Spatial correspondence between areas of concentration of Patagonian scallop (*Zygochlamys patagonica*) and frontal systems in the southwestern Atlantic

EUGENIA BOGAZZI,[1,2,]* ANA BALDONI,[2] ANDRÉS RIVAS,[3] PATRICIA MARTOS,[2,4] RAÚL RETA,[2,4] J. M. (LOBO) ORENSANZ,[3] MARIO LASTA,[2] PATRICIA DELL'ARCIPRETE[3,5] AND FRANCISCO WERNER[6]

[1]*Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina*
[2]*Instituto Nacional de Investigación y Desarrollo Pesquero, PO Box 175, Mar del Plata B7602HSA, Argentina*
[3]*Centro Nacional Patagónico, CONICET, 9120 Puerto Madryn, Argentina*
[4]*Universidad Nacional de Mar del Plata, Mar del Plata B7602HSA, Argentina*
[5]*Universidad Nacional de la Patagonia Austral, Sede Caleta Olivia, Santa Cruz, Argentina*
[6]*Marine Sciences, CB 3300, University of North Carolina, Chapel Hill, NC 27599-3300, USA*

ABSTRACT

It has been hypothesized that the geographical location of scallop beds in extensive shelf regions mirrors hydrographic structures (e.g. frontal systems) that favor the retention/concentration of pelagic larvae. Large, discontinuous concentrations of the Patagonian scallop (*Zygochlamys patagonica*) are known to have occurred recurrently (for more than 30 yr) at certain geographical locations over the extensive Patagonian shelf. These stocks, exploited since 1996, currently support one of the most important scallop fisheries in the world. Here, we investigate whether those aggregations are spatially coincidental with major frontal systems. Several pieces of information were used: historical survey data documenting the geographic distribution of the Patagonian scallop beds, catch and effort data from the commercial fleet, oceanographic data on frontal systems, and remote sensing imagery. We found that large-scale aggregations do match the location of three major and very different frontal systems in the southwestern Atlantic: the Shelf-Break Frontal System, the Northern Patagonia Frontal System, and the Southern Patagonia Frontal System. We describe the three frontal systems and their associated scallops fishing grounds and discuss which processes can contribute to sustaining the productivity of the scallop grounds in each case.

Key words: benthic fishery, frontal systems, metapopulation, Patagonian scallop, shelf-break front, shelf-sea front, southwestern Atlantic

INTRODUCTION

Metapopulations of benthic invertebrates, including scallops, are structured as collections of subpopulations of sedentary residents interconnected by larval dispersal, with different patterns and degrees of connectivity (for scallop examples see Orensanz *et al.*, in press). Formal and conceptual models have been developed to investigate connectivity in specific oceanographic scenarios (e.g. Werner *et al.*, 1996) and to simulate the dynamics of metapopulations under simplified connectivity assumptions (e.g. Morgan and Botsford, 2001). According to Sinclair's (1987) 'member/vagrant hypothesis', geographic patterns and variability of abundance (i.e. metapopulation structure and dynamics) could be explained by dispersal/retention mechanisms. Under this hypothesis, the location of subpopulations of benthic metapopulations should mirror, at least to some extent, the workings of hydrographic features (e.g. frontal systems) that, coupled with larval behavior, have the potential to retain (and/or concentrate) pelagic larvae. The recurrent spatial location of self-sustaining scallop populations, in particular, has been explained using a 3D numerical circulation model (Tremblay *et al.*, 1994).

Frontal systems, defined as areas where there are steep gradients in oceanographic variables, are usually associated with high biological productivity (Mann, 1992). They constitute important feeding and/or reproductive habitats, often acting as retention/

**Correspondence*. e-mail: ebogazzi@inidep.edu.ar

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concentration areas for pelagic larvae or as barriers to dispersal (e.g. Tremblay and Sinclair, 1992, for the George Bank sea scallop stocks). The Patagonian scallop (*Zygochlamys patagonica*) stocks of the southwestern Atlantic offer an opportunity to test the hypothesis that biological processes (e.g. as revealed by large macro-scale distribution patterns) match oceanographic features in the water column (e.g. frontal systems). Stocks of Patagonian scallop are widely distributed over the southwestern Atlantic Shelf Large Marine Ecosystem (SSAS LME; Bisbal, 1995; Fig. 1). Large, discontinuous, recurrently located concentrations have been observed for more than 30 yr, and exploited since 1996 (Lasta and Bremec, 1998; Ciocco *et al.*, in press). The SSAS has an uneventful topography, gently sloping toward the shelf edge without steep macro-gradients in substrate texture. Thus, the recurrent discontinuity of scallop aggregations is an intriguing phenomenon, one that cannot be explained solely in terms of benthic habitat. This observation prompted the hypothesis that the location of scallop beds could be associated with areas of high productivity, or otherwise suitable for the retention, concentration and/or survival of pelagic

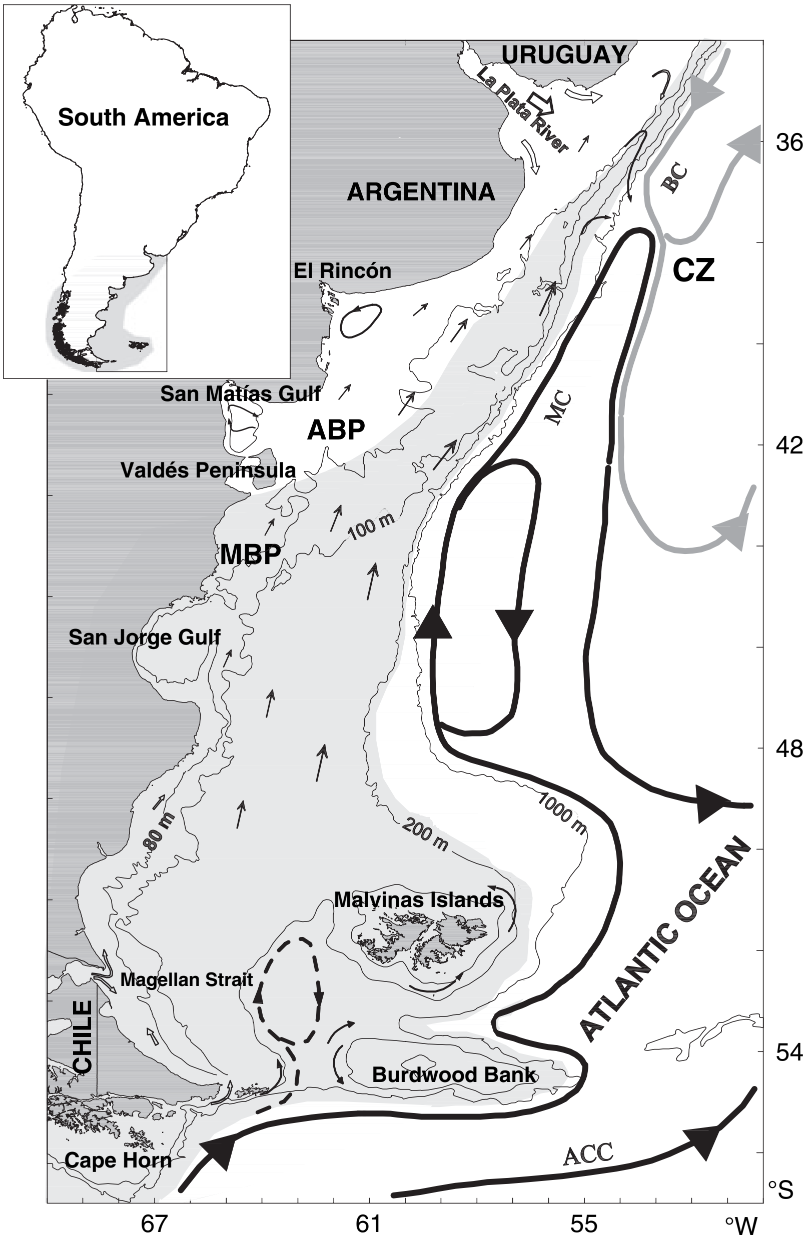


Figure 1. Southwestern Atlantic Shelf (SSAS): schematic circulation, showing the Malvinas (MC), Antarctic Circumpolar (ACC) and Brazil Currents (BC), and the Confluence Zone (CZ). Arrows indicate the general circulation pattern over the continental shelf; empty arrows represent continental runoff. The shaded area represents the Magellan Biogeographic Province (MBP), unshaded area in the northern Argentine shelf corresponds to the Argentine Biogeographic Province (ABP). Adapted from Piola and Rivas (1997). Inbox: distribution range of *Zygochlamys patagonica*.

larvae. The dynamics of several commercially important fish stocks in the region have been associated with oceanographic structures, mostly with frontal systems, some of which have been previously described (e.g. Glorioso and Flather, 1995; Sabatini and Martos, 2002).

In this study we bring together several pieces of information: historical survey data documenting the geographic distribution of the Patagonian scallop beds, catch and effort data from the commercial fleet, oceanographic data on frontal systems, and remote sensing imagery. Many of these data have never before been analyzed. Here, we integrate them to investigate whether the distribution pattern of scallop aggregations matches major frontal systems, and consider hypotheses that may explain emerging patterns. Results are discussed in the context of current ideas on the structure, connectivity and dynamics of exploited metapopulations of benthic invertebrates with pelagic larvae.

STUDY SYSTEM

Study area

The study area (Fig. 1) includes the Argentine and Uruguayan shelves south of 35°S, which extend offshore with a gentle slope. The texture of the substrate is rather homogeneous, predominately soft sediments composed mainly of sand, with variable shell content (Parker *et al.*, 1997).

The boundary oceanic circulation is influenced by two major currents: the southward flowing subtropical Brazil Current (BC) and the northward Sub-Antarctic flow of the Malvinas (= Falkland) Current (MC), both with axes nearly parallel to the continental slope and turning eastwards at the Confluence Zone (CZ). The BC is warm, saline, and relatively oligotrophic. In contrast, the MC branches off the Antarctic Circumpolar Current (ACC), carrying low salinity, cold, and nutrient-rich Sub-Antarctic water. The two-current system forms a distinctive ecological boundary, which outlines the eastern limit of SSAS LME and separates it from the Southwest Atlantic Basin. The opposite flows of subtropical and Sub-Antarctic waters define a strong frontal structure in the CZ between 35 and 40°S (Gordon and Greengrove, 1986). The CZ is a highly dynamic region with a complex array of eddies, rings and filaments (Gordon, 1989), high spatial–temporal variability (Garzoli and Giulivi, 1994) and enhanced phytoplankton biomass (Brown and Podestá, 1997), constituting an important biogeographic boundary between assemblages of subtropical and Sub-Antarctic origin. The shelf waters result from the mixing of ACC, MC and Patagonian Current (PC) waters and continental runoff, and are modified by water and energy exchange with the atmosphere (Guerrero and Piola, 1997). The PC is characterized by low salinity contributed by Southeast Pacific waters and continental waters from Magellan Strait and Fueguian Channels moving northward along the coast (Guerrero and Piola, 1997).

The SSAS is characterized by a general northeastward circulation and a noticeable large amplification of the oceanic semidiurnal tides toward the coast and south of 40°S. Tidal energy dissipation concentrates off El Rincón, northeast of Valdés Peninsula, both ends of San Jorge Gulf and, to a lesser degree, northwest of Malvinas (=Falkland) Islands. Along the shelf break the diurnal tides are strong and resonate with northward propagating continental shelf waves. North of 40°S tidal circulation is relatively weak and circulation is driven mainly by the winds (Palma *et al.*, 2004).

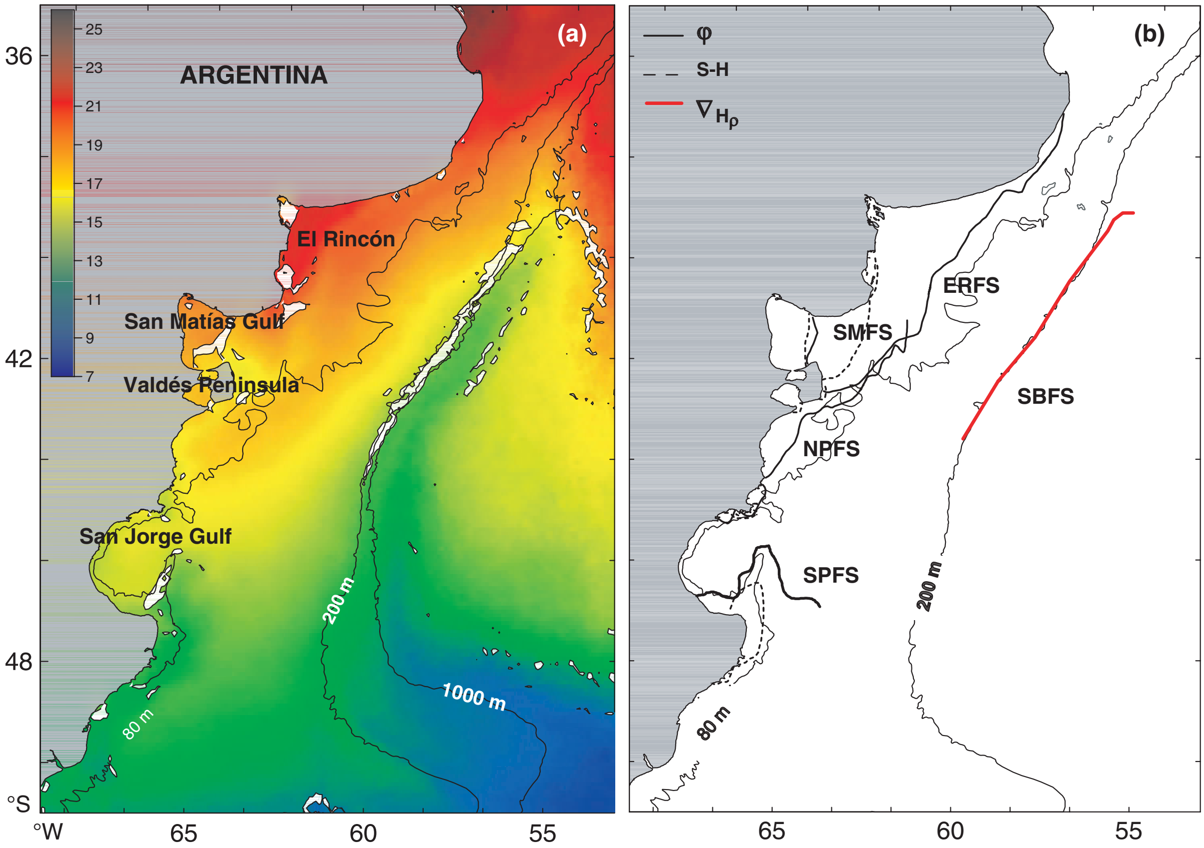
The frontal systems of the SSAS we deal with in this study include the Shelf-Break Frontal System (SBFS), representing the transition between shelf and MC waters (Martos and Piccolo, 1988), the tidal Northern Patagonian Frontal System (NPFS, Sabatini and Martos, 2002) and the Southern Patagonian Frontal System (SPFS, Guerrero and Piola, 1997) (Fig. 2). These fronts differ from each other in the main forcing, as well as in their temporal and spatial scales. The San Matías Frontal System (SMFS, Glorioso and Flather, 1995) is not analyzed in detail for reasons discussed later. The Río de la Plata River estuarine front (Guerrero *et al.*, 1997) and El Rincón Frontal System (ERFS, Fig. 2; Guerrero and Piola, 1997) were not considered in this study because they are outside the range of distribution of the Patagonian scallop.

These frontal zones have been recognized as areas of high productivity, being associated with high nutrients, phytoplankton and chlorophyll-*a* concentrations (Carreto *et al.*, 1995), shellfish and finfish stocks (Brunetti *et al.*, 2000), spawning, eggs and larvae (Sánchez *et al.*, 1998), and micro and mesozooplankton aggregations (Thomson *et al.*, 2001).

The Patagonian scallop and its fishery

The Patagonian scallop inhabits soft bottoms, mainly 'reclining' in muddy–sandy substrate (Stanley, 1970). The species, which dominates the epibenthic community of scallop fishing beds (Bremec and Lasta, 2000), is a suspensivore feeding mainly on phytoplankton (Schejter *et al.*, 2002). Its geographic range extends from Chiloé Island in the SE Pacific (42°S)

Figure 2. (a) Surface thermal fronts based on satellite imagery: mean SST for January (12-yr average of monthly means, data from NOAA/Pathfinder, 9-km resolution images); shown in white are zones where surface thermal gradient >0.05°C km^{-1}. (b) Frontal systems based on hydrographic data. Northern Patagonia Frontal System (NPFS), Southern Patagonia Frontal System (SPFS), San Matías Frontal System (SMFS) and El Rincón Frontal System (ERFS) are indicated by the critical contours of stability (φ) based on mean summer conditions from all years analyzed (ERFS from Lucas, unpublished data; NPFS from Ehrilch *et al.*, 2000; SPFS calculated by us). The SMFS and SPFS are also indicated by the Simpson–Hunter stratification parameter (S–H, Glorioso and Flather, 1995). The Shelf-Break Frontal System (SBFS) is represented by the maximum surface horizontal gradient of density ($\nabla_{H\rho}$, red line).



south to Cape Horn (55°56′S), and on the southwestern Atlantic northwards to off the Río de la Plata River estuary (35°50′S) (Fig. 1, inset). Biogeographically it is a cold-temperate species characteristic of the Magellan Biogeographic Province. Large aggregations are known to occur only on the Atlantic side of its range, where at least six high-density areas (described later) have been recognized by several exploratory and fishing cruises on the Patagonian Shelf and off northern Argentina and southern Uruguay (Lasta and Bremec, 1998). Additionally, an experimental fishing survey conducted in 2002 found five commercially significant concentrations on the Malvinas (= Falkland) Islands Shelf (Bizikov and Middleton, 2002).

The Atlantic stocks have been commercially exploited since 1996 by eight factory trawlers that process the catch at sea (six operated on the Argentine and two on the Uruguayan shelf). With catches on the order of 50 000 tons yr^{-1}, this now ranks among the most important scallop fisheries in the world (Ciocco *et al.*, in press). Starting in 1999, the resource was shared with Uruguay (one vessel) in the Common Fishing Zone. After 2001, and in accordance with international law, each country has had the exclusive right to exploit this sedentary species on its own continental shelf.

MATERIALS AND METHODS

Oceanographic data

The oceanographic data used in this study, obtained between 1982 and 2001, consist of high-resolution conductivity, temperature and depth (CTD) records and temperature measurements using discrete water bottle samples (6% of the total database records). The number of stations was 980 for the NPFS, 475 for the SPFS, and 462 over the outer shelf and continental slope (SBFS). CTD data were collected with a Meerestechnik Elektronik sound and Seabird series SBE19 or SBE911+ profilers (accuracy for temperature: 0.01°C month^{-1}; for conductivity: 0.001 S m^{-1} month^{-1}), which were calibrated by measuring water samples with a salinometer and reversing thermometers.

The stability parameter φ (Simpson, 1981), which represents a measure of the work needed to mix the water column, was calculated for every CTD profile taken in December (for NPFS) and January (for SPFS). A critical contour, which allowed mapping the boundary between homogenous and stratified regimes during summer, was selected by comparing the contour with the distribution of vertical properties. The mean conditions for NPFS and SPFS systems were represented by φ values of 40 J m^{-3} (Ehrlich *et al.*, 2000) and 150 J m^{-3}, respectively, calculated on the basis of stability data for all years. Data available for the Valdés Peninsula region (years 1984, 1986, 1988, 1993–96, 1998 and 1999) were used previously by Sabatini and Martos (2002). The dataset corresponding to San Jorge Gulf corresponds to the 1995–2000 period. Stability parameters calculated by A. Lucas (University of California, San Diego, CA, USA, unpublished data; φ parameter) and Glorioso and Flather (1995; Simpson–Hunter parameter: S–H) for the study area were considered (see Fig. 2b). Small differences observed between φ and S–H critical contours result from the different factors and datasets used for the calculations. For the slope zone the frontal position was determined with the maximum horizontal gradient of density. Surface data were from March 1994 and bottom (up to 150 m) data were from summer cruises. CTD stations were regularly spaced at intervals varying from 11 to 41 km along transects. In order to characterize the annual regime of bottom temperature, data were selected according to the depth range where the fishing grounds were located.

Satellite data

Monthly averaged sea surface temperature (SST) data were downloaded from NOAA/NASA AVHRR Oceans Pathfinder database for the period 1987–98 (http://podaac.jpl.nasa.gov/sst/, date of last access 9 July 1999; day data, 35–53°S, spatial resolution 9 km). Temperature gradients were estimated as centered finite differences. Based on the location of the Simpson–Hunter parameter contours (Glorioso and Flather, 1995) gradient values ≥0.05°C km^{-1} were considered as indicative of a thermal front.

Surveys and fishery data

Definition of scales

Definition of spatial scales follows Orensanz and Jamieson (1998) and Orensanz *et al.* (in press). Two spatial scales are considered meaningful in the context of this study. The large scale corresponds to metapopulations or (equivalently) fishing grounds: collections of sedentary subpopulations or (equivalently) fishing beds connected among them by larval dispersal at a rate that is meaningful for ecological-time population dynamics. The intermediate scale corresponds to subpopulations or fishing beds. Here we do not deal with small-scale processes, pertinent to ecological interactions taking place in the neighborhood of individuals.

Exploratory survey data

Historical information from technical and scientific reports and personal communications was considered to document the geographic distribution and spatial and temporal persistence of the Patagonian scallop beds. This includes geographic position of hauls performed by several exploratory and fishing surveys of benthic and demersal species which explored the SSAS between 1925 and 2003 (Dell, 1964; Olivier and Scarabino, 1972; Bastida *et al.*, 1981; Lasta and Zampatti, 1981; Dupaul and Smolowitz, 1994). An extended list is available from the senior author upon request. All data, including commercial trips directed to Patagonian scallop, were spatially sorted with a grid of 0.4° latitude by 0.4° longitude cells. A cell was classified as 'absence' when all hauls in it had zero scallops caught. The spatial resolution was chosen in order to attain the minimum oceanographic spatial resolution (0.5°) for the shelf-break area, where fishing activity was most intense.

Data from commercial operations

Between January 1995 and December 2003, five factory vessels (Argentine fleet) completed 277 commercial trips and 560 000 fishing hauls in the area between 36 and 55°S. The vessels operated non-selective bottom otter trawls with booms (head and foot rope, between 17 and 22 m long; Lasta and Bremec, 1997). Average towing speed was 7.4 km h^{-1}. Trawling activity was continuous during the day; duration of a trip ranged between 20 and 40 days. Depending on speed and other technical characteristics, any vessel could complete 40–60 tows day^{-1} per net (Ciocco *et al.*, in press). Towing time was variable depending on year and location, lasting up to 40 min.

The information obtained during an experimental fishing trip in 1989 in the area bound by 43°S, 63°W, 46°S and 65°W (Lasta, 1992) was included in the analysis. The trip was 24 days long, and 3963 hauls were performed with towing times ranging between 4 and 7 min. Data on fishing activity were obtained from logbooks and on-board observers, providing temporally and spatially detailed catch and effort information. In the logbooks, fishers recorded a haul position every 4 h; location of hauls performed in between were associated with the first recorded datum.

Analysis of these data reflects fishermen behavior aimed at maximizing the catch. The number of hauls was considered a measure of effort allocated to each 0.4° latitude by 0.4° longitude cell. The cells selected as 'suitable' (profitable) were those with more than 200 hauls made during each trip. This value represents approximately 2 days of fishing work (10% of the effort exercised by a single vessel during a short trip). From a fisherman's point of view this allocation of effort would indicate a profitable area.

Fishing effort applied on the Uruguayan Sector (north of 37°S, see Fig. 6) was determined based on the Argentine fleet activity. A new regional fishery started in 2003 in an area under provincial jurisdiction in the San Jorge Gulf region, where the industrial fleet managed by the federal administration is not allowed to operate. Exploratory surveys and information from the F/V 'Wiron III' in this area were utilized to describe the fishing aggregation. Besides the industrial fishery, artisanal boats landed small commercial catches in San Jorge Gulf (Ciocco *et al.*, in press), San Matías Gulf (E. Morsan, Instituto de Biología Marina y Pesquera 'Almirante Storni', Rio Negro, Argentina, unpublished data) and Punta Arenas (Chile), but no data were available for this study.

RESULTS

Frontal systems

Major maximum thermal gradient areas were revealed by satellite imagery data to the southwest of San Jorge Gulf, off southeast Valdés Peninsula, at the mouth of San Matías Gulf and over the shelf break, from 39 to 45°S (Fig. 2a). Coastal fronts located in the El Rincón area (ERFS, between 37 and 42°S) and at the mouth of San Matías Gulf were also clearly identified, but are not analyzed for reasons discussed below. Surface thermal gradients observed east of the shelf edge are associated with the MC retroflection (Fig. 2a). These thermal gradients ($>0.05°C\ km^{-1}$) persisted from the austral spring to the autumn (October–May) in the 12 yr analyzed. The identification of surface frontal zones from satellite imagery is coincidental with the critical contour of the φ and S–H parameters reported by other authors (Glorioso and Flather, 1995; Lucas, unpublished data) and those calculated for the southwestern Atlantic Shelf as part of our study (Fig. 2b). Small differences observed in the location of the ERFS between the thermal surface gradient (Fig. 2a) and the contour of φ (Fig. 2b) can be explained in terms of the choice of the critical value of the latter and the depth of the water column, which could modify the onshore–offshore position of the contour. Similar fronts were detected in remote images of SST gradients by Bava *et al.* (2002).

In this study we describe three frontal systems, two of them detectable by satellite imagery within the range of the geographic distribution of the Patagonian scallop: the SBFS and the SPFS (Fig. 2b). A third one, the NPFS, which includes the Valdés tidal front, is not well captured in satellite images for reasons discussed below.

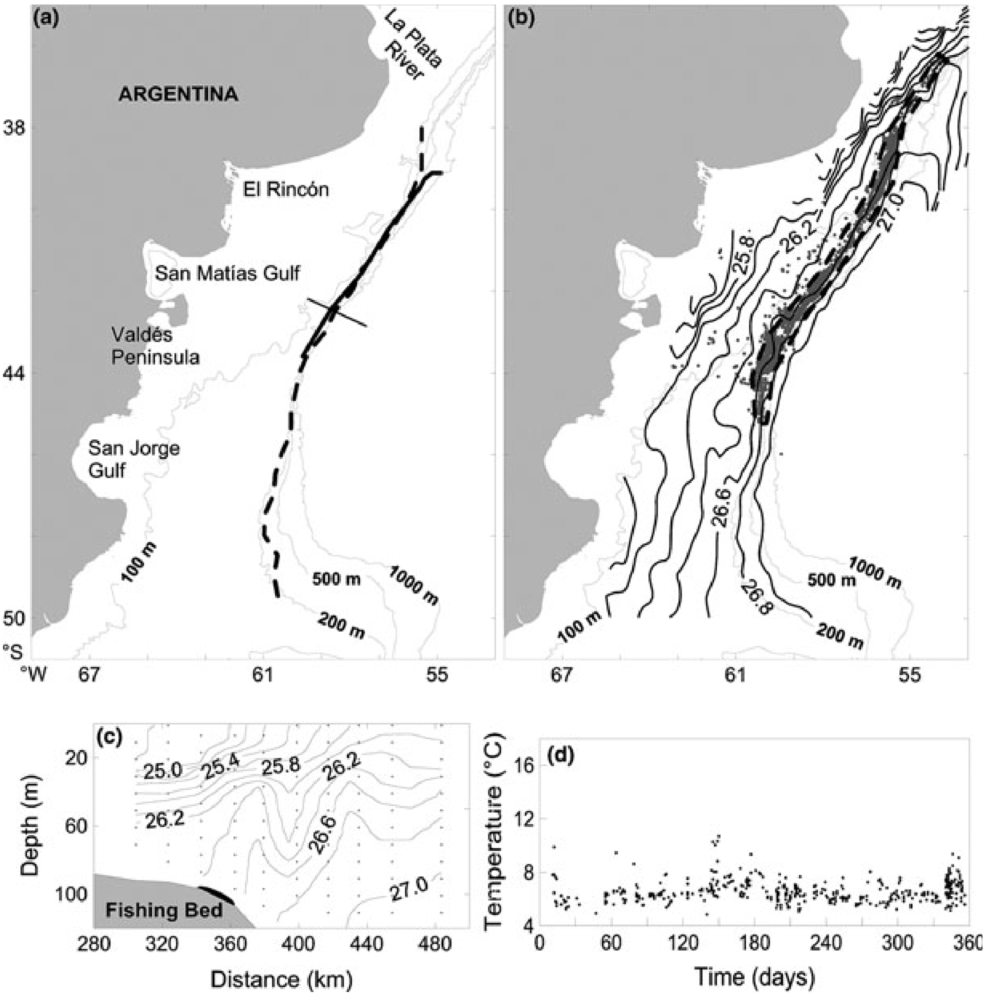
Shelf-Break Frontal System

A weak density gradient, roughly coincidental with the shelf break, forms the boundary between shelf waters (less saline) and slope waters (saltier, nutrient rich) (Fig. 3a,b). This transition defines a gradual horizontal increase of density (on the order of $0.01\ kg\ m^{-3}\ km^{-1}$) over the whole water column throughout the year. Additionally, the differential heating between these two regimes increases the temperature of surface layers during warm periods, resulting in the formation of a surface thermal-density front. At the surface the SBFS develops from spring to autumn with the maximum gradient during the summer. Development and horizontal gradient of the front are forced mainly by the progress of the seasonal thermocline–pycnocline (southward and seaward) and variation in the position of the MC (mainly interannual variability, e.g. Garzoli and Giulivi, 1994).

At the surface the SBFS has been defined between 39 and 44°S, but turns seaward north of 40°S, following the gyre of the MC core ($\sigma_{t150m} = 27\ kg\ m^{-3}$, Figs 2a and 3b). However, the interface between shelf and slope waters, defined by the $26.8\ kg\ m^{-3}$ isopycnal on the bottom, is observed southward to 49°S following the 200-m isobath (Fig. 3a). On the other hand, north of 38°S the intensification of the bottom horizontal gradient shows the interaction between shelf waters, influenced by the Río de la Plata River, and MC and BC waters over the slope (Fig. 3b).

As a result of the development of the summer thermocline the surface temperature of shelf waters

Figure 3. Shelf-Break Frontal System (SBFS). (a) Location of the front in March of 1994 at the surface (solid line), and average from December to March period, 1982–2002 at the bottom (dashed line). The straight line represents transect location. (b) Distribution of bottom water density during the December 1993–March 1994 period, and position of hauls made by the commercial fleet reported between 1995 and 2003 (dots). Dashed line bounds the section of the fishing grounds selected for temperature analysis. (c) Density distribution along transect for March 1994. Dark area over the bottom represents the range of shelf-break scallop beds. (d) Annual variation of bottom temperature over the fishing beds.



reaches 16°C, while temperature over the slope is around 11°C. This stratification corresponds to the density distribution of a region in which the vertical density gradient varies horizontally, changing from large values in the shelf summer pycnocline to smaller values in the deep water offshore (Fig. 3c). The frontal boundary is approximately 40 m thick over the slope, while its cross-shelf intersection with the outer shelf spans between 80 km (surface) and 40 km (bottom). Despite seasonal intensification and development, the density gradients at the foot of the front are indeed present even during winter. Below 50 m depth, at the shelf edge, the shelf-water density ranged from 26.4 to 27 kg m^{-3}, giving a cross-frontal density difference of 0.6 kg m^{-3} between the 100- and 150-m isobaths (Fig. 3c).

The typical density structure of the SBFS in the southwestern Atlantic, where density increases monotonically offshore, defines a retrograde front where the frontal isopleth's slope is opposite to the cross-shelf topography. A subsurface anticyclonic eddy (convergent), with horizontal scale in the order of 40 km, was observed over the upper slope between 40 and 90 m depth associated with an upwelling (Fig. 3c). Furthermore, cross-frontal mid-level intrusions appear to occur at times along the SBFS, except during late winter (August and September), their thickness varying from 5 to 40 m. The bottom temperature in the area remains between 5 and 8°C (Fig. 3d); higher values correspond to points farther north of 37.5°S, associated with the presence of the BC over the slope.

Northern Patagonian Frontal System

A major tidal frontal zone is located near Valdés Peninsula, extending southward off the Patagonian coast from ca. 42 to 45°S (Fig. 2b). The turbulence generated by high tidal currents keeps the well-mixed shallow waters separated from the deeper stratified water. The front starts forming in the early spring, as a seasonal thermocline develops and persists through the autumn, when stratification declines; the steepness of the gradient is maximal during the summer. The average position of the system estimated over this period shows an overall NE–SW alignment following closely the bathymetry and isopycnal contours (75–80 m, Fig. 4a). It is located on average 50 km offshore in the south, and ca. 80 km offshore in the northern zone (Fig. 2b). However, interannual fluctuations move it between 80 and 120 km off the northern coast of Valdés Peninsula and between 20 and 100 km off Isla Escondida (Fig. 4a, also shown by Ehrlich *et al.*, 2000). As a consequence of the bathymetric configuration and topographic shoals located SE and NE of Valdés Peninsula the rate of tidal energy dissipation is enhanced from south to north. Bottom density, which is controlled by temperature, increases offshore. The 26.0 kg m^{-3} isopycnal defines the seaward limit of maximal gradient, indicative of the frontal position (Fig. 4b). A sharp pycnocline between 20 and 40 m depth separates the upper and bottom waters; the

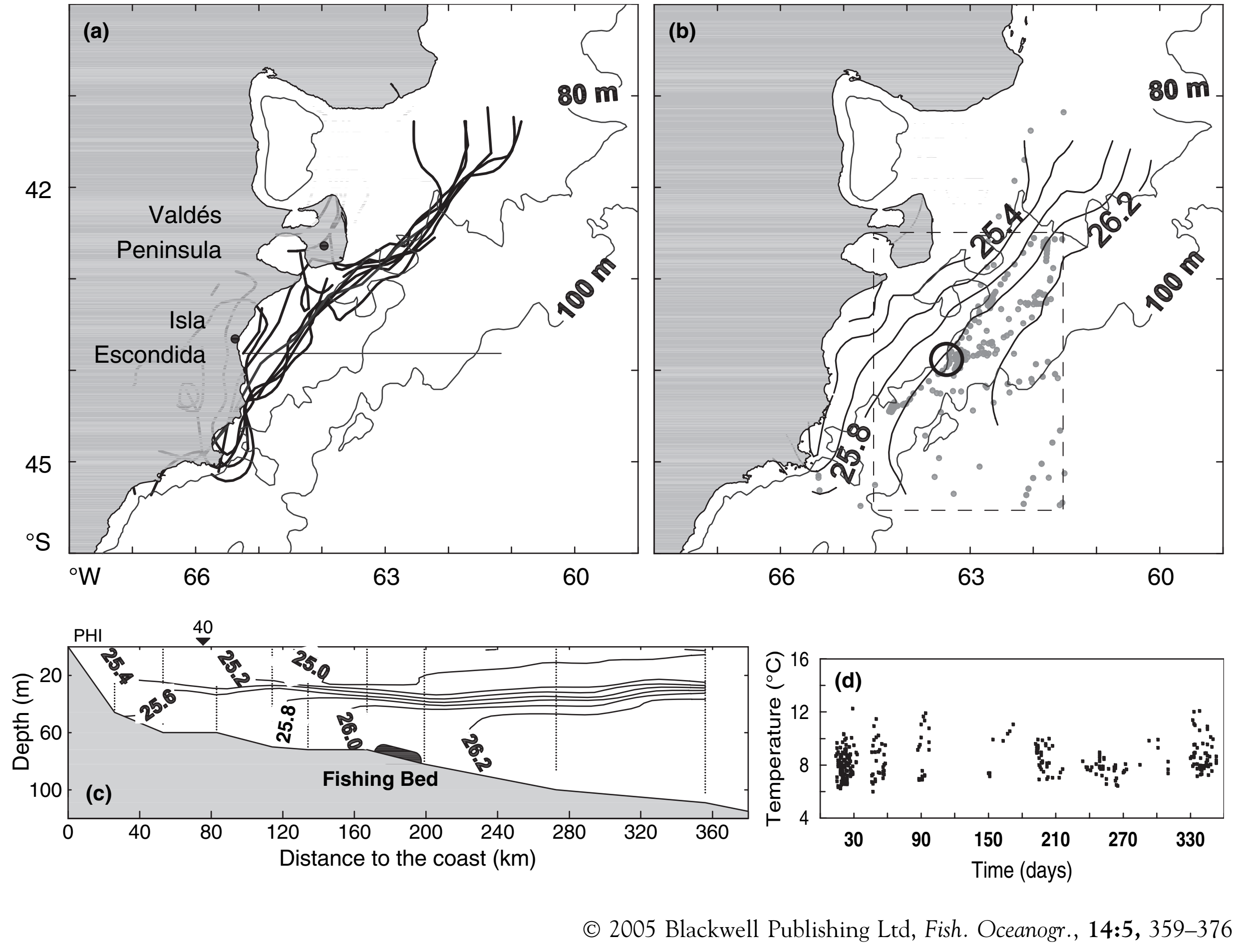


Figure 4. Northern Patagonia Frontal System (NPFS). (a) Inter-annual variability in the position of the front; critical contours of stability (φ) shown for 9 yr. The straight line represents transect location. (b) Distribution of bottom water density in December 1993, and position of commercial hauls reported during 1989 and 1995–2003 (dots); the circle bounds the area where most of the fishing effort was allocated. Dashed line bounds the section of the fishing ground selected for temperature analysis. (c) Transect for December 1993, showing density distribution; station locations indicated by dotted lines. Critical φ-values shown at the top. Dark area over the bottom represents the core scallop bed. (d) Annual variation of bottom temperature over the fishing bed (deeper than 80 m).

isopycnals define horizontal gradients as they intersect the surface ($0.0036\ \mathrm{kg\ m^{-3}\ km^{-1}}$) and bottom ($0.0033\ \mathrm{kg\ m^{-3}\ km^{-1}}$). The bottom signal is *ca.* 100 km offshore from the surface signal (Fig. 4c).

Off Isla Escondida the homogeneous side of the front presents lower surface temperature than the stratified zone, but the lowest temperatures in the area occur offshore from the 80-m isobath at the bottom layers, ranging between 12 and 6°C over an annual cycle (Fig. 4d). The density field shown (Fig. 4c) corresponds to surface temperatures of 12°C on the well-mixed and 14°C on the stratified side. Temperature variability at the bottom is significantly lower than at the surface, with a minimum during the autumn–winter months.

Tidal currents, density fields and (to a lesser extent) wind-driven circulation dominate the mean flow in the area. Direct current measurements indicate a mean flow parallel to the local isobaths, with increasing intensity seawards (Rivas, 1997). In the frontal zone there is a noticeable difference between the periodic components of the flow (semidiurnal component around $40\ \mathrm{cm\ s^{-1}}$) and the mean value (lower than $2\ \mathrm{cm\ s^{-1}}$; Rivas, 1997).

Southern Patagonia Frontal System

The SPFS develops from the Magellan Strait to the south of the San Jorge Gulf (Guerrero and Piola, 1997). This thermohaline front represents the transition between tidally mixed low-salinity waters of the PC and seasonally stratified more saline waters of the continental shelf. Therefore, it is forced mainly by advection of cold and low salinity waters of the PC and strong tidal currents over the shelf. The northern frontal configuration, between ca. 45.5 and 48°S, is associated with the 80-m isobath, which contours a prominent shoal in the vicinity of Cape Tres Puntas (Fig. 5a). Interannual variations in the mean position of the front were small between the summer months of 1995, 2000 and 2001 (Fig. 5a). During the summer the well-mixed waters over the shoal are surrounded by two stratified regions with a thermocline between 30 and 50 m depth (Fig. 5c), defining a bottom density gradient of $0.012\ \mathrm{kg\ m^{-3}\ km^{-1}}$ (Fig. 5b). The area of maximum surface–bottom density difference is located to the west of the shoal ($0.037\ \mathrm{kg\ m^{-3}\ km^{-1}}$), where the contours come close to the bottom (Fig. 5b). During the winter, when shelf waters are vertically homogeneous, the salinity gradient between the PC and shelf water persists and maintains the frontal density distribution. The presence of a little bank (shallower than 50 m) is noticeable to the east of the shoal where an alteration of the pycnocline shows an anti-cyclonic gyre and the well-mixed area widens (Fig. 5c). Bottom temperature in the study area remains between 6 and 14°C (Fig. 5d) during the year; values higher than 12.5°C correspond to summer data for the homogeneous zone.

Scallops

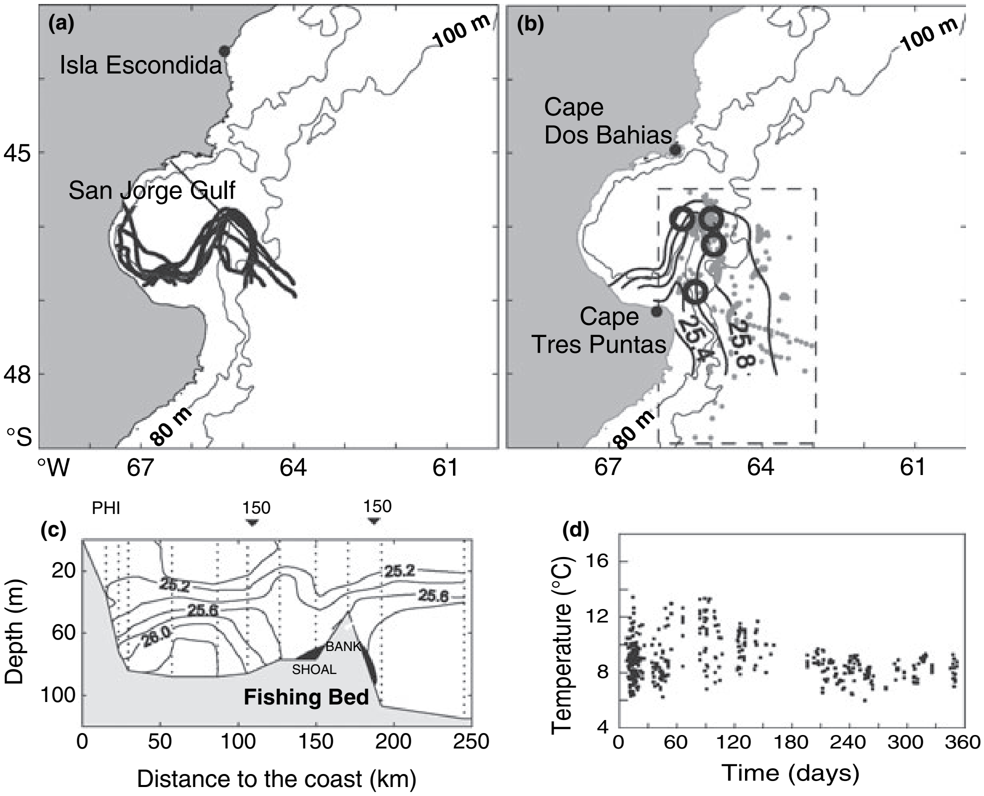
The Patagonian scallop is distributed in the southwestern Atlantic from off La Plata River to Tierra del Fuego (55°S) (Fig. 6a,b). The species is virtually absent north of San Matías Gulf and inshore of the 50 m isobath, where two warm-temperate scallop species (*Aequipecten tehuelchus* and *Flexopecten felipponei*) occur, and beyond mid-slope depths (Fig. 6a,b).

Six discontinuous large-scale aggregations were identified on the shelf between 36° and 48° using fishing intensity (effort allocated per unit area) as a proxy for abundance. Those aggregations are naturally grouped into three major regions suitable for commercial fishing (Fig. 6b, Table 1): the Sea Bay, Tres Puntas and Shelf-Break grounds.

There is consistent indication that beds of the Shelf-Break ground were trawled during exploratory surveys conducted by the FRV 'Walther Herwig' in 1966 (anonymous cruise reports). At the spatial scale dictated by the resolution of the analysis, the ground is composed of a string of four discontinuous aggregations spread along the shelf break. Most of the annual fishing effort applied during the study period (98–100% of the hauls) was allocated to this ground (Table 1), between 38 and 45°S (Fig. 6c). Fishing beds are located within a 20–70-km-wide strip, in a depth range of 81–195 m. Although fishing effort has increased steadily over the whole region, some areas proved more suitable than others (Fig. 6c). Factors other than abundance determine suitability of a bed for commercial harvesting. It was noticed by fishers, for example, that scallop beds associated with the shelf break at 48°S are profitable in terms of catch per unit effort but, because of depth (close to 200 m) and strong bottom currents, they are unsuitable for fishing operations. In spite of these biases fishing intensity appears to be a good indicator at the resolution scale required by this study.

The Sea Bay ground, located off Isla Escondida between 75 and 84 m deep (Fig. 4b,c), was discovered in 1973 during a survey conducted by FRV 'Prof. Siedlecki' (J.M. Orensanz, unpublished data) and found again during exploratory fishing surveys conducted by FRVs 'Walther Herwig' and 'Shinkai Maru' in 1978–79 (Lasta and Zampatti, 1981). It was

Figure 5. Northern end of the Southern Patagonia Frontal System (SPFS). (a) Inter-annual variability in the position of the front; critical contours of stability (one per year) for the period 1995–2001. The straight line represents transect location. (b) Distribution of bottom water density in January 2001, and position of hauls reported during 1989 and 1995–2003 (dots); circles bound areas where fishing intensity was highest. Dotted line bounds the section of the fishing ground selected for temperature analysis. (c) Transect for January 2001, density distribution. Critical φ-values shown at the top. Dark area over the bottom represents the approximate location of fishing beds. (d) Annual variation of bottom temperature over the fishing bed.



intensively fished in 1989 and lightly in 1995, 2001 and 2002 (Table 1).

The presence of high concentrations of Patagonian scallops close to Cape Tres Puntas was first detected in 1973 during an exploratory survey conducted by FRV 'Prof. Siedlecki' (J.M. Orensanz, unpublished data). The Argentine commercial fleet revealed the existence of the Tres Puntas ground, located to the east and around Cape Tres Puntas shoal (Fig. 5b,c). The area was fished in 1989, 1997, 1999 and 2003. Exploratory surveys and a recently developed local fishery extended the known distribution of the aggregation toward the inside of San Jorge Gulf, under provincial jurisdiction, where patches occur around the shoal between 60 and 100 m depth (Fig. 7). Despite good catches, quality and high muscle production, fishermen found trawling difficult due to the rocky bottom and topographic configuration.

No commercial fishing data were available for San Matías Gulf. Exploratory surveys found small beds at 130 m deep in the south-center part of the gulf (approximately at 42°S), and along the northern coast, between 70 and 90 m (E. Morsan, unpublished data).

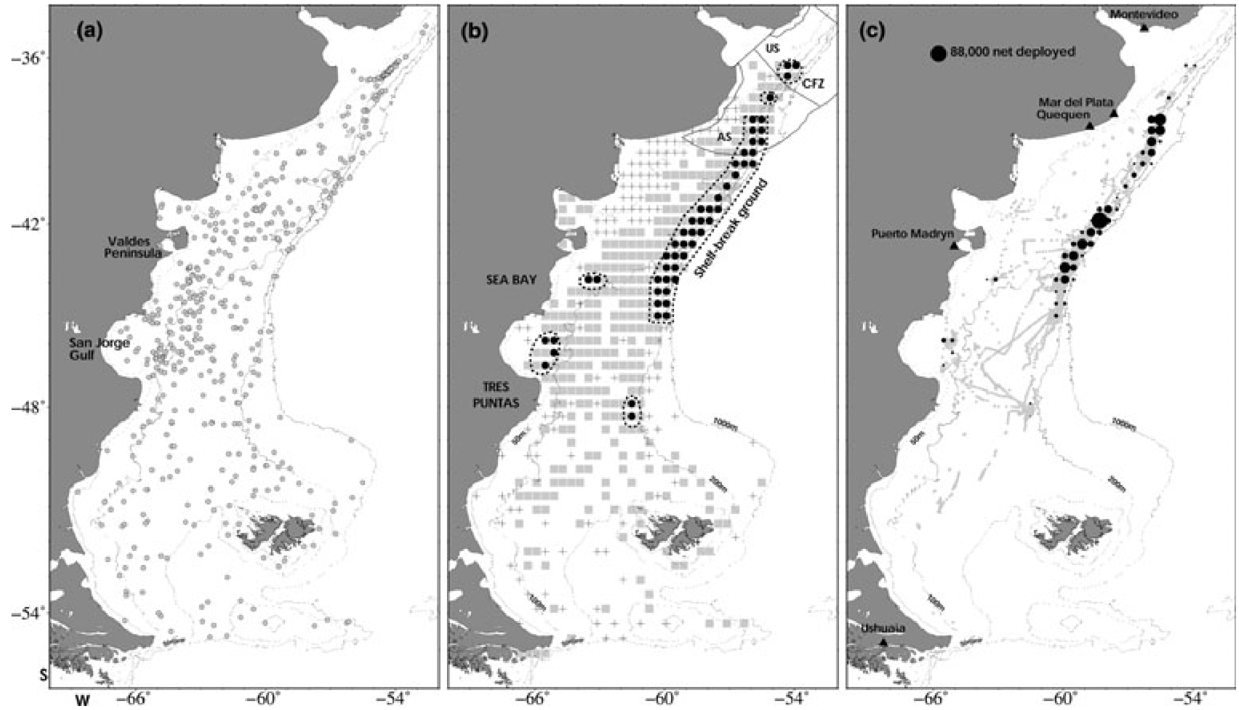
Overlay and matching

Consistent spatial correspondence was found between the main fishing aggregations of Patagonian scallop and the locations of the three frontal zones (Fig. 7). Between 39 and 44°S and along the shelf-break, the SBFS overlays the most productive fishing grounds, with beds located right beneath the surface density gradient (Fig. 7). It is in that latitudinal range where the narrow continental slope brings the core of the MC closer to the shelf break (200-m isobath). Although less suitable for fishing, the latitudinal distribution of the ground continues up to 36°S to the north, and to 49°S to the south. The beds span the cross-shelf intersection zone between shelf and slope waters as it occurs at the bottom, under the influence of a typical retrograde isopleth structure (Fig. 7).

Table 1. Fishing effort exercised by commercial vessels (see text) on Patagonian scallop grounds.

Ground	Location	Reported by	Period	Area fished	Commercial nets deployed	Suitability of the area
Sea Bay	Southeast of Península de Valdés (off Isla Escondida)	'Sea Bay Alpha'	1989	Off Isla Escondida	6670	–
		Argentinean fleet	1995–97, 1999, 2001–03	43–44°S		–
Tres Puntas	San Jorge Gulf	'Sea Bay Alpha'	1989	Near Cabo Tres Puntas	10 902	High muscle production. Difficulties to operate
		Argentinean fleet	1997, 1999 and 2003			
Shelf break	Between 38 and 45°S	Argentinean fleet	1995–2003	Along the shelf break off the 100-m isobath. Highest fished area around 42°S	532 918	Recognized as most suitable area
	North of 38°S	'Holberg' (Uruguayan vessel)	1999	Only in the CFZ (ca. 80% of activity vessel was performed south of 37°S)	unavailable data	The largest CPUE was obtained at 36°40′S. North of 36°15′S the catches decreased abruptly. Highest density in the CFZ found at 36°20′ (Gutiérrez and Defeo, 2002)
		Argentinean fleet	1995–2003	Mostly close to 37°30′S	5052	–
	Between 48 and 49°S	Argentinean fleet	1996–97, 1999, 2001 and 2002	Close 200-m isobath between 48 and 49°S	1293	Difficulties to operate due to environmental conditions

Figure 6. (a) Effort distribution allocated by exploratory surveys that provided information about Patagonian scallop distribution. Gray dots show haul positions for historical non-commercial surveys. (b) Distribution of the Patagonian scallop, *Zygochlamys patagonica*, over the southwestern Atlantic Shelf (SSAS), based on scientific and commercial cruises from 1925 to 2003. Shaded cells are those from where this species was recorded at least once. A '+' indicates that scallops were absent from stations trawled/dredged in the cell; blank cells indicate no data. Cells where more than 200 commercial hauls were allocated during 1989 and 1995–2003 are indicated with a solid dot. Sea Bay, Tres Puntas and Shelf-Break grounds indicate major aggregations found. CFZ: Common Fishing Zone (Argentina-Uruguay), AS: Argentine Sector, US: Uruguayan Sector. (c) Spatial distribution of effort directed to Patagonian scallop by the Argentine fleet (commercial cruises). Black dots show effort measured as nets-deployed allocated per cell during 1989 and 1995–2003; gray dots indicate single-haul positions. Top black dot indicates maximum size of circle, corresponding to 88 000 nets deployed within a cell.



The Sea Bay ground is associated with the NPFS front, occupying the central-south part of its latitudinal distribution. The ground is located on the stratified side, coinciding with the position of the bottom frontal signal (Fig. 7).

The Tres Puntas Bed is shaped as a series of patches located around the Cape Tres Puntas Shoal, associated with the mean position of the northern area of the SPFS (Fig. 7). The patches occur in the transition zone and are subjected to stratified and well-mixed waters depending on seasonal and interannual variability.

DISCUSSION

Distribution of the Patagonian scallop in the SSAS

Our review of various sources of information indicates that, at the scale of the SSAS, the Patagonian scallop occurs over a wide latitudinal range (Fig. 6a) and across diverse hydrographic regimes (Fig. 1). North of 45°S its abundance is generally low shoreward of the SPFS, temperature probably becoming a limiting factor. North of 40°S, a region characterized by the ERFS (Fig. 2a), the Patagonian scallop vanishes from the inner shelf as bottom temperature rises above 9°C, the upper limit tolerated by the species (Heilmayer *et al.*, 2001).

Three major areas of aggregation or grounds (*sensu* Orensanz and Jamieson, 1998) have been identified in the SSAS: Shelf-break, Sea Bay and Tres Puntas, the latter two known as potential fishing grounds for as long as 30 yr. Each of these grounds is characterized by internal heterogeneity expressed in the patchy distribution of density (Lasta *et al.*, 2001). The structure at this scale has been studied for some areas of the Shelf-Break ground using geostatistical methods (Lasta *et al.*, 2001). Aggregations differ from each other with regard to composition of the benthic communities (Bremec and Lasta, 2000) and biological characteristics such as

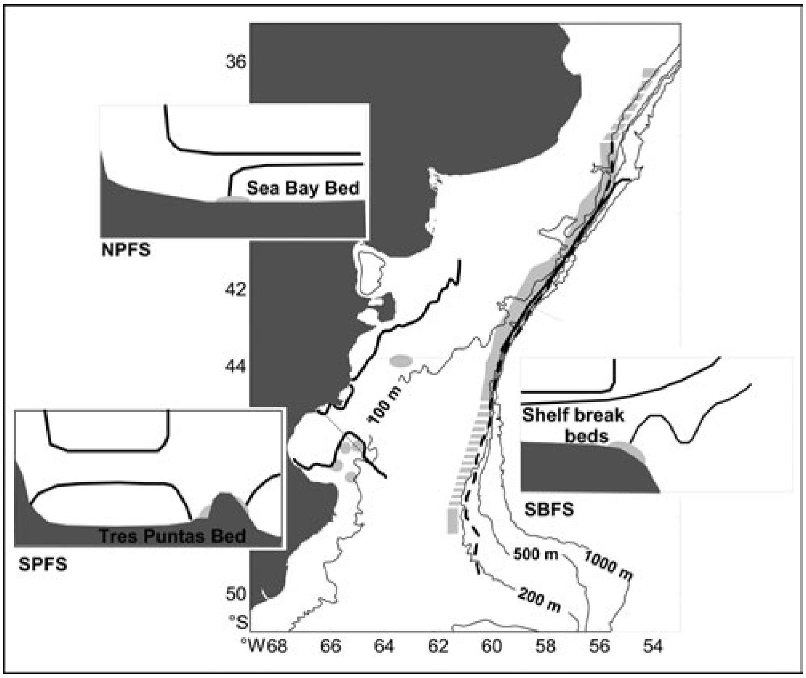


Figure 7. Schematic representation of the spatial correspondence between three frontal systems (solid lines for surface and dashed for bottom signal) and Patagonian scallop beds (shaded areas); straight lines indicate transects. Boxes: vertical structure of the fronts along the transects. Gray areas indicate location of scallop beds.

relative muscle weight of scallops (meat yield; Lasta and Bremec, 1998). The latter determines the quality of the product, which is lowest in the Sea Bay and highest in the Shelf-Break ground. Although substrate is generally a determining factor of scallop spatial distribution (e.g. Stokesbury and Himmelman, 1993), the large-scale distribution of the Patagonian scallop does not appear to be related to characteristics of the substrate over the uneventful bottom-scapes of the SSAS. The only noticeable exception is the absence of scallops from the silty central basins of coastal gulfs (San Jorge, Nuevo, San José and San Matías; Fig. 1).

The location of major Patagonian scallop aggregations matches three major frontal zones that define oceanographic and biological discontinuities over the SSAS: the Shelf-Break ground with the SBFS, the Sea Bay ground with the NPFS, and the Tres Puntas ground with the northern segment of the SPFS. This matching may result from two families of processes: increased productivity at and/or beneath frontal systems, or hydrographic mechanisms that, together with larval behavior, facilitate the retention and/or concentration of pelagic larvae. Among post-settlement factors, food availability at the bottom depends on the concentration of planktonic biomass at the surface and benthopelagic coupling processes (Valiela, 1995). Food supply from the plankton to the bottom is thought to be a major factor for the persistence and recurrent location of scallop populations (Orensanz *et al.*, in press).

One general pattern, three different scenes

The three frontal systems associated with major aggregations of Patagonian scallops in the SSAS are structurally very different from each other, yet all correspond to areas of high productivity.

The NPFS was partially described by several authors (Glorioso and Simpson, 1994; Sánchez *et al.*, 1998) and fully described by Sabatini and Martos (2002). A well-defined annual cycle and development of the seasonal thermocline starting in early October characterizes the stratified side (Rivas and Piola, 2002). Differential wind/tidal forcing characterize environmental differences along the front, defining northern (off Valdés Peninsula) and southern (off Isla Escondida) areas that are reflected by planktonic communities (Sabatini and Martos, 2002). A very narrow mixed sector brings the front very close to the coast and frequently does not show a signal at the surface (Sabatini and Martos, 2002), which could explain the weak surface thermal gradient in the satellite imagery. In addition, the spatial resolution used in the satellite imagery is probably lower than that required to show the very small surface gradient of temperature observed in some years. The front is highly productive during the spring and summer, with enhanced phytoplankton biomass and high chlorophyll-*a* concentration (Carreto *et al.*, 1981). In the area off Isla Escondida these concentrations occur in the surface layer of the stratified side, where red tides often develop (Carreto *et al.*, 1986), while nitrate concentration is consistently higher on the mixed side (Carreto and Benavídes, 1990). Growth of phytoplankton populations could be explained by at least two mechanism of transport across the front, moving either cells or nutrients: the spring-neap cycle and baroclinic eddies (Mann and Lazier, 1991).

The circulation pattern in the adjacent of San Jorge Gulf, where the northern end of the SPFS develops, is characterized by a coastal northward jet carrying cold and low-salinity water and an anticyclonic gyre present throughout the year (Palma *et al.*, 2004). The jet diverges into two branches when it reaches the tip of the gulf: one flows into the gulf along the coast, while the other continues toward the NNE (Palma *et al.*, 2004). Seasonal differences in transport, mainly due to wind stress variability and secondarily to fluctuations of freshwater discharge (Sabatini *et al.*, 2004), could explain the variability observed in the mean position of the front. Furthermore, the area is characterized by the enhanced energy dissipation associated with a noticeable topographic configuration: the Cape Tres Puntas Shoal and the adjacent bank. Interaction between these dominant oceanographic factors may result in local energetic processes such as intensification of frontal structure, surface convergence and upwelling–downwelling, which can significantly influence the local distribution of pelagic and benthic organisms. Phytoplankton concentrations as well as scallop assemblages seem to form patches in the frontal zone, which could be explained by the mixed-layer dynamic (Franks, 1997). The peak levels of primary production, typical of a temperate-sea cycle, coincide with the persistent physical structure. The phytoplankton cycle is characterized by two well-defined chlorophyll-*a* maxima; the main one develops during spring and the secondary during autumn (Cucchi Colleoni and Carreto, 2003). As is the case in tidal fronts, the spring-neap cycle may also be proposed as a cross-frontal exchange mechanism which enhances the productivity of the system (Mann and Lazier, 1991).

In contrast to shelf sea fronts, the mean position of the SBFS (and shelf-break fronts in general) is more or less stationary, as it is entirely controlled by the location of the shelf-break (Gawarkiewicz and Chapman, 1992). Within the range of influence of the MC over the slope, phytoplankton blooms involving dinoflagellates (Negri *et al.*, 1992) and coccolithophorids (Gayoso and Podestá, 1996) appear narrow on satellite imagery, while they widen south of 45°S (Brown and Podestá, 1997). The northern penetration of the MC during winter months is coherent with the maximum of nitrate concentration (Carreto *et al.*, 1995) and saltier bottom waters observed over the shelf-break at 39°S at that time. By the end of the winter, when the water column is well mixed, heat is mixed downwards and nutrients from deeper waters would be mixed upwards (upward nutrient flux). The annual phytoplankton growth cycle is characterized by two well-defined chlorophyll-*a* maxima. The main peak occurs during spring (the spawning season of the Patagonian scallop; Campodónico *et al.*, 2001) and the secondary peak during the autumn, when the thermocline breakdown begins (Carreto *et al.*, 1995). This process is accompanied by a shift in the chlorophyll-*a* maxima from the surface to the pycnocline and by decreasing nitrate concentration in the euphotic layers of the shelf due to phytoplankton activity (Carreto *et al.*, 1995). Several processes influence the circulation and exchange that may explain enrichment and high productivity over the SBFS. Some of them, like topographic waves over the slope (Olson *et al.*, 1988) and mesoscale processes along the edge of the MC, were previously suggested (Glorioso and Flather, 1997). Eddies and mid-level intrusions were density-compensated features present mostly at the thermocline (pycnocline) level of the SBFS. The turbulent exchange between interleaved layers of shelf and slope water can greatly enhance the net exchange of water properties, including heat, salt, nutrients and plankton, across the frontal zone. Equivalent exchange mechanisms have been identified over other shelf edges elsewhere in the world: internal waves (Mazé, 1987), mid-level intrusions (Welch, 1981), interleaving and double diffusive processes (Voorhis *et al.*, 1976), and shelf-break eddies which may be a prime agent of cross-shelf exchange (Garvine *et al.*, 1988). In addition, the detachment of the bottom boundary layer (BBL) is thought to play a fundamental role in the enrichment of the euphotic zone at the shelf-break frontal boundary (Houghton *et al.*, 1994). In a stratified flow, water parcels are forced out of the BBL into the water column, along isopycnal surfaces (Gawarkiewicz and Chapman, 1992). In the northern part of the SBFS the food items of *Z. patagonica* were found to be planktonic, mainly Sub-Antarctic diatoms and dinoflagellates (Schejter *et al.*, 2002). The period of higher cell abundance in gut contents (November, Schejter *et al.*, 2002) and maximum growth in tissue mass (Valero, 2002) are matched by the peak of spring primary production. Weak stratification at this time and the occurrence of vertical movements (displacements between 5 and 40 m) produced by internal tides, together with episodic wind stress (Glorioso and Flather, 1995; Rivas, 1997), are some coupling mechanisms that may facilitate the sinking of algal cells from the euphotic zone to the scallop benthic habitat.

Connectivity and metapopulation structure

Relative to the processes considered in this study, aggregations of Patagonian scallops in the SSAS can be conveniently conceptualized as a two-scale pattern: an array of a few large- (macro-) scale aggregations (equivalent to fishing grounds), each of them consisting of clusters of dense subpopulations (equivalent to fishing beds). Given what is known about circulation in the SSAS, connectivity is arguably higher among beds within a ground than among grounds. Thus, each large-scale aggregation can be defined as a separate metapopulation, their dynamics governed by two families of processes: connectivity between metapopulations and larval retention in the vicinity of the parental stock. These correspond, respectively, to vagrancy and membership in terms of Sinclair's (1987) hypothesis.

Although 'marine metapopulations' have become fashionable only during the last decade, the conceptual model has a long history in scallop research (e.g. Fairbridge, 1953; Sinclair *et al.*, 1985; Orensanz, 1986, as 'megapopulations'). Metapopulation arrangements investigated in different studies range from collections of subpopulations that share a common larval pool (Fairbridge, 1953; Orensanz, 1986; Thouzeau and Lehay, 1988), usually confined to semi-enclosed bays with significant tidal circulation, to 'archipelagos' of self-sustaining subpopulations (Sinclair *et al.*, 1985; Sinclair, 1987; Young, 1994; Arnold *et al.*, 1998), in which larval retention in the vicinity of the parental stock is purportedly significant. Correspondence between observed patterns of distribution and oceanographic features has been regarded as support for the second model ('inductive approach' *sensu* Sinclair *et al.*, 1985, p. 5). Matching between major frontal systems and large-scale aggregations of Patagonian scallops reported by us contributes that type of evidence. Oceanographic features that have been associated with retention include shelf fronts, trapping by gyres and eddies, interaction between coastal topography and wind or tidally induced circulation, and estuarine-like circulation (Orensanz *et al.*, in press). Although relationships between stock location and oceanographic features are frequently invoked, they have been rarely substantiated by process-oriented studies (the 'deductive approach' *sensu* Sinclair *et al.*, 1985, p. 5).

Opportunities for cross-shelf transport between grounds of the inner shelf (Tres Puntas and Sea Bay) and the shelf break are not well understood. Connectivity along the inner shelf (inshore of the 100-m isobath) and along the shelf edge must be asymmetrical, with beds to the south–southwest being likely sources of larvae for beds located toward the north–northeast. In the area of the NPFS the mean flux measured (lower than 2 cm s^{-1}; Rivas, 1997) is an order of magnitude lower than the tidal component (40 cm s^{-1}; Rivas, 1997). At a monthly time-scale (the order expected for the pelagic stage) the trajectory of an inertial particle would follow the typical position of the front, being advected to the NE at about 50 km $month^{-1}$ (Sánchez *et al.*, 1998) and, so, retained within the region of the Sea Bay ground. Notice that, as pointed out by Cowen *et al.* (2000), the relative significance of dispersal and retention is largely a matter of scale. In the case of SBFS, the northward flow of the Malvinas (= Falkland) Current, nearly parallel to the continental slope, and a clockwise (cyclonic) gyre over the middle Patagonian Shelf (Palma *et al.*, 2004) support the hypothesis of a convergent northward flow along the shelf break. This implies, as noticed by Gutiérrez and Defeo (2002) for the northern end of the shelf break, that larvae must be transported mostly toward the northeast.

Our description of major frontal systems of the SSAS suggests some mechanisms for larval retention within metapopulations. Sinclair *et al.* (1985) observed that along the shelf of the northwestern Atlantic scallop beds tend to occur in zones of transition between tidally mixed (inshore) and stratified (offshore) waters. This pattern is very similar to the correspondence of the Sea Bay ground with the NPFS observed by us. In some documented cases recruitment appears to be associated with the seasonal development of an upper layer of warm water (Tremblay and Sinclair, 1992). Studies of the ontogeny of behavior and settlement of *Placopecten magellanicus* larvae kept in experimental mesocosms revealed that in stratified water larvae are confined to the upper layer, above the thermocline (Pearce *et al.*, 1996), implying that settlement should increase in areas where (and/or at times when) water stratification is disrupted. Orensanz *et al.* (1991) noticed that the Sea Bay ground matches the stratified region offshore from the NPFS, prompting the hypothesis that a mechanism of this nature operates in this system as well. In the case of the SPFS, although circulation is complex (especially with regards to topographically steered flows) and not completely understood, there are opportunities for physical and biological retention/concentration mechanisms (e.g. energetic processes like surface convergence and upwelling–downwelling) that may explain the presence of the associated scallop beds.

Larvae are not passive particles; larval dispersal is influenced by factors other than water circulation: diffusion, survival, and active behavior in the water column (Cowen *et al.*, 2000). Vertical and horizontal larval swimming behaviors, coupled with mesoscale and submesoscale circulations, may alter their transport trajectories enhancing ecological time-scale retention close to the source population (Werner *et al.*, 1993; Botsford *et al.*, 1998). Even subtle responses to environmental cues can have a strong influence on larval retention/dispersal. In a comparative study of two populations Manuel and O'Dor (1997) and Manuel *et al.* (1997) found that larvae respond in the same way to the daily light cycle, but differ in their response to tidal cues. Horizontal transport resulting from vertical migration was considered by the authors as the most likely selective pressure to create and maintain different behaviors against the homogenizing effects of larval dispersal. Ultimately, understanding of factors governing the large-scale distribution of the Patagonian scallop will require surveys of larval distribution in the field and experimental work on larval behavior.

Information about oceanography of the SSAS and large-scale distribution of Patagonian scallop stocks should be the basis for simulation modeling of larval dispersal under different assumptions about (or scenarios for) larval dispersal and resulting patterns of connectivity and larval retention/advection, an approach best illustrated by the research conducted by Tremblay *et al.* (1994) on the *Placopecten magellanicus* stocks from the Georges Bank.

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