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Oceanographic conditions off Coastal South America in relation to the distribution of Burmeister's porpoise, *Phocoena spinipinnis*

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Abstract: Historical data (1965-2000) of temperature, salinity, and dissolved oxygen (0 and 50m) were analyzed to understand the seasonal variability of the oceanographic conditions associated to the distribution of *P. spinipinnis* from Paita, Peru (05°01'S, 81ºW), in the Pacific Ocean, to Santa Catarina, Brazil (28°48'S, 49°12'W), in the Atlantic. The variability of historical average data was associated with different processes as a function of the geographical position and seasonality. These variations have different expressions along each coast as a function of the circulation system in each ocean. The northern boundary of the distribution of *P. spinipinnis* for the Pacific coast at Paita (5°S) is coincident with the westward turn of the Humboldt Current, as it is incorporated into the South Equatorial Current. In the Atlantic, the northern boundary for the species seems to be associated with the Atlantic Subtropical Convergence (30-40°S). The high temperature (>24°C) and salinities (>36psu) registered at the surface and at 50m between the coast and 20nm were coincident with the known northern limit of the distribution of this species on both coasts of South America. We propose the existence of three oceanographic areas within the distributional range of *P. spinipinnis*: (1) from Paita, Peru to south of Arauco Gulf, Chile, that has the influence of the Humboldt Current, and a developed oxygen minimum zone (OMZ); (2) from south of Arauco Gulf to south of La Plata River, Argentina, which shows the influence of the Cape Horn and Malvinas Currents, respectively, as well as downwelling processes, freshwater contributions from fjords, glaciers and rivers; and (3) from La Plata River to Santa Catarina, Brazil, which is characterized by the influence of the Brazil Current, and the freshwater contributions of the basin of La Plata River and the estuarine system of Patos Lagoon, south Brazil. The presence of the OMZ is possibly a factor in the separation of groups (1) and (2) along in the Chilean coast. In addition, we propose that Burmeister's porpoise presents a continuous distribution throughout this range from Paita, Peru to La Plata River basin, Argentina, being able to reach Uruguayan and Brazilian waters under certain oceanographic conditions (intrusion of colder and less saline waters toward the north associated with the Subtropical Convergence).

Resumen: Datos históricos (1965-2000) de temperatura, salinidad y oxígeno disuelto (0 y 50m) fueron analizados para comprender la variabilidad estacional de las condiciones oceanográficas asociadas a la distribución de *P. spinipinnis* desde Paita, Perú (05°01'S, 81ºW) en el Océano Pacífico, hasta Santa Catarina, Brasil (28°48'S, 49°12'W). La variabilidad de los datos promedios históricos fue asociada con diferentes procesos como una función de la posición geográfica y estacionalidad. Estas perturbaciones tienen diferentes expresiones en cada costa en función de los sistemas de circulación en cada océano. El limite norte de la distribución de *P. spinipinnis* en la costa Pacifico en Paita (5°S), es coincidente con la zona donde la Corriente de Humboldt gira al oeste y se incorpora a la Corriente Ecuatorial. En la costa Atlántica, el limite norte para esta especie parece estar asociada a la Convergencia Subtropical del Atlántico (30-40°S). Altas temperaturas (>24°C) y salinidades (>36psu) registradas en superficie y 50m de profundidad entre la costa y 20nm fueron coincidentes con el limite norte conocido de la distribución de esta especie en ambas costas de Sudamérica. Nosotros proponemos tres áreas oceanográficas asociadas con la distribución de *P. spinipinnis*: (1) desde Paita al sur del Golfo de Arauco, Chile, que tiene la influencia de la Corriente de Humboldt y la zona de mínimo oxígeno (ZMO); (2) desde el sur del Golfo de Arauco hasta el Río de La Plata, Argentina, la cual muestra la influencia de las Corrientes del Cabo de Hornos y Malvinas respectivamente y procesos de hundimiento, contribuciones de agua dulce desde los fiordos, glaciares y ríos; y (3) desde el Río de La Plata hasta Santa Catarina, Brasil, la cual esta caracterizada por la influencia de la Corriente de Brasil y los aportes de agua dulce desde la cuenca del Río de La Plata y del sistema estuario de la Lagoa dos Patos, en el sur de Brasil. Probablemente, la presencia de la ZMO es un factor importante en la separación de los grupos (1) y (2) a lo largo de la costa chilena. Además, proponemos que la marsopa espinosa presenta una distribución continua a lo largo de su rango desde Paita, Perú hasta la bacía del Rio de la Plata, Argentina, siendo capaz de alcanzar aguas uruguayas y brasileras bajo ciertas condiciones oceanográficas (entrada de aguas frías y menos salinas hacia el norte asociada a la Convergencia Subtropical).

Keywords: *Phocoena spinipinnis*, Burmeister's porpoise, distribution, oceanographic condition, Atlantic Ocean, Pacific Ocean.

Introduction

The distributions and movements of marine mammals are clearly influenced by their oceanic environment. As indicated by Hastie *et al*. (2005), although such relationships are inherently dynamic, distributions have been related to a range of environmental determinants, including sea surface temperature (*e.g.* Selzer and Payne, 1988; Forney, 2000; Baumgartner *et al*., 2001; Benson *et al*., 2002; Hamazaki, 2002; Piatkowski *et al*., 2002; Littaye *et al*., 2004; Jonhston *et al*., 2005; Tynan *et al*., 2005), salinity (*e.g.* Selzer and Payne, 1988; Forney, 2000; Tynan *et al*., 2005), and water depth (*e.g.* Ross *et al*., 1987; Gowans and Whitehead, 1995; Baumgartner, 1997; Davis *et al*., 1998; Carretta *et al*., 2001; Benson *et al*., 2002; Trukhin, 2003; Tynan *et al*., 2005). However, the importance of these determinants appears to vary between regions and species, a feature that highlights

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the need to focus studies on the role of oceanography in dolphin habitat selection on a regional basis. In addition, the distribution, abundance and foraging success of top trophic level predators in marine systems, such as sharks, seabirds, pinnipeds, and cetaceans, are determined by large-scale oceanographic patterns and their effect on prey distribution and abundance (Smith *et al.*, 1986; Ainley *et al.*, 1995a, b; Kenney *et al.*, 1995; Pyle *et al.*, 1996; Tynan, 1997; Sydeman and Allen, 1999; Forney, 2000; Benson *et al.*, 2002). In marine systems, heterogeneity of productivy is the result of complex interactions of wind, currents, and land masses (Johnston *et al.*, 2005).

Burmeister's porpoise, *Phocoena spinipinnis* (Burmeister, 1865) is an endemic species of coastal waters of South America, from Santa Catarina, southern Brazil (28°48'S, 49°12'W) to Paita Bay, northern Peru (05°01'S, 81ºW) (Brownell and Praderi, 1982; Simões-Lopez and Ximenez, 1989; Jefferson *et al.*, 1993). However, it is unclear whether or not this species is present continuously throughout this range (Klinowska, 1991; Jefferson *et al.*, 1993; Goodall *et al.*, 1995a;Reeves *et al.*, 2003). This species has been assumed to have a coastal distribution, preferring shallow waters, and indeed most of the sightings have been nearshore (Goodall *et al.*, 1995b). In general, few sightings and movements of *P. spinipinnis* have been reported (*e.g.* Aguayo, 1975; Donoso-Barros, 1975; Würsig *et al.*, 1977; Guerra *et al.*, 1987; Reyes and Oporto, 1994; Van Waerebeek *et al.*, 2002, Heinrich *et al.*, 2004[4]).

Burmeister's porpoise is associated with a broad range of water temperatures. At the southern limit of its distribution near Cape Horn and Tierra del Fuego, water temperatures range from 3°C in June (austral winter) to about 9°C in the summer months (Brownell and Praderi, 1982). In the north, the species appears to be associated with temperate waters in the two major northward flowing currents off South America, the Humboldt and the Malvinas Currents (Brownell and Clapham, 1999).

The Humboldt and Cape Horn Currents are the most important currents in the Southeast Pacific, and the distribution of *P. spinipinnis* in this region is associated with both currents. These currents are born by the bifurcation of West Wind Drift or Antarctic Circumpolar Current center at 45°S. The Humboldt Current has a northward direction from central Chile (40°S) to northern Peru, where it is incorporated into the South Equatorial Current near to 5°S at Paita, Peru (Bakun *et al.*, 1999). The Cape Horn Current has a southward direction, and passes around the continent through the Drake Passage, influencing both east and west coasts of South America (Pickard, 1973).

On the Atlantic coast, the distribution of Burmeister's porpoise is associated with the Brazil and the Malvinas Currents. The Brazil Current originates where the westward flowing trans-Atlantic South Equatorial Current bifurcates into two currents, the North Brazil and the Brazil Currents, with the latter branch having a southward direction (Peterson and Stramma, 1990; Stramma *et al.*, 1990). The Malvinas Current is a branch of the Circumpolar Current and flows northward along the continental shelf of Argentina until it reaches the Brazil Current offshore La Plata River (Legeckis and Gordon, 1982; Garzoli, 1993; Vivier and Provost, 1999). Both currents converge generating the Atlantic Subtropical Convergence or Brazil-Malvinas confluence, which lies between 33-38°S along the continental margins of Brazil, Uruguay, and Argentina, and it is considered a major transitional oceanic domain in the Southwest Atlantic (Figure 1) (Olson *et al.*, 1988; Podesta *et al.*, 1991).

The habitat where *P. spinipinnis* is known to occur shows sectors favorable to upwelling processes, as in the case of the Humboldt Current, which presents several centers of coastal upwelling (Strub *et al.*, 1998; Tarazona and Arntz, 2001). In the case of the Brazil Current, the upwelling is associated with the cyclonic meanders in the region of the Southeast Brazil Bight or Santos Bight (24-26°S) (Campos *et al.*, 2000). Another difference between the Pacific and Atlantic Oceans is the presence of oxygen minimum zones (OMZs). The OMZs are present along the Pacific coast, at midwater depth in the open ocean where dissolved oxygen concentration falls below 0.5ml l^{-1} (Kamykowski and Zentara, 1990; Levin *et al.*, 1991).

To date, few studies have been conducted to determine the effect of oceanographic features and environment variables on the distribution and movements of *P. spinipinnis* (*e.g.* Würsig *et al.*, 1977; Simões-Lopes and Ximenez, 1993). However, to understand the movements of *P. spinipinnis* it is first necessary to know its distribution at regional scales and mesoscales (10s to 100s of km), and later to fine scales (1 to 10 km).

The purpose of the present study is to examine the wide distribution of *P. spinipinnis* at regional and temporal mesoscales in relation to oceanographic conditions. Specifically, to explore why Burmeister's porpoise is present in the Pacific and Atlantic Oceans, we hypothesize that the distribution of *P. spinipinnis*, from Santa Catarina, southern Brazil (28°48'S, 49°12'W) to Paita Bay, northern Peru (05°01'S, 81ºW) is associated with oceanographic conditions (*e.g.*, temperature, salinity, and dissolved oxygen) and circulation systems (*e.g.* currents, upwelling and donwelling process), because these variables are directly related with seasonal productivity, and with prey distribution and abundance.

[4] Heinrich, S., Hammond, P., Christie, C. and Fuentes, M. (2004) Localized distribution and habitat use of Burmeister's porpoises (*Phocoena spinipinnis*) in the Chiloé Archipiélago, Southern Chile. Pages 164-165 *in* Abstracts, 11° Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur y 5[to] Congreso de la Sociedad Latino Americana de Especialistas en Mamíferos Marinos, 11-17 September, Quito, Ecuador.

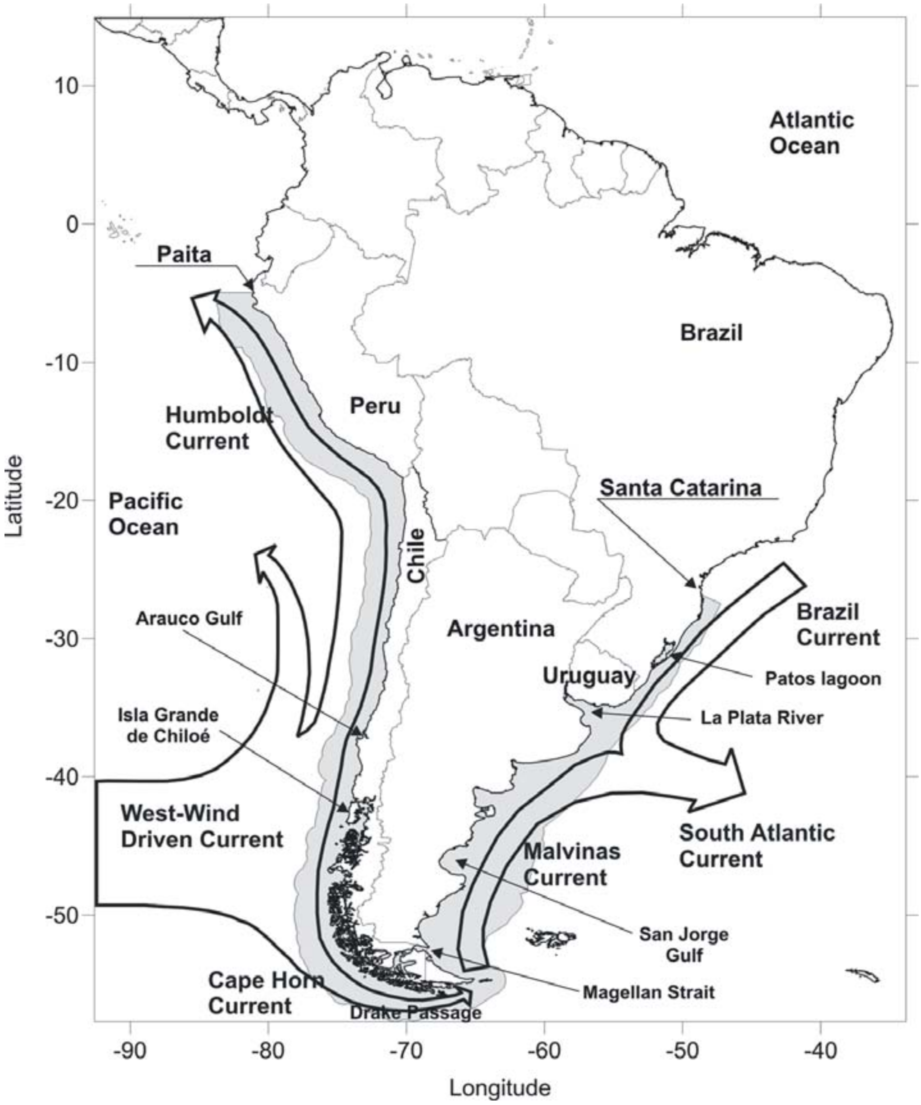

Figure 1. Study area from Paita, Peru (5°01'S) in the Pacific to Santa Catarina, Brazil (28°48'S) in the Atlantic off South America and schematic diagram of the main currents.

Material and Methods

Study area

The study area corresponds to the known distribution of *P. spinipinnis*, from Paita, Peru (5° 01'S) in the Pacific coast to Santa Catarina, Brazil (28° 48'S) in the Atlantic coast of South America. Temperature (°C), salinity (psu) and dissolved oxygen (ml l^{-1}) data at surface and 50m of depth, and between the coast and 20 nautical miles (nm) for the Atlantic and Pacific coast were analyzed to understand the seasonal variability of the oceanographic conditions associated with the distribution of *P. spinipinnis*. Although Burmeister's porpoise is considered a coastal species (Brownell and Praderi, 1982, 1984; Goodall *et al.*, 1995a), it has been found up to 50km from the coast of north-central Argentina, at a depth of 60 m (Corcuera, 1991), and at least 20km from the coast of Valdivia, Chile (Oporto and Brieva, 1994). Considering these antecedents, we used the 20-nm offshore boundary, because we analyzed the oceanographic conditions associated with the distribution of Burmeister's porpoise at large- and mesoscale and not at fine-scale. If we had conducted the analyses at fine scale, we would only be describing the local variability and would not be able to explain the broad distribution of this species.

For the spatial analysis we used as oceanic boundary the isobath of 100m of depth in the Atlantic Ocean. In the Pacific Ocean, we fixed as oceanic boundary the distance of 20nm offshore, because the 100m isobath is very close to the coast (Figure 1). The definition of season used follows austral schedule: summer (January-March); fall (April-June); winter (July-September); and spring (October-December). However, only the summer and winter distributions will be discussed in detail, as the pattern found for temperature, salinity and dissolved oxygen concentration during the fall and spring corresponded to intermediate conditions between the patterns of summer and winter presented here.

Data sources and processing

Historical data of temperature, salinity, and dissolved oxygen from 1965 to 2000 were used in the analysis of oceanographic conditions. The data were downloaded from the servers of WOCE (World Ocean Circulation Experiment) and NCEP (National Centers for Environmental Prediction). The program Ocean Data View (Schlitzer, 2004) was used for making the selection of all the stations used in this study, and for transforming all data into the same format. The next step was to export the oceanographic data to Microsoft Access, with the purpose of generating for each variable (temperature, salinity and dissolved oxygen) the historical average every 5 minute of latitude and longitude for each season and depth (surface and 50m), respectively. After that, kriging with linear semi-variogram was used to generate georeferenced images using the program Surfer 8.0 (BOSS International, Madison, WI, USA). Finally, program TNTMips 6.7 Lite (MicroImages, Inc., Lincoln, NE, USA) was used to carry out the spatial analysis of the unsupervised classification methods of self-classification (cluster) using the images of temperature, salinity and dissolved oxygen for each depth and season. This method is based on neuronal networking computing techniques, and was designed to recognize natural groups of spectral patterns in a sample of the input data and to produce a consistent class identification in response to input of similar patterns during classification of the entire images (Microimages, 2001). Finally, an image was generated with the three parameters according to depth and season, respectively.

Results

General conditions

A total of 104424 oceanographic stations were selected to carry out the analysis of the historical average conditions. The number of oceanographic stations for the Pacific and Atlantic were different. About 61% (64358) of the oceanographic stations corresponded to the Pacific. However, the numbers of stations for each season were similar, especially in the Pacific. The distribution the all oceanographic station used in this study is shown in Figure 2.

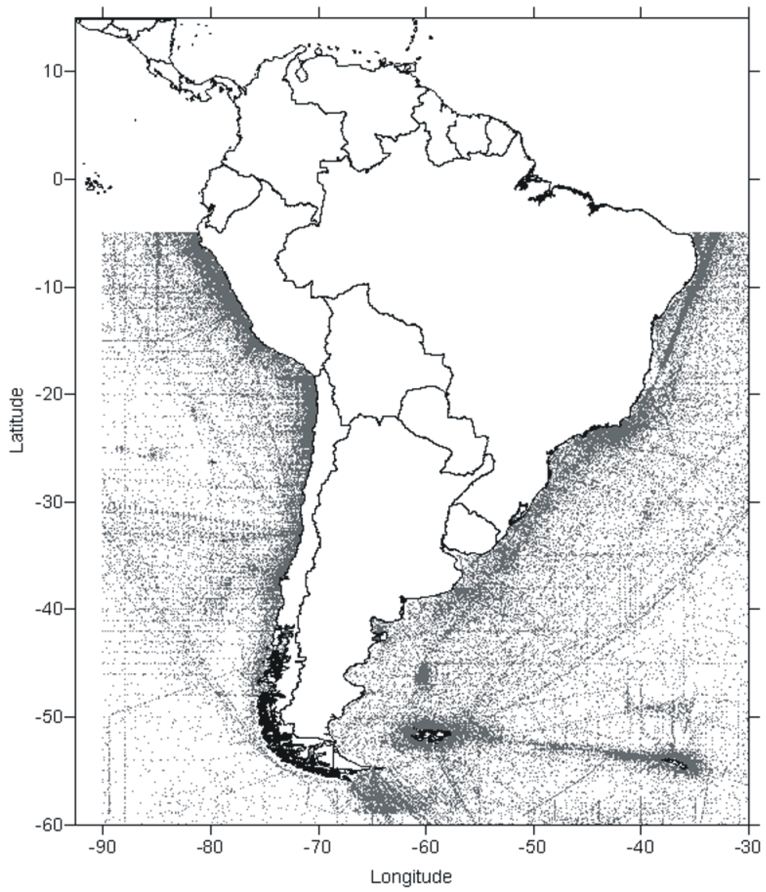

Figure 2. Oceanographic stations used by season from 1965 to 2000 for the Atlantic and Pacific Oceans.

The average historical data between the coast and 20nm showed great variability in the three parameters analyzed (temperature, salinity and dissolved oxygen) (Table 1). In summer, the maximum temperature observed at surface was 29.1°C and 26.6°C in the Atlantic and Pacific, respectively (Table 1). At 50m, the maximum temperature in summer was 24°C in the Atlantic and 26.3°C in the Pacific. The minimum temperatures (2.6-2.8°C) were recorded at the surface in the Atlantic (in autumn) and Pacific (in summer) (Table 1). At 50m, the minimum temperature was lower in the Pacific (Table 1). Thermal inversions were also observed in the Pacific due to the influence of colder freshwater sources.

The maximum salinities (>36psu) were registered at 50m for both the Atlantic and Pacific, respectively. In surface waters, the minimum salinities were observed in austral summer (0.040psu) for the Atlantic and austral spring (0.140psu) for the Pacific (Table 1).

In the Atlantic, the range of dissolved oxygen was from 2.99 to 8.00ml l^{-1}, while that in the Pacific was from 0.02 to 10.98ml l^{-1}. The minimum concentrations of dissolved oxygen were recorded in the Pacific, both at the surface and 50m of depth (Table 1).

Spatial analysis

- Temperature

The images of average temperature at the surface and 50m of depth in austral summer showed gradual increase in temperature from south to north (Figures 3a,d). In summer, the Pacific coast presented an increment in surface temperature (14°C to 22°C) from ~ 41°S (off Isla Grande de Chiloé, Chile) at 05°S (off Paita, Peru). This increase was also observed from the coast to offshore (Figure 3a). The isotherms were semi-perpendicular to the coastline, and were associated with the upwelling process. From 41°S to the Drake Passage the isotherms were perpendicular to the coast and the surface temperature decreased from 14°C to # 6°C (Figure 3a). In the Atlantic, the surface temperature in summer was similar to that of the Pacific. At 46°S, the isotherms change the orientation from semi-perpendicular to parallel to the coast, but in the Pacific the temperature increased toward the coast (Figure 3a).

In the austral winter, the minimum surface temperature was similar (6°C) in both oceans. However, differences were observed in the maximum surface temperature in the Pacific and Atlantic coasts. The isotherm of 14°C in the Atlantic coast was missing, while that in the Pacific was found at 28°S. In the Pacific between 5°S and 10°S, an intrusion of water warmer than 18°C was observed from offshore toward the coast. In the Atlantic, the isotherms were perpendicular to the coast, and associated with discharges of rivers, such as Río de la Plata (Figure 3c).

The image of temperature at 50m of depth in summer and winter showed that in the Pacific the isotherms tend to be perpendicular to the coast from the Drake Passage to near 29°S, with temperatures >5°C and 14°C, respectively. However, lower temperatures were observed at the coast from 29°S northwards. In the Atlantic, from 50°S to the north, the isotherms presented a tendency to be parallel to the coast, and the

Table 1. Minimum and maximum values of temperature, salinity and dissolved oxygen from Paita, Peru (5° 01'S) in the Pacific to Santa Catarina, Brazil (28°48'S) in the Atlantic off South America between 1965 to 2000, by depth (surface and 50m) and season.

OCEAN	DEPTH (m)	SEASON	TEMPERATURE (°C)		SALINITY (psu)		DISSOLVED OXYGEN (ml l^{-1})	
			min	max	min	max		
Atlantic	0	Summer	19.3	29.1	0.040	35.800	3.80	8.00
		Fall	2.6	25.1	0.440	35.651	2.99	8.00
		Winter	11.5	21.1	0.070	35.519	4.43	8.00
		Spring	13.2	23.8	0.430	35.817	3.09	8.00
	50	Summer	15.8	24.0	34.976	35.855	2.73	5.52
		Fall	2.6	23.3	33.785	36.272	2.83	7.45
		Winter	16.3	19.5	31.932	35.845	3.69	6.03
		Spring	14.5	19.4	35.364	35.960	3.44	5.42
Pacific	0	Summer	2.8	26.6	1.289	35.668	0.08	10.98
		Fall	4.8	23.3	9.999	35.796	0.87	9.89
		Winter	4.7	21.5	12.496	35.486	1.44	9.20
		Spring	5.2	24.2	0.140	35.429	0.15	9.42
	50	Summer	5.9	26.3	5.000	36.008	0.03	7.60
		Fall	8.0	21.2	30.259	35.190	0.02	6.69
		Winter	5.2	19.2	27.440	35.540	0.02	8.00
		Spring	6.0	23.6	22.024	35.500	0.02	7.01

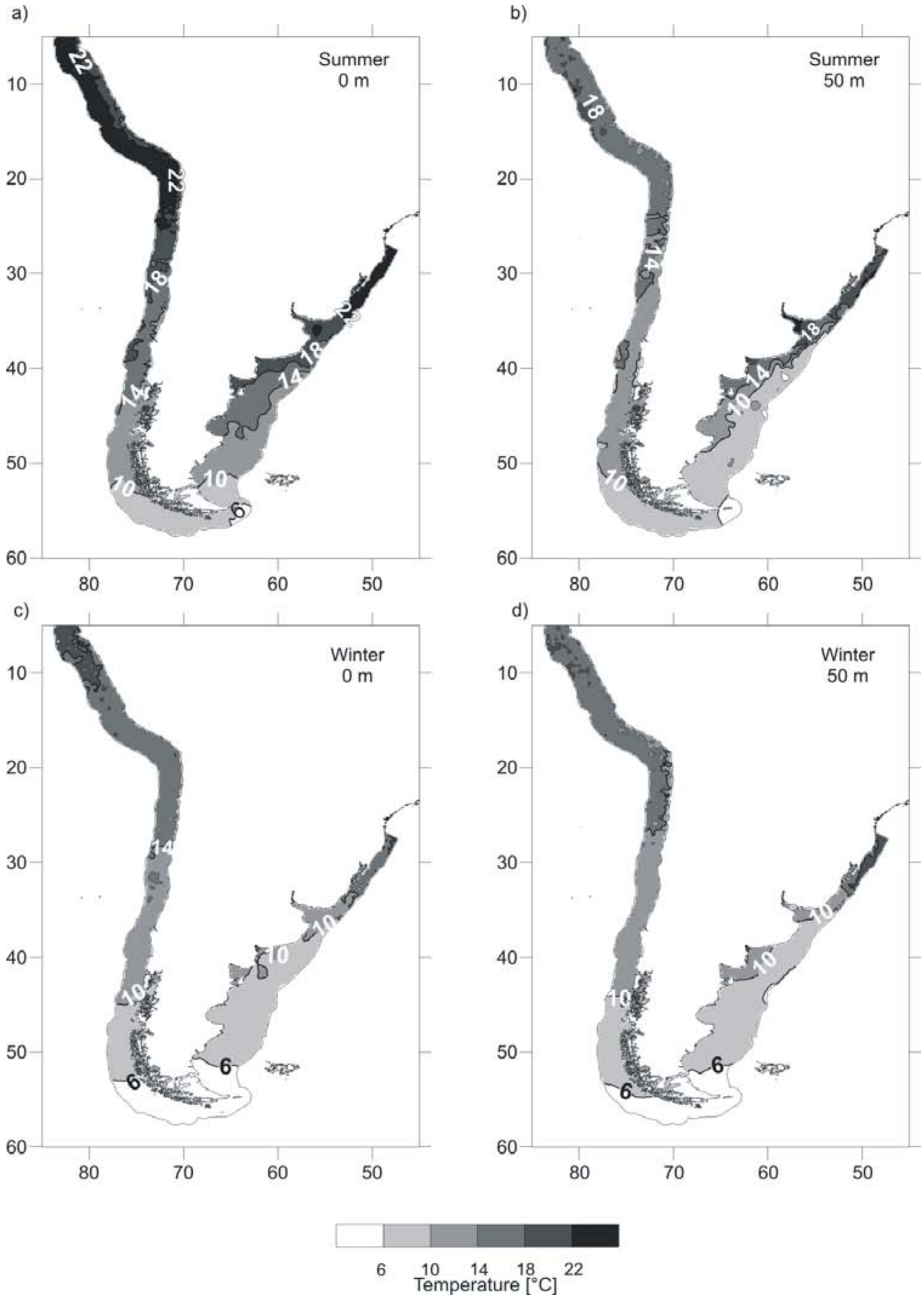

Figure 3. Historical average temperature: a) summer 0m, b) summer 50m, c) winter 0m and d) winter 50m.

temperature was greater than 10°C (Figures 3b,d).

- *Salinity*

In the Atlantic and Pacific, both at the surface and 50m, salinity increases from south to north. Higher salinities ($ 35psu) were observed near the northern boundary of the study area off the Peruvian and Brazilian coasts (Figures 4a,d). In summer, the salinity off the Argentine coast at the surface and 50m was between 33-34psu. This was similar to the Chilean coast south of 33°S (Figures 4a,b). However, in the Pacific the salinity increases gradually at the surface (>35 psu) and offshore north of 26°S, but in winter this limit moves further northwards (Figures 4c,d). The minimum salinity observed reflects the contributions of freshwater from fjords, glaciers, and rivers, mainly in the Atlantic, where there is a great contribution of freshwater from the basin of the La Plata River. In the Pacific, lower surface salinities were observed in the zone of channels and fjords, due to the contributions of freshwater from precipitation, draining, rivers, and glacier

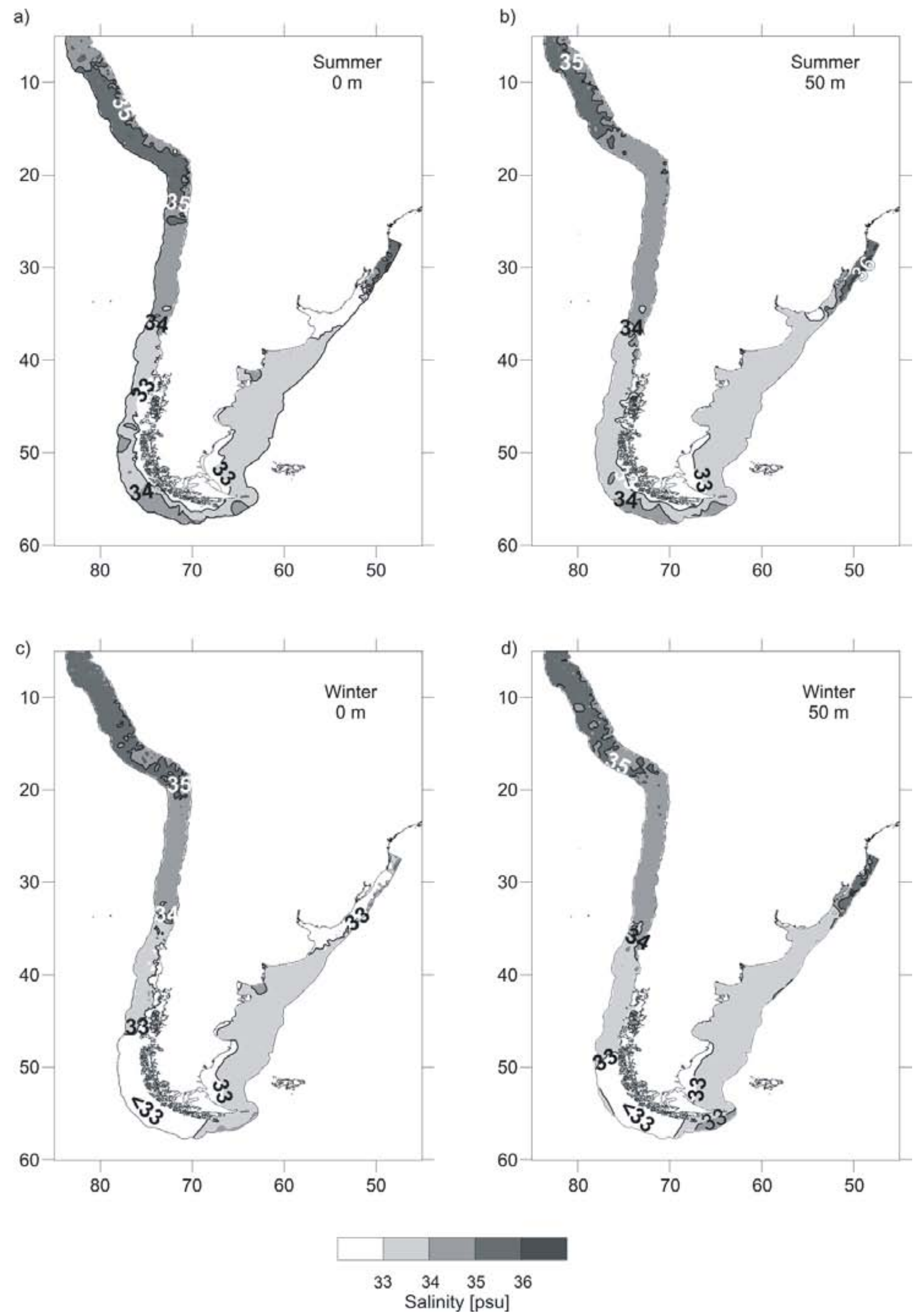

Figure 4. Historical average salinity: a) summer 0m, b) summer 50m, c) winter 0m and d) winter 50m.

melting.

- *Dissolved oxygen*

The dissolved oxygen concentration in the Atlantic and Pacific increases from the north southwards, both at the surface and at 50m (Figures 5a,d). However, there is a decrease in dissolved oxygen from surface to depth in the Pacific. The lower concentration of dissolved oxygen was associated with the influence of the OMZs, and in the coastal zone of the Peruvian coast, the upper limit of OMZs was closer to the surface.

The Patagonia area presented the greater dissolved oxygen concentrations (>6ml l^{-1}) (Figures 5a,d). These waters are mixed during the winter by the action of winds, which increase the thickness of the Ekman Layer.

On the continental shelf of Argentina, the Malvinas Current transports more oxygenated water to the north (Figures 5c,d). Off the Brazilian and Uruguayan coasts the water is less oxygenated, between 4-6ml l^{-1}, with a minimum near to 2ml l^{-1} in the area of Patos Lagoon,

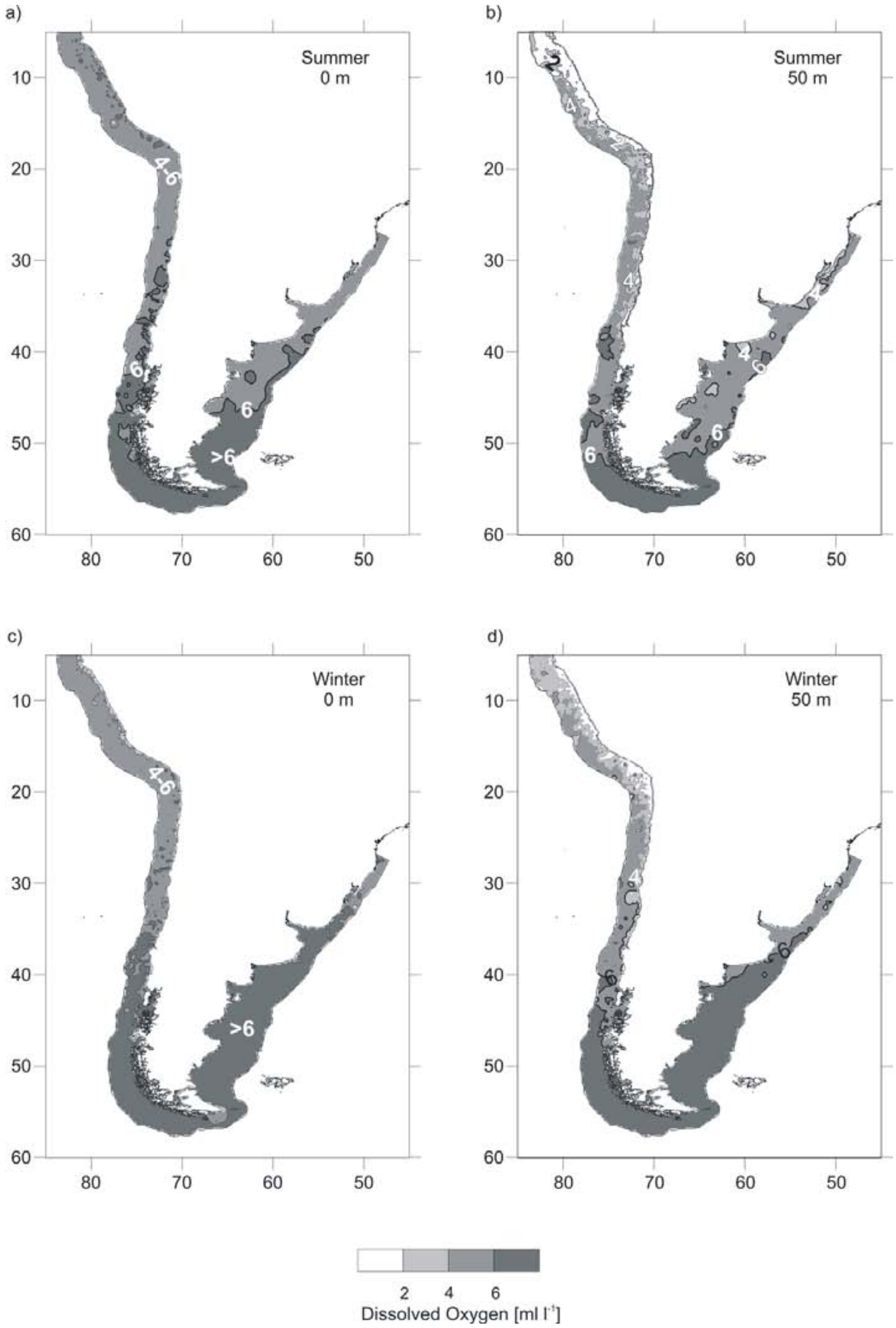

Figure 5. Historical average dissolved oxygen: a) summer 0m, b) summer 50m, c) winter 0m and d) winter 50m.

south Brazil (32°S; 49°W) (Figure 5b). In the Pacific, north of 40°S the dissolved oxygen concentration was between 4-6ml l^{-1} (Figures 5a,c), and near the coast at 50m upwelling water from the OMZs, with values <0.5ml l^{-1} was observed (Figures 5b,d).

- *Self-classification*

The self-classification method shows that the image obtained for the surface generated three different groups (Figure 6). The first group was associated with more temperate and saline waters, and it was present in fall, winter and spring from northern Peru (5°S) to ~40°S in the Pacific (Figures 6b,c,d). In summer, this group presented a minimum distribution from 5° to 33°S (Figure 6a). Off the Atlantic coast, this group showed a minimum distribution in winter from 38° to 28°S (Figure 6c), and with fluctuations along the coast from La Plata River to the north, especially in summer and fall.

The second group includes the austral waters, and their

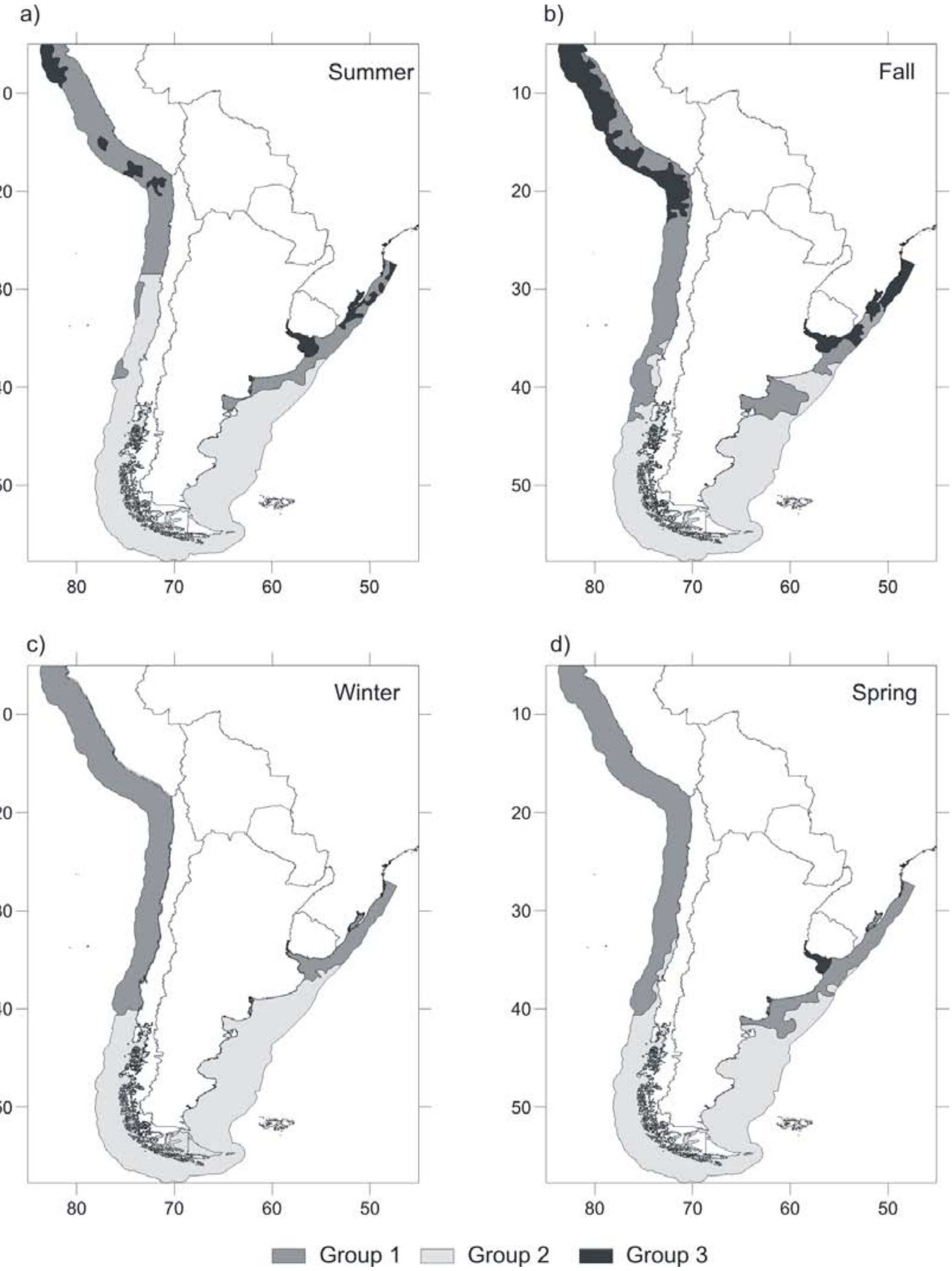

Figure 6. Groups generated for each season at the surface by self-classification methods.

associated seasonal fluctuations. In the Atlantic, this group was associated with the Malvinas Current in all four seasons, and in the Pacific it was associated with the Cape Horn Current in fall, winter, and spring (Figures 6b,c,d). In summer, this group expands its distribution to the north (~40°S to 33°S), where there is the influence of the Humboldt Current and the upwelling waters (Figure 6a).

The third group in the Pacific coast was associated with an intrusion of oceanic waters from offshore toward the Peruvian coast. In the Atlantic this group has a contribution of freshwater from the riverine basins discharging along the Uruguayan and Brazilian coasts (*e.g.*. La Plata River, Patos Lagoon) as well as runoff (Figures 6a,b). The first and the second groups were present year-round, but the third group was absent in winter (Figure 6c).

At 50m, the self-classification method showed the same groups observed at the surface (Figures 7a,b,c). However, in spring a fourth group was created in the austral zone from the Magellan Strait in the Pacific to south of San

Jorge Gulf, off Argentina, in the Atlantic (Figure 7d).

Based on the results of this study, we propose three oceanographic areas relevant to the distribution of *P. spinipinnis*:

(1) The first area, from Paita, northern Peru (5°S), to south of the Arauco Gulf, Chile (~39°S), has the influence of the Humboldt Current, which involves upwelling that carries water rich in nutrients, colder, more saline and low in oxygen, and also contains an oxygen minimum zone (Figure 8);

(2) The second area, from south of Arauco Gulf to south of La Plata River (~38°S) shows the influence of Cape Horn and Malvinas Currents, and involves downwelling processes, and freshwater contributions from fjords, glaciers and rivers (Figure 8);

(3) The third area, from La Plata River to Santa Catarina, Brazil (28°S) is characterized by the influence of the Brazil Current, and the freshwater contributions of the basin of La Plata River and the estuarine system of Patos Lagoon (Figure 8).

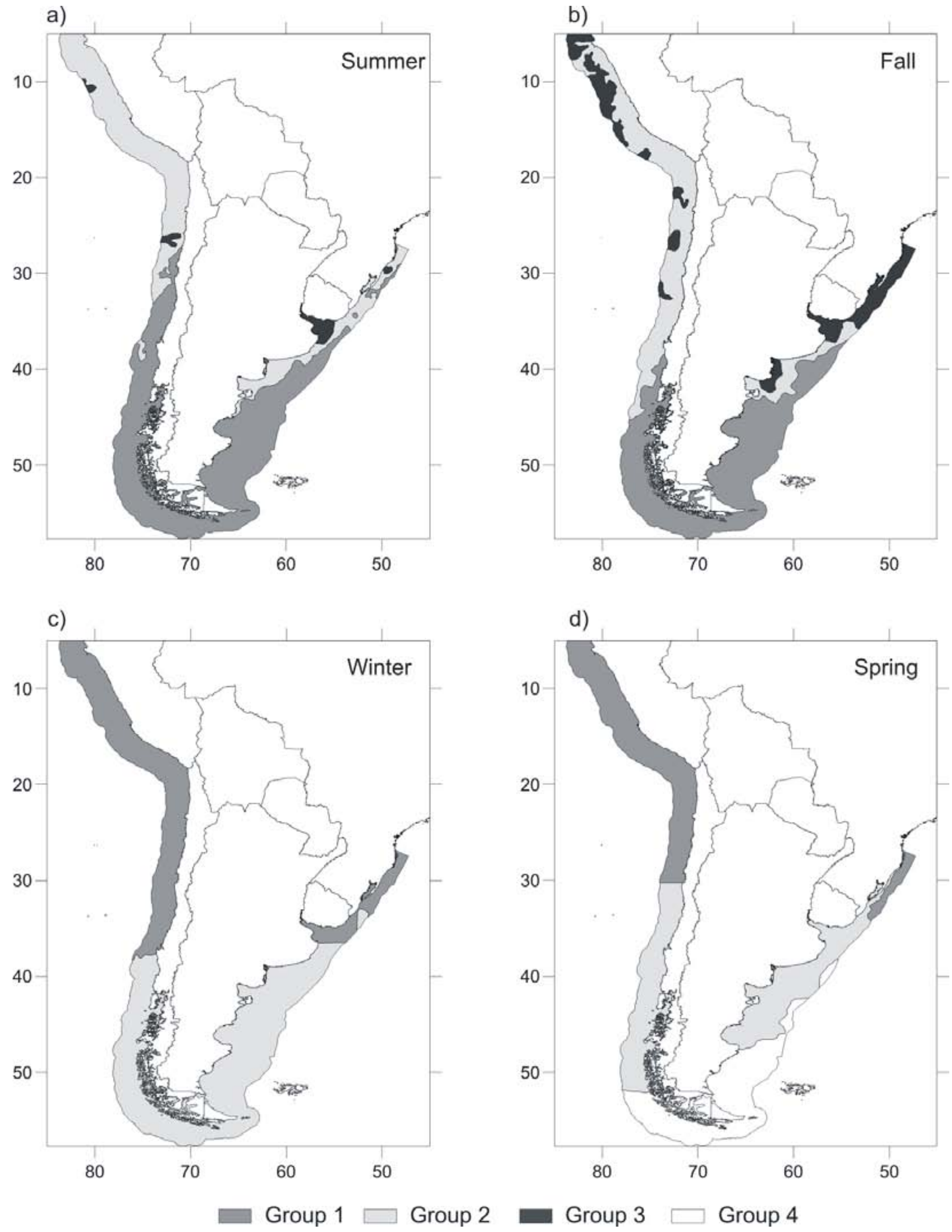

Figure 7. Groups generated for each season at 50m by self-classification methods.

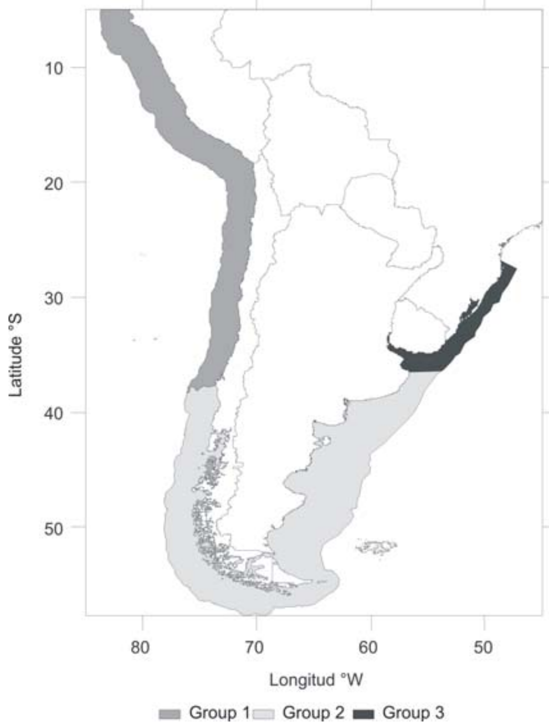

Figure 8. Proposed oceanographic zones associated with the distributions of *Phocoena spinipinnis*.

Discussion

The variability of average historical data of temperature, salinity, and dissolved oxygen analyzed in this study is associated with different processes related to the geographical position and the influence of seasonality. This has been described by several authors (*e.g*. Lima *et al*., 1996; Piola *et al*., 2000; Blanco *et al*., 2001; Rivas and Piola, 2002; Sabatini *et al*., 2004).

Results from this study clearly show the influences of oceanographic conditions on the distribution of Burmeister's porpoise in both oceans. The characterization of the oceanographic conditions showed that the northern boundary of the distribution of *P. spinipinnis* for the Pacific coast at Paita, Peru (5°S) is coincident with the westward turn of the Humboldt Current, as it is incorporated into the South Equatorial Current. In the Atlantic, the northern boundary seems associated with the Atlantic Subtropical Convergence (30-40°S), as was originally proposed by Brownell and Clapham (1999) and Goodall *et al*. (1995a). In addition, the high temperatures (>24°C) and salinities (>36psu) recorded at the surface and 50m between the coast and the 20nm boundary were coincident with the known northern limit of the distribution of *P. spinipinnis* on both coasts of South America (Goodall *et al*., 1995a,b; Reyes and Van Waerebeek, 1995; Brownell and Clapham, 1999).

The characterization of the oceanographic conditions from Paita, Peru to Santa Catarina, Brazil showed a clear separation in three major areas. The differences in distribution of *P. spinipinnis* between the different oceanographic areas is based on an assumption of seasonal variations of the parameters examined.

The first oceanographic area, from Paita, northern Peru (5°S) to south of Arauco Gulf, Chile (~39°S) is characterized by the presence of the Humboldt Current and an OMZ, with an average temperature between 14-22°C, salinity between 34-35psu, and dissolved oxygen from values lower than 1 to 6ml l^{-1}. These characteristics are coincident with the seasonal ranges of surface temperature and salinity observed by Blanco *et al*. (2001).

The influence of the Humboldt Current System in the first area is very important, because a significant exchange of heat and CO_2 takes place between the ocean and the atmosphere due to upwelling of sub-surface, cold, nutrient-rich, CO_2-saturated waters. This fertilization of the photic zone increases primary production and the uptake of CO_2 (Escribano *et al*., 2003). The Humboldt Current System with its coastal upwelling ecosystem off Peru and Chile is recognized as a highly productive region, sustaining large fisheries of anchovies and sardines (Alheit and Bernal, 1983; Mann and Lazier, 1991; Walsh, 1991). Burmeister's porpoise occurring in the upwelling system might be particularly vulnerable to local depletion as they inhabit a very rich, but unstable environment (*e.g*. due to recurring El Niño events). Detailed studies of stomach contents of porpoises from Peru and Chile have shown that their most common prey were primarily anchovy (*Eugraulis ringens*), hake (*Merluccius gayi*), and jack mackerel (*Trachurus murphyi*) (Torres *et al*, 1992; Reyes and van Waerebeek, 1995).

Although cetaceans are highly mobile predators and their distribution is dynamic, habitat selection often seems to correspond with hydrographic domains associated with bathymetric features (Baumgartner, 1997; Moore *et al*., 2000), so the assumption of some annual pattern of cetacean distribution and abundance seems warranted. Probably, the presence of the OMZs in the southeastern Pacific Ocean, from the latitude of the Galápagos Islands (~1°S) to southern Chile (~40°S) (Gallardo, 1963; Rosenberg *et al*., 1983; Arntz *et al*., 1991), is an important factor in the separation of two oceanographic areas observed in this study for the Chilean coast, and its limit seems to be south of the Arauco Gulf (~39°S) (Gutierrez *et al*., 2000). According to time series data in northern Chile (1980 to 1997, JGOFS and FONDAP-HUMBOLDT Projects), the oxycline is located at 50m of depth at the coast, and at 100m of depth in oceanic waters. However, this limit has been detected in shallower waters at 10m during strong El Niño, as the event of 1997-1998.

The upper limit of OMZs presents a great vertical intra and interannual variability associated with dynamic processes in the system (Morales *et al*., 1999). The upper and lower boundaries of OMZs have been characterized as sites of enhanced biological and biogeochemical activity (Wisher *et al.*, 1995), including the coupling of nitrification and denitrification processes (Anderson *et al.*, 1982). In addition, OMZs represent an effective barrier of vertical distribution and diversity of plankton, micronekton, and benthic species or assemblages, though some organisms are adapted to these extreme conditions (Wisher *et al.*, 1995).

The second oceanographic area proposed here is from south of the Arauco Gulf, Chile to south of La Plata River, Argentina (~38°S). This group is characterized by the influence of the Cape Horn and Malvinas Currents, and freshwater contributions (especially from fjords, glaciers and the La Plata River Basin) with temperature values between 6°-22°C, salinity between 33-35psu and dissolved oxygen between 2-6ml l^{-1}. The maximum record of temperature associated with a Burmeister's porpoise sighting ranged between 17.5° and 19.5°C (summer) in San José Gulf, Argentina (Würsig and Würsig, 1980) and Tierra del Fuego to near Cape Horn, average from 4°C (winter) to 9°C (summer) (Goodall *et al.*, 1995a).

The low value of salinity recorded in spring off the Pacific coast was associated with the melting of glaciers at that time. The excess of precipitation in the Southeast Pacific and continental runoff from southern Chile reduced the salinity over the shelf of the Atlantic coast to values <33.9psu (Deacon, 1933; Lusquiños and Valdéz, 1971). Several authors observed the remarkable permanent salinity minimum existing off southern Chile (Silva and Neshyba, 1979; Neshyba and Fonseca, 1980; Sievers and Nowlin, 1989; Silva *et al.*, 1997). According to these authors, the main driving forces in this zone are contributions of freshwater from rivers, runoff, rain and glaciers; mixing of freshwater with saline waters; subsurface advection of more saline waters with oceanic origin, and vertical mixing by wind shear.

There are two types of freshwater discharges over the Patagonian shelf, in Argentina.The first is related to drainage of continental rivers along the coast of southern Patagonia, and the second is the inflow of diluted waters from the Magellan Strait (Panella *et al.*, 1991). Although there is only scant information about the magnitude of the influx of the relatively fresher waters from the Magellan Strait, the water mass structure of the Patagonian shelf is strongly influenced by a freshwater 'tongue', which has its salinity minimum in that region and is known as the Patagonian Current (Sabatini *et al.*, 2004). This is similar to what was observed in this study (Figure 4).

In the second oceanographic area we proposed, the salinity minimum (>33psu) at 50m depth in the Atlantic indicates that the contributions of freshwater are concentrated at the surface, and do not reach 50m, with the exception of the low salinity observed in winter (31.93psu). This can be attributed to a stronger mixing of the water column that would allow the dilution of water at this depth with surface freshwaters. In the Pacific there was a larger contribution of freshwater in the water column, corresponding to that found by Dávila *et al.* (2002), who determined the large effect of freshwater offshore in fall. With regard to dissolved oxygen, the highest concentrations were found in the southern zone (for both Pacific and Atlantic coasts), and were associated with the turbulent mixing of the water column by the wind action. This mixing is more intense because of the continual passage of frontal systems, especially in the Pacific coast, where the concentrations are larger than in the Atlantic coast at 50m.

In this area, sightings of Burmeister's porpoise have been made at least 20km from coast of Valdivia, Chile, especially in winter when sardines move offshore (Oporto and Brieva, 1984), in mouths of rivers and estuaries (Aguayo, 1975), and appear to be fairly common in bays off the intricate channels of Tierra del Fuego in the southernmost part of the range (Goodall *et al.*, 1990; 1995), and in San José Gulf, Argentina (Würsig and Würsig, 1980). Heinrich *et al.* (2004) mention that Burmeister's porpoises from Chiloé Archipelago (42°-43°S) seemed to prefer significantly deeper waters (mean depth=37m) and further from shore (mean distance to shore=963m).

The third oceanographic area proposed here, from La Plata River to Santa Catarina, Brazil (28°S), is characterized by the influence of the Brazil Current, and the freshwater contributions of the La Plata River basin and the estuarine system of Patos Lagoon. This is coincident with that observed by Piola *et al.* (2000), who analyzed historical hydrographic data in the upper layer over the continental shelf off eastern South America and concluded that there is a widespread influence of continental discharge, primarily from La Plata River Basin and locally from Patos Lagoon.

During the austral winter, the low-salinity plume reaches 28°S, while in summer it is constrained to south of 32°S. The seasonal variability of the along shore extent of the low-salinity plume, presumably induced by variations in the wind stress, is larger than the changes induced by the variability in river discharge.

The Subtropical Convergence has enormous importance to the geographical distribution of the South American biota. This convergence, which in the summer is located at the latitude of Montevideo (Uruguay), can reach Florianópolis (Brazil) during winter, creating rich fishing areas (CARPAS, 1964). This would explain the occasional presence of *P. spinipinnis* in Brazil, because the three records of Burmeister's porpoise for Brazil were in spring 1986, near the Uruçanga river mouth, Santa Catarina state (28°48'S) (Simões-Lopez and Ximenez, 1993). The second and third record were on the coast of Rio Grande do Sul, in summer 1986 (32°40'S; 52°26W) (Pinedo, 1989), and summer 2000 off Farol Berta (30°23.9'S; 50°17.2'W) (Ignacio Moreno, GEMARS, pers. comm.). These records were coincident with the intrusion of colder and less saline waters northwards. According to Silva *et al.* (1984), in these latitudes, salinities between 33-36psu, and the surface temperature tends to be lower near shore (16-22°C), gradually rising in deeper waters offshore (23-27°C). In addition, Pimenta (2001) analyzed the variability of the La Plata plume by simulations with a numerical model as a function of wind stress and intensity of river discharge, including the effect of La Niña and El Niño periods and found that the average speed of the plume along the shore was directly related to the intensity of the outflow, and the northward extent of the plume along the shelf varied from 850 km to 1550 km, for La Niña and El Niño, respectively. Considering these conditions, we propose that the habitat of Burmeister's porpoise in the Atlantic is associated with the Subtropical Convergence. When intrusions of colder and less saline waters occur northwards, *P. spinipinnis* can move to the north, reaching the latitude of Florianópolis (28°48'S; 49°12'W), southern Brazil. Silva *et al*. (1984) reveal upwelling areas to the north of the Santa Catarina coast, as well as in the region between Santa Marta Cape and Florianópolis.

The movements of cetaceans and other mobile marine predators are driven primarily by physical oceanographic conditions, particularly at lower trophic levels (Angel, 1994; Fiedler *et al*., 1986; Benson *et al*., 2002). The feeding ecology of Burmeister's porpoise is not well known, but regional differences in feeding habits are likely.

Considering the existing information on Burmeister's porpoise based on sightings, strandings and incidental captures (Corcuera *et al*., 1995; Goodall *et al*., 1995a,b; Reyes and Van Waerebeek, 1995) from Paita, Peru to Santa Catarina, Brazil, and the oceanographic characterization of habitat of *P. spinipinnis* obtained in this study, we propose that Burmeister's porpoise presents a continuous distribution throughout this range from Paita, Peru, to La Plata River Basin, Argentina, being able to reach Uruguayan and Brazilian waters under certain oceanographic conditions (*e.g*. intrusion of colder and less saline waters toward the north associated to the Subtropical Convergence).

Better information on spatial and temporal variation of the diet and habit use of *P. spinipinnis*, combined with feeding behavior are necessary to improve current models of prey consumption. The results provide useful information use in understanding the ecology of Burmeister's porpoise, and hopefully will help managers address concerns about the potential impacts of anthropogenic activity on this species. The analyses presented in this study may also provide relevant habitat information for a number of other marine mammal species present in the study area.

Conclusions

Our results support a clear separation of the distribution of Burmeister's porpoise into three large areas: (1) from Paita, northern Peru (5°S), to south of the Arauco Gulf, Chile (~39°S) with the influence of the Humboldt Current and OMZ; (2) from south of Arauco Gulf to south of La Plata River, Argentina, (~38°S) associated with the Cape Horn and Malvinas Currents, as well as freshwater contributions; (3) from La Plata River to Santa Catarina, Brazil (28°S), with the influence of the Brazil Current, and the contributions of freshwater from La Plata River Basin, Argentina and the estuarine system of Patos Lagoon, south Brazil. The presence of OMZ is an important factor in the separation into two groups off the Chilean coast (~39°S). The characterization of the oceanographic conditions showed that the northern boundary of the distribution of *P. spinipinnis* for the Pacific coast at Paita (5°S) is coincident with the westward turn of the Humboldt Current, as it is incorporated into the South Equatorial Current. Off the Atlantic coast, the northern boundary seems associated with the Atlantic Subtropical Convergence (30-40°S). The high temperatures (>24°C) and salinities (>36psu) registered at the surface and at 50m between the coasts and the 20nm boundary were coincident with the known northern limit of the distribution of this species on both coasts of South America. In addition, we propose that Burmeister's porpoise presents a continuous distribution throughout this range from Paita, Peru to La Plata River Basin, Argentina, being able to reach Uruguayan and Brazilian waters under certain oceanographic conditions (*e.g*. intrusion of colder and less saline waters toward the north associated to the Subtropical Convergence).

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