

Cross-front variations in adult abundance and recruitment of Patagonian scallop (*Zygochlamys patagonica*) at the SW Atlantic Shelf Break Front

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We studied cross-front variations in adult abundance and recruitment of Patagonian scallop (*Zygochlamys patagonica*) and their relationship with the Shelf Break Front and satellite-derived chlorophyll *a* in the Southwest Atlantic between 38°S and 39°30'S. Integrated data from commercial fleets (CF, 1996–2005), research cruises (RC, 1998–2005), sea surface temperature (SST; 1985–1997), and satellite-derived chlorophyll *a* (CSAT; 1998–2004) were included in the analysis. One-way ANOVA was used to assess differences in recruitment and scallop abundance in a cross-front direction. The abundance of scallops was greatest (RC > 200 kg h⁻¹) closer to the onshore side of the front or beneath it, and the East–West extension of scallop beds (~40 km) matched the seasonal zonal displacement of the front (~37 km). The highest CSAT gradients were west of or matched the position of the front. The annual mean position of the front correlated with the spatial variability in recruitment within areas where the species recruited successfully (RC > 2000 h⁻¹). The spatial variability in adult abundance and recruitment of scallops is strongly related to the spatial variability in the position of the front and with the high CSAT concentrations associated with it.

Keywords: abundance, marine fronts, recruitment, scallops, Southwest Atlantic, spatial pattern, *Zygochlamys patagonica*.

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Introduction

Marine fronts are usually associated with high biological primary production promoted by physical mechanisms that affect planktonic organisms, such as vertical fluxes, retention, and convergence (Mann and Lazier, 1991). At large scales, spawning of fish (many economically important) and aggregations of their larvae occur associated spatially with fronts (Acha *et al.*, 2004). Moreover, species abundance and community diversity are usually greater in these areas than in the surrounding waters (Dauwe *et al.*, 1998). Therefore, marine fronts play a key role in marine systems, because of the transfer of primary production to upper trophic levels, and because the physical mechanisms favour the aggregation of organisms (Olson, 2002; Acha *et al.*, 2004).

The convergence of water masses at a frontal interface may aggregate and retain benthic invertebrate larvae, which then settle, supplying recruits to the seabed (Sinclair, 1987; Acha *et al.*, 2004). Moreover, many benthic species depend on benthopelagic coupling mechanisms by which food particles, generated in the euphotic layer, sink to the bottom (Billet *et al.*, 1983; Bett *et al.*, 2001). Therefore, frontal variability (i.e. position and extension, which can change within and among years) may have consequences on (i) recruitment (Shanks, 1995; Alexander and

Roughgarden, 1996), (ii) the distribution and abundance of benthic species (Nodder *et al.*, 2003), or (iii) all the processes that contribute to a dynamic community (Dewicke *et al.*, 2002). Although these factors are important in understanding patterns in species abundances and community functions, few studies have aimed to understand those processes better (Josefson and Conley, 1997).

The Patagonian scallop (*Zygochlamys patagonica*) is a suspension-feeder that inhabits soft substrata from Chiloé Island in the SE Pacific (42°S) to Cape Horn (56°S), and in the Southwest Atlantic north to 35°S, the latitude of the mouth of the Río de la Plata (Bogazzi *et al.*, 2005). At large scales, important aggregations of this species match the location of three major frontal systems: the Shelf Break Front (SBF), the Northern Patagonian Front, and the Southern Patagonian Front (Bogazzi *et al.*, 2005). Under the influence of the SBF and along the 100-m isobath, the most profitable scallop beds are located, and they produce ~50 000 t of commercial scallops annually (Lasta and Bremec, 1998; Orensanz *et al.*, 2006). The fishery, certified as sustainable by the Marine Stewardship Council in 2006, has been prosecuted since 1996, and it is an important one for Argentina, which

deploys a factory fleet to harvest the resource (Ciocco *et al.*, 2006). In addition to the large-scale association of scallop aggregations with frontal systems, observations at higher resolution (~ 40 km) suggest that their spatial distribution varies in a cross-front direction (Lasta *et al.*, 2001), probably as a result of variability in the SBF.

Given these antecedents, we evaluate the hypothesis that scallop distribution varies in a consistent pattern across the axis of the front. With this purpose, we integrated high-resolution data from fishery research cruises (RC, dredge benthic samples), fishing fleets (logbooks and observer data), satellite-derived sea surface temperature (SST), satellite-derived chlorophyll *a* (Chl *a*), and *in situ* CTD data to determine the relationship between recruitment and adult abundance of Patagonian scallop and both spatial variability of the SBF and surface Chl *a* concentration.

Material and methods

Study area

The study was performed in an area under the influence of the SBF, located between $38^{\circ}00'$ and $39^{\circ}30'S$ (Figure 1) in the Argentine Sea (SW Atlantic). The SBF is a thermohaline front characterizing the offshore border of the continental shelf. Its inner boundary is located between the 90- and 100-m isobaths (Martos and Piccolo, 1988). The front has a West–East extension of ~ 80 km at the surface and 40 km at the seabed (Bogazzi *et al.*, 2005). It is the result of the meeting of warm (6.5 – 21°C), fresher (33.2 – 33.8 psu), nutrient-poorer (1 – $8 \mu\text{g}$ at l^{-1} nitrate; $<1 \mu\text{g}$ at l^{-1} phosphate) shelf waters of Subantarctic origin with colder (4.5 – 6°C), more saline (33.8 – 34.2 psu), nutrient-rich (10 – $27 \mu\text{g}$ at l^{-1} nitrate; $>1 \mu\text{g}$ at l^{-1} phosphate) waters of the Malvinas Current (Martos and Piccolo, 1988; Lutz and Carreto, 1991; Carreto *et al.*, 1995; Brandini *et al.*, 2000). The front shows strong gradients in the thermal field ($>0.08^{\circ}\text{C km}^{-1}$; Martos and Piccolo, 1988), mainly during summer, but salinity gradients

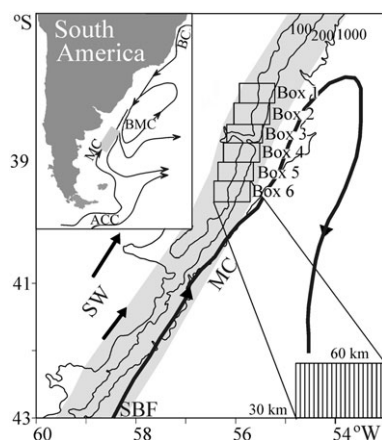


Figure 1. The study area in the Southwest Atlantic. Boxes divide the scallop grounds in a cross-front direction. The schematic cells within each box are shown in the lower right corner. The grey area represents the location of the SBF, and arrows indicate the direction of flow of Shelf Waters (SW). The contours correspond to the 100, 200, and 1000-m isobaths. Inset: schematic circulation, showing the Brazil Current (BC), Malvinas Current (MC), Brazil Malvinas Confluence (BMC), and Antarctic Circumpolar Currents (ACC). Adapted from Piola and Rivas (1997).

are weak ($0.002 \text{ psu km}^{-1}$; Romero *et al.*, 2006). The typical density structure of the SBF defines a retrograde front in which the slope of frontal isopleths is opposite to that of the cross-shelf topography. Mesoscale oceanographic processes such as a sub-surface anticyclonic eddy and cross-front mid-level intrusions (thickness 5–40 m) have been identified in the area (Bogazzi *et al.*, 2005). The location of the SBF varies seasonally at 38 – 39°S , moving offshore during summer and onshore during spring and autumn (Carreto *et al.*, 1995). It has been suggested that upwelling at the shelf break could lead to the development of the strong band of Chl *a* shown in satellite images (Romero *et al.*, 2006). This is a quasi-continuous band, between 38 and 50°S , characterized by a strong annual cycle with maximum values during spring and summer (Saraceno *et al.*, 2004).

Variability of the SBF system

Annual and seasonal mean climatologies in SST gradients were used to locate the SBF mean position and to determine its variability. Although the front is haline, we employed SST to study the position of the front and its dynamics, because the spatial and temporal resolution of satellite data is better than the *in situ* data available for both salinity and temperature. However, density sections were drawn to describe the general front structure and the connection between surface and bottom conditions. The oceanographic data used in characterizing the vertical structure of the front correspond to density (σ_t , kg m^{-3}) synoptic sections computed from depth profiles of temperature and salinity measured with a Sea-Bird 19 and 911 CTD. CTD stations were regularly spaced at intervals varying from 10 to 43 km along-transects run to encompass the condition of the front in summer (February 2004), autumn (May 2000), and spring (November 1993). Samples to calibrate salinity data were taken at bottom depths, and the temperature sensor maintained the factory calibration.

The SST gradients were computed using a centred difference scheme based on 13 years (1985–1997) of satellite data of the Pathfinder + Erosion monthly climatology at 9.28×9.28 km resolution (Casey and Cornillon, 1999, 2001). Years covered by the satellite information do not match those with biological data and cannot be used to explain the occurrence of years with high or low values of catch per unit effort (cpue). Climatological analyses of satellite-derived chlorophyll *a* concentration were employed based on 7 years (1998–2004) of sea surface colour images from Standard Mapped Images (SMIs), supplied by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS). The SMIs are derived from level-3 monthly binned data and mapped with a resolution of $0.09 \times 0.09^{\circ}$ (corresponding to $\sim 7.8 \times 10$ km in the study area), in a two-dimensional array of equidistant cylindrical projection. Following Yoder (2000) and Romero *et al.* (2006), the satellite-derived sea surface chlorophyll *a* concentration is referred to as CSAT (mg m^{-3}).

Cross-front variability in adult scallop abundance and recruitment from two sources of data

Recruitment and adult scallop abundance: research cruise data
To evaluate the relationship between the position of the front and scallop abundance, a scallop ground which include three beds was divided into six boxes, located at different latitudes. Inside each, 20 cross-front cells (~ 3 km longitude by 30 km latitude) were created (Figure 1). Data were assigned to the cells according to the initial position of the tows obtained by GPS (± 20 m). Data from RC (1998–2005) on the cpue of recruits (cpue R, number h^{-1}),

corresponding to scallops <16 mm total height (i.e. up to 1 year old; Lomovasky *et al.*, 2008), and cpue of adults (cpue A, kg h^{-1}), scallops that reach the commercial size (>55 mm total height, individuals 4–14 years old; Lomovasky *et al.*, 2008) were used. RC were performed annually, and station locations (tows) were regularly spaced at ~ 6 km intervals. The vessel operated with a non-selective dredge 2.5 m wide, with a mesh size of 10 mm and an efficiency of 43% (Valero, 2002). The standard towing time and speed were 10 min and 5.5 km h^{-1} , respectively. Data from the unsorted catch (UC) were used to estimate the scallop catch. Total UC was weighed (± 1 kg), and subsamples (± 0.1 kg) were obtained randomly. The scallops present in the subsamples were counted, weighed, and measured to the nearest millimeter. The null hypotheses of no differences in cpue (recruits or adult scallops) across the front were evaluated with one-way ANOVA, and *post hoc* differences between averages were evaluated with a Bonferroni test. The cpue data were ln-transformed to satisfy ANOVA assumptions (Zar, 1984).

Commercial scallop abundance: commercial fleet data

The relationship between the position of the front and adult scallop abundance was evaluated with data from commercial fleets (CF, 1996–2005; cpue F), using the scheme described above. CF completed 331 fishing trips (1 trip ~ 30 d) during the study period, making an average of 50 tows d^{-1} (range 30–80 tows d^{-1}). The vessels operated non-selective bottom otter trawls 13 m long, with a mesh size of 100 mm, headrope and footrope 17 and 22 m long, respectively (Lasta and Bremec, 1998), and with an efficiency of 48% (Valero, 2002). UC per tow was assessed visually (extent of codend filling), based on categories of 10% before it was opened on deck. The UC weight for different proportions of codend fullness (20, 50, 80, and 100%) was determined by weighing a series of tows. A full net was estimated to contain 2298 kg of UC (Lasta and Bremec, 1998). Scallop catch was estimated from the scallop yield: subsamples (10 kg) were taken randomly from the UC, and scallop and bycatch portions were weighed (± 0.1 kg). The cpue of commercial scallops (cpue F) was calculated based on their proportion in the yield. Based on an underlying error of 15% in biomass estimates from a collection of 30 samples per boat, the use of more than one subsample per tow would only reduce the uncertainty by 2% (Lasta *et al.*, 1998).

Results

Variability of the SBF system

There was weak evidence of the SBF in the northern part of the study area around $38^{\circ}30'S$ (boxes 1 and 2, Figure 2). Maximum SST gradients reached $0.02^{\circ}\text{C km}^{-1}$ during austral autumn and winter at the western side of box 1, where the mean annual position of the front is located. Maximum gradients of $\sim 0.02^{\circ}\text{C km}^{-1}$ were in autumn at the eastern side of box 2. The SBF front becomes clearer south of box 2 (boxes 3–6), SST gradients increasing gradually southwards and towards the shelf break, reaching values of $0.05^{\circ}\text{C km}^{-1}$. The eastern side of most boxes was influenced by the biggest gradients in SST, mainly during spring and summer. The mean seasonal position of the front had greater spatial variability than the mean annual position, with an onshore displacement during austral autumn (April–June) and winter (July–September), and more offshore positions during summer (January–March) and spring (October–December). Zonal displacement of the SBF mean position may reach

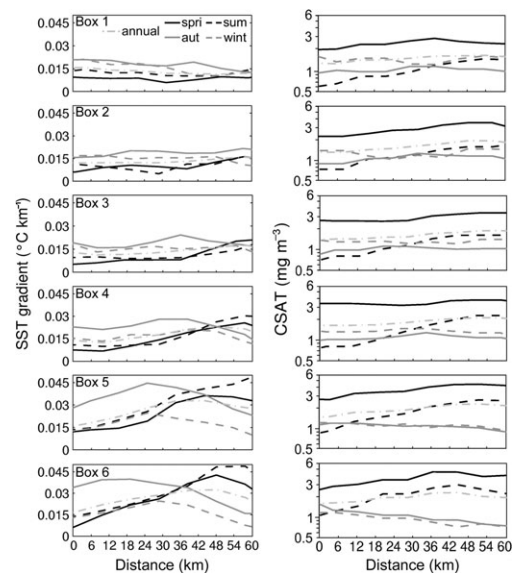


Figure 2. Annual and seasonal mean climatologies of SST gradients ($^{\circ}\text{C km}^{-1}$) and derived surface chlorophyll *a* concentrations (CSAT, mg m^{-3}) crossing the shelf break in each box.

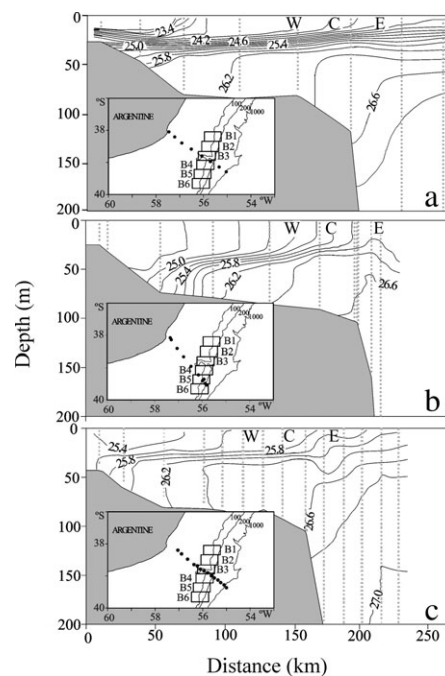


Figure 3. Vertical fields of density (σ_t , kg m^{-3}) along sections sampled during the austral (a) summer, (b) autumn, and (c) spring, crossing the shelf break (see insets).

~ 37 km (boxes 5 and 6; Figure 2), with extreme locations (on- and offshore) in autumn and summer.

Vertical sections of density show at the surface a similar spatial pattern of SST gradient fields (Figure 3). The maximum surface gradient of the isopycnals (SBF) during summer and spring is offshore (Figure 3a and c), whereas in autumn the accentuated gradient of density was onshore (Figure 3b). Slope waters appear to be more influenced by the Malvinas Current in spring, shown by the displacement up to 150 m deep of the 27.0 isopycnal (Piola and

Gordon, 1989), whereas in summer the same isopycnal was deeper than 200 m (not shown). During autumn, this feature is not observed, probably because the section extension is limited offshore. The strongest vertical stratification was during summer, at the western side of the box, reaching up to $0.12 \text{ kg m}^{-3} \text{ m}^{-1}$, diminishing during autumn and spring to a value around $0.04 \text{ kg m}^{-3} \text{ m}^{-1}$. The highest CSAT concentrations were at the western location of the SBF in most climatological seasons (Figure 2; note the logarithmic scale for CSAT). However, in the boxes under strong influence of the front (boxes 3 and 5), the highest values of CSAT during spring were related to a central-western position crossing the front. Maximum CSAT values increased up gradually to the south, attaining values of 5 mg m^{-3} .

Cross-front variability in adult scallop abundance and recruitment from two sources of data

Recruitment and adult scallop abundance: research cruise data

The cpue of recruits (cpue R) varies in a cross-front direction for almost all boxes with successful recruitment (Table 1). The spatial correlation between the patterns of distribution of higher values of cpue R (Figure 4) and of annual SBF position (Figure 2) is easily seen. A Bonferroni test revealed that the highest averages (e.g. $13\,935 \text{ h}^{-1}$, $n = 7$, $\text{s.d.} = 23\,643$; box 2), located in central positions within the scallop bed (Figure 4), were significantly different from the rest. In box 3, probably because of low statistical power, the Bonferroni test was unable to identify the source of the differences detected by the ANOVA. The largest values of mean cpue R were in central-eastern positions of the bed, although there was an exception in box 4 where the highest values were in a central-western position. In 2000 and 2001, when there was successful recruitment, the cpue was, on average, $>2000 \text{ h}^{-1}$ in almost all tows (i.e. throughout the scallop bed). In other years, however, when recruitment was less ($<500 \text{ h}^{-1}$ in almost all tows), the spatial pattern was heterogeneous, only a few patches having above-average recruitment (Figure 4).

The cpue A varies in a cross-front direction for almost all boxes, except for box 4 (Table 1). In the northern boxes, the differences were caused by lower averages, $\sim 60 \text{ kg h}^{-1}$, on the western side of the scallop bed in contrast to the higher values in central or

Table 1. Summary of ANOVA results by box.

Box and parameter	d.f. effect	MS effect	d.f. error	MS error	F	p-level
Box 1 Cpue A	10	32.186	173	11.802	2.727	0.004
Cpue R	9	16.181	172	2.357	6.685	<0.001
Box 2 Cpue A	10	43.897	142	10.734	4.089	<0.001
Cpue R	10	13.241	142	1.414	9.366	<0.001
Box 3 Cpue A	12	35.274	146	13.591	2.595	0.004
Cpue R	12	26.186	148	2.267	11.551	<0.001
Box 4 Cpue A	8	18.307	88	14.215	1.288	0.260
Cpue R	8	0.795	89	0.957	0.830	0.578
Box 5 Cpue A	10	20.435	194	13.401	1.525	0.133
Cpue R	10	12.261	258	0.837	14.645	<0.001
Box 6 Cpue A	12	11.822	76	10.425	1.134	0.346
Cpue R	12	5.104	77	1.388	3.678	<0.001

The analysis contrasts the cpue of scallop recruits (cpue R, numbers h^{-1}) and the cpue of adult scallops (cpue A, kg h^{-1}) at the SBF with those in surrounding areas. The data were obtained from RC. d.f., degrees of freedom; MS, mean square.

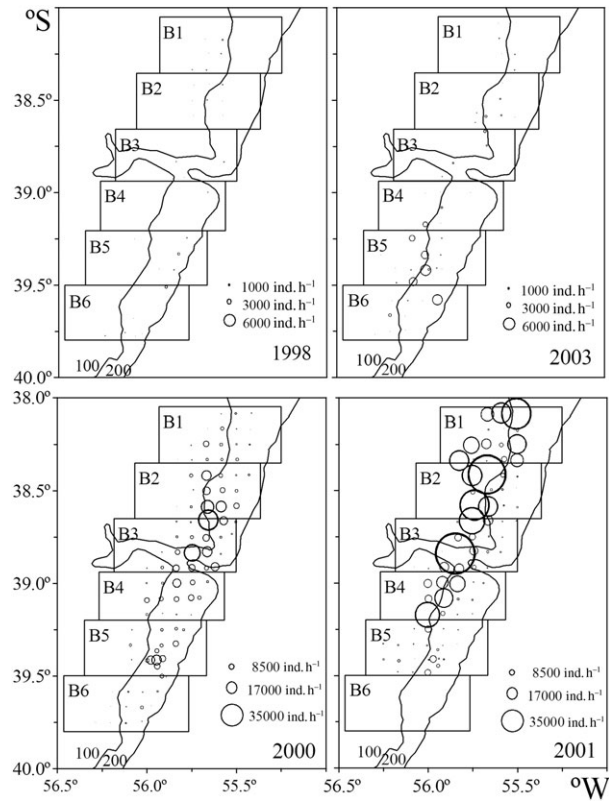


Figure 4. Cross-front distribution of cpue of scallop recruits (cpue R: numbers h^{-1}). The years 1998 and 2003 represent poor recruitment years, and 2000 and 2001 represent successful recruitment years (note the change of scale in the symbol). The contours correspond to the 100 and 200-m isobaths.

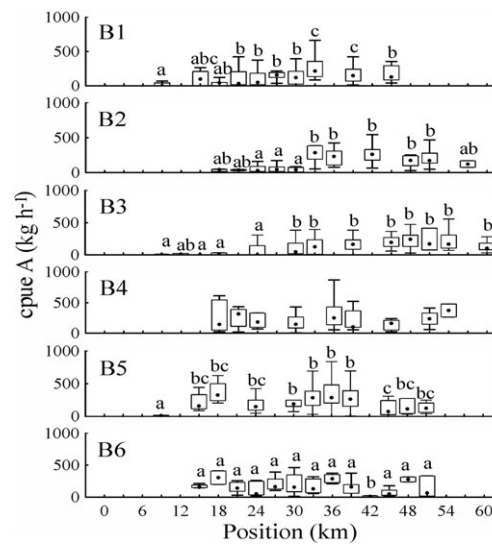


Figure 5. Box-plot of the cross-front distribution of the cpue of adult scallops (cpue A: kg h^{-1}) according to their position from the western side of each box. Letters indicate differences in the average cpue A from the Bonferroni *post hoc* test.

eastern areas, with values, on average, $\sim 220 \text{ kg h}^{-1}$. The highest mean cpue A was 371 kg h^{-1} ($n = 7$, $\text{s.d.} = 342$) in a central position of the bed in box 2 (Figure 5). Although there were

Table 2. Summary of ANOVA results by box.

Box	d.f. effect	MS effect	d.f. error	MS error	F	p-level
1	10	1.703	1 280	0.194	8.790	<0.001
2	10	2.318	512	0.182	12.727	<0.001
3	12	7.043	791	0.379	18.576	<0.001
4	10	4.187	636	0.211	19.886	<0.001
5	13	2.759	510	0.177	15.593	<0.001
6	9	2.046	431	0.133	15.410	<0.001

The analysis contrasts the cpue of commercial scallops (cpue F, $t h^{-1}$) at the SBF with that in the surrounding areas. The data were obtained from the CF. d.f., degrees of freedom; MS, mean square.

differences across the front, the southern boxes showed no clear spatial pattern.

Commercial scallop abundance: CF data

Commercial scallop cpue (cpue F) varied in a cross-front direction in all boxes (Table 2). There were two clear cross-front patterns and an intermediate version (Figure 6). One pattern presents the lowest mean cpue F, located at the western side, and the larger mean cpue F in the central part of the bed (box 3). The opposite spatial pattern shows the largest mean values of cpue F at the western side of the scallop bed (boxes 1 and 2). The intermediate pattern in the rest of the boxes shows several peaks in cpue F. The Bonferroni analysis showed that almost all values of cpue F were different from each other. The highest was $12 t h^{-1}$ ($n = 7$, s.d. = 3.16) in box 2, although it was well away from the front. Although differences in a cross-front direction were detected for all boxes, in box 3 only was there a spatial distribution similar to that of cpue A in the first three boxes. Box 3 had considerable variability in cpue F, ranging between $1.50 t h^{-1}$ ($n = 30$, s.d. = 0.43) and $11.69 t h^{-1}$ ($n = 38$, s.d. = 8.5).

Discussion

Our results have revealed that seasonal variability in the position of the front and the location of the surface CSAT maximum correlates spatially with a zone of high recruitment probability and adult scallop abundance. The highest values of scallop abundance were in central–eastern areas within the scallop bed, matching the highest gradients in SST and CSAT concentration at the surface. Therefore, scallop abundance seems to be closely related to oceanographic processes.

The zonal displacement of the SBF is close to the cross-shelf break extension of Patagonian scallop beds (~ 37 km). This pattern suggests that the autumn (spring) mean climatological position of the SBF may determine the westernmost (easternmost) limit of the scallop bed, because spawning of scallops takes place mainly between spring and early autumn (Walossek and Waloszek, 1986; Campodónico *et al.*, 2008). This seasonal spatial variability in the position of the SBF is seemingly associated with the dynamics of the Malvinas Current (Carreto *et al.*, 1995), and seasonal variations in front intensity may be related to sea–air heat fluxes, horizontal advection (Saraceno *et al.*, 2004; Romero *et al.*, 2006), and/or coastal-trapped waves (Saraceno *et al.*, 2005). Moreover, density sections (Figure 3) show shelf waters with moderate to strong pycnoclines during warmer months, and the water column at the shelf break (near

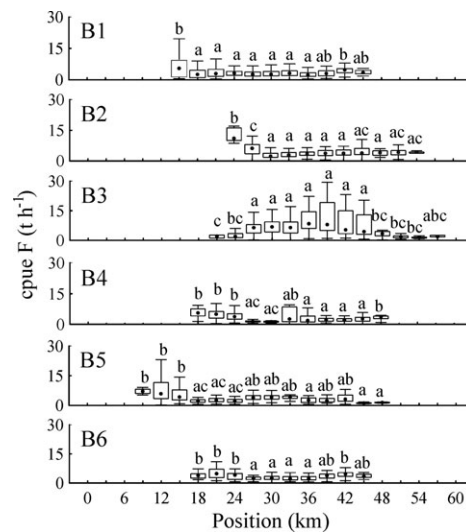


Figure 6. Box-plot of the cross-front distribution of the cpue of the commercial scallop fishery (cpue F, $t h^{-1}$) at the SBF according to the position of the tows. Letters indicate differences in the average cpue F from the Bonferroni *post hoc* test.

the location of the scallop beds) shows weaker stratification. This situation could promote benthopelagic coupling (larval settlement, food supply to adults), along with dynamic processes such as inertial tide mixing and/or internal waves (Mann and Lazier, 1991).

Blooms of CSAT occur at the shelf break mainly during spring and early summer, and maxima are located onshore of the SBF (Romero *et al.*, 2006). Although we found some differences between the spatial patterns in SST and CSAT concentration, possibly because of the different years in the climate dataset, the CSAT maximum during spring and summer were located both onshore and above the SBF. Therefore, despite the different years being analysed, CSAT maximum concentrations showed a clear relationship with front position.

The strong association between larval retention systems and recruitment is widely recognized (Sinclair *et al.*, 1985), but their effect on community structure (“supply side ecology”; Lewin, 1986) in offshore communities is poorly understood. For the Patagonian scallop, the cross-front pattern of the highest cpue of recruits in the central–eastern portion of the bed (the western position of the SBF) could be a complex phenomenon which implies that the front constrains zonal displacement of larvae, but allows their drift along the front and their subsequent return to the seabed (Shanks, 1995). Mechanisms to explain this process, once larvae are near or in the frontal zone, may involve accumulation caused by the convergence of currents (Shanks, 1995), vertical mixing of the water column, larval transport to the seabed by fluid injection along the isopycnal surfaces (Richards, 1990), or larval transport by internal waves or tides (Pineda, 1991, 1994). There was no distinct pattern in the spatial distribution of scallop recruits in the southern boxes, probably because of the small number of recruits there, and because of their patchiness during the study period.

The highest CSAT concentrations during spring and summer were west of the front, suggesting that food supply could be a major factor in determining the persistence and greatest abundances of scallops in the area, reinforcing recruitment patterns.

This pattern was confirmed by RC, considered more representative of scallop distribution, because factors that control the allocation of fishing effort could promote the patterns obtained from commercial data (Orensanz *et al.*, 2006). The spatial pattern of scallops across the front obtained from RC suggests that food availability on the western side of the scallop beds is not as good as on the eastern side. A similar pattern was found at other fronts, where chlorophyll levels in sediments (Josefson and Conley, 1997) and more labile organic material (Nodder *et al.*, 2003) are closely associated with the pattern of variation in benthic biomass. Interannual variability in CSAT could also be responsible for the several peaks in commercial cpue in the southern boxes. It is important to note, however, that although the substratum is generally assumed to be a determinant of the spatial distribution of scallops (Katsanevsky, 2005), the spatial distribution of Patagonian scallops at a macroscale does not appear to be related to substratum characteristics over the fairly uniform substrata of the SW Atlantic (Bogazzi *et al.*, 2005). Moreover, high densities of diatoms in the area (Gayoso and Podestá, 1996), a high rate of diatom sedimentation even during stratified condition (Hansen and Josefson, 2001) and the confirmation of greater diatom abundance in the stomach contents of scallops during summer (Schejter *et al.*, 2002) support our interpretation that food availability plays an important role in the mesoscale distribution patterns of the Patagonian scallop.

To conclude, front activity in the SW Atlantic appears to generate strong structure in the recruitment of the Patagonian scallop, and that pattern remains stable in terms of the distribution of adults. The spatial variability we observed in scallop abundance seems to be a result of (i) the effect of frontal variability on recruitment and/or (ii) spatial variability in the food supply to the scallop beds. This may be an example of how surface oceanographic patterns are closely related to recruitment localization and the abundance of a benthic species (a commercial fishery resource in this case).

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