Marine fronts at the continental shelves of austral South America[☆]
Physical and ecological processes

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Abstract

Neritic fronts are very abundant in austral South America, covering several scales of space and time. However, this region is poorly studied from a systemic point of view. Our main goal is to develop a holistic view of physical and ecological patterns and processes at austral South America, regarding frontal arrangements. Satellite information (sea surface temperature and chlorophyll concentration), and historical hydrographic data were employed to show fronts. We compiled all existing evidence (physical and biological) about fronts to identify regions defined by similar types of coastal fronts and to characterize them. Fronts in austral South America can be arranged in six zones according to their location, main forcing, key physical variables, seasonality, and enrichment mechanisms. Four zones, the Atlantic upwelling zone; the temperate estuarine zone; the Patagonian tidal zone and the Argentine shelf-break zone, occupy most of the Atlantic side. The Chile–Peru upwelling zone, on the Pacific, is the largest and best-known region. The Patagonian cold estuarine zone encompasses the tip of South America, connecting the Pacific and Atlantic oceans, and remains poorly studied. When observed at a continental scale, the Pacific coast dominated by two large frontal zones appears simplest than the Atlantic coast in terms of frontal richness. The extension of the continental shelf in the Atlantic coast allows for the development of a great diversity of mesoscale fronts. Though frontal zones we defined are extensive areas of the continental shelves, fronts inside the zones are comparatively small areas. Even so, they play a paramount role in ecological processes, allowing for high biological production; offering feeding and/or reproductive habitats for fishes, squids, and birds; acting as retention areas for larvae of benthic species; and promoting establishment of benthic invertebrates that benefit from the organic production in the frontal area.
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1. Introduction

A common-sense view of the marine environment as a fluid medium would probably imply progressive changes and smooth gradients in physical properties. Sharp boundaries, however, are actually quite widespread and are generally known as "fronts"... Le Fèvre (1986)

In general, a front can be thought as a meeting of waters. Circulation at the fronts is usually associated with a density difference between the two waters, which generates a convergence at the surface or bottom boundary and maintains the front as a sharp transition, approximating an interface, even in the presence of diffusive effects (Largier, 1993). Fronts are an integral part of the sea, of its fluid processes and of its ecological functions.

The fronts are caused by diverse forcing such as tides, continental run-off, currents convergence, wind, solar heating, bathymetry, etc. There is no agreement about the classification of fronts, but a partial listing of those occurring in neritic waters would include tidal fronts, shelf-break fronts, upwelling fronts, estuarine fronts, plume fronts, and fronts associated with geomorphic features such as headlands, islands, and canyons (Mann and Lazier, 1996).

Fronts are zones of increased mixing both laterally and vertically, the result of which often is increased primary and secondary production (Olson and Backus, 1985). It is well accepted that fronts are likely to be characterized by high phytoplankton biomass and in many cases, enhanced activity at higher trophic levels as well (Le Fèvre, 1986; Largier, 1993; Mann and Lazier, 1996). Marine populations exist in a moving fluid medium that is highly structured and often turbulent. Moreover, primary organic production in the sea must take place in the illuminated surface layers which tend to be isolated from sources of necessary plant nutrients. Thus, essentially, the entire living system of the ocean is crucially dependent on various processes by which organisms and materials are transported and redistributed (Bakun, 1994). Fronts are usually vertically inclined interfaces between water masses of different properties, where nutrient rich waters are moved up. Nutrient pumping due to stratification weakening or disruption generates enrichment in the photic zone, enhancing primary production at fronts. If the frontal region is sufficiently long-lived, populations of herbivorous zooplankton will increase, and convergence concentrates zooplankton in the front promoting secondary production. Fronts are also important in benthic productivity. Benthic invertebrates take advantage of primary production and detritus generation in the photic zone (Largier, 1993; Mann and Lazier, 1996).

High food availability at fronts attract nekton organisms (fish, squids, etc.), transferring the energy to higher trophic levels. Free swimmers like tunas, swordfish or sperm whales detect fronts by sophisticated sensorial systems (Olson, 2002). Strong convergence velocities associated with fronts are very efficient in accumulating floating matter along the convergence line. Flotsam often includes detritus such as dust, foam and timber (Bowman, 1978). Bakun (1994) stressed the widespread attraction of fish and other marine animals to drifting objects, and proposed this as a mechanism of front detection.

Coastal birds like gulls and terns, may detect prey aggregations by using visual cues, both by direct location of prey or identifying the active presence of other subsurface predators (large fish, seals, whales, dolphins and even penguins) which drive preys close to the surface. Pelagic seabirds, like large albatrosses and petrels, may travel thousands of kilometers during their foraging flights and may use olfactory cues to detect remote sources of food like zooplankton, fishes or squids which concentrate at fronts (Nevitt, 1999).

The physics of fronts provides unique opportunities for various types of organisms, while at the same time, an acute set of physiological challenges. Some fauna would use fronts as prime foraging grounds making use of the fact that some organisms are at a disadvantage in the front because of thermal, haline or nutritional stresses (Olson, 2002).

Marine environment at austral South America is poorly studied from a systemic point of view. Notwithstanding, there is enough information to show that this region is rich in coastal fronts, having different forcing, and temporal and spatial scales. Marine front patterns may be seen as part of the structural complexity of the pelagic realm at the seascape scale. Satellite information (sea surface temperature and chlorophyll concentration), and historical hydrographic data, were employed to show fronts. We compiled all existing evidence to identify regions

defined by similar types of coastal fronts and to characterize them. Our main goal is to compare Pacific versus Atlantic coasts regarding their frontal arrangements, and to develop a holistic view of physical and ecological patterns and processes, at austral South America.

2. Data sources and methodology

The geographic domain covered in this review corresponds to the coastal zone in the Southern Cone of South America (20° to 60°S) (Fig. 1). On the Atlantic side this area coincides with the Southeast South American Shelf Large Marine Ecosystem, as described by Bisbal (1995). On the Pacific coast it corresponds to the Humboldt Current Large Marine Ecosystem (e.g. Sherman, 1988).

We are considering neritic fronts with a range in spatial scale from thousands of kilometers (e.g. the Chilean–Peruvian upwelling) to tens of kilometers (e.g. some tidal fronts on the Atlantic coast of Tierra del Fuego). Fronts of smaller spatial scale are not well studied for the area, and have presumably a more localized effect on biological processes.

We employed information coming from different bibliographic sources, several of them rather cryptic ("gray literature"), normally not available to the international scientific community. Frequently, data analysis were made without having in mind the concept of "ocean fronts"; and the studies of biological processes were in many cases highly dissociated from physical oceanography. All this information was thus reinterpreted in the light of bio-physical interactions at marine fronts concepts (e.g. Olson, 2002), bringing new insights from current knowledge.

The synoptic capability of present thermal and ocean color satellite sensors, was employed to generate two images of the entire study area, which allowed us to show thermal fronts and chlorophyll concentrations at frontal areas. Monthly Level 3 SeaWifs images, corresponding to chlorophyll-*a* concentration in mg m^{-3}, were provided by the SeaWiFS Project NASA/Goddard Space Flight Center and ORB-IMAGE (http://seawifs.gsfc.nasa.gov/). All images for the period 1997–2001 were corrected to geographic coordinates (lat–lon), and subset images were generated for the study area.

Sea Surface Temperature (SST) estimates were obtained from the Advanced Very High Resolution Radiometer (AVHRR) onboard the NOAA-14 polar orbiting satellite. Level 1B local area coverage (LAC) data were acquired through the NOAASatellite Active Archive (SAA) (http://www.saa.noaa.gov) and the CENPAT receiving facility at Puerto Madryn, Argentina. Forty relatively cloud free AVHRR scenes, for the period February 25 to March 15 of 1999, were processed to obtain SST images using the Erdas Imagine software with the goal of generating a mean SST map of the entire study area. The composite SST map is employed to show thermal fronts.

Isopleths of mean surface salinity of specific regions are presented in order to display salinity fronts. We employed 8387 oceanographic stations (CTD and castings) coming from the National Institute for Fisheries Research and Development (INIDEP-Argentina); and from the Argentine Oceanographic Data Center (CEADO). Frontal extension was defined by the maximum horizontal gradients of physical properties.

We summarized the physical oceanographic features of the coastal fronts in order to identify large coastal regions characterized by similar frontal forcing. After that, we compiled and condensed the information about main ecological processes of each region. We draw a holistic view of frontal patterns and ecological processes, and finally made a general comparison between the Pacific and the Atlantic coasts.

3. Results

3.1. The coastal fronts at the Atlantic margin. Oceanographic features

From a continental perspective, the Atlantic coastline is relatively straight from 20°S to the Río de la Plata (Figs. 1 and 2). The South Brazilian Bight is a conspicuous feature of the southern Brazilian coast, which lies between Cape Frio (23°S) and Cape Santa Marta Grande (28°40′S). From Río de la Plata to Tierra del Fuego, there are several major coastal embayments (Blanca Bay and the Gulfs of San Matías, San Jorge and Nuevo), and the headland of Península Valdés (Fig. 2). The
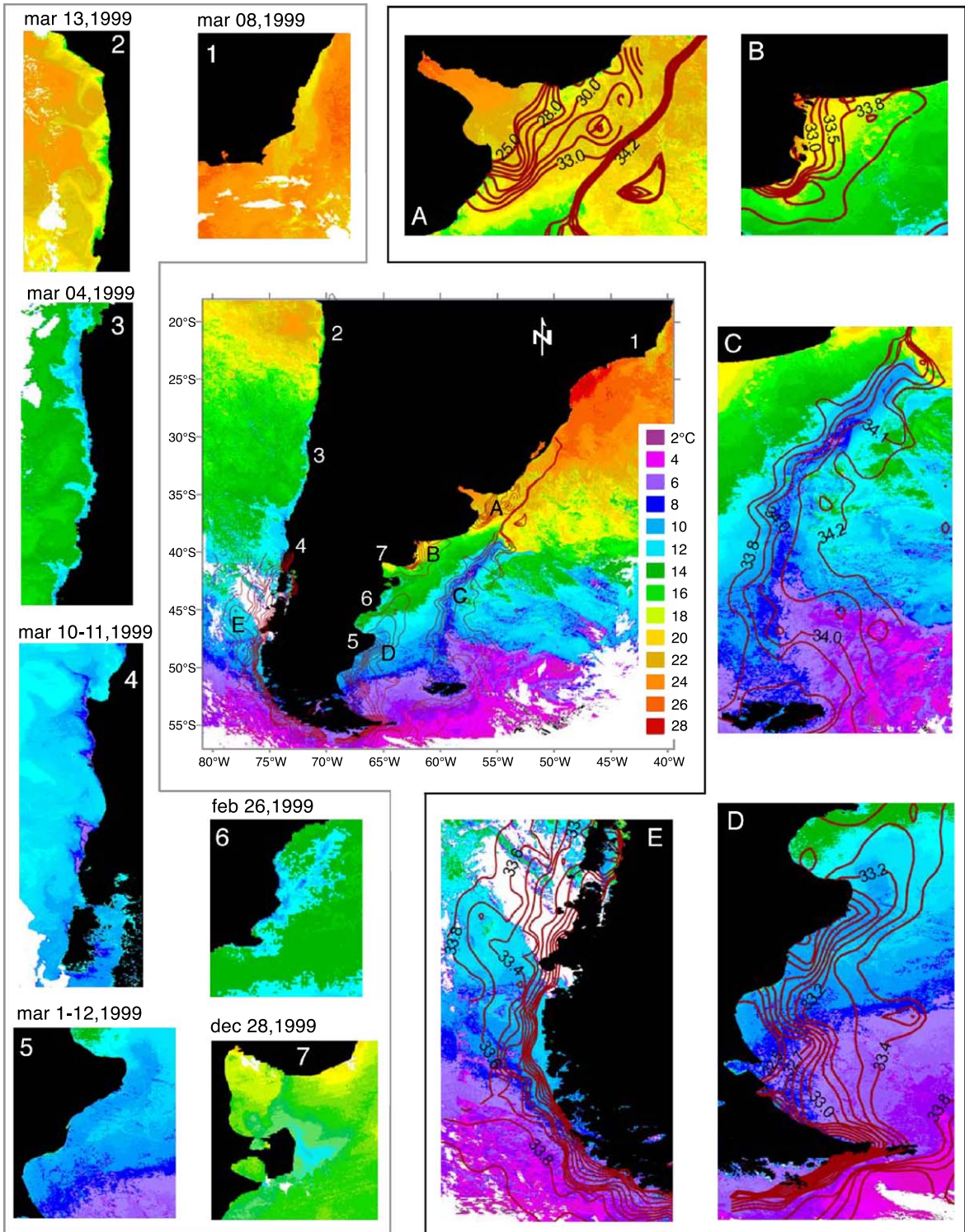
extension of the continental shelf off Argentina (ca. 1,000,000 km^2) produces an exceptionally large Neritic Province. The average distance from shore to the shelf-break ranges from about 50 km (Cape Frío) to more than 800 km (off southern Patagonia). The open ocean circulation is dominated by the opposite flow of the Brazil (subtropical) and the Malvinas (subantartic) currents (Fig. 2). Both currents meet, in average, at 36°S (Olson et al., 1988). In this area, referred to as the Brazil/Malvinas Confluence, the two flows turn offshore in a series of large amplitude meanders.

3.1.1. The Cape Frío upwelling

Cape Frío (23°S) is characterized by wind induced upwelling on the coast, and shelf-break upwelling driven by the meandering pattern and eddy activity of the Brazil Current (Castro and Miranda, 1998; Campos et al., 2000) (Fig. 1). During the summer, divergence due to the coastal upwelling pumps water inshore in the bottom layers. In the presence of meander-induced upwelling near the shelf-break, the combination of the two effects results in a strong mechanism capable of bringing the cold and nitrate rich South Atlantic Central Water (SACW), from the slope regions to near the coast (diagram box in Fig. 2). During winter, when coastal upwelling is diminished, practically only the meander-induced upwelling occurs (Campos et al., 2000). The amount of freshwater discharged by rivers onto the inner shelf is scarce and the nutrient enrichment depends on the pumping of the SACW from the slope.

3.1.2. The Cape Santa Marta Grande upwelling

The area off Cape Santa Marta Grande in the Brazilian shelf (28°45′S) is characterized by locally upwelling events, mainly during spring and summer (Emilsson, 1961; Matsuura, 1986; Castello, 1990).

Shelf water off Cape Santa Marta Grande is evenly stratified, with warm saline water at the surface driven by the SW Brazil Current overlying much cooler, fresher, and nutrient-rich SACW. The bottom is rather steep and narrow, as the shelf is just slightly over 100 km wide. The summer season is characterized by moderate dominant NE winds that force an upwelling condition at the coast (Matsuura, 1986). Less frequently, a downwelling condition is observed when winds reverse to a SW direction.

3.1.3. The Patos Lagoon estuary

The Patos Lagoon is the world's largest choked lagoon. About 80% of the lagoon is a freshwater system, but at its southern limit (32°S) the lagoon connects to the ocean by means of a deep (15 m) and narrow inlet (800 m). There, brackish waters and fringing marshes comprise an estuarine ecosystem of about 1000 km^2. Tidal energy is scarce due to amphidromic conditions presented at 30–32°S (Odebrecht and Castello, 2001). As a result, the main forcing controlling water dynamics and salinity distribution are regional precipitation (700–3000 m^3 s^{-1} annual mean freshwater run-off, with maximum in winter/spring), and wind patterns (northeasterly winds promote flushing while the southerly winds force saltwater into the estuary) (Odebrecht and Castello, 2001; Seeliger, 2001). Lagoon discharge into the shelf generates a low density and stable surface water layer. This plume extends for about 50 km offshore (Odebrecht and Castello, 2001).

3.1.4. The Río de la Plata estuary

The Río de la Plata is an extensive and shallow coastal plain estuary at 35–36°S (Fig. 1). It receives freshwater from the second largest South American basin, with a mean discharge of 22,000 m^3 s^{-1} (Framiñan and Brown, 1996). The system is characterized by strong vertical stratification: freshwater flows seaward on the surface while denser shelf water intrudes along the bottom, taking the shape of a salt

Fig. 1. Temperature and salinity fronts at the continental shelves of austral South America. Sea Surface Temperature composite image (NOAA-14 from 2-25-1999 to 3-13-1999). Isopleths of salinity for selected areas. Numbers represent subsets of thermal fronts; letters represent subsets of salinity fronts. (1) Cape Frío upwelling, (2) Southern Peru upwelling, (3) Northern Chile upwelling, (4) Central Chile upwelling, (5) Southern Gulf San Jorge tidal front, (6) Northern Gulf San Jorge tidal front, (7) Península Valdés tidal front. (A) Río de la Plata estuarine front (2490 stations), (B) El Rincón estuarine front (1200 stations), (C) Argentine shelf-break front (5580 stations, see also the thermal gradient), (D) Atlantic Patagonia cold estuarine front (2304 stations), (E) Pacific Patagonia cold estuarine front (890 stations). NOAA LAC Level 1B data were acquired at the SAA (Satellite Active Archive) of the NOAA (National Oceanic and Atmospheric Administration). (available at http://www.saa.noaa.gov/swig-bin/WWWdisplay).
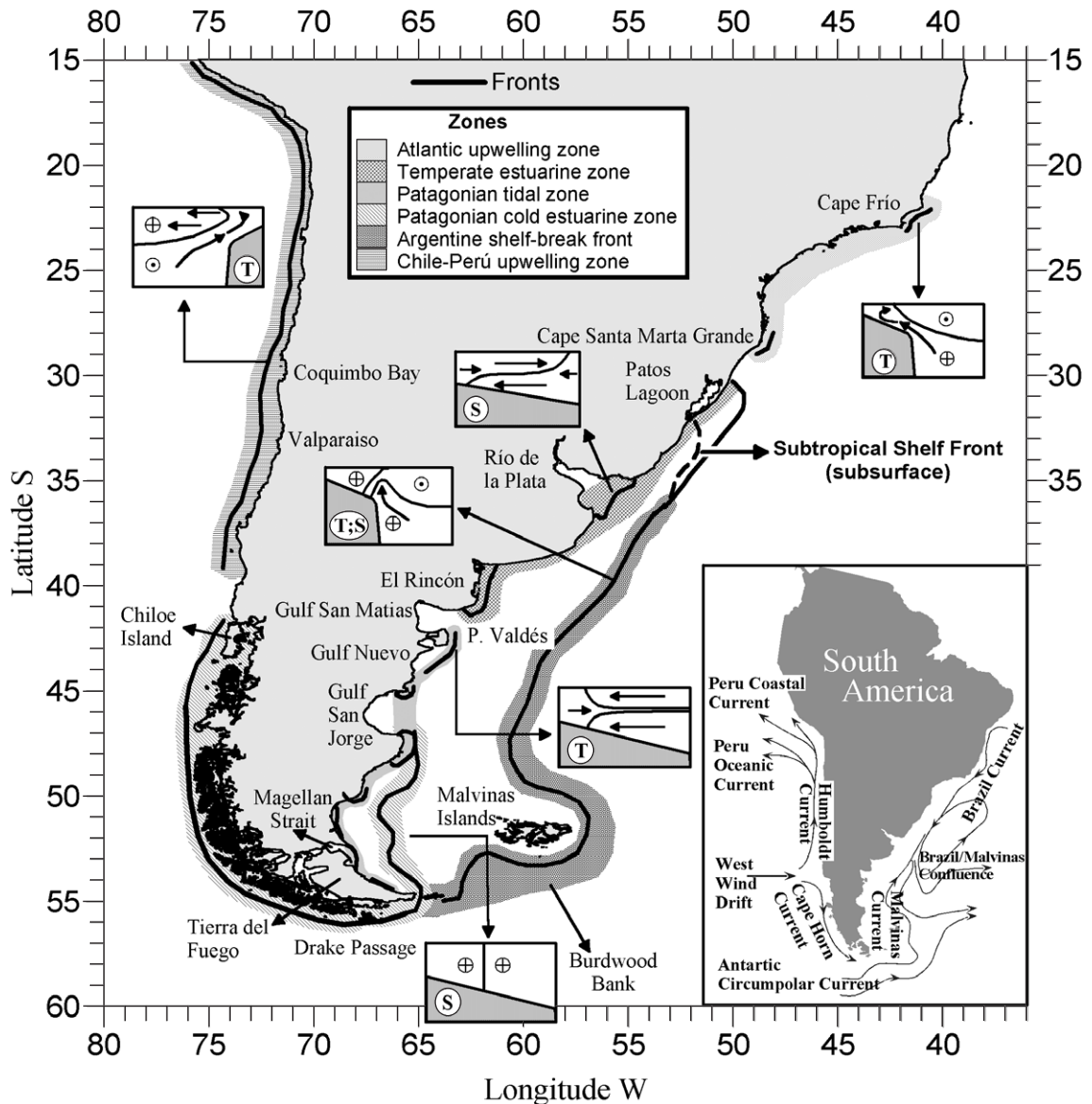
Fig. 2. Frontal zones in austral South America. Diagram boxes represent vertical structure of the fronts: black lines show the density surfaces, arrows show water flow, circles with a cross show currents flowing into paper, circles with a dot show currents flowing out of paper. "T" or "S" refers to the main variable featuring the front (temperature or salinity, respectively). Insert: Main currents and general surface circulation at austral South America.

wedge (see the diagram box in Fig. 2). The dynamics of the upper water layer discharging over the continental shelf is mainly driven by wind stress, while the bottom layer is topographically controlled (Guerrero et al., 1997). A disruption of water column stratification and mixing of the salt wedge occurs after several hours of strong onshore winds (>11 m s^{-1}) (Guerrero et al., 1997). In the inner estuary, the flocculation of suspended matter at the tip of the salt wedge and resuspension of sediment due to tidal current friction at the bottom forms a turbidity front (Framiñan and Brown, 1996).

3.1.5. The El Rincón estuary

The coastal regime in the region called El Rincón (39°S–41°S, depth < 40 m) is characterized by vertical homogeneity due to tidal forcing, and a coastal front separating diluted coastal water, coming from the Negro and Colorado rivers (960 m^3 s^{-1} total average discharge), and shelf waters. Salinity gradient is increased by the presence in the continental shelf of high saline waters originated in Gulf San Matías (a major coastal basin isolated from the shelf by a 60 m sill). The front, oriented North–South, encloses an area of 10,000 km^2 showing weak seasonality (Fig. 1). Bathymetry and the mean shelf circulation contribute in maintaining this front (Guerrero and Piola, 1997; Guerrero, 1998; Lucas et al., submitted).

3.1.6. The Península Valdés tidal front

The Península Valdés tidal mixing front (Fig. 1) is a mesoscale (100–1000 km) thermal front, observed in spring and summer, that defines the boundary between stratified (offshore) waters and a coastal, vertically mixed body of water (see the diagram box in Fig. 2). The stratification of shelf waters is induced by surface warming during spring and summer periods, and the mixing of the coastal water is forced by vertical shear induced by tidal currents at particular topographic shoals southeast and northeast of the peninsula (Carreto et al., 1986; Glorioso, 1987). Wind stress on the surface layer also contributes to the formation and maintaining of the homogeneous side of the front. The structure of the front is maintained until autumn when stratification of shelf waters decays. Frontogenesis begins in spring.

The Atlantic Patagonian continental shelf has high levels of dissipation of tidal energy (Simpson and Bowers, 1981; Glorioso, 1987). That of Península Valdés is the best known tidal front for the region, but some minor and less studied tidal fronts exists southward (Fig. 1). Sabatini et al. (2000) showed a front at 51°S, and Glorioso and Flather (1995), from predictions of a barotropic model, proposed the existence of tidal fronts southward reaching 55°S.

3.1.7. The Atlantic Patagonia cold estuarine front

Water masses on the northern extreme of the Drake Passage, north of the Subantarctic front, are diluted due to an excess of rainfall on the SE Pacific (see

Section 3.2.1) and the continental discharge along the W coast of South America. The flow towards the Atlantic, known as Cape Horn Current (Fig. 2), enters the continental shelf through the Le Maire Strait contributing to the low salinity water south of the Magellan Strait. In the continental shelf, this water is further diluted by continental run-off, mainly by the diluted waters of the Strait of Magellan. Several basins drain along this strait collecting the abundant rainfall (>2000 mm year^{-1}) and thaw during summer. This coastal water mass is also wind driven by dominant westerly winds. A diluted plume, vertically mixed by tides and the wind stress (see the diagram box in Fig. 2) is traced 200 km off-shore (100 m depth) and 800 km northward, reaching the southern limit of Gulf San Jorge and meeting the coastal tidal front here located (Fig. 1). Though this plume remains vertically homogeneous in salinity, thermal stratification in the northern sector has been reported (Krepper and Rivas, 1979).

Glorioso and Flather (1995) have shown that local wind field generate a large anticlowise circulation cell in southern Grande Bight. The model predicts that associated divergence of the flow may induce a compensating upwelling motion as was observed by Sánchez et al. (1995).

3.1.8. The Argentine shelf-break front

Near the Argentine continental shelf-break the subantartic shelf waters meet the cooler and more saline waters of the Malvinas current, thus producing a thermohaline front (Martos and Piccolo, 1988; Lutz and Carreto, 1991). The shelf-break front is a permanent feature that characterizes the border of the shelf (Fig. 1). The inner boundary lies between the 90 and 100 m isobath. During summer the front presents mild gradients in the density and thermal fields but is weak in the salinity field. During winter only salinity controls the density gradient. The gradients are strongest during autumn (Martos and Piccolo, 1988). The geographical location of the front may vary according to the dynamics of the Malvinas Current, for which cyclical variations—including semiannual, annual and biannual periods—have been reported (Olson et al., 1988; Fedulov et al., 1990). Carreto et al. (1995) have shown that at 38–39°S the front varies seasonally, moving offshore during summer and onshore during spring and autumn.

The shelf-break front may be followed from the Burdwood Bank along the shelfbreak to the east, around Malvinas Islands (Guerrero et al., 1999) and northwards up to the Brazil/Malvinas Confluence (Fig. 1). This confluence, generated at the meeting of the major oceanic currents in the Southwestern Atlantic, produces an extended region of interrelated fronts extending offshore to the oceanic domain. Piola et al. (2000) have shown an extension of the Brazil/Malvinas confluence over the shelf, defining a thermohaline sub-surface front between subtropical shelf waters and subantartic shelf waters (Fig. 2). This subtropical shelf front is located near the 50 m isobath at 32°S and extends southwards towards the shelf-break near 36°S. The front locates beneath a low-salinity surface layer generated by the discharge of the Río de la Plata and Patos Lagoon.

3.2. The coastal fronts at the Pacific margin. Oceanographic features

The Pacific Andean coastline is characterized by high relief, a relatively narrow shelf bordering a deep trench, and small drainage basins. The shelf reaches up to 100 km off northern Peru, becomes very narrow or absent off northern Chile (23–33°S), and wider again off southern Chile (Strub et al., 1998; Kellog and Mohriak, 2001). In Peru and northern Chile, the coastal region is a narrow desert belt that receives almost no rain (Kellog and Mohriak, 2001). Southern Chile contains one of the major fjord regions of the world. South of Chiloé Island the mainland coast (42–56°S) is separated from the Pacific Ocean by a large number of archipelagos, channels, and islands, and characterized by numerous and small river basins. Many glaciers are conspicuous features south of 46° (Pickard, 1971; Jaramillo, 2001). The large-scale circulation is characterized by a broad eastward West Wind Drift current at approximately 43°S that splits into an equatorward Peru (or Humboldt) Current and a poleward Cape Horn Current (Fig. 2). The Peru Current is a north-flowing, cold water, eastern boundary current. Two branches, which diverge at the latitude of northern Chile, may be identified in it: the Peru Oceanic Current and the Peru Coastal Current. Between them and southward flows the weak and irregular Peru Subsurface Countercurrent, which transports subtropical waters and occasionally reaches

the surface (Strub et al., 1998; Longhurst, 1998; Kjerfve et al., 2001; Tarazona and Arntz, 2001). The Cape Horn Current (Fig. 2) moves southward and interacts with the estuarine circulation in the complex fjords becoming less saline and with higher oxygen values. These properties are limited to the region next to the coast at 42°S (in the upper 20 m) but extend approximately 100 km offshore at 51°S (Strub et al., 1998). At the latitude of the Magellan Strait (52°30′S), Atlantic, Pacific and Antartic waters interact strongly (Medeiros and Kjerfve, 1988). The Cape Horn Current flows towards the Atlantic across the Drake Passage, and their highly buoyant waters are further diluted by continental run-off from the Magellan Strait on Atlantic side.

3.2.1. The Pacific Patagonia cold estuarine front

There is great scarcity of information about the frontal zone we intend to characterize here (see Pickard, 1971; Silva and Neshiba, 1979; Strub et al., 1998). South of 42°S, the shelf is several hundred kilometers wide and is covered with scattered islands offshore of the fjords (Fig. 2). Surface forcing is dominated by strong poleward winds and heavy precipitation (2500 mm year^{-1} in average) during frequent storms (Strub et al., 1998). The interior sea formed by the Chilean austral channels, some lakes and fjords, is basically formed by a two-layer structure. Due to continental runoff, these waters have very low salinity in the surface layer of 20–30 m thick. Surface layer deepens offshore (Pickard, 1971; Strub et al., 1998; Dávila et al., 2002). The interaction between subantartic waters and the diluted waters from the fjords define a coastal salinity front occurring between 42° and 56°S (Böehnecke, 1936; Silva and Neshiba, 1979; Gordon et al., 1982; Dávila et al., 2002). The front is present during the whole year with strongest gradients during summer. Salinity increases from 33.0 near the coast up to 33.8 offshore. Two zones of very low salinity are observed in the around 44–46°S and 52–53°S (Dávila et al., 2002). The southward wind stress should induce Ekman water transport, piling up freshwater near the coast (Dávila et al., 2002), maintaining the front as a narrow band parallel to the coast. The front bounds the Pacific coast and the tip of the continent reaching the Atlantic Ocean, and meeting the "The Tierra del Fuego cold estuarine front", as defined in Section 3.7 (Fig. 1).

3.2.2. The Chilean–Peruvian upwelling front

The continental shelf in this zone is very narrow. The break of shelf occurs at 200 m, within 10–20 km of the shoreline, and the slope itself is relatively steep. From Valparaiso (33°S) southward, the shelf widens and reaches 50 km off Chiloé islands (Longhurst, 1998). Trade winds blow northward and parallel to the Chilean–Peruvian coast. The Coriolis force together with friction forces in the water column generates a deflection towards the left (Southern Hemisphere) that causes Ekman transport perpendicular to the coast, forcing deeper water to rise and forming an upwelling of nutrient rich and cooler waters (Tarazona and Arntz, 2001). The coastal upwelling system of the Peru–Chile Current belongs to the most productive regions in the world oceans (Fig. 1).

Coastal divergence and cyclonic wind-stress curl near the coast give rise to extensive upwelling features, prominent in satellite imagery of temperature and chlorophyll fields (Figs. 1 and 3). Images show also that upwelling occurs seasonally (Longhurst, 1998). Sea surface temperature tends to increase towards the west and north, thus creating both a zonal and latitudinal gradient, respectively, the former being mainly a consequence of coastal upwelling (Tarazona and Arntz, 2001) (Fig. 1).

The Chilean and Peruvian regions show slight differences in upwelling characteristics. Upwelling favorable winds are relatively lighter along the Chilean coast, though still persistent and favorable, and their maximum potential for forcing upwelling at the coast occurs in the vicinity of Valparaiso (33°S). In the Peruvian region, upwelling chlorophyll plumes do not extend as far offshore as those in the Chilean coast. Upwelling is restricted to relatively shallow depths, and occurs as numerous small coastal upwelling cells, from which relatively small plumes (<100 km in Peru but 200–300 km in the Chilean region) of cool water may be entrained offshore (Fig. 1). In addition to the cool filaments, the Chilean region is characterized by meanders and eddies, which develop and decay on the scale of a few days to a few tens of days. All the persistent centers of upwelling are apparently topographically locked to the vicinity of capes and submarine topographic features. South 20°S it is mainly subantartic water of the equatorward coastal current which upwells, though northern 15°S

equatorial subsurface water is upwelled in normal years (Longhurst, 1998).

3.3. The frontal zones of austral South America

Taking into account geographic location and main physical forcing, which in turn, are related to the nutrient enrichment mechanism, we defined 6 frontal zones (Fig. 2). Two of them are composed by one large continuous front, so they are in some sense, self-defined (i.e. the Argentine shelf-break front zone; the Patagonian cold estuarine zone). Though the Chile–Perú upwelling manifests as numerous small cells, we considered it as a unique front due to contiguousness of the cells, and to the continuity of the main forcing (wind) over the zone. So we defined the Chile–Perú upwelling zone. The Atlantic upwelling zone, the temperate estuarine zone, and the Patagonian tidal zone are composed by several discrete fronts. We defined the extension of these zones on the basis of the northernmost and southernmost fronts of each type. The zones are homogeneous regarding frontal types and main forcing (winds; continental runoff; and tides, respectively).

3.3.1. The Atlantic upwelling zone

It extends from 23°S to about 29°S (Fig. 2), encompassing the upwellings of Cape Frío and Cape Santa Grande. This region presents medium primary production, with blooms of short duration and low intensity, but important in this tropical (oligotrophic) region (Fig. 3) (Lins-da-Silva et al., 1988; Valentin and Coutinho, 1989).

Zooplankton maxima are observed during summer, in coincidence to the strongest upwelling occurrence. Zooplankton composition varies with the dominance of different water masses, being those of the Brazil Current richer in species than the cold waters (Valentin, 2001). Medusae, Ctenophora and salps are the main components of the macrozooplanktonic biomass. Dense populations of the filter-feeding salp *Thalia democratica* contribute to rapid decrease of primary biomass (Valentin, 2001). Active predators such as the Hydromedusae *Rhacostoma atlantica* (small fishes) and *Olindias sambaquiensis* (fish eggs and larvae) are very abundant (Mianzan and Guerrero, 2000).

Benthic communities of rocky shores show high diversity, characterized by rich algal communities,
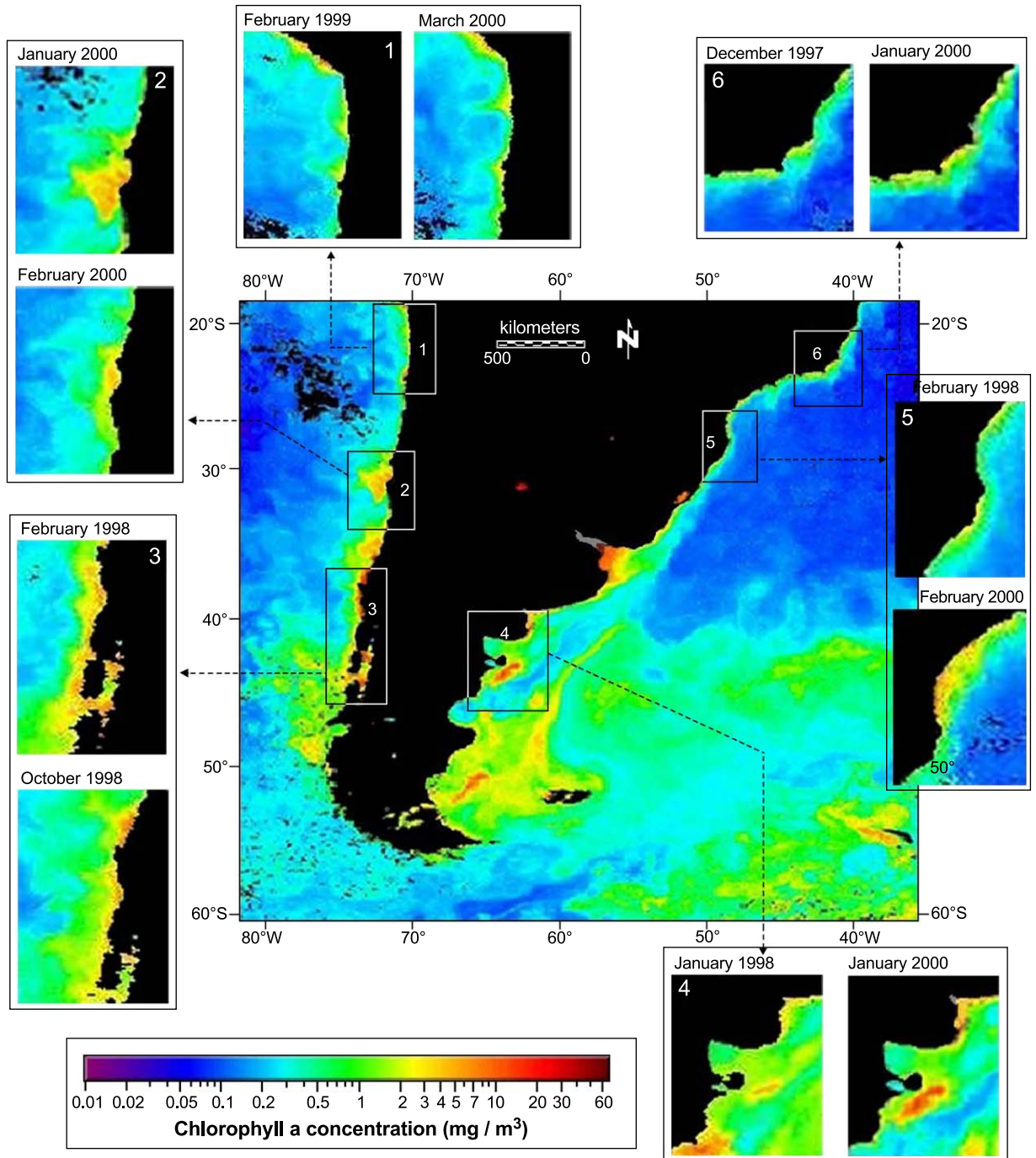
Fig. 3. Productivity of marine fronts. Chlorophyll a concentration (SeaWiFS) composite image of austral South America. Inserts show details and temporal variability in: (1) Southern Peru upwelling. (2) Northen Chile upwelling. (3) Península Valdés tidal front and El Rincón estuarine front. (4) Cape Santa Marta Grande upwelling. (5) Cape Frío upwelling. (6) Shelf-break front. Images provided by the SeaWiFS Project, NASA/Goddard Space Flight Center and ORBIMAGE (available at http://seawifs.gsfc.nasa.gov/SEAWIFS/IMAGES/SEAWIFS_GALLERY.html).

mussels and dense populations of cirripeds. Organic enrichment of inner shelf sediments by upwelling promotes the presence of detritivorous bivalves like *Nucula puelcha* and *Corbula patagonica* (Valentin, 2001).

The presence of neritic squids is related to the productivity of the region. Arrivals of *Loligo sanpaulensis* recruits coincide with coastal upwelling (Haimovici and Perez, 1991). Small pelagic fishes spawn in relation to the upwelling. The Brazilian sardine (*Sardinella brasiliensis*), spawn in an enriched environment directly downstream from the Cape Frío upwelling (Bakun and Parrish, 1990), and recruitment variability has been related to variations in upwelling events frequency (Matsuura, 1996). The Argentine anchovy, *Engraulis anchoita*, spawns in the cool upwelling regions, during late spring to early summer (Fig. 4A) (Bakun and Parrish, 1991).

Breeding colonies of birds, mainly gulls and terns, locate near the upwelling (Fig. 4B). The South American tern (*Sterna hirundinacea*) seems to be highly dependent of resources such as sardines and anchovies, which concentrate in the frontal area (Antas, 1991; Valentin, 2001).

3.3.2. The temperate estuarine zone

It extends south of Cape Santa Marta Grande, about 30°S, to the Negro river mouth (41°S), encompassing three large estuarine fronts: Patos Lagoon, Río de la Plata and El Rincón (Fig. 2). During fall and winter, the diluted surface waters from the Río de la Plata flow in a NNE direction along the Uruguayan coast in response to the Coriolis force, mixing with freshwater run-off from the Patos Lagoon (Odebrecht and Castello, 2001). In those occasions, a large frontal area is formed between Río de la Plata and Cape Santa Marta Grande (see Piola et al., 2000). In spring and summer, dominant onshore winds force surface waters of the Río de la Plata southward, along the Argentine coast. However, examining a historical data bank, a connection between the Río de la Plata and El Rincón waters has not been detected (Lucas et al., submitted).

This zone is characterized by high biological production, which sustain important artisanal and coastal fisheries in Brazil, Uruguay and Argentina. In the Patos Lagoon benthic microalgae, submersed and emersed macrophytes and marsh plants are responsible for most of the primary production. Phytoplankton become more important during the frequent saltwater intrusions in spring and summer (Seeliger, 2001). In the inner Río de la Plata estuary high turbidity constrains photosynthesis, thus phytoplankton is relatively poor. High concentrations of detrital biomass (pheopigments, C.A.R.P., 1989), tintinnids, and bacteria would constitute the main energy supply for primary consumers. Phytoplankton becomes more important in the outer estuary, where mixing of estuarine and marine waters enhances light penetration.

The copepod *Acartia tonsa* is the most abundant component of the estuarine zooplankton in the Patos Lagoon and in the Río de la Plata. In the lagoon, seasonal and annual changes in the planktonic community are due to seawater intrusion (marine copepods and benthic invertebrate larvae) or high freshwater flushing (cladocerans, freshwater copepods and larvae of some limnic fishes) (Seeliger, 2001). In the inner Río de la Plata estuary, the convergence of water masses and the strong picnoclines produce the accumulation and retention of plankton (Mianzan et al., 2001a). Plankton is mainly located in the lower saline layer, with the highest biomasses aggregated immediately below a halocline along the Río de la Plata salt wedge (Madirolas et al., 1997). Gelatinous plankton, mainly *Mnemiopsis maccradyi* (Ctenophora), *Iasis zonaria* (Salp) and *Lychnorhiza lucerna* (Scyphozoa), concentrates near the outer side of the front (Mianzan and Guerrero, 2000; Mianzan et al., 2001b; Alvarez Colombo et al., 2003).

The estuarine zone is characterized by soft bottoms, mainly inhabited by infaunal benthic organisms such as polichaetes and bivalves. Crustaceans are also important. The high deposition of suspended matter support the dense beds of the deposit feeding clam *Mactra isabelleana*. The croaker, *Micropogonias furnieri*, mainly prey on these clams which would constitute a linkage between detritus and fish (Giberto, 2001).

High incidence of reproductive activity of fishes has been detected in or near the estuarine fronts (Fig. 4A), notably by *Brevoortia aurea* and fishes of Family Sciaenidae like *M. furnieri*, *Cynoscion guatucupa* and *Pogonias cromis* (Weiss, 1981; Castello, 1986; Sinque and Muelbert, 1997; Macchi and Acha, 1998; Acha et al., 1999a; Acha and Macchi, 2000; Macchi and Acha, 2002). These estuaries play a paramount role as
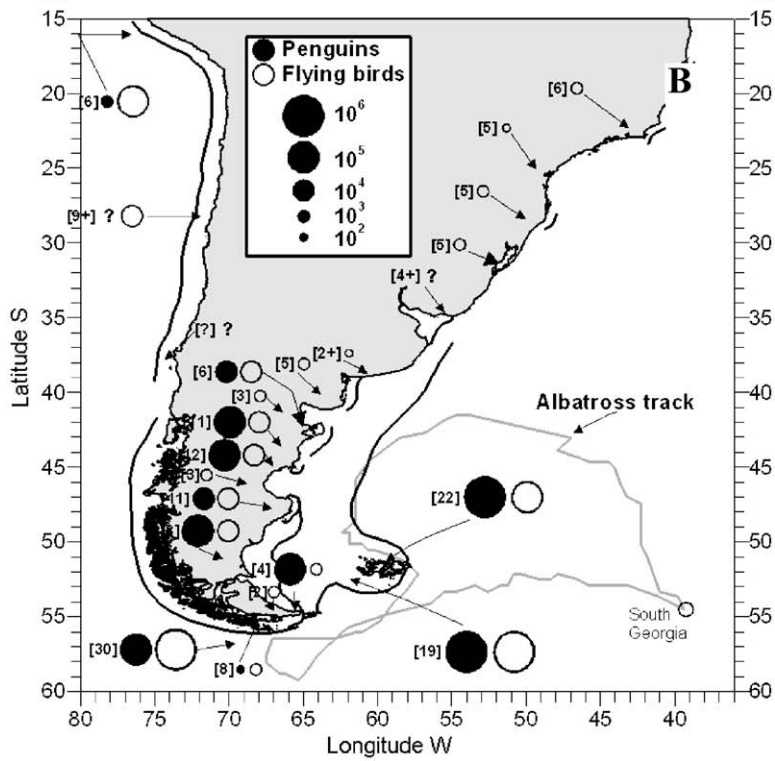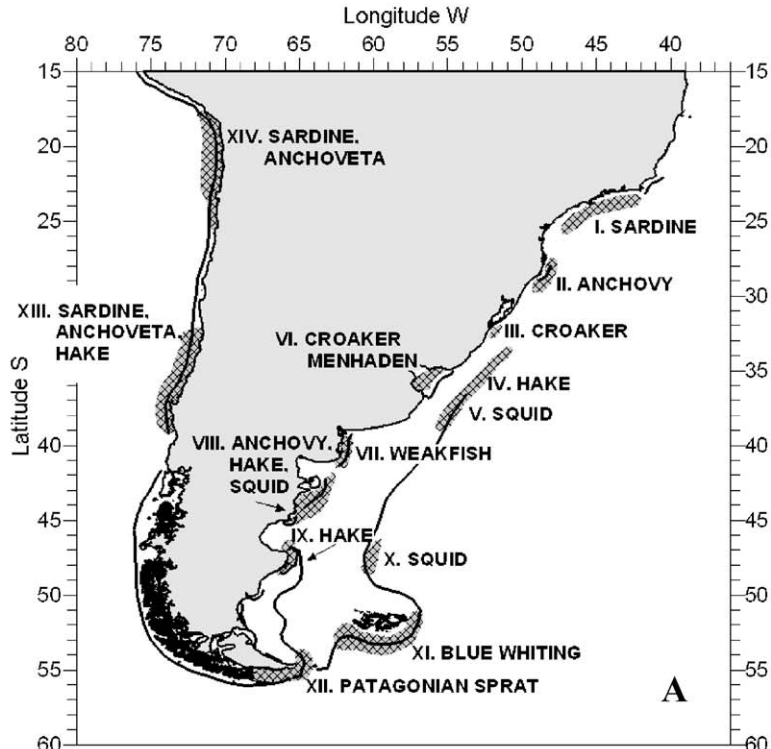
nursery grounds for fishes, both for those spawned inside the estuary, and for those spawned in the adjacent marine waters which colonize then the estuarine environment. Juveniles take advantage of the abundant food and high temperatures for growth (Sinque and Muelbert, 1997; Lasta, 1995).

Breeding colonies of seabirds are mainly composed by coastal species which forage close to the shoreline or in estuarine habitats (Fig. 4B). Estuaries are also wintering or refueling areas of migratory species coming from southern Patagonia, northern South America and even the northern Hemisphere (Antas, 1991; Escalante, 1991; Canevari et al., 1998; Favero et al., 2001a; Copello and Favero, 2001). Common Terns (*Sterna hirundo*), Black Skimmers (*Rynchops niger*) and other less abundant like other terns and gulls, heavily prey on juvenile fishes (Favero and Lasta, 2000; Silva et al., 2000, Favero et al., 2000a,b; 2001a,b; Mauco et al., 2001; Mariano-Jelicich et al., in press). The most important breeding areas in the Temperate Estuarine Zone are found close to El Rincón front, where large Kelp Gulls, South American Terns, and small cormorant colonies have been reported (Yorio et al., 1998a) (Fig. 4B).

3.3.3. The Patagonian tidal zone

It includes the Atlantic Patagonian coast from north of Peninsula Valdés (42°S) to Staten Island (55°S) (Fig. 2). Nutrient enrichment is largely dependent on intensified vertical mixing in the homogeneous side of these fronts. Carreto et al. (1986) demonstrated that this front is highly productive during spring and summer (Fig. 3). In some occasions the stratified zone can be dominated by the toxic dinoflagellate *Alexandrium tamarense* (= *Gonyaulax excavata*), whereas chain-forming diatoms are abundant in the homogeneous sector (Carreto et al., 1986).

Diverse size fractions of zooplankton occur at different sectors of the front. Microzooplankton (mostly copepods eggs and nauplii) mainly occupy the transitional zone, in coincidence with the maximum values of chlorophyll-*a* (Viñas and Ramírez, 1996). Mesozooplankton (primarily calanoid copepods) show maximum values in the stratified zone (Möhlenkamp, 1996). Macrozooplanktonic gelatinous biomass is dominated by *Mnemiopsis leidyi* (Ctenophora) and *Aequorea* spp. (Hydromedusae). Ctenophores are more abundant in the frontal interface and in the highly stratified side (Alheit et al., 1991; Mianzan and Guerrero, 2000; Alvarez Colombo et al., 2003). Nongelatinous macrozooplankton was nearly evenly distributed across the front, represented by the crustacean *Pterosquilla* sp., euphausids, pycnogonids, tomopterids, the cephalopods *Rossia tenera* and *Illex argentinus*; and larvae of commercial fishes such as *E. anchoita*, *Merluccius hubssi* and *Genypterus blacodes* (Mianzan and Guerrero, 2000). The tidal fronts seems to be the axis for the distribution of adult anchovy shoals that track annual changes in the frontal location (Hansen et al., 2001). Spawning of *E. anchoita*; *M. hubssi* and the squid *I. argentinus* is related with those fronts (Fig. 4A) (Ehrlich and de Ciechomski, 1994; Acha et al., 1999b; Brunetti and Ivanovic, 1999). Larvae occurred in the stratified side of the front. Hake larvae occurred at the bottom layer, whereas anchovy larvae and squid paralarvae were more frequent in the upper layer (Brunetti and Ivanovic, 1999; Viñas and Santos, 2000).

Large concentrations of the Patagonian scallop, *Zygochlamys patagonica*, match the location of the tidal front near Península Valdés. Orensanz et al. (1991) have suggested that the front might function as a larval retention area, concentrating the scallop larvae on their stratified size. Another large Patagonian scallop concentration, the Tres Puntas Bed, locates near the southern limit of the Gulf San Jorge, probably related to the tidal front (Lasta and Bremec, 1998).

The shoreline from Valdés Peninsula to Staten Island shows seabird colonies usually much diverse

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Fig. 4. Use of neritic fronts by squids, fishes and birds. (A) Examples of several species spawning in relation to frontal zones (redrawn from: I. Bakun and Parrish, 1990; II. Matsuura and Kitahara, 1995; III. Sinque and Muelbert, 1997; IV. Ehrlich and de Ciechomski, 1994; V. Brunetti and Ivanovic, 1999; VI. Acha et al., 1999a,b; Acha and Macchi, 2000; VII. Macchi and Acha, 1998; VIII. Sánchez and de Ciechomski, 1995; Ehrlich and de Ciechomski, 1994, Brunetti and Ivanovic, 1999; IX. Ehrlich and de Ciechomski, 1994; X. Brunetti and Ivanovic, 1999; XI. Sánchez and de Ciechomski, 1995; XII. Sánchez et al., 1997; XIII. Bernal et al., 1997; Vargas et al., 1997; Castro et al., 2000; XIV. Bernal et al., 1997). (B) Birds breeding colonies. Size of circles proportional to the number of bird pairs; number between brackets is the number of species in the colonies. Gray line shows one foraging flight of 7470 km in 13 days, tracked by satellite of a Wandering Albatross breeding at South Georgia Islands (redrawn from Tickell, 2000).

and larger than those reported for northern latitudes in the Atlantic (Fig. 4B). Bird species include surface (gulls and terns) and pursuit diving predators (cormorants and penguins). Penguin (*Spheniscus magellanicus*) colonies range from 10,000 to 250,000 pairs (Yorio et al., 1998b). The occurrence of birds colonies may be related with the availability of breeding grounds and with high prey abundances in the coastal fronts. Available data show that large terns (*Thallasseus* spp) mainly prey upon anchovy (*E. anchoita*) and Atherinids (*Odonthestes* sp.) (Quintana and Yorio, 1997).

3.3.4. The Argentine shelf-break zone

Although physical processes involved in the shelf-break front are poorly understood, in situ (Hubold, 1980a,b; Lutz and Carreto, 1991; Carreto et al., 1995) and remote sensing measurements (Podestá, 1997) have shown the high productivity of this front (Fig. 3). Remote sensing by the Coastal Zone Color Scanner (CZCS) has shown near surface concentrations of phytoplankton pigments along the shelf-break through spring and summer. In contrast, phytoplankton biomass across most of the shelf decreased rapidly following the spring bloom (Podestá, 1990).

The large phytoplankton biomass along the shelf-break is probably the result of enhanced supply of nutrient-rich Malvinas current waters into the euphotic zone (see the diagram box in Fig. 2), which could happen through a variety of processes such as small-scale eddies and/or internal waves (coupled with episodic wind stress). Additionally, the interleaving of water masses at the front could enhance vertical stability, retaining phytoplankton cells in the euphotic zone (Podestá, 1990).

Sabatini and Alvarez Colombo (2001) have shown high zooplankton concentrations associated to this front during summer–early autumn. Ehrlich (2000) has reported the highest densities of eggs and early larvae of the Argentine hake, *Merluccius hubbsi*, in the shelf-break front during fall–winter. The location of this spawning site (35–37°S) (Fig. 4A) would be related to the abundance of zooplanktonic preys for larvae, and to dynamic conditions (Ekman transport) allowing larval retention on the Argentine shelf (Ehrlich, 2000). The front plays an important role in the northward feeding migration of the hake (*M. hubbsi*), and the anchovy (*E. anchoita*), as the fish are closely

associated to it for 5–6 months of the year. While *M. hubbsi* and *E. anchoita* coincidentally migrate off-shore and then northward along the slope in autumn, the former actively preys on the latter (Brandhorst and Castello, 1971; Podestá, 1990). Myctophiids are the most abundant small pelagic fish in the area, and their larvae occurred throughout the year (Sánchez and de Ciechomski, 1995). Dense concentrations of shortfin squid *I. argentinus* occur along the shelf-break in late fall (Otero et al., 1981). Squid is increasingly found in stomach contents of hake during this season (Angelescu and Cousseau, 1969; Cordo, 1981).

The life cycles of two spawning stocks of *I. argentinus* are related to the shelfbreak front (Fig. 4A) (Brunetti et al., 1988). The egg masses of the Southpatagonic Stock (autumn spawners) would be carried northward by Malvinas Current along the shelf-break front, reaching Brazil–Malvinas Confluence where higher temperatures accelerate development and hatching occurs. The spawning grounds of the Bonaerensis–Northpatagonic Stock (winter spawners) are close to the west side of Brazil–Malvinas Confluence (Brunetti and Ivanovic, 1992).

Dense beds of the Patagonian scallop (*Z. patagonica*) locate in coincidence with the shelf-break front between 90 and 150 m, from about 38°30′ to 43°. This spatial pattern is attributed to the high productivity of the front (Lasta and Bremec, 1998).

Females of the Patagonian elephant seal (*Mirounga leonina*), which breed and molt on the shores of Península Valdés, cross the continental shelf to feed near the shelf-break front, predating mainly on squids (Campagna et al., 1994, 1998).

The concentration of preys along the shelf-break front zone is exploited by a large number of pelagic seabirds as albatrosses and large petrels which mostly breed in archipelagos of the southernmost tip of South America (e.g. Diego Ramírez archipelago, Staten Islands) and Malvinas (Falkland) Islands (Schlatter, 1984; Croxall et al., 1984; Schiavini et al., 1998) (Fig. 4B). Some species like the Black-browed albatross (*Thalassarche melanophrys*), the Wandering albatross (*Diomedea exulans*), the Southern Giant Petrel (*Macronectes giganteus*) or the White-chinned Petrel (*Procellaria aequinoctiallis*) (all of them breeding in South Georgia and/or Falkland Islands) use to forage in the Patagonian shelf and along the shelf-break from 60°S up to 35°S in the Brazil/Malvinas Confluence

(Prince et al., 1998; González-Solís et al., 2002; Huin, 2002). Diet of the Black-browed albatrosses is mainly composed by fish, squid, crustaceans and jellyfish, mostly obtained not farther than 500 km from the colonies (Cherel and Klages, 1998; Tickell, 2000). The bulk of the diet of Wandering albatrosses is composed only by squid and fish, which could be taken thousands of kilometres from the colony (see satellite track examples in Fig. 4B) (Cherel and Klages, 1998; Prince et al., 1998).

3.3.5. The Patagonian cold estuarine zone

This zone extends along Pacific and Atlantic coasts, encompassing the southern tip of South America. It extends southward 42°S (Chiloé Island) on the Chilean side, and southward 46°30′ (south of Gulf San Jorge) on the Argentine part (Figs. 1 and 2). Biological knowledge about this zone is scarce. On the Pacific side, it is mainly referred to the inshore zones (the fjords, channels, and islands). The estuarine waters here are relatively poor in nutrients, being the oceanic subantartic waters the main source of nutrients (Silva and Neshiba, 1979). From Chiloé southward, satellite imagery show summer blooms of chlorophyll that extend 200–300 km offshore (Longhurst, 1998), probably related to the front (Fig. 3).

On the Atlantic side, the Fuegan spratt (*Sprattus fuegensis*) spawns in a highly energetic hydrographic front off Tierra del Fuego (Fig. 4A) and recruits in the coastal region off southern Patagonia (Sánchez et al., 1995, 1997). Eggs and larvae were collected off the coast of Tierra del Fuego. Larvae were collected also in large densities all along the Fuegan Atlantic coast off the Magellan strait, and to a minor extent in the coastal region of Santa Cruz, in correspondence to the shelf fronts described for the area by Glorioso and Flather (1995) (see Section 3.3.3).

Data on birds from southern Chile is very scarce, with the exception of Diego Ramirez Archipelago (56°30′S; 68°40′W) where about 30 breeding seabird species have been reported, some of them reaching abundances of one million adults (Schlatter, 1984). Albatrosses (mainly Grey-headed albatrosses, *Thalassarche chrysostoma*) and large petrels (e.g. Giant petrels, *M. giganteus*) use to forage far away from the coasts both in the Atlantic and the Pacific oceans along the continental shelves). However, other medium sized or small petrels (e.g. 2 millions of individ-

uals of Blue petrels, *Halobaena caerulea*) may feed close or in association to neritic fronts. Coastal birds showing shorter feeding trips like gulls, terns, cormorants and penguins are much less abundant in this islands (Fig. 4B) (Schlatter, 1984).

3.3.6. The Chile–Peru upwelling zone

The zone here described is part of a larger ecosystem extending between 4°S and about 40°S along the western coast of South America. High primary production characterizes this system (Fig. 3). MacIsaac et al. (1985) described the primary production cycle in a segment of the upwellings at 15°S. It is possible to recognize a number of zones along the axis of the plumes. The innermost is the intense upwellings zone characterized by high nutrient concentration but low phytoplankton biomass. The following zone offshore presents a thermocline due to solar heating; photosynthesis is increasing as well as nutrient uptake. In the next zone, all processes occur at maximal rates producing rapid accumulation of biomass and depletion of nutrients. In the external zone nutrient depletion occurs, so that the cells experience nutrient limitation.

In Northern Chile, satellite images of sea surface temperature shown that upwelling intensity is greater in summer, and decreases in the winter months (Barbieri et al., 1995). CZCS data showed maximum pigment concentrations in winter and minimum in summer (Thomas, 1999), that is 180° out of phase with monthly averaged upwelling favourable winds. Pigment patterns along the Chilean coast were probably controlled by the interaction of upwelling with circulation patterns unconnected to local wind forcing (Thomas, 1999).

Field studies showed high chlorophyll-*a* concentrations associated with bay and/or capes and with the presence of cold waters originated by upwelling at 23°S (Rodriguez et al., 1996; González et al., 2000). In contrast, oceanic waters showed low concentrations (González et al., 2000). Significant grazing impact by planktonic Crustaceans (calanoid and cyclopoid copepods, and euphausiids) and the salp *Salpa fusiformis* were reported (González et al., 2000). Upwelling takes place intermittently year-round, suggesting that secondary production is not limited by food. Advection, consequently, must play an important role in structuring the spatial distribution of copepods such as

Calanus chilensis (one of the main herbivores of the system). Population losses from upwelling and offshore transport may be compensated by rapid turnover rates of cohorts (Escribano, 1998).

The most abundant fishes in the Humboldt Current system are sardines, anchovies, mackerel and hakes, which maintain important fisheries (Vargas et al., 1997). The anchoveta *Engraulis ringens*, with its wide distributional range (4°S through 42°S), has been found in two major spawning areas: southern Peru through 25°S, and the Talcahuano area (35°S through 38°S) (Fig. 4A). Although spawning may occur intermittently during most of the year, reproduction peaks during the austral winter (Castro et al., 2000). Near Central Chile, anchoveta and common sardine (*Clupea benticki*) concentrations were mainly associated to the development of coastal upwelling events. Jack mackerel (*Trachurus murphyi*) were largely associated with the strong thermal gradient next to the warmer oceanic waters (Yañez et al., 1996).

Two main spawning areas have been reported for hake (*Merluccius gayi gayi*) on the Chilean coast, located around 32°30′–35°00′S and 36°00′–40°00′S (Fig. 4A). These regions have been indicated as retention areas of high productivity, due to the effect of the bottom bathymetry on the direction of the geostrophic flow. This produces anticyclonic rings that prolong the presence of rich upwellings waters with high food availability for hake larvae. Highest larval concentrations were related to moderate upwelling index values (Bernal et al., 1997; Vargas et al., 1997).

At least nine coastal seabird species breeds along central and northern Chile, excluding the archipelagos located hundreds of kilometres offshore (Fig. 4B) (Schlatter, 1984). For the Peruvian coasts, the Humboldt Penguins (*Spheniscus humboldti*) and other five coastal flying bird species (mostly cormorants) have been reported (Duffy et al., 1984). All these birds are pursuit divers which predate on the small pelagic fishes abundant in the upwelling fronts.

Variable numbers of humpback whales (*Megaptera novaeangliae*) may be resident year-round in the Humboldt Current, taking advantage of the prey abundance associated to the coastal upwelling. These individuals are out of phase with the standard seasonal north–south migratory movements (Papastavrou and Van-Waerebeek, 1997).

The Chilean–Peruvian upwelling zone is under strong and direct effect of "El Niño" Southern Oscillation (ENSO) phenomenon. Its effects on oceanographic and ecological processes of the region are very well documented (Pauly and Tsukayama, 1987; Mann and Lazier, 1996; Longhurst, 1998; Tarazona and Arntz, 2001). The region is exposed to a great inter-annual variability. ENSO events occur every 2–7 years (mean 4 years), but in 1982–1983 an ENSO event occurred with a severity that is considered occurring with a periodicity of 100 years or more. The consequences of decrease in productivity cascaded all the way from phytoplankton through herbivores to disappearance of fish stocks such as hake, anchovy, sardines, and jack mackerel. ENSO events produced also strong alterations of the invertebrate benthic community, loss or variations in the reproduction of seabirds due to starvation and/or collapse of nests in penguins (e.g. Culik et al. 2000; Vargas 2000), and starvation of marine mammals.

4. Discussion

Marine fronts are abundant at the continental shelves of austral South America, covering several scales of space and time. Winds, tides, freshwater discharges, and oceanic currents are their main forcing. Those forcing, interacting with geomorphological features such as bottom topography and coastal bearing, produce several types of fronts that can be arranged in six zones according to their geographic locations, main forcing, key physical variables, seasonality, and enrichment mechanisms (Fig. 2). These frontal zones cover all the neritic ecosystems of austral South America.

Though frontal zones we defined are extensive areas of the neritic province, it must be stressed that fronts inside the zones are comparatively small areas (see Figs. 1 and 3). Even so, when all the evidence is put together it becomes clear that they play a paramount role in ecological processes of the ocean (e.g. Figs. 3 and 4), allowing for an exceptionally large primary production; offering adequate feeding and/or reproductive habitats for nektonic species such as fishes and squids; acting as retention areas for larvae of benthic species and so promoting establishment of adult beds. Those benthic beds

benefit also from the organic production increased in
the frontal area. Fronts also attract mammals in
search of feeding. Breeding birds need great quanti-
ties of high quality food that concentrate near fronts.
Birds feeding at fronts represent a linkage between
marine and terrestrial ecosystems with a net transport
towards the last. At a continental scale, a good visual
correlation exists between the distribution of coastal
seabird colonies and coastal fronts in the Atlantic,
which could constitute hot spots with high food
availability (Fig. 4B). Moreover, the distribution of
seabirds at sea and the structure of seabirds assemb-
lages is influenced by the presence of fronts and the
physical structure of the ocean (Veit, 1995). The
Atlantic shelf break front is also an important feed-
ing area but mainly used by pelagic seabirds to
forage (e.g. albatrosses and petrels). Fishing activity
is very high at the shelf break front and the inter-
actions between pelagic seabirds and fishing vessels
produce important seabird mortalities (Stagi and Vaz-
Ferreira, 2000; Favero et al., in press). The Pacific
coast of South America is occupied by coastal sea-
birds, but also by pelagic seabirds coming from
distant breeding areas such as Australia and New
Zealand (Tickell 2000).

Upwelling fronts locate in areas with narrow
continental shelves, where oceanic circulation is
close the coastline. These upwellings show seasonal
variability, which is stronger in the Atlantic coast.
High frequency variability manifests as pulses (up-
welling/downwelling) in the Atlantic coast, and as
intensifying/weakening of the upwelling condition in
the Pacific side. Moreover, Pacific upwelling zone is
under direct and strong influence of ENSO events.
Environmental variability could give the advantage
to small pelagics (sardines and anchovies) over more
specialized (e.g. demersal) species which are able to
establish and maintain themselves in other ecosys-
tems, feeding at a somewhat higher trophic level
(Bakun and Parrish, 1991). This seem to be the cases
for the Chilean–Peruvian upwelling, and the Cape
Frío and Cape Santa Marta Grande upwellings. The
temperate estuarine zone and the shelf-break zone are
less variable systems, dominated by nektonic species
feeding at higher trophic levels such as sciaenids,
flatfishes, coastal sharks and rays; and hake and
squid, respectively. Fronts in the Patagonian tidal
zone represent an intermediate condition where an-

chovies, hake and squids are the key species of the
system.

Some of the frontal zones are under the effects of
the El Niño Southern Oscillation (ENSO) cycle. The
most striking case is the Chilean–Peruvian upwelling,
but fronts on the Atlantic side are also affected.
Among the main alterations forced by ENSO in South
America are perturbed rainfall patterns that induce
changes in the hydrological balance of some water-
sheds. In the watersheds connected to the Atlantic
temperate estuarine zone, ENSO produces an excess
of rainfall thus producing an increase in riverine
discharge, affecting the hydrodynamics of the estuar-
ies and probably increasing their fertilization effects
on the adjacent ocean. Through ''bottom-up'' control-
ling forces, the variability observed at the basal levels
in the food chains can be transmitted to the upper
levels, reaching top predators. For example, the diet
and foraging patterns of some coastal seabird species
like the Common Tern, seems to be affected by long-
term variability in the Río de la Plata runoff, also
strongly correlated with ENSO (Mauco and Favero,
2003). The effects of ENSO on the Atlantic upwelling
zone and the Patagonian cold estuarine zone have not
been studied. Some variability degree of Malvinas
Current could be related to the Antarctic Circumpolar
Wave (White et al., 1998), which in turn seems to be
related to El Niño activity (White and Peterson, 1996),
but its potential effects on the shelf-break front has not
been studied.

There is agreement on the faunal and floristic
relations between the Southeastern Pacific and South-
western Atlantic (Boschi, 2000 and references there-
in). The biogeographic Magellanic Province extends
from the north of Chiloé Island, encompasses the tip
of South America and reaches the continental shelf of
the Atlantic Patagonia. The extended frontal zone
from Chiloé Island southward, reaching the cold
estuarine front on Atlantic Patagonia and the Atlantic
shelf-break front (Figs. 1 and 2), could be a transport
system for organisms into the Magellan Province.
These fronts are dynamic features that undergoes
formation with an increase in horizontal velocity
along the front, probably generating a jet (a cross
frontal secondary circulation should also exists)
(Olson, 2002). Horizontal water movement along the
front can provide both food resources and a mecha-
nism to carry holoplanktonic organisms and also

planktonic larvae of fishes and benthic invertebrates from one ocean to the other. In the case of larger nekton, it is clear that they can both actively seek out the frontal interface or swim across it to find preferred habitats. It is assumed that all of these taxa interact with the frontal environment by changing their behaviour based on clues provided by the physical and biological attributes of the front (Olson, 2002). In our case, salinity appears as the key variable, but temperature seems to be also associated to these fronts from 53° to the south and bounding Tierra del Fuego (Fig. 1). Following the ideas by Olson (2002) for swordfish in the North Atlantic, it may be thought that Magellan fishes may employ salinity as a clue to outline the frontal location. Isohalines would define a coordinate system in which fishes can navigate performing along-frontal excursions around both Patagonian coasts.

The Pacific coast, dominated by two large frontal zones, appears simplest than the Atlantic in terms of frontal richness when observed at a continental scale (Fig. 1). This seems true despite of several small-scale fronts in southern Chile (mainly fjord type estuaries with effects probably at a local scale); and variation at some extent along the more than 2000 km of the Chilean–Peruvian upwelling. In the Atlantic coast, the extension of the continental shelf allows for the development of a great diversity of mesoscale fronts, especially from 32° southward. Economic and ecologically important species such as hake, anchovy and shortfin squid take advantage of fronts encompassing different zones, i.e. the shelf-break front and tidal fronts near Península Valdés, having the opportunity to exploit organic production peaks at different moments within the annual cycle, and/or to modulate environmental variability.

Life distribute in the oceans in an uneven way. Our results show that frontal spatial pattern can help in understanding life configuration at the spatial scale of the austral South American region. Moreover, marine fronts must be recognized as key oceanographic structures to understand feeding and reproductive strategies and migratory patterns of local populations. Future studies would greatly benefit from a better focus onto the frontal regions described for the region, and from an integration of physical and biological processes. Due to the differential distribution of fronts in each coast, austral South America seems to be a suitable scenario to study the effect of frontal richness on some extensive properties of the continental shelf ecosystems such as biological diversity, population richness of the species, key species life histories, and ecosystems resilience facing perturbations such as ENSO events or Global Climatic Changes, whose effects produce alterations on main frontal forcing such as wind and run-off configurations.

Acknowledgements

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