UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

TESE DE DOUTORADO

VARIAÇÃO GEOGRÁFICA DO BOTO-DE-BURMEISTER, *PHOCOENA SPINIPINNIS* (BURMEISTER, 1865) (CETACEA: PHOCOENIDAE) NAS COSTAS ATLÂNTICA E PACÍFICA DA AMÉRICA DO SUL

DANIZA MARCELA MONTSERRAT MOLINA SCHILLER

PORTO ALEGRE – RS, 2006.

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DANIZA MARCELA MONTSERRAT MOLINA SCHILLER

Tese de Doutorado apresentada ao Curso de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Doutor em Ecologia.

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PORTO ALEGRE – RS, 2006.

A meu filho Maximiliano (MAX)
A meus Pais Irma Schiller e Luis Molina

> ***"O rio atinge seus objetivos porque aprendeu a contornar obstáculos"***
> **(Lao-Tsé)**

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RESUMO

Um total de 142 crânios do boto-de-Burmeister, *Phocoena spinipinnis* depositados em museus e coleções cientificas da Argentina, Brasil, Chile, Peru e Uruguai foram utilizados para explorar a variação geográfica em relação ao tamanho e forma do crânio de *P. spinipinnis*. Ademais, foi realizada uma caracterização oceanográfica da área de distribuição do boto-de-Burmeister através de dados históricos de temperatura, salinidade e oxigênio a 0 e 50m de profundidade na costa Atlântica e Pacifica. As idades dos animais foram obtidas pelas leituras das GLGs na dentina. A idade mais alta atingida por ambos os sexos foi de 10 anos. Medições na dentina mostraram dimorfismo sexual na primeira GLG e diferenças geográficas entre botos do Peru e Atlântico. Três tipos de anomalias foram registrados nos dentes, e a linha marcadora parece estar associada ao “El Niño”. Vinte e oito caracteres métricos foram utilizados para explorar o dimorfismo sexual e crescimento. A maturidade física do crânio foi estabelecida quando o comprimento côndilo-basal atingiu 95% do comprimento total (≥266mm nos machos e ≥277mm nas fêmeas). Diferenças no tamanho e forma do crânio foram analisadas através de morfometria tradicional e geométrica. Os resultados revelaram dimorfismo sexual, sendo as fêmeas maiores do que os machos. As diferenças em tamanho e forma concentraram-se principalmente na região rostral e neurocrânio. Foi observada variação geográfica entre os botos do Atlântico, Chile e Peru. *P. spinipinnis* do Peru são de menor tamanho em relação a os botos do Chile e Atlântico. Botos do Chile apresentam um tamanho e forma intermediária, e os botos do Atlântico são maiores (especialmente na região orbital, altura do crânio e região rostral). A distância de Mahalanobis mostrou maior separação entre os botos do Peru e do Atlântico, e menor distância entre os exemplares do Chile e Atlântico. A morfometria geométrica explica com maior clareza as diferenças entre botos do Chile e Atlântico, especialmente nas vista ventral e lateral. A correlação entre variáveis ambientais e morfométricas através da análise de correlações canônicas e dos quadrados mínimos parciais de dois blocos sugere que as diferenças observadas no tamanho e na forma dos crânios têm uma importante influência espacial, associada à variabilidade sazonal das condições oceanográficas presentes nos dois oceanos e diretamente relacionada às três áreas oceanográfica propostas neste estudo: (1) de Paita, Peru (05°01’S, 81ºW) até o sul do Golfo de Arauco, Chile (~39°S); (2) do sul do Golfo de Arauco até o sul do Rio da Prata (~38°S); e (3) do Rio da Prata até Santa Catarina, Brasil (28º48’S; 49°12W). Adicionalmente, propõe-se que *P. spinipinnis* apresenta uma distribuição contínua desde Paita, Peru ate a bacia do Rio da Prata, Argentina, podendo alcançar águas uruguaias e brasileiras em determinadas condições oceanográficas (entrada de águas mais frias e menos salinas com direção ao norte, associadas à Convergência Subtropical).

Palavras-chave: *Phocoena spinipinnis*, boto-de-Burmeister, dimorfismo sexual, variação geográfica, morfometria tradicional, morfometria geométrica, determinação da idade, distribuição, anomalias, condições oceanográficas.

ABSTRACT

A total of 142 skulls from Burmeister's porpoises, *Phocoena spinipinnis* from museums and scientific collections from Argentina, Brazil, Chile, Peru and Uruguay were analyzed to explore the geographical variation in relation to size and shape on skulls of *P. spinipinnis.* In addition, an oceanographic characterization of the area of distribution of Burmeister's porpoise by historical data of temperature, salinity and oxygen the 0 and 50m of depth on the Pacific and Atlantic coast was carried out. The age of the animals was obtained by reading the Growth Layer Group in dentine. The oldest male and female were 10 years of age. Measurements in dentine showed sexual dimorphism in the first GLG and geographic differences between porpoises from Peru and Atlantic. Three types of anomalies were recorded in teeth, and the marker lines seem to be associated to "El Niño". Twenty-eight characters were used to explore sexual dimorphism and growth. Physical maturity of the skull was established when 95% of condylobasal length was attained (≥266mm in the males and ≥277mm in the females). Differences in size and shape of skull were analyzed by traditional and geometric morphometrics. The results revealed sexual dimorphism, being the females larger than male, and the differences in size and shape are concentrated mainly in the rostral region and neurocranium. Geographic variation between porpoises from Atlantic, Chile, and Peru was observed. *P. spinipinnis* from Peru are smaller compared to porpoises from Chile and Atlantic. Porpoises from Chile have an intermediate shape, and porpoises from Atlantic are larger (mainly related to orbital region, skull height and rostral region). The distance of Mahalanobis showed more separation between porpoises from Peru and Atlantic, and less distance between specimens from Chile and Atlantic. Geometric morphometrics was more useful for show differences between specimens from Chile and Atlantic, especially in the ventral and lateral views. The correlation between environmental and morphometric variables by canonical analysis and two-block partial least squares suggests that the differences observed in the size and shape of skulls would have an important spatial influence, associated to the seasonal variability of the oceanographic conditions present in the two oceans, and directly related to the three oceanographic areas proposed in this study: (1) from Paita, Peru (05°01'S, 81ºW) to south of Arauco Gulf, Chile (~39°S); (2) from south of Arauco Gulf to south of La Plata River, Argentina (~38°S); and (3) from La Plata River to Santa Catarina, Brazil (28º48'S; 49°12W). In addition, it is proposed that *P. spinipinnis* presents a continuous distribution 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).

Keywords: *Phocoena spinipinnis*, Burmeister's porpoise, sexual dimorphism, geographic variation, traditional morphometrics, geometric morphometrics, age determination, distribution, anomalies, oceanographic condition.

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INTRODUÇÃO GERAL

A Família Phocoenidae esta constituída por seis espécies: boto comum, *Phocoena phocoena*; boto-de-Dall, *Phocoenoides dalli*; boto-de-Burmeister, *Phocoena spinipinnis*; boto-de-óculos, *Australophocaena dioptrica*, boto sem nadadeira, *Neophocaena phocaenoides*, e vaquita, *Phocoena sinus* (BERTA *et al.,* 2006). Em geral são animais pequenos, no máximo com 2,5m de comprimento, rostro indiferenciavel da cabeça, a qual tem aparência arredondada, dentes pequenos e em forma de espatula, nadadeira dorsal pequena ou ausente (JEFFERSON *et al*., 1993). Estas espécies em sua maioria apresentam uma distribuição costeira e estão sujeitas à exploração pelas comunidades costeiras, porem é particularmente vulnerável a mortalidade acidental pelas atividades de pesca, degradação do habitat (poluição, tráfego marítimo e diminuição importante das espécies-presa pela pesca intensiva dos recursos) (BJØRGE & DONOVAN, 1995).

O boto-de-Burmeister*, Phocoena spinipinnis* foi descrita por BURMEISTER (1865) com apenas um exemplar capturado na boca do Rio da Plata, Argentina. A origem do nome científico *Phocoena spinipinnis* é do grego *phokaina* (boto) ou do latim *phocaena* (boto) e *spinna* (que tem espinhas) e *pinna* (asa ou nadadeira). Também é conhecida por seu nome vulgar como: marsopa espinosa (em Espanhol), golfinho espinhoso (em Português) e Burmeister's porpoise (em Inglês) (BROWNELL & PRADERI, 1982, 1984; PINEDO, 1989; JEFFERSON *et al*., 1993; BJØRGE & DONOVAN, 1995). Esta espécie despertou grande interesse, embora tenham se passado muitos anos até que outros exemplares fossem coletados na Argentina (GALLARDO, 1917), Chile (PÉREZ-CANTO, 1896; PHILIPPI, 1893, 1896) e Peru (ALLEN, 1925). Após a década de 60, os registros e estudos nas costas pacífica e atlântica tornaram-se mais comuns.

O boto-de-Burmeister é pequeno e robusto, o comprimento médio é de aproximadamente 1,5m. A coloração é variável, na região dorsal é escura e homogênea, na região ventral é ligeiramente mais clara e ao redor dos olhos geralmente existe uma mancha circular mais escura. A espécie possui o menor número de dentes do gênero *Phocoena*, de 14 a 16 pares de dentes na maxila e de 17 a 19 pares de dentes na mandíbula. Possui uma nadadeira dorsal característica, sua forma é similar a um triângulo reto de base larga e apresenta pequenos tubérculos (dentículos dérmicos), pequenas projeções semelhantes a espinhos, característicos de *P. spinipinnis* (Figura 1) que originaram o nome cientifico e popular (BURMEISTER, 1865; PRADERI, 1971; BROWNELL & PRADERI, 1982, 1984; HETZEL & LODI, 1993; JEFFERSON *et al.*, 1993 BJØRGE & DONOVAN, 1995).

P. spinipinnis ocorre em águas da América do Sul (BROWNELL & PRADERI, 1982). Sua distribuição na costa atlântica estende-se desde Santa Catarina (28º 48'S, 49º 12' W), sul do Brasil até Terra do Fogo e Canal de Beagle (PRADERI, 1971; PILLERI & GIHR, 1972; WÜRSING *et al.*, 1977; GOODALL, 1978; PINEDO, 1989; SIMÕES-LOPES & XIMÉNEZ, 1989). Na costa do pacífico, o Boto-de-Burmeister ocorre desde a Bahia de Paita, norte do Peru (05º05'S) até o estreito de Magalhães, sul do Chile (ALLEN, 1925; CLARKE, 1962; AGUAYO, 1975; GASKIN *et al.*, 1987; REYES & VAN WAEREBEECK, 1995). Os Botos-de-Burmeister, além de possuírem hábitos discretos (são aparentemente tímidos), não costumam aproximar das embarcações. O tamanho do grupo geralmente varia entre 1 e 6 indivíduos (GOODALL *et al.*, 1995a; HEINRICH *et al.*, 2004). Contudo, VAN WAEREBEECK *et al.* (2002) reportou em setembro 2001 um grupo de 150 indivíduos próximo à Ilha Guañape, centro-norte do Peru (08º28'04''S, 78º58'16.7''W).

No Peru, *P. spinipinnis* é a segunda espécie mais capturada em pesca, sendo as capturas tanto acidentais como intencionais (READ *et al.*, 1988; VAN WAEREBEEK & REYES, 1990, 1994; VAN WAEREBEEK *et al.*, 2002). Outrossim, sua carne é comercializada para o consumo humano (CLARKE, 1962; GRIMWOOD, 1969; MITCHELL, 1975; CLARKE *et al.*, 1978; BROWNELL & PRADERI, 1982, 1984; READ *et al.*, 1988;

VAN WAEREBEEK & REYES, 1990). No sul do Chile ocorre captura acidental nas redes de pesca artesanal e a gordura dos botos assim capturados são utilizadas como isca para a captura da *centolla*, *Lithodes antarcticus* (e.g., REEVES 2003). No Uruguai e Argentina, capturas acidentais ocorrem em redes de pesca, ainda que em menor freqüência (CASTELLO, 1974; GOODALL, 1978; BROWNELL & PRADERI, 1982).

O Boto-de-Burmeister está incluído na categoria "dados insuficientes" (*Data Deficient*) da Lista de Espécies Ameaçadas de Extinção da União Internacional para a Conservação da Natureza (IUCN) (REEVES *et al*., 2003), pois a informação disponível sobre a historia de vida, distribuição, movimentos, abundância e estrutura da população é ainda escassa (PRADERI, 1971, BROWNELL & PRADERI, 1982, 1984; PINEDO, 1989; CORCUERA *et al*., 1995; GOODALL *et al*., 1995a, b; REYES & VAN WAEREBEECK, 1995; VAN WAEREBEEK *et al*., 2002; REEVES *et al*., 2003).

Diferenças no tamanho corporal foram observadas entre botos da costa do Pacífico e do Atlântico. Comprimentos máximos de 182 – 183 cm foram registrados nos exemplares do Peru (REYES & VAN WAEREBEEK, 1995). Este comprimento foi similar ao registrado na costa chilena (n=28) (BRIEVA & OPORTO, 1990). Contudo, na costa atlântica se registraram exemplares com comprimentos máximos de 196 – 200 cm (BROWNELL & PRADERI, 1984; CORCUERA *et al*., 1995; GOODALL *et al*., 1995b).

A descrição do crânio de *P. spinipinnis* e análises da morfometria craniana são raras (BURMEISTER, 1865; ALLEN, 1925; NORRIS & MCFARLAND, 1958; NOBLE & FRASER, 1971; PRADERI, 1971; PILLERI & GIHR, 1972, 1974; BROWNELL & PRADERI, 1982, 1984; PINEDO, 1989; SIMÕES-LOPES & XIMENEZ, 1989; CORCUERA *et al*., 1995; REYES & VAN WAEREBEEK, 1995) e a maioria baseados em um único exemplar ou alguns indivíduos. O dimorfismo sexual já foi documentado em crânios de exemplares sexualmente adultos coletados no Peru (REYES & VAN WAEREBEECK, 1995).

BROWNELL & PRADERI (1982, 1984) e CORCUERA *et al.* (1995) baseados em diferenças no tamanho corporal sugeriram que *P. spinipinnis* apresentaria duas populações isoladas na América do Sul: uma no Oceano Pacífico e outra no Atlântico. CORCUERA *et al.* (1995) propõem que os exemplares do Uruguai e da Província de Buenos Aires pertenceriam à mesma população. Mas para esclarecer esta questão faz-se necessária a realização de estudos de variação geográfica (considerando a morfologia e a genética de exemplares coletados ao longo de toda sua distribuição). Recentes estudos apóiam a diferenciação genética entre *P. spinipinnis* do Peru e Chile-Argentina (ROSA *et al.*, 2005).

Mudanças no tamanho e estrutura etária de uma população são esperadas quando esta é submetida a capturas. Geralmente o tamanho corporal médio e idade reprodutiva diminuem (JENNINGS *et al.*, 2001). Por outro lado, fatores ambientais associados com a interrupção ou mudança nos hábitos alimentares também podem influir no crescimento do indivíduo (LOCKYER, 1990, 1995; MANZANILLA, 1987). LOCKYER (1990) sugere que a variação temporal observada na média da maturidade sexual e taxa de crescimento da baleia-fin, *Balaenoptera physalus* da Islândia, foi uma resposta denso-dependente a mudanças na abundância da presa. Tanto efeitos ambientais como antrópicos (captura direta ou acidental, poluição e tráfego marítimo em ambientes costeiros) podem causar relações denso-dependentes, que poderiam refletir no tamanho do indivíduo, maturidade sexual e tamanho populacional (FOWLER, 1987). PERRIN *et al.* (1976) encontrou diferenças em parâmetros de história de vida entre duas populações de *Stenella attenuatta* expostas a diferentes níveis de exploração.

Muitas espécies de pequenos cetáceos são ameaçadas devido aos altos níveis de mortalidade acidental e/ou direta, e à degradação do habitat. Contudo, nos últimos anos consideráveis esforços têm sido realizados para o estabelecimento de medidas de conservação e manejo dessas populações (REEVES *et al.*, 2003). A primeira etapa neste manejo é definir as populações envolvidas, e uma ferramenta para definir populações de mamíferos são as análises de variação geográfica baseadas em variáveis morfológicas e genéticas. Como uma conseqüência, a variação geográfica tem sido extensivamente estudada em animais (GOULD & JOHNSTON, 1972) e uma variedade de técnicas estatísticas têm sido desenvolvidas para clarificar esses padrões (THORPE 1976, 1980, 1983; NEFF & MARCUS, 1980). Esses estudos proporcionam a base para a descrição de unidades de estoques utilizadas para avaliar e manejar essas espécies (SCHNELL *et al.*, 1986).

Em mamíferos marinhos, o crânio tem sido muito utilizado em estudos da variação geográfica, através da morfometria tradicional (método linear) (PERRIN, 1975; SCHNELL *et al.*, 1986; PINEDO, 1991; AMANO & MIYAZAKI, 1992; PERRIN *et al.*, 1994; BARRETO, 2000; AMANO *et al.*, 2002; BEASLEY *et al.*, 2002; BRUNNER, 2002; BRUNNER *et al.*, 2002; HIGA *et al.*, 2002; JEFFERSON 2002; RAMOS *et al.*, 2002; OLIVEIRA *et al.*, 2005). Contudo, as estruturas morfológicas num organismo têm dois componentes (tamanho e forma) e a forma é mais informativa para definir entidades biológicas na natureza (PATTON & BRYLSKI, 1987; ATCHLEY *et al.,* 1992).

A morfometria geométrica é um novo método que começou a ser desenvolvido no início dos anos noventa, sendo chamada de “a revolução em morfometria” (ROHLF & MARCUS, 1993). A morfometria geométrica abrange uma série de técnicas que visam descrever e representar a geometria das formas estudadas. É capaz de descrever e localizar mais claramente as regiões de mudanças na forma, e de reconstruir graficamente estas mudanças. Esta descrição é feita através do estabelecimento de pontos anatômicos de referência em estruturas homólogas, os chamados marcos anatômicos. Este método tem maior robustez na análise e exclui os fatores de posição, orientação e tamanho na análise da forma

(ROHLF, 1990, 1993, 1996, 2001; BOOKSTEIN, 1991, 1996; ROHLF & MARCUS, 1993; SLICE, 1996; BOOKSTEIN, 1998; MONTEIRO & REIS, 1999; ZELDICH *et al.*, 2004). Em mamíferos marinhos, este método foi recentemente aplicado em crânios de pinípedes para estudos ontogenéticos (SANFELICE, 2003), dimorfismo sexual (OLIVEIRA *et al.*, 2005) e em variação geográfica (HIGA *et al.*, 2002; MONTEIRO-FILHO *et al.*, 2002; DREMER, 2005).

Estudos sobre o grau de variação morfológica, genética ou comportamental desenvolvidos em cetáceos possibilitam entender melhor os processos evolutivos a nível intra-específico, na medida em que permitem visualizar as variações que podem estar ocorrendo dentro de uma espécie. O conhecimento do grau de variação morfológica intra-específica (tanto no espaço como no tempo) pode fornecer informações sobre a estrutura das populações e seus padrões de movimentação (PINEDO, 1991). O estudo de variações morfológicas fornece informações de aspectos funcionais importantes para a ecologia de uma espécie, como o tamanho e a forma de certos órgãos têm efeitos sobre o grau de adaptação do organismo ao ambiente (WIIG, 1992). Portanto, esses estudos podem fornecer maiores informações sobre os padrões de movimento e estruturas de estoques, através da identificação de ecotipos (formas locais que devem seus atributos a efeitos seletivos de um determinado ambiente) e de variações sazonais na presença destes em um determinado local.

A grande variedade de condições oceanográficas existentes ao longo da distribuição de *P. spinipinnis*, somada à grande plasticidade exibida, leva a pensar que esta espécie apresentaria algum tipo de variação geográfica.

OBJETIVOS:

Geral:

Analisar a variação geográfica em crânios de *Phocoena spinipinnis* ao longo da costa Atlântica (Brasil, Argentina e Uruguai) e Pacífica (Peru e Chile) da América do Sul.

Específicos:

1) Caracterizar as condições oceanográficas associadas à distribuição de *P. spinipinnis* com base em dados históricos de temperatura, salinidade e oxigênio dissolvido ao longo das costas Pacífica e Atlântica (Capitulo 1);
2) Definir, identificar e caracterizar os grupos de camadas de crescimento (GLGs) nos dentes de *P. spinipinnis* e analisar possíveis variações das GLGs entre exemplares das diferentes localidades ao longo da costa Atlântica e do Pacífico (Capitulo 2);
3) Analisar o dimorfismo sexual e o padrão de crescimento em crânios de *P. spinipinnis* (Capitulo 3);
4) Verificar a existência de variação geográfica em relação ao tamanho e forma em crânios de *P. spinipinnis* (Capitulo 4).

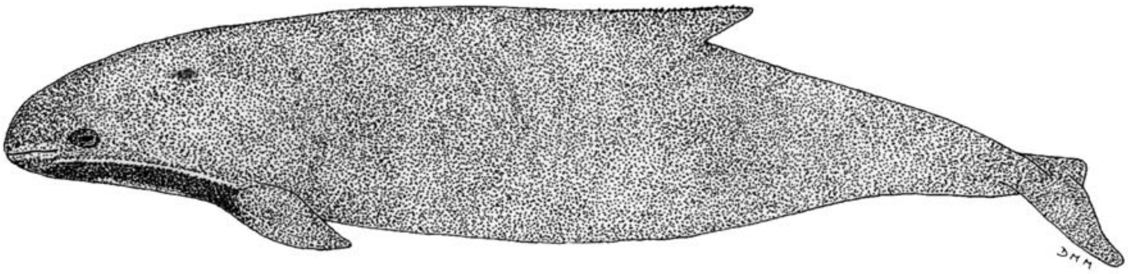

Figura 1. Boto-de-Burmeister*, Phocoena spinipinnis.*

CAPITULO 1

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 at 0 and 50m of depth) 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 local circulation system. 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 Currents, 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 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), 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 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-Lopes and Ximenez, 1989; Jefferson *et al*., 1993). However, it is unclear whether the 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.

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[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 5to Congreso de la Sociedad Latino Americana de Especialistas en Mamíferos Marinos, 11-17 Septiembre, Quito, Ecuador.

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 area 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 process, as 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, for 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 system (*e.g.,* currents, upwelling and donwelling process), because these characteristics are directly related with seasonal productivity, and with prey distribution and abundance.

Materials 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 60m (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 for carrying 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 responses 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. The average historical data between the coast and 20nm showed a 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 registered 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 freshwaters.

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 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 registered 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 of 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, which was associated with 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 a difference with the Pacific was that 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 coast. 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 above 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 toward north. In the Atlantic, from 50°S to the north, the isotherms presented a tendency to be parallel to the coast, and the 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 fresh water from fjords, glaciers, and rivers, mainly in the Atlantic, where there is a great contribution of fresh water from the basin of the La Plata River. In the case of the Pacific, the lower surface salinities were observed in the zone of channels and fjords, due to the contributions of freshwater from precipitation, draining, rivers, and glacier melting.

- *Dissolved oxygen*

The dissolved oxygen concentration in the Atlantic and Pacific increases from the north southward, both at the surface and at 50m (Figures 5a,d). However, there is a decrease in dissolved oxygen from the 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, 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 than the image obtained for the surface presented three 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 28ºS (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 fluctuations in the annual cycle. In the Atlantic, this group was associated with the Malvinas Current in the 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 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 Currents, and the freshwater contributions of the basin of La Plata River and the estuarine system of Patos Lagoon (Figure 8).

Discussion

The variability of average historical data of temperature, salinity, and dissolved oxygen analyzed in this study are 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 the large fisheries of anchovy and sardine (Alheit and Bernal, 1983; Mann and Lazier, 1991; Walsh, 1991). Burmeister's porpoise 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 principally 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 with time series data in northern of 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 present 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 this time. The excess of precipitation in the Southeast Pacific and continental runoff from southern Chile reduce 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 forcings 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 fresh water 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 fresh waters. In the Pacific there was a larger contribution of fresh water 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), 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), 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 (Guerrero *et al.*, 1997). The zone between 30ºS and 40ºS has a high variability in physical and chemical properties and represents an ecotone of high biological diversity. Peaks of phytoplankton biomass have been found associated with frontal structures (Gayoso and Podestá, 1996).

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-Lopes 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 850km to 1550km, 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 Florianopolis (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 may be 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 the 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 behaviour are necessary to improve current models of prey consumption. The results provide information of potential use in understanding the ecology of

Burmeister's porpoise, and hopefully will help managers address concerns about the potential impacts on this species due to anthropogenic activity. 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 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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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	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

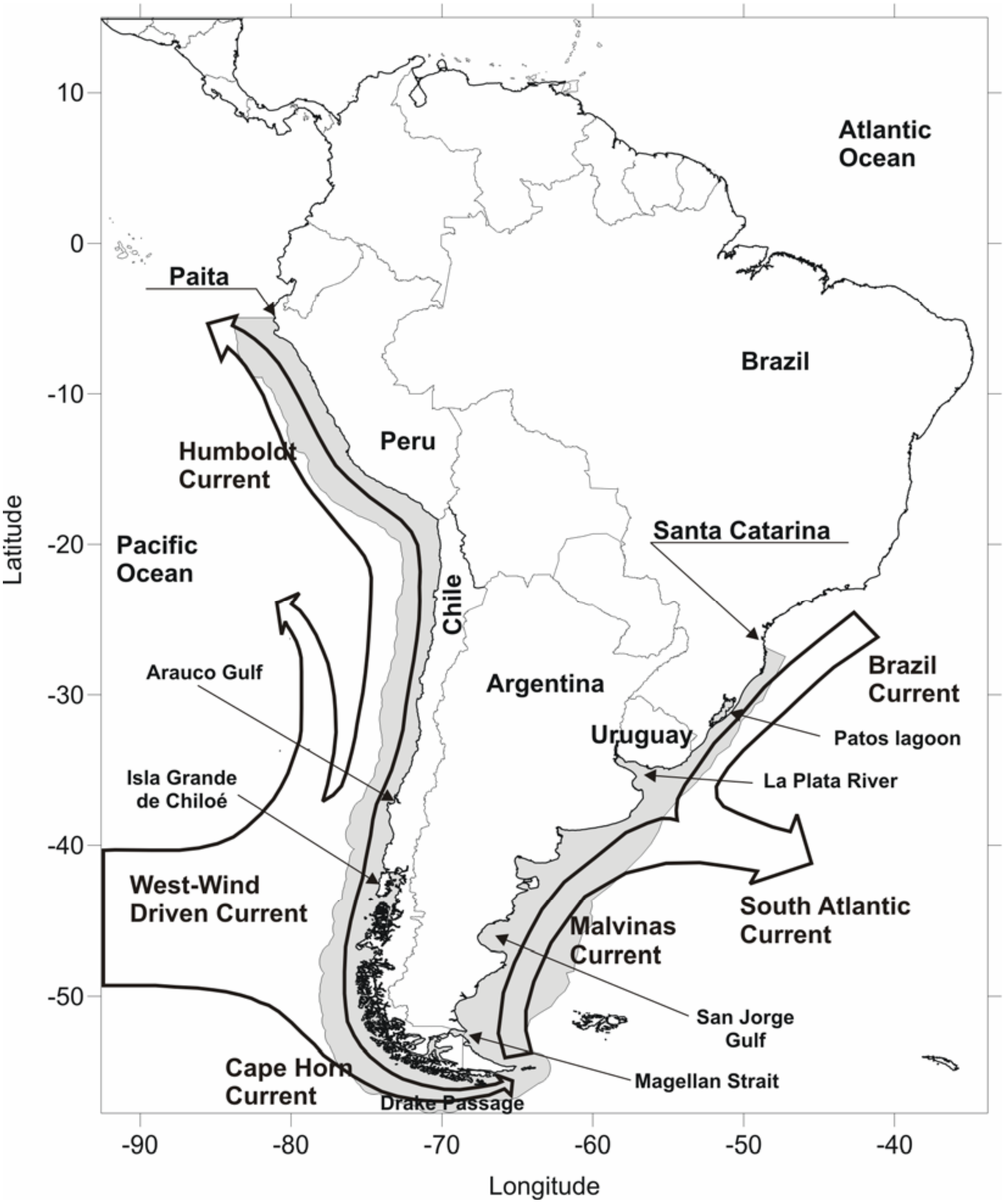

Figure 1. Study area from Paita, Peru (5° 01'S) in the Pacific to Santa Catarina, Brazil (28° 48'S) in the Atlantic off South America and schematic diagram of the main currents.

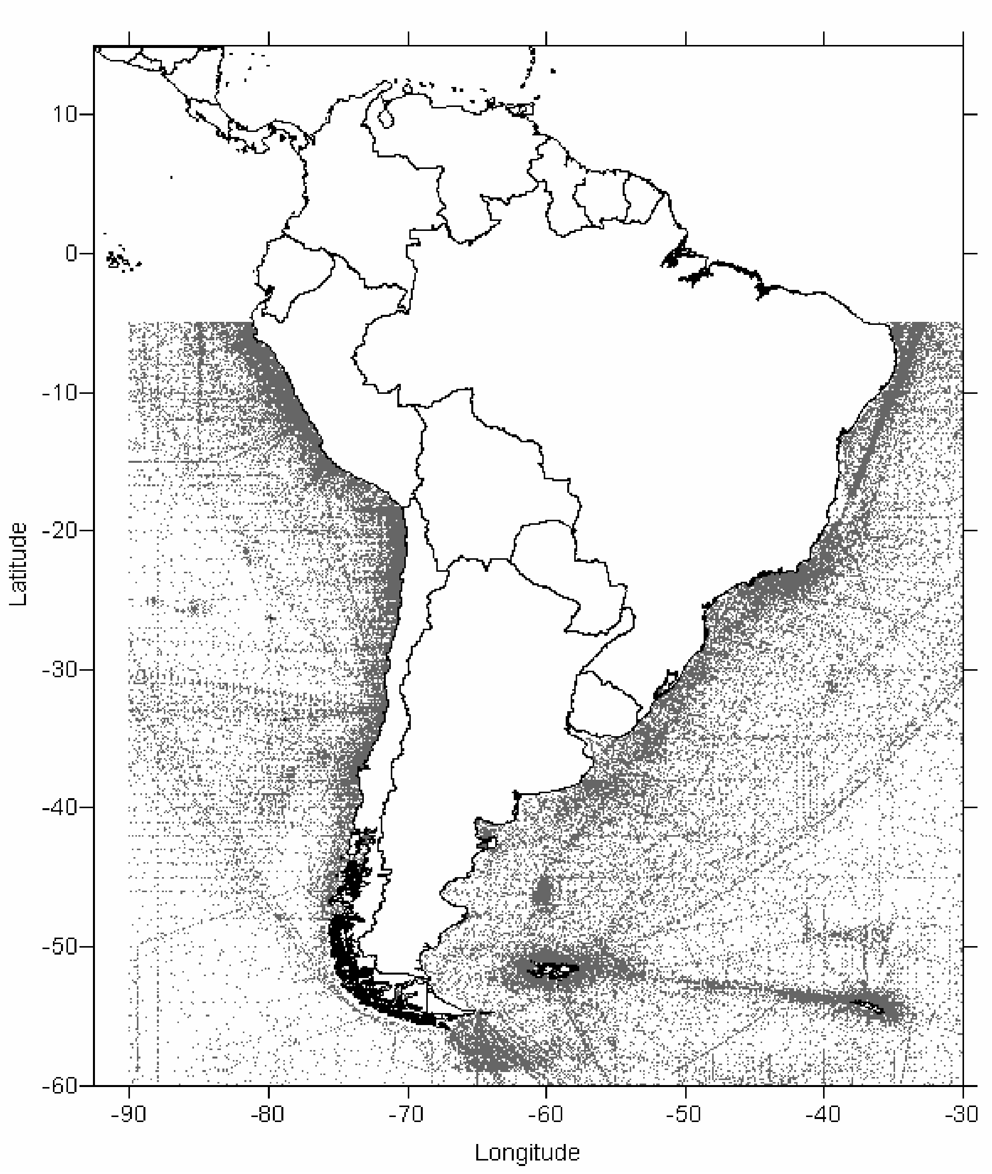

Figure 2. Oceanographic stations used by season from 1965 to 2000 for the Atlantic and Pacific Oceans.

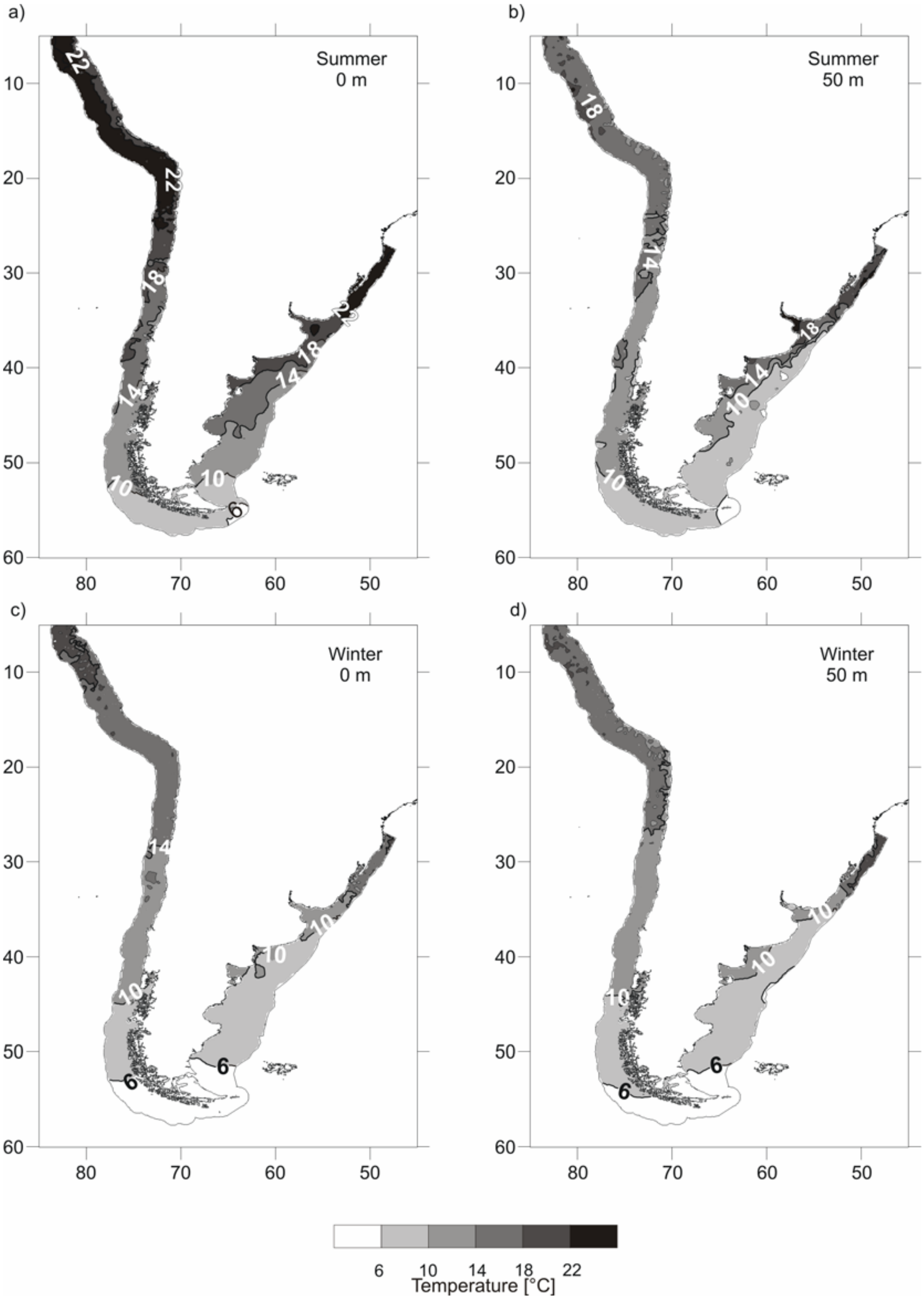

Figure 3. Historical average temperature: a) summer 0m, b) summer 50m, c) winter 0m and d) winter 50m.

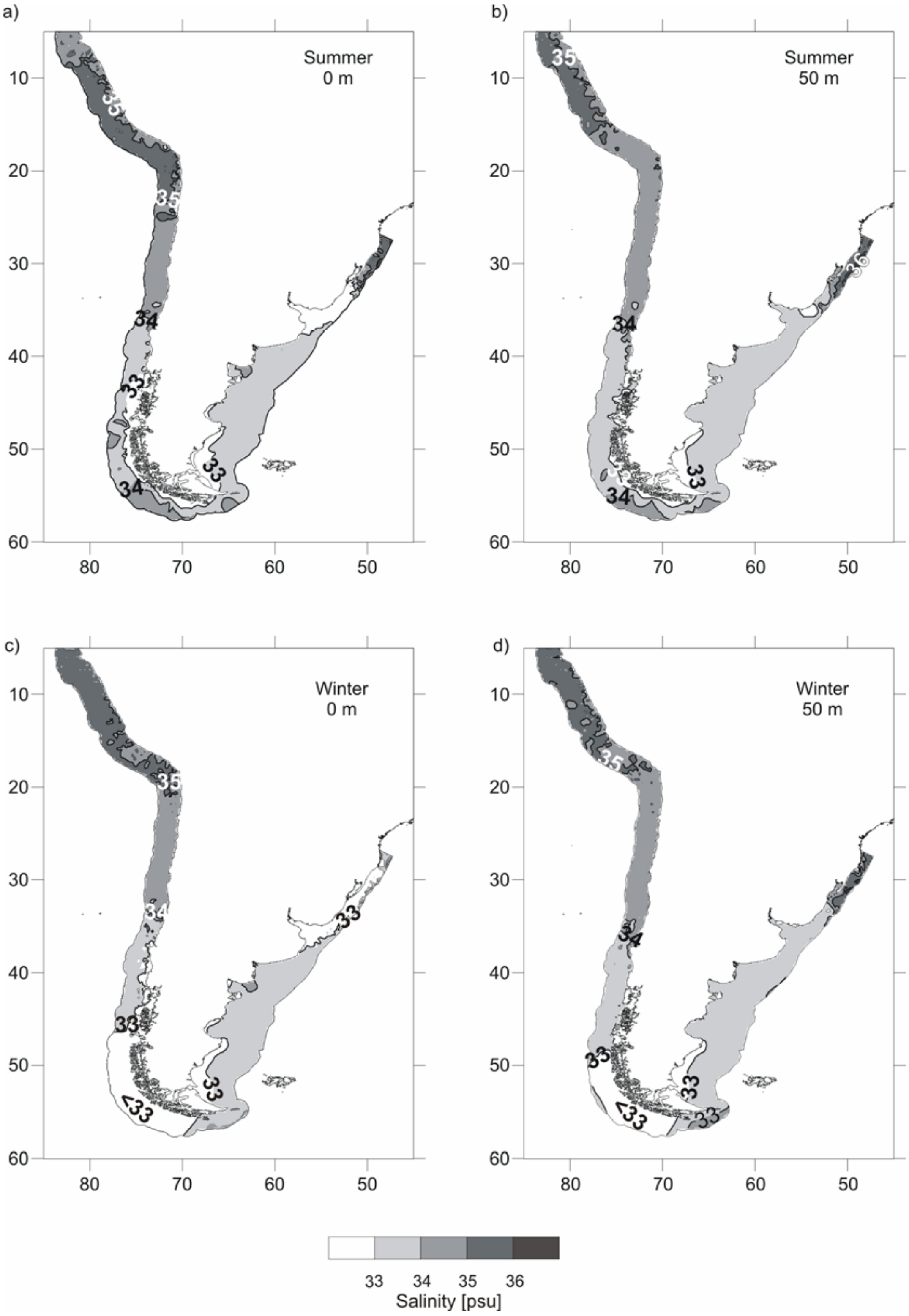

Figure 4. Historical average salinity: a) summer 0m, b) summer 50m, c) winter 0m and d) winter 50m.

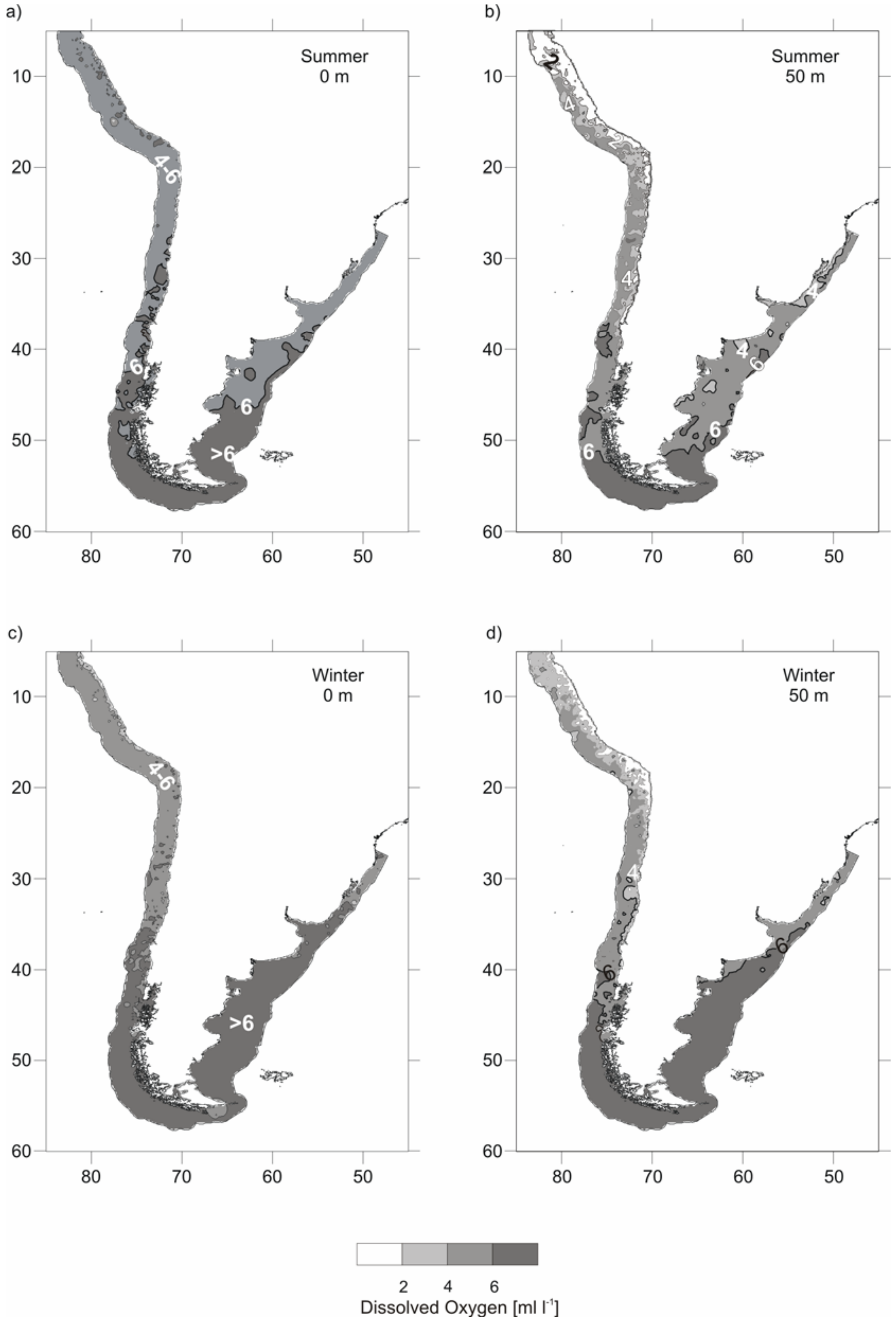

Figure 5. Historical average dissolved oxygen: a) summer 0m, b) summer 50m, c) winter 0m and d) winter 50m.

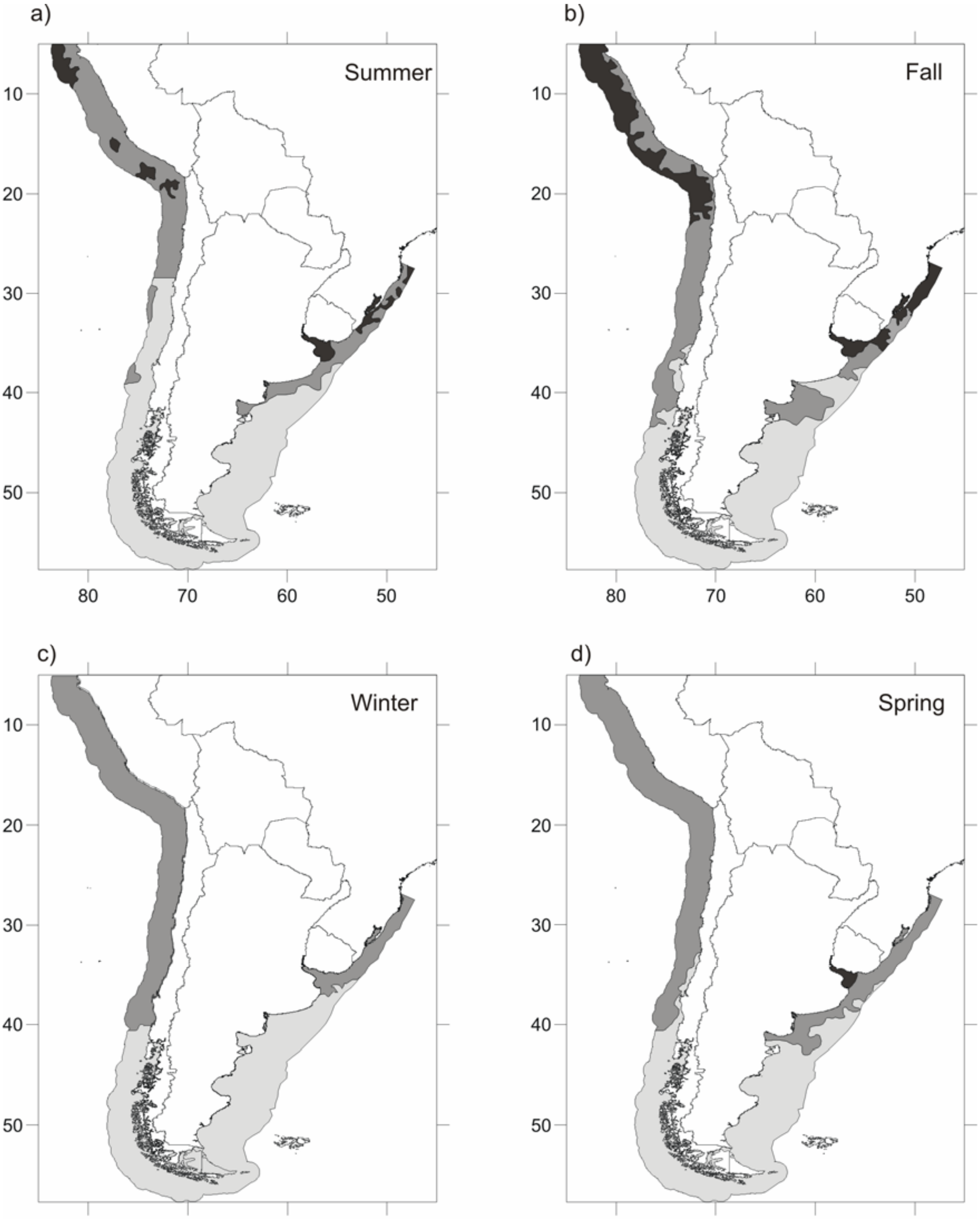

Figure 6. Groups generated for each season at the surface by self-classification methods.

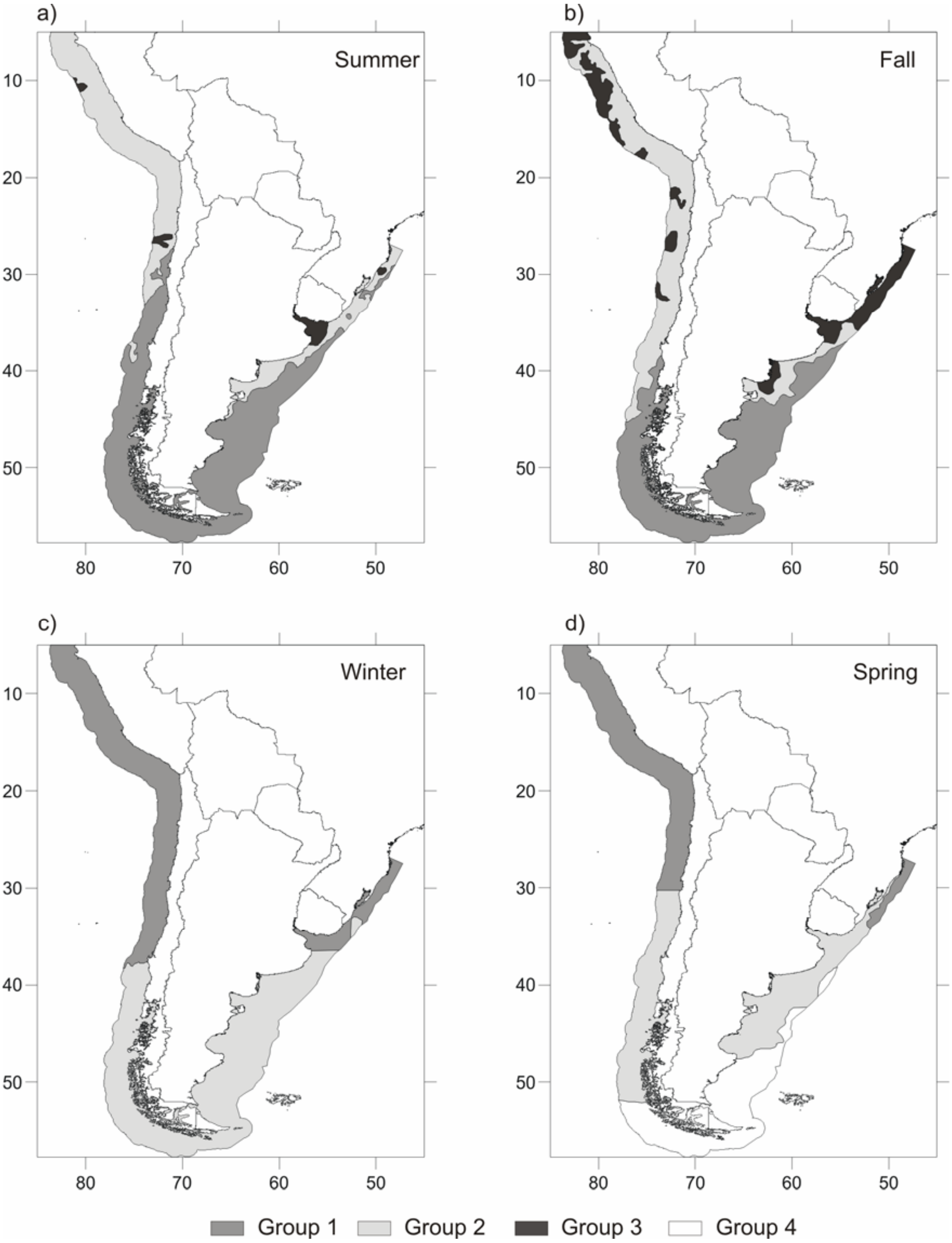

Figure 7. Groups generated for each season at 50m by self-classification methods.

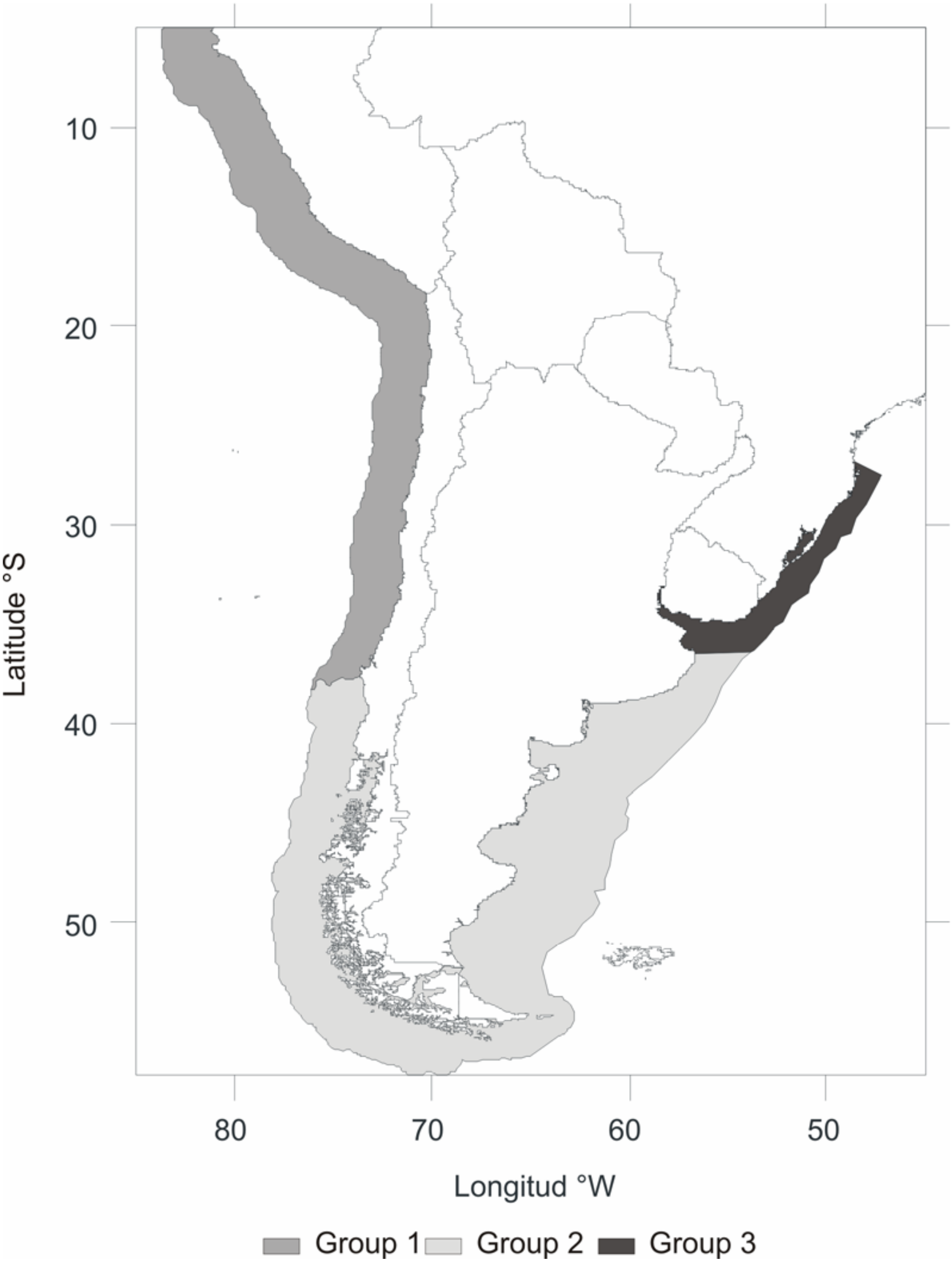

Figure 8. Proposed oceanographic zones associated with the distributions of *Phocoena spinipinnis*.

CAPITULO 2

GROWTH LAYER PATTERNS IN TEETH FROM THE BURMEISTER'S PORPOISE, *PHOCOENA SPINIPINNIS* FROM ATLANTIC AND PACIFIC COASTAL WATERS OF SOUTH AMERICA.

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ABSTRACT

A total of 89 teeth from *P. spinipinnis* from museums and scientific collections from Peru, Chile, Argentina, Uruguay and Brazil were analyzed. Thin 25 µm sections were used to describe Growth Layer Groups, accessory layers and tooth anomalies. The number of dentinal GLGs in the sample ranged from 0 to 10. In cementum, GLGs were absent in most of the individuals. Measurements in dentine showed sexual dimorphism in the first GLG (P = 0.0013, df = 40, t-value=3.4436). The first GLG showed significant difference by geographic area between Peru and the Atlantic specimens (P = 0.0069, df = 39, t-test = 2.8483), and the central accessory layer in the first GLG also presented a significant difference between Chile and the Atlantic specimens (P = 0.006, df = 8, t-test = 3.7026). Three types of anomalies (marker lines, cemental disturbance and dentinal resorption) were recorded in teeth of seven individuals from Peru collected between 1984 to 1998. The marker lines seem to be associated with environmental factors, because these marker lines are coincident with “El Niño” events.

Key words: *Phocoena spinipinnis*, Burmeister’s porpoise, GLGs, age estimation, growth layers, ENSO, marker lines, anomalies.

INTRODUCTION

Age determination in any animal population is fundamental for understanding the biology of individuals and population dynamics, and provides useful information for conservation and management procedures (*e.g*. Scheffer and Myrick 1980, Molina-Schiller and Pinedo 2004).

The use of teeth in age determination in cetaceans has been addressed generally (Perrin and Myrick, 1980). For porpoises, different techniques have been used for age determination, *e.g*., harbour porpoise, *Phocoena phocoena* (Nielsen 1972, Gaskin and Blair 1977, van Utrecht 1978, Stuart and Morejohn 1980, Noldus and de Klerk 1984, Manzanilla 1987, Watts and Gaskin 1989, Read 1990, Bjørge *et al*. 1995, Hohn and Lockyer 1995, Kvam 1995), Burmeister's porpoise, *Phocoena spinipinnis* (Manzanilla 1987; Crespo *et al*. 1994[1]; Corcuera *et al*. 1995), finless porpoise, *Neophocaena phocaenoides* (Shirakihara *et al*. 1993).

Potential information that might be inferred from teeth includes general health, maturity, sex, reproductive history and the occurrence of environmental events affecting general status (Lockyer 1995). Mineralization anomalies in teeth as a mean for identifying stress during the animal's lifetime, and the possibility of such interpretations from variations in zonation and GLGs patterns in teeth have been raised by several researchers, *e.g*., parturition lines (Klevezal' and Myrick 1984), suckling lines (Bengtson 1988) and hypocalcified lines associated with the El Niño phenomenon off Peru (Manzanilla 1989). The interpretation of mineralization anomalies may indicate genetic stock differences or different types and levels of environmental stress (Lockyer 1995, 1999).

Burmeister's porpoise is endemic to coastal waters of South America (Brownell and Praderi 1982; Reeves *et al*. 2003). Information about life history, abundance, distribution,

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[1] Crespo, E. A., A. C.Schiavini, M. G. Perez Macri, L. Reyes and S. Dans. 1994. Estudios sobre determinación de edad en mamíferos marinos del Atlántico Sudoccidental. Pages 31-55 *in* Anales IV Reunión de Trabajo de Especialistas en Mamíferos Acuáticos de América del Sur.

movements, population structure and trends is limited (Corcuera *et al.* 1995, Goodall *et al.* 1995a, Reyes and Van Waerebeeck 1995, Reeves *et al.* 2003). Furthermore, it is unclear whether the species is present continuously throughout its range (Goodall *et al.* 1995b, Corcuera *et al.* 1995, Reeves *et al.* 2003). It has been suggested that Pacific and Atlantic Burmeister's porpoise comprise two different stocks, a hypothesis which is consistent with size differences observed between individuals from Northern Argentina and Peru-Chile (Brownell and Praderi 1984, Corcuera *et al.* 1995). Recent studies include genetic differentiation among Burmeister's porpoises from Peru and Chile-Argentina (Rosa *et al.* 2005), geographic variation among skulls from Peru, Chile and Atlantic (Argentina, Brazil, and Uruguay) (Molina-Schiller 2006).

The goal of the present study was to define, identify, and characterize growth layer groups (GLGs) and to explore possible variations of GLGs patterns among Burmeister's porpoises from different localities along the Pacific (Peru and Chile) and Atlantic coast of South America.

MATERIALS AND METHODS

The sample

Teeth of 89 *P. spinipinnis* (27 females, 45 males, and 17 of unknown sex) were examined to characterize growth layers (Fig. 1, Table 1). The teeth were obtained from museums and scientific collections from the following locations and years: Peru, 52 porpoises (from 7 localities), were a mixture from incidentally, directly-caught or stranded at seven localities du ring the period 1984 to 2001, mainly from 1984-1987, and 1998-2001; Chile samples from 3 localities consisted of 22 incidentally caught or stranded porpoises during the years 1986 to 2004, including two additional individuals collected from central Chile in 1894 and 1967; Argentina samples included 12 individuals from 6 localities collected from incidental catch and stranding events during the period 1975 to 2002, with an additional specimen collected in 1903; Brazilian samples comprised two porpoises stranded at two localities on 1986 and 2000, respectively; a single stranded specimen from Uruguay was obtained in 2002 (Fig. 1, Table 1).

No *a prori* selection of specimens using sex or length class was made. The sexes were known (n = 36) or estimated (n = 37) by discriminant functions from skulls with know sex (Molina-Schiller 2006).

Tooth preparation and age determination

Most of the teeth were stored dry for more than 28 years, and exceptionally teeth of three individuals were stored dry for more than one hundred years. Due to these procedures, a large number of teeth became very dry, cracked and split.

For most individuals at least one tooth was available for preparation. The teeth were decalcified with RDO®, a fast commercial decalcifier, composed of a mixture of acids (see Myrick *et al.* 1983). Decalcification time ranged from 1 to 12 h, depending on the size or volume of the tooth (*i.e.*, teeth from smaller animals required less time using the RDO guide to decalcification). The sections were considered ready when flexible, bending in the center, and then were rinsed in running tap water for 24 h. From each tooth, longitudinal thin sections 25 µm thick were obtained using a freezing microtome, and the teeth were cutting according to the criterion used by Scheffer and Myrick (1980), Bjørge *et al.* (1995), Hohn and Lockyer (1995), and Kvam (1995). Then two or three on-center sections were stained free-floating in 100 ml Harris's haematoxylin for 5 min and rinsed in running tap water for 24 h to eliminate excess of stain (Molina and Oporto 1993). Tooth sections were immersed in 50 % and 100 % glycerine for 30 min, respectively, to dehydrate and were mounted on glass slides in pure glycerine (Myrick *et al.* 1983, Hohn *et al.* 1989).

The GLGs in the dentine and cementum were read using a compound microscope 10-50X under transmitted light. The interpretation of annual layer groups is based on Scheffer and Myrick (1980) and Nielsen (1972). This author observed in *P. phocoena* the equivalence of a GLG for every year of age, using tetracycline marking in one known-age individual. Considering that the GLG deposition patterns have not been established for *P. spinipinnis*t, in this study we also assumed that one GLG represent one year of growth.

Only on-center and “close-to-center” sections were used for GLG readings. “Close-to-center” sections were defined according to Pinedo and Hohn (2000) (*i.e.*, apex of GLGs round and with 60 % of the whole extension of the pulp cavity visible). The resolution of each GLG was evaluated according to the conspicuousness of boundary layers, consistency and continuity of layers along the whole length of the tooth section in the dentine and cementum (Hohn *et al*. 1989, Pinedo and Hohn 2000, Molina-Schiller and Pinedo 2004). Two GLGs readings were conducted by the first author with intervals of at least two weeks. When differences were found, a third reading was performed and selected, under the assumption that skill and accuracy increased with time.

In dentine, four measurements were taken perpendicularly to the bottom of the neonatal line using an ocular micrometer in a compound microscope (Carl Zeiss) with transmitted light at powers from 10 to 50X (see Fig. 2). The neonatal line was used as reference to measure the first GLG. The second and third GLGs were measured using the previous GLG as reference. In addition, the first accessory layer on the first GLG was measured (Fig. 2A). Cementum GLGs were counted, but not measured.

Statistical analyses

The thickness (relative widths) of the first three GLGs and accessory layer on the first GLG were analized by geographic area (Peru, Chile and Atlantic) and sex. Differences between means were analised by Student *t*-test for independent samples by groups, and two-way analysis of variance was applied to test interaction between sex and geographic area for each measurement (Zar 1999). All statistical analyses were performed using the software Statistics 6.0 for Windows. The teeth from specimens with unknown sex were not included in statistical analyses.

The three geographic area (Peru, Chile and Atlantic) defined in this study were based in studies of geographic variation of skulls of *P. spinipinnis* psysically mature (Molina-Schiller 2006). In that study, discriminat analyses and canonical analyses showed significant differences ($\alpha = 0.05$) between skull from Peru ($n = 60$), Chile ($n = 28$), and Atlantic (n=14). In addition, samples from Argentina ($n = 11$), Uruguay ($n = 2$) and Brazil ($n = 1$) were examined, and the two-way analysis of variance indicated no difference between localities at α=0.05. Therefore, the specimens from Argentina, Brazil and Uruguay were pooled in a single group named “Atlantic”.

Anomalies

Each tooth specimen was examined to register the anomaly type, number and position, sex and geographic area. Five major categories of mineralization anomaly were defined: pulp stones, marker lines, mineralization interference, dentinal resorption and cemental disturbance (Myrick 1988, Lockyer 1993, 1995, 1999). At least two teeth were examined when the anomaly was registered, to confirm that different teeth from the same individual presented similar growth anomalies and patterns.

RESULTS

Age frequency distribution

The Student t-test showed that the age frequency distribution by sex was not significant between geographic areas ($P > 0.05$). The maximum number of GLGs presented in the dentine was ten for both females and males from Peru. In the Atlantic sample the oldest female had 9 GLGs and the oldest male had 7 GLGs. In Chile the maximum number of GLGs in males was 7 and females 5 GLGs (Table 1). In all teeth examined the pulp cavity was not completely occluded. Due to this fact, all the age obtained here were based in dentinal GLGs.

Dentine

In dentine, the neonatal line was observed as a narrow translucent layer (about 15 μm) in all individuals. The conspicuousness of the neonatal line allowed its use as a point of reference in the measurement of the first GLGs (Fig. 2A).

The first GLG was formed by an opaque layer followed by a translucent (or unstainable) layer. The boundary of the first GLG was easy to identify due to the difference in intensity of the coloration between the first and second GLGs (Figs 2A, B, C).

The Student *t*-test showed sexual dimorphism in relative width of first GLG ($P = 0.0013$, df = 40, t-value = 3.4436), with males grater than females (Table 2). This value was larger in males from Chile (380 μm, $n = 3$), followed by those from Peru (371.30 μm, $n = 23$), and the Atlantic males (362.50 μm, $n = 2$). In females, the relative width of the first GLG was larger in a single female from Chile (350 μm, $n = 1$), followed by those from Peru (348.33 μm, $n = 6$), and the Atlantic (312.86 μm, $n = 7$) (Table 2). In addition, the relative width of first GLG showed significant difference by geographic area between Peru and the Atlantic specimens ($P = 0.0069$, df = 39, t-test = 2.8483) (Table 2).

About mid-way through the first GLG a distinct accessory layer was observed in some individuals (Figs 2A, B, C), however, accessory layer were more prevalent in teeth of males from Peru (*n* = 11), and absent in females from Peru (Table 2). The accessory layer of the first GLG can cause problems, as it can be erroneously considered as boundary between the first and second GLGs. One of the criteria used to distinguish accessory layers was to follow the line of the GLG until the bottom of the tooth. In most cases accessory layers finished before reaching half the length of the root. The mean distance between the central accessory layer on the first GLG and the neonatal line was larger in males than in females, and presented significative differences between Chile and the Atlantic porpoises (*P* = 0.006, df = 8, *t*-test = 3.7026) (Table 2).

In the second GLG the opaque and translucent layers were more defined, and the identification of the limit between the second and the third GLGs was usually detected by the intense coloration of the opaque layer (Figs 2A, B, C). The second GLGs was narrower than the first GLG, and although the relative width was larger in teeth of porpoises from Peru that those from Chile and the Atlantic, the differences were no significative (Table 2).

The third GLG was measured similarly to the previous GLGs (Figs 2A, B, C). In general, the males showed relative width larger than females and the third GLGs were larger in teeth from Peru, followed by individuals from the Atlantic and Chile (Table 2).

Cementum

In cementum, the GLGs were observed as a thin opaque layer followed by a thick translucent layer (Fig. 2A). However, the GLGs were visible in few individuals (n=8). In addition, the number of GLGs in cementum tended not to correspond in all cases with the number of GLGs in dentine (Figs 2, 3A, 3C).

Anomalies

Three types of anomalies (marker lines, cemental disturbance and dentinal resorption) were recorded in teeth of *P. spinipinnis* (Table 3). The incidence of anomalies was observed only in seven individuals (five males and two females) from Peru (n = 52) collected between 1984 and 1998 (for two individuals the date of collection was unknown) (Table 3). Anomalies were generally noticed in older specimens with more than 6 GLGs, and 22 (42.3 %) of Burmeister's porpoises from Peru were older than 6 yearsr of age (Table 1). All individuals analyzed were physically mature (Molina-Schiller 2006), except the female NN5 with 5.5 years of age. Data on sexual maturity are unknown, except for the sexually mature male JSM 227 (Manzanilla 1987).

Marker lines were recorded in six (11.5 %, n = 52) of the 52 animals from Peru, but were absent in samples from other areas (Table 3). This anomaly was observed as a narrow (about 15 µm) and waving translucent layer (hipocalcified line) in all individuals (Fig. 3). The number and position of marker lines were noted (Table 3). This anomaly was observed in four males with ages between 3.5 – 9 years of age, and two females of 5.5 and 7.5 years of age (Table 3, Figs 3A, B, C, D, 4A). The information on date of death, age at death and sequential ages where marker lines occurred permitted a calculation of the calendar year in which the anomaly appeared in the tooth (Table 3). In particular, a marker line appears in the same years (1982 to 1984) for several Burmeister's porpoise (Table 3). In addition, the male (JSM 227) presented two marker lines in the dentine (Table 3, Figs 3A, B). This hypocalcified marker line seems to be associated with environmental factors, because the dates of formation of these marker lines are coincident with "El Niño" Southern Oscillation (ENSO) events (Table 3).

Teeth from four (7.7 %, *n* = 52) Peruvian porpoises showed cemental disturbance (Table 3; Fig. 4B, C, D), while dentinal resorption was registered in a single male (1.9 %, *n* = 52) (Table 3, Fig. 4A).

DISCUSSION

The age frequency distribution showed that the porpoises forms Peru are older than specimens from Chile and Atlantic, whereas those females from Chile were younger than porpoises from Atlantic; however, these differences were not significative, possibly due to small size sample. In general, few young individuals (less than 2 years) were observed in the sample, perhaps this has relation with the different methods of collect of Burmeister´s porpoises (stranding; gillnet incidental or direct mortality).

The GLGs patterns observed for *P. spinipinnis* is similar to those previously described for other porpoises, *e.g.*, *Phocoena phocoena* (Nielsen 1972, Kvam 1995, Gaskin and Blair 1977, Scheffer and Myrick 1980, Bjørge *et al.* 1995), *Phocoena spinipinnis* (Manzanilla 1987, Corcuera *et al.* 1995). The first GLG appears to be the most complicated in terms of growth, frequently with a pronounced stained accessory layer at the mid-zone, which could be misinterpreted as the end of the first GLG. This accessory lamina has previously been observed in *Tursiops truncatus* (Hohn 1980), *Globicephala macrorhynchus* (Kasuya and Matsui 1984, Lockyer 1993), *Inia geoffrensis* (Silva 1995), *Cephalorhynchus eutropia* (Molina and Oporto 1993, Molina and Reyes 1996), *Pontoporia blainvillei* (Pinedo and Hohn 2000), and *Arctocephalus australis* (Molina-Schiller and Pinedo 2004).

The GLGs observed in cementum were few visible in most of the individuals. For this reason, it was not possible to correlate the number of layers in dentine with the number of layer in the cementum. This has also been observed in *P. phocoena* (Nielsen 1972, Kvam

1995), C. *eutropia* (Molina and Oporto 1993). On the other hand, is possible that the cemental thickness is correlated with the placement in the jaw and the related stresses.

The relative width of the first GLG was larger in males than in females from three geographic areas, evidencing sexual dimorphism in teeth of *P. spinipinnis*. Van Utrecht (1969) and Nielsen (1972) using other methods, also found sexual dimorphism on teeth of *P. phocoena*. These authors showed a corresponding difference for males and females in the distance between the cervical limit of the cementum and the point where the neonatal line ends against the cementum.

Geographic variation was observed in the relative width of first GLG between Peru and the Atlantic porpoises, and the mean distance between the central accessory layer on the first GLG and the neonatal line presented significative differences between Chile and the Atlantic porpoises. Although, the sample size of teeth of *P. spinipinnis* from Peru was larger than sample size from Chile and Atlantic, the relative width of the first GLG might be used as a guide to geographical variation between specimens from Peru and the Atlantic coast. Some evidences suggest that the characteristics of GLGs seem to differ in animals from various regions (Bjørge *et al.* 1995). These differences are probably related to environmental factors. Analyses of historical data (1965-2000) of temperature, salinity, and dissolved oxygen (0 and 50m depth) were analyzed to understand the seasonal variability of the oceanographic conditions associated with the distribution of *P. spinipinnis* from Paita (05°01'S, 81ºW)-Peru to Santa Catarina (28°48'S, 49°12'W)-Brazil (Molina-Schiller *et al.* 2005). These authors, proposed three oceanographic areas: (1) from Paita to south of Arauco Gulf-Chile, that has the influence of Humboldt Current, and an oxygen minimum zone (OMZ); (2) from south of Arauco Gulf to South of La Plata River, showing the influence of 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 which is characterized by the influence of Brazil Currents, and the freshwater contributions of the hydrographic basin of the La Plata River and the estuarine system of Patos Lagoon. On the other hand, the results obtained in this study are coincident with differences in morphometrics between skulls of mature physically *P. spinipinnis* from Peru and Chile (from San Antonio ~33º 30'S to south), and between skulls from Peru and the Atlantic coast (Argentina, Brazil and Uruguay) (Molina-Schiller 2006), and Rosa *et al.* (2005) has shown genetic differentiation among Burmeister's porpoises from Peru and Chile-Argentina.

Although measurements of GLGs obtained in this study were useful as guidelines for defining GLGs in dentine and to explore possible variations of GLGs among Burmeister's porpoises from different localities along the South America coast, they should be used with caution. The true definition and validation of GLGs can only be determined when the animals are time-marked with tetracycline or other periodic extractions). However, measurements and relative widths of GLGs are useful as guidelines, reducing the probability of interpreting accessory layers as limits of GLGs (Hohn *et al.* 1989, Pinedo and Hohn 2000). In addition, it is necessary to mention that the differences in relative width of the first GLG and central accessory lamina by geographic area and sex are an initial analysis. In addition, we have been particularly interested in knowing the growth layer patterns of teeth from the north-central Chilean coast, and evaluating possible differences with Burmeister's porpoise from Peru.

Three types of mineralization anomalies (marker lines, dentinal resorption and cemental disturbance) can be recognized in Burmeister's porpoise, but a low incidence of anomalies in teeth *P. spinipinnis* was evident. The anomalies were only registered in 13.5 % (n = 7) of all samples from Peru (n = 52). As might be expected, the incidence of anomalies tends to increase with age, but each type has a different level of incidence. In general, the anomaly type and patterns of incidence in the two sexes were similar for marker lines and cemental disturbance. This suggests that in general, susceptibility to the causative factors of these anomalies is not sex-specific. Dentinal resorption was only registered in a single individual. By contrast Myrick (1988) found that resorption was highest in female *Stenella longirostris*, and Lockyer (1993) observed that incidence of dentinal resorption and cemental disturbance appears to be greater in males of *G. macrorhynchus*.

The generally low incidence of anomalies suggests that occurrence may be both uncommon and spontaneous (Lockyer 1995). The types of anomaly may be inter-related, and affected to varying degrees by the same internal and/or external factors (Lockyer 1993).

The marker line identified in this study is a waving hypocalcified layer of 15 µm similar in thickness to the neonatal line. The appearance of marker lines might be associated with interruption or change in regular feeding habits, caused by environmental events, because the formation of these marker lines is coincident with "El Niño" events. The Humboldt Current System with its coastal upwelling ecosystem off Peru and Chile is recognized as a highly productive region, sustaining the large fisheries of anchovy and sardine (Alheit and Bernal 1993, Walsh 1991, Mann and Lazier 1991). Burmeister's porpoise in the upwelling system might be particularly vulnerable to local depletion as they inhabit a very rich, but unstable environment (*e.g.*, recurrent El Niño events), because El Niño is more intense along the Peruvian coast, than along the Chilean coast. This might explain the lack of marker lines in teeth of *P. spinipinnis* from central Chile and the Atlantic coast.

Manzanilla (1989) reported a correlation in timing of the appearance of hypocalcified dentinal layers in teeth of dusky dolphins, *Lagenorhynchus obscurus*, off Peru with the El Niño event of 1982-83. The anomalous layer, described as the "El Niño mark" (ENM) comprised of a pair of hypocalcified incremental layers about 75 µm wide within the 1983 GLG. The feature appeared predominantly, but not exclusively, in adult females. Manzanilla ascribed dietary deficiencies as the cause of the tooth anomalies. Teeth of other species did not display ENM's. Although the anomalous layer observed by Manzanilla (1987) showed characteristic similar to marker line observed in this study, differences in the thickness were evident. On the other hand, this author did not find anomalies in teeth of *P. spinipinnis*, whereas we found a marker line of 15 µm in the adult male specimen, JSM 227, analyzed by Manzanilla (1987). Probably these differences have relation with the accuracy of the technique used in this study, and consequently more conspicuousness of GLGs.

Other evidence of a connection between tooth anomalies and environmental factors is the study realized by Lockyer (1993) on marker lines in teeth of free-living *Globicephala melas* mass-stranded off Iceland and Faroes, and the independent correlation of appearance of such lines in particular years in animals separated both in time and geographic space in the northeast Atlantic. This may be indicative of an external environmental crisis, similar in impact to the El Niño event off Peru. If the anomalies in teeth (*e.g.* marker lines) can be associated with environmental events, it would be a powerful tool to analyze climate changes and to interpret life history events.

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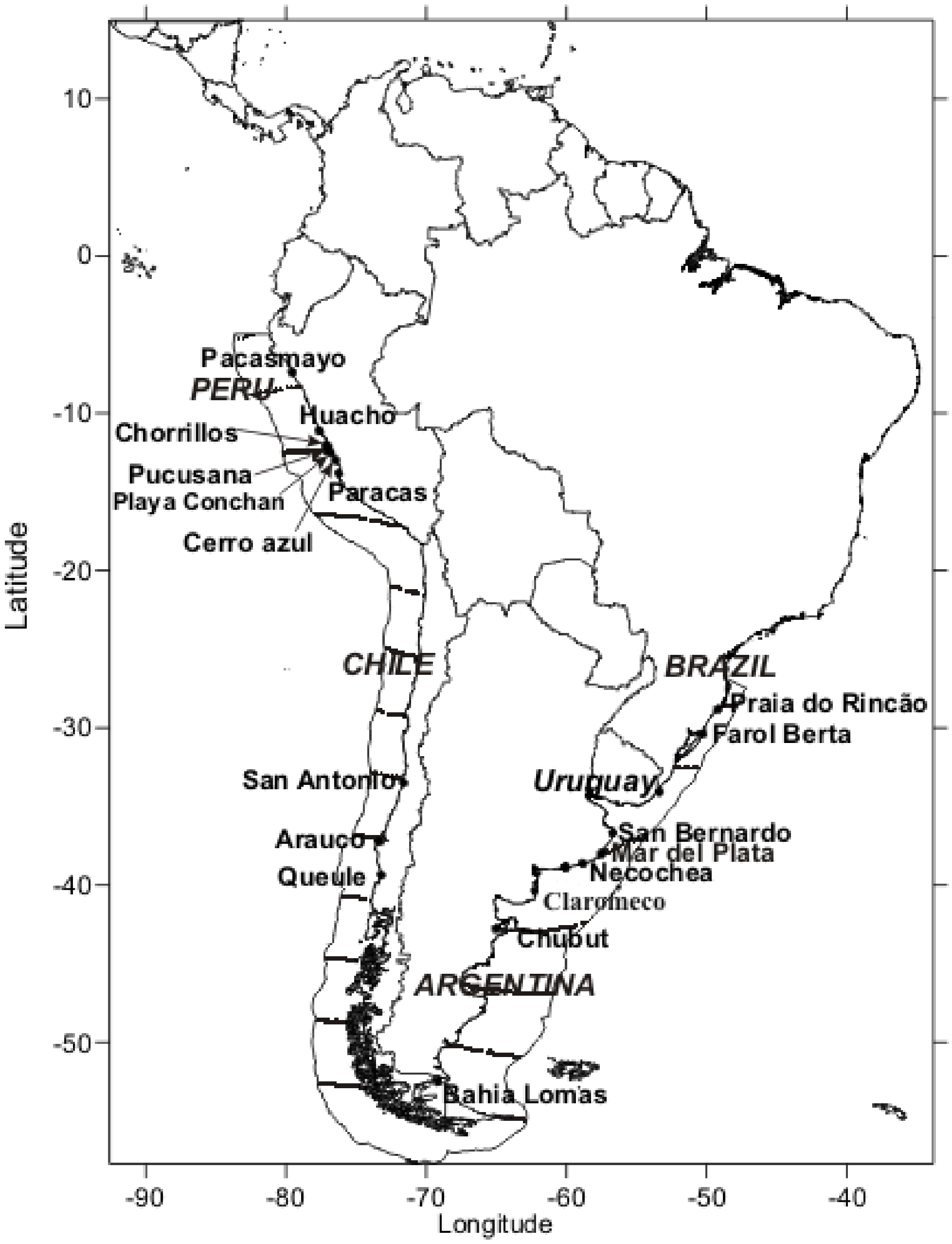

Figure 1. Geographical location of *Phocoena spinipinnis* sampling sites in South America coast (Peru, Chile, Argentina, Uruguay and Brazil).

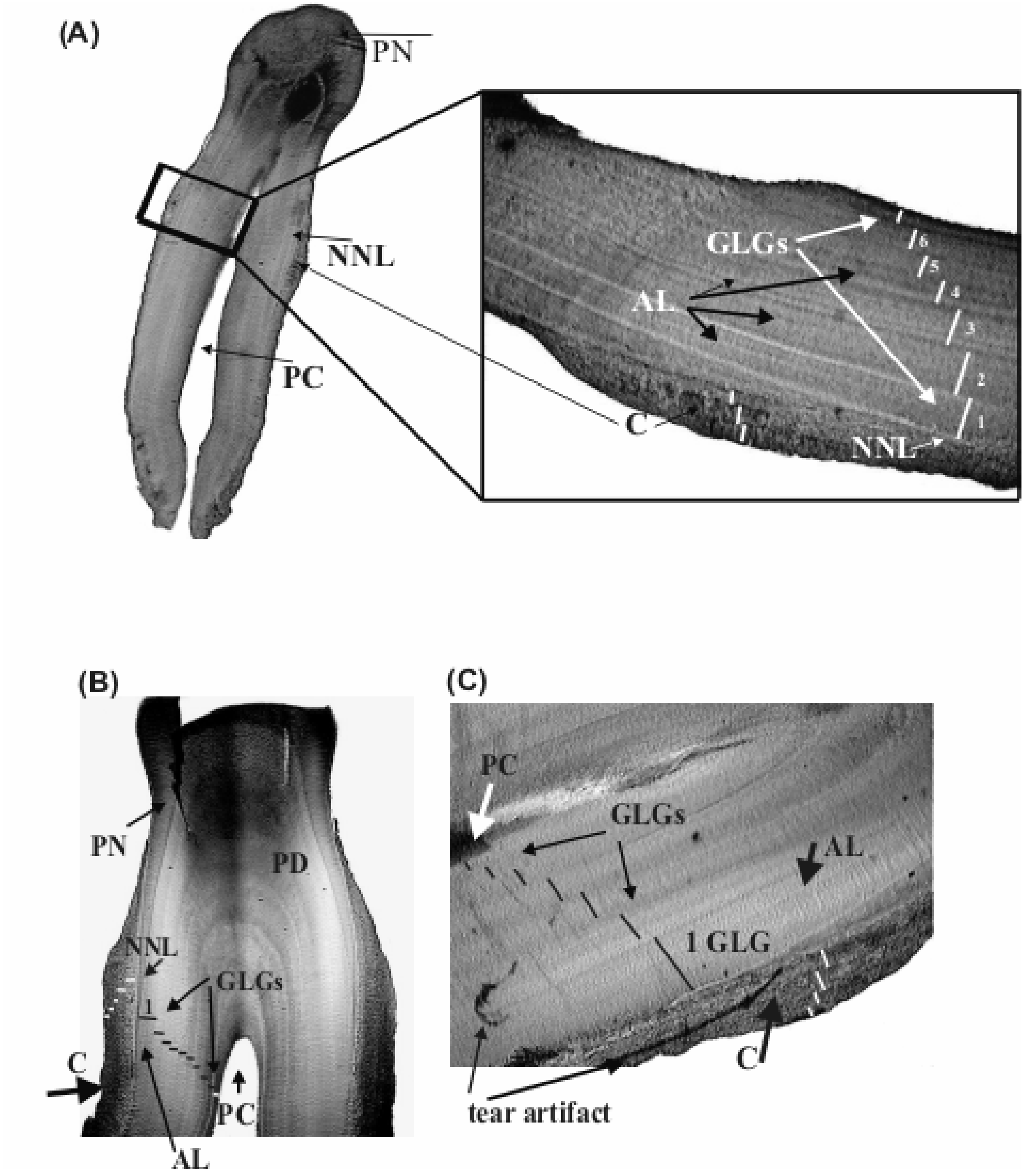

Figure 2. Longitudinal decalcified and stained thin sections of *Phocoena spinipinnis* tooth, showing the location of measurements of first third GLGs and accessories layers in dentine. (A) Male (ACO 10) with 6.5 GLGs (10X), (B) female (JCR 1628) with 10 GLGs (10X), and (C) female (CENPAT P2) with 7 GLGs (10X). AL = accessory layer, C = Cementum, GLGs = Growth Layer Groups, NNL = neonatal line, PC = pulp cavity, PD= postnatal dentine, PN = prenatal dentine.

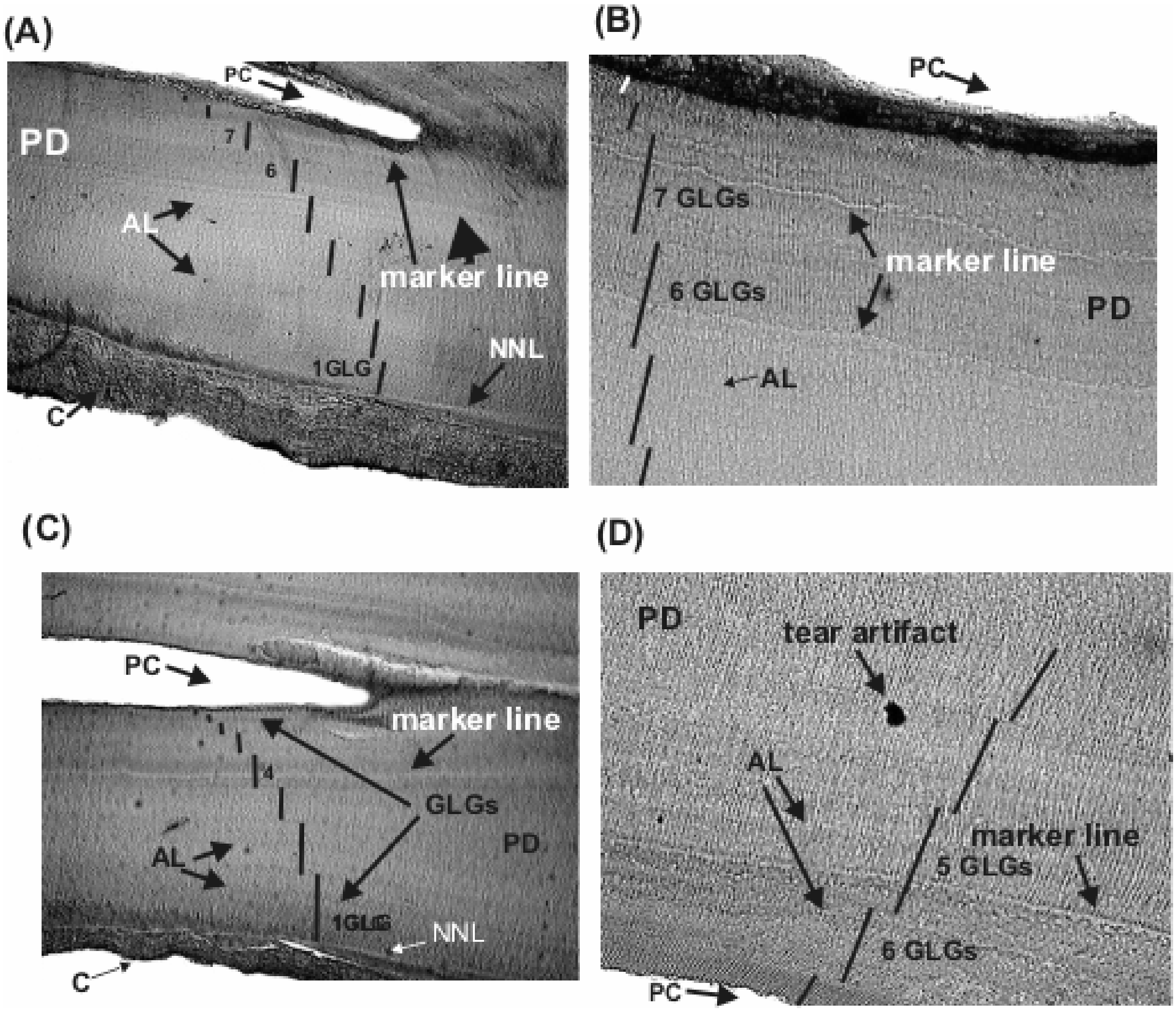

Figure 3. *P. spinipinnis* tooth section showing marker lines in dentine. (A) Male (JSM 227) with 9 GLGs (10X), (B) Zoom of position of marker line in dentine of male JSM 227 (10X) (C) Female (JCR 271) with 7.5 GLGs (10X), and (D) Male (JCR 76) with 6.5 GLGs (10X). AL = accessory layer, C = cementum, GLGs = Growth Layer Groups, NNL = neonatal line, PC = pulp cavity, PD= postnatal dentine, PN = prenatal dentine.

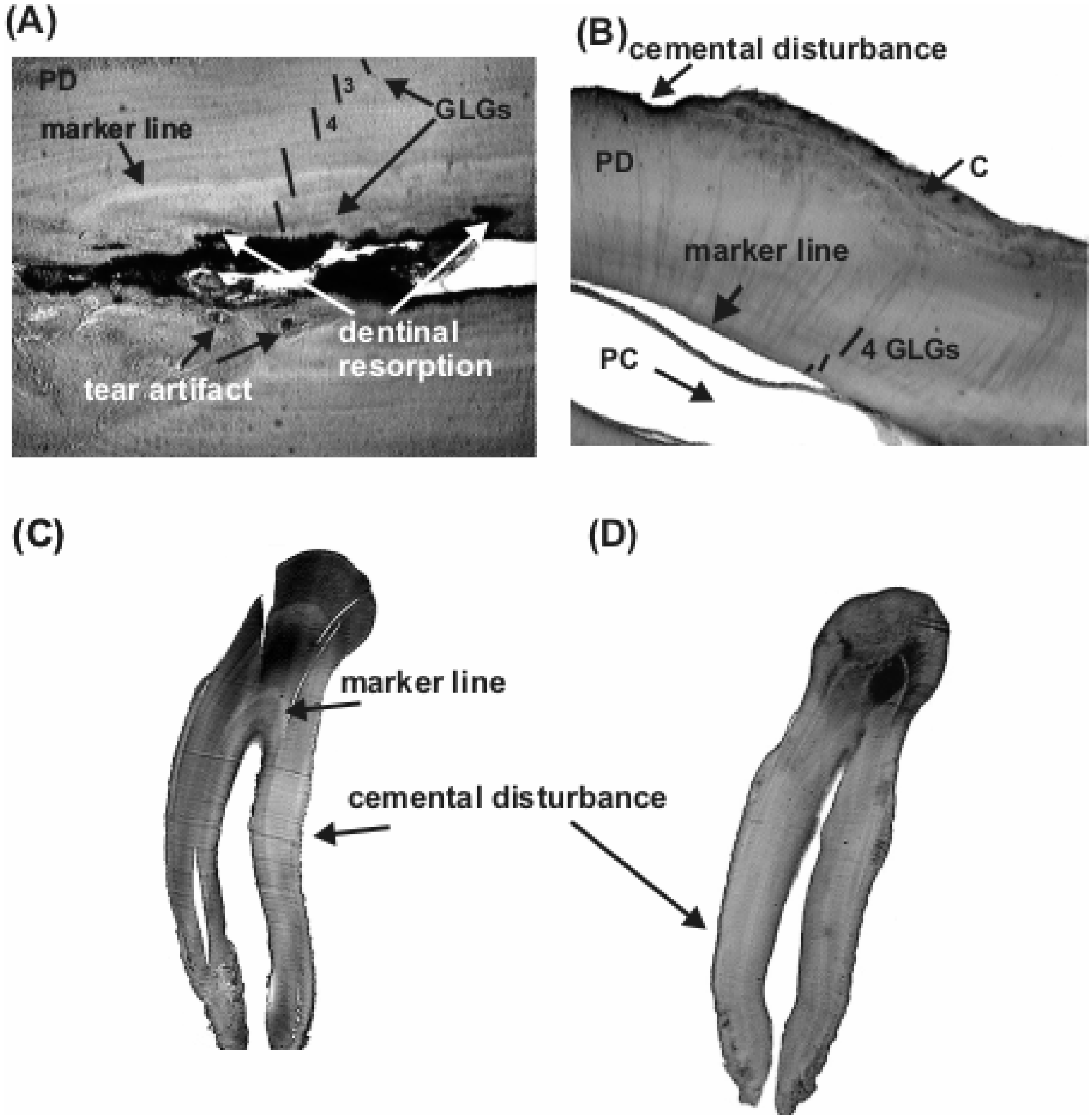

Figure 4. *P. spinipinnis* tooth section showing anomalies in dentine (marker line and dentinal resorption) and cementum (cemental disturbance). (A) Male (NN4) with 6 GLGs (10X) (B) female (NN5) with 5.5 GLGs (10X), (C) Male (JCR 125) with 3.5 GLGs (4X), and (D). Male (ACO 10) with 6.5 GLGs (4X). C = cementum, GLGs = Growth Layer Groups, PC = pulp cavity, PD= postnatal dentine, PN = prenatal dentine.

Table 1. Sample size of teeth used for GLGs analysis, by age (GLGs), sex and geographic area.

Geographic area	Peru		Chile			Atlantic				
Locality	Peru		Chile			Argentina			Uruguay	Brazil
Ages (GLGs)	Female	Male	Female	Male	Unknown Sex	Female	Male	Unknown sex	Male	Female
<1	---	---	---	2	5	---	---	---	---	---
1	---	4	---	1	9	---	1	---	---	---
2	2	6	1	---	---	1	---	---	---	---
3	2	5	---	1	---	---	---	2	---	---
4	1	3	---	---	---	---	---	---	---	1
5	1	6	1	---	---	1	---	---	---	---
6	5	4	---	---	---	1	1	---	---	---
7	2	2	---	2	---	2	---	1	1	1
8	---	---	---	---	---	1	---	---	---	---
9	2	5	---	---	---	1	---	---	---	---
10	1	1	---	---	---	---	---	---	---	--
Total by Locality	16	36	2	6	14	7	2	3	1	2
Total by Geographic area	52		22			15				

Table 2. Measurements (µm) of the first three GLGs and accessory layer on first GLG by sex and geographic area obtained in males and females dentine of *P. spinipinnis.* All measures were taken on “on-center” cuts.

	Dentine	Females						Males					
Geographic Área	Measurement	n	Mean	Min.	Max.	SD	CV (%)	n	Mean	Min.	Max.	SD	CV (%)
Peru	Accessory layer		-----	-----	-----	-----	-----	11	210.90	150	275	43.23	20.50
	1st GLG	6	348.33	315	375	19.15	5.50	23	371.30	325	450	32.73	8.81
	2nd GLG	6	267.50	210	300	32.98	12.33	18	265.00	200	310	38.08	14.37
	3rd GLG	5	175	150	200	25	14.29	11	185.91	150	250	26.91	14.47
Chile	Accessory layer	1	250	250	-----	-----	-----	2	237	225	250	17.68	7.44
	1st GLG	1	350	350	-----	-----	-----	3	380	340	425	42.72	11.24
	2nd GLG	1	200	200	-----	-----	-----	3	253.33	210	275	37.53	14.81
	3rd GLG	1	125	125	-----	-----	-----	2	127.50	127.50	150	31.82	24.96
Atlantic	Accessory layer	2	137.50	125	150	17.68	12.86	1	225	225	225	-----	-----
	1st GLG	7	312.86	225	375	55.44	17.73	2	362.50	350	375	17.68	4.88
	2nd GLG	6	249.17	200	300	42.48	17.05	2	250	250	250	0.00	0.00
	3rd GLG	6	169.17	100	225	44.77	26.46	2	150	110	190	56.57	37.72

Table 3. Incidence of mineralization anomalies in *P. spinipinnis* teeth from Peru.

Individual	Number of GLGs	Sex	Data collected	Physical Maturity*	Data estimated from birth	Number of anomalies	Data formation GLGs	Position of anomaly in dentine	Type of anomalies	Oceanographic Condition (ENSO)
JSM 227	9	Male	21-Mar-86	M	1977	2	1982-83	6th GLG	marker line	El Niño
							1983-84	7th GLG	marker line	Niño
JCR 76	6.5	Male	11-Nov-84	M	1978	2	1982-83	5th GLG	marker line	El Niño
									cemental disturbance	------
NN4	6	Male	Without data	M	-------	2	without data	5th GLG	marker line	------
								6th GLG	dentinal resorption	------
JCR 125	3.5	Male	27-Dec-84	M	1981	2	1983-84	3rd GLG	marker line	Niño
									cemental disturbance	
ACO 10	6.5	Male	10-Jan-98	M	1992	1	1992-93	1st GLG	cemental disturbance	------
JCR 271	7.5	Female	04-May-85		1978	1	1981-82	4th GLG	marker line	Normal-Niño
NN5	5.5	Female	Without data	I	-------	2	without data	4th GLG	marker line	------
									cemental disturbance	------

*Dates obtained from skulls of *P. spinipinnis* (Molina-Schiller 2006), M = physically mature, I = physically immature

CAPITULO 3

Growth and sexual dimorphism in skulls of Burmeister's porpoise (*Phocoena spinipinnis*)

Crecimiento y dimorfismo sexual en cráneos de marsopa espinosa (*Phocoena spinipinnis*)

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ABSTRACT

Skulls from 142 Burmeister's porpoises *Phocoena spinipinnis* (27 males, 18 females and 97 of unknown sex) deposited in museums, personal and scientific collections in Peru, Chile, Argentina, Uruguay and Brazil were analyzed. Twenty-eight cranial measurements were used to explore sexual dimorphism, and the growth pattern of *P. spinipinnis*. Discriminant functions were obtained for males and females for which sex was known. The growth layers groups (GLGs) in the dentine from teeth were counted. The oldest male and female were both 10 years of age. Growth parameter values obtained by Gompertz model fitted to condylobasal length–at-age of males and females *P. spinipinnis* showed a differentiated development between sexes. In females, only this character presented a high correlation with age ($r \geq 0.80$). The asymptotic growth at 95% was estimated for each variable. In males, differences were observed in the stabilization of the asymptotic growth of the variables selected with $r \geq 0.80$. Considering that the median age of all variables selected was 3 years, we suggest that males attain physical maturity about the 3 years of age. We considered appropriate the use of the asymptotic length attained at 95% of condylobasal length as a criteria of attainment of physical maturity in the skull of P. *spinipinnis*. Thus, the males attain physical maturity when the condylobasal length is ≥ 266mm, while that the females attain physical maturity when the condylobasal length is ≥ 277mm. Hotelling T^2 test and discriminant functions using metric characters showed sexual dimorphism both in physically mature and physically immature skulls. Discriminant functions were also obtained for all skulls according to the physical maturity. The sexual dimorphism observed in skulls of physically mature *P. spinipinnis* showed the females are larger than males.

Key words: *Phocoena spinipinnis*, Burmeister's porpoise, growth, age estimation, physical maturity, sexual dimorphism.

RESUMEN

Cráneos de 142 marsopas espinosas *Phocoena spinipinnis* (27 machos, 18 hembras y 97 de sexo desconocido) depositados en museos, colecciones personales y científicas de Perú, Chile, Argentina, Uruguay y Brasil fueron analizados. Veintiocho mediciones craneales fueron utilizadas para explorar el dimorfismo sexual y el patrón de crecimiento. Funciones discriminantes fueron obtenidas para machos y hembras de sexo conocido. Fueron contados los Grupos de Capas de Crecimiento (GLGs) en la dentina de los dientes. La edad máxima registrada para ambos sexos fue de 10 años. Los parámetros de crecimiento obtenidos por el modelo de Gompertz en la longitud condylobasal de machos y hembras de *P. spinipinnis* mostraron un desarrollo diferenciado entre sexos. En las hembras, sólo esta variable presentó una alta correlación con la edad ($r \geq 0.80$). Para cada variable se estimó el crecimiento asintótico al 95%. En machos, se observaron diferencias en la estabilización del crecimiento asintótico de las variables seleccionadas con $r \geq 0.80$. Considerando que la mediana de la edad de todas las variables seleccionadas fue de 3 años, se sugiere que los machos alcanzarían la madurez física alrededor de los 3 años de edad. Se considera además que el uso de la longitud condylobasal al 95% como criterio de madurez física en el cráneo de *P. spinipinnis* es apropiado. De esta forma, los machos alcanzarían la madurez física cuando la longitud condylobasal es ≥266mm, mientras que las hembras alcanzarían la madurez física cuando la longitud condylobasal es ≥277mm. Utilizando caracteres métricos, el test Hotelling T^2 y funciones discriminantes mostraron dimorfismo sexual en cráneos físicamente adultos y físicamente jóvenes. Funciones discriminantes también fueron obtenidas para todos los cráneos según la madurez física. El dimorfismo sexual observado en cráneos de adultos mostró que las hembras de *P. spinipinnis* son de mayor tamaño que los machos.

Palabras clave: *Phocoena spinipinnis*, marsopa espinosa, crecimiento, estimación de edad, madurez física, dimorfismo sexual.

INTRODUCTION

Life-history studies include growth in size and the schedules of transitions between developmental stages as important elements of the relationships between organisms and their environment (Roff 1992, Stearns 1992, Klingenberg 1996). The study of somatic growth is also very important in order to understand the biology of a species, as well as being a tool for stock identification (Barreto & Rosas 2006). The use of growth models allows its parameterization, and is a useful tool for the comparison of data on growth (Gulland 1976).

The quantitative description of growth curves for morphometric characters gives a basis for assessing the ontogenetic patterns underlying differences in morphological structure (Creighton & Strauss 1986). Several growth models have been used in marine mammals studies. The Gompertz model has been used to describe growth in belugas, *Delphinapterus leucas* (Stewart 1994); harp seals, *Phoca groenlandica* (Innes et al. 1981), and some Pinnipeds species (McLaren 1993), and franciscana, *Pontoporia blainvillei* (Ramos et al. 2002). The von Bertalanffy growth model has been widely used to describe asymptotic growth in fishes (Misra 1986), as well as to a variety of long-live mammals such as polar bears, Ursus *maritimus*, harbour porpoise, *Phocoena phocoena,* harp seal, *Phoca groenlandica,* South American sea lion, *Otaria flavescens*, South American fur seal, *Arctocephalus australis*, walrus, *Odobenus rosmarus rosmarus,* and bottlenose dolphin, *Tursiops truncatus* (Kinsgsley 1979, Stuart & Morejohn 1980, Innes et al. 1981, Rosas 1989, Molina-Schiller and Pinedo 2004, Knutsen and Born 1991, Barreto 2000). Richards growth model has been used in *Odobenus rosmarus rosmarus* (Garlich-Miller & Stewart 1998). In taxonomical and stock identification studies, it is recommended that comparisons among different geographic populations be preceded by identification of the individual variation in adults that occur within populations (Perrin 1984, Schnell et al. 1985). However, before identifying variation at the population levels, studies of the ontogenetic variation and age estimation are required to select the physically mature individuals to avoid selecting traits related with development, *i.e*., those expressed by physically immature individuals (Pinedo 1991, Klingenberg 1996, Calzada et al. 1997, Brunner 2000, Molina-Schiller & Pinedo 2004, Sanfelice 2003).

Burmeister's porpoise, *Phocoena spinipinnis* is an endemic species of South America (Brownell & Praderi 1982; Reeves et al. 2003). Information about life history, distribution, movements, and population structure is limited (Corcuera et al. 1995, Goodall et al. 1995a, Reyes & Van Waerebeeck 1995, Reeves et al. 2003). Differences in size were observed between Burmeister's porpoises from northern Argentina and Peru-Chile, and it was suggested that Pacific and Atlantic Burmeister's porpoises comprise two different stocks (Brownell & Praderi 1984, Corcuera et al. 1995). Recently Rosa et al. (2005) observed genetic differentiation among Burmeister's porpoises from Peru and Chile-Argentina.

Although skull description and some cranial morphometrics of Burmeister's porpoises have been published (*e.g*., Burmeister, 1865; Allen, 1925; Noble and Fraser, 1971; Praderi, 1971; Pilleri and Gihr, 1972, 1974; Brownell and Praderi, 1982, 1984; Pinedo, 1989; Simões-Lopes and Ximénez, 1989; Reyes and Van Waerebeek, 1995) most reports were based on either a single or a few specimens. The majority of Burmeister´s porpoise specimens deposited in scientific collections is of individuals of unknown sex, which preclude their use in several osteological studies. Considered this situation, the goal of this study was to use skull characters of Burmeister's porpoise to explore the species sexual dimorphism and growth pattern.

MATERIALS AND METHODS

Study area and specimens examined

Skulls from 142 Burmeister’s porpoises (27 males, 18 females and 97 specimens of unknown sex) kept in several museums, scientific and personal collections were included in the study. The database comprised Peru samples (20 males, 11 females and 53 specimens of unknown sex) obtained from 7 localities, including incidentally, directly-caught or stranded animals collected over a wide period from 1984 to 2001, mainly from 1984-1987; Chile samples (4 males, 3 females, and 31 specimens of unknown sex) obtained from 5 localities, which consisted of 22 specimens taken from a mixture of stranding and incidental catches, during the period 1986 to 2004, with two individuals collected from central Chile in 1894 and 1967; Argentina samples (3 males, 3 females, and 10 specimens of unknown sex) obtained from 6 localities from incidental catch and stranding, during the period 1975 to 2002; Uruguay samples (2 specimens of unknown sex) from 2 localities were obtained by strandings in 2002 and another with unknown date; and Brazil samples (1 female, and a specimen of unknown sex) from 2 localities were collected from stranded animals in 1986 and 2000 (Figure 1, Appendix I).

Analysis of metric characters

Thirty-seven cranial measurements from 142 skulls of Burmeister´s porpoises were taken with a 300mm digital caliper. However, only twenty-eight measurements (Figure 2) were utilized in the analysis due to missing or broken bones in some skulls. Sample sizes, therefore, varied for each recorded measurement. Twenty-one measurements were based on those taken for *P. spini*pinnis (Brownell and Praderi, 1982; Brownell and Praderi, 1984; Pinedo, 1989; Simões-Lopes and Ximénez, 1989; Reyes and Van Waerebeek, 1995), *P. phocoena* (Stuart and

Morejohn, 1980; Noldus and de Klerk, 1984; Yurick and Gaskin, 1987), Dall's porpoise, *Phocoenoides dalli* (Amano and Miyazaki, 1992), spectacled porpoise, *Phocoena dioptrica* (Perrin et al., 2000), *Neophocaena phocaenoides* (Amano et al., 1992; Jefferson, 2002). Seven new measurements were added: Height of rostrum at midlength; width of premaxillae at base of nares; greatest width of frontal; least distance between occipital condyles; width of palate at midlength of rostrum; greatest width of pterygoid and distance from maxilar to occipital crest (Figure 2). All measurements were taken by DMS, thereby eliminating the potential problem of inter-observer bias. The number of teeth and/or presence of alveoli in each mandibular and maxillary branch were counted. However, in several samples from Argentina (n=4), Chile (n=34), and Peru (n=28), the mandibles were missing, therefore, seven measurements (length of lower tooth row; length of mandibular symphysis; height of mandible; mandible length; mandible width; number of lower right teeth; number of lower left teeth) were not included in the analysis.

Sex determination using only specimens of known sex

Twenty-eigth characters were examined to explore the sexual dimorphism on skulls of 45 *P. spinipinnis* of known sex (27 males and 18 females) using General Linear Models (GLM) and stepwise discriminant analysis (Zar 1999, Hair 1984). Considering that few specimens of known sex were available, two new variables, longitude and latitude of sampling site were included in the analysis for obtaining a discriminant function for male and female independent of geographic area.The discriminant functions obtained using squared Mahalanobis distances from group centroids were applied to the individuals of unknown sex. A discriminant score function was performed to ascertain sex. All statistical analyses were performed using Statistic Program 6.0 for Windows.

Growth and age estimation

The Gompertz equation was used to describe cranial development for each linear variable according to sex and to determine which variable better correlated with age (McLaren 1993). In addition, the results obtained with the Gompertz growth model were compared with von Bertalanffy growth model (1957) and Richards growth model (1959). The Gompertz equation is expressed by: $S_t = A_\infty \times e^{-e^{-k(t-t_0)}}$, were: S_t is the value of the measure at age t; A_∞ is the asymptotic length (*e.g.*, the average length the species reaches if it grows indefinitely); t is a unit of time in years (estimated from growth layer groups present in each tooth); k is the growth-rate constant, t_0 is the hypothetical age at which the species have length equal zero;), and e is the natural logarithm base. The adjustment of the growth models to the data was done minimizing the sum of squared residuals using the interaction quasi-Newton method (non-linear module) of the Statistics Program 6.0. for Windows. Growth curves were calculated for males and females without considering their geographical origin, because the number of skulls with teeth was limited, especially for females (e.g., Peru, males=36, females=16; Chile, males=6, females=2; Argentina, males=2, females=7; Uruguay, male=1; and Brazil, females=2).

Ages were estimated from counts of the growth layer groups (GLGs) in the dentine using decalcified and stained thin sections. Teeth were decalcified with RDO® (a rapid commercial bone decalcifier), and cut longitudinally using a freezing microtome. On-center sections 25 µm thick were stained in Harris' hematoxylin and examined under transmitted light according to Myrick et al. (1983), Molina & Oporto (1993), Molina-Schiller (2006).

The age at attainment of physical maturity (t) in the skull was obtained when the asymptotic length attain 95% of the growth curve for each variable. Only variables with a high correlation (r≥0.80) in the growth curve were selected for growth analysis. When (t) were different, median was obtained (age of all variables selected) and considered as the age at attainment of physical maturity.

Sexual dimorphism according to the physical development of the skull

All skulls (n=142) of Burmeister's porpoises were separate according to the physical development of the skull. Differences between males and females physically mature and physically immature were examined by Hotelling T^2 multivariate test, and stepwise discriminant analysis (Hair 1984). A discriminant score function was performed to ascertain sex of *P. spinipinnis* physically mature and physically immature. All statistical analyses were performed using Statistic Program 6.0 for Windows.

RESULTS

Sex determination using only specimens of known sex

Descriptive statistics for cranial measurements of *P. spinipinnis* of known sex from Peru, Chile, and Atlantic are showed in Tables 1, 2, 3.

All the skulls with known sex were classified correctly using the squared Mahalanobis distances from group centroids. The discriminant analysis classified fourteen variables as dimorphic: length of orbit-LO; greatest width of premaxilla-GWP; height of rostrum at midlength-HR; longitude-sampling site; distance from maxilar to occipital crest-DMO; width of rostrum at base-WR; greatest width of temporal fossa-GWT; distance from tip of rostrum to anterior nares-DRN; condylobasal length-CBL; latitude-sampling site; greatest postorbital width-GPOW; greatest width of pterygoid-GWP; length of pterygoid-LP, and greatest preorbital width-GPRW (Wilks' Lambda=0.21253; F(14,21)=5.5578, P=0.0002) (Table 4). The discriminant functions (n=37) were 100% successful in the classification of sex. In order to determine sex, the measurements were replaced in both functions, and the sex attributed corresponded to the one with the highest value in the discriminant function.

Discriminant functions obtained were applied in 97 individuals of unknown sex (Figure 3a), and the skulls were classified as follows: Peru (38 males, 15 females), Chile (15 males, 16 females), Atlantic (Argentina, 4 males and 6 females), Uruguay (2 males), and Brazil (1 females). All the skulls were classified correctly using the posteriori classification. The sex composition of the whole sample is shown in Figure 3b.

Growth

The ages of the examined skulls varied from 0 to 10 years in males and of 2 to 10 years in females (Fig. 4). The parameters of fitted Gompertz curves presented better correlation between the metric variables-at-age for males and females of *P. spinipinnis*, because Richards and von Bertalanffy growth models did not converge.

The correlation coefficient (r) obtained through the Gompertz model revealed that in males ten characters (35.71%) presented a larger correlation with the age ($r \geq 0.80$). The variables expressing higher correlation with age in males were condylobasal length ($r=0.93$), followed by distance from tip of rostrum to external nares ($r=0.92$), and length of rostrum ($r=0.91$) (Table 5). In addition, five characters (width of rostrum at midlength, width of premaxillae, distance from tip of rostrum at pterygoid hamuli, width of palate at midlength of rostrum, and length of orbit) did not present correlation with age (Table 5).

In females only condylobasal length ($r=0.86$) presented a larger correlation with age ($r \geq 0.80$), followed by length of rostrum from base ($r=0.66$) (Table 5). In addition, the parameters were not estimated for fourteen characters in females, and five characters in males because the growth model did not converge (Table 5). It this is probably linked to the sample size utilized in this study. In females, the lack of some age classes was evident (e.g., absence of females between 0 and 2 years of age). The absence of animals that "anchor" the beginning of the curve could result in low estimates of k and t_0 (e.g., Rosas et al. 2003).

The growth constant (k) presented different patterns for males and females. In males, the condylobasal length showed faster growth (k=0.79) than in females (k=0.27) (Table 5), whereas the length of rostrum from base presented a faster growth in females (k=1.07) than in males (k=0.96) (Table 5). In males the skull height (k=0.97) presented the faster growth, followed by length of rostrum from base (k=0.96), and width of rostrum at base (k=0.87). A slower growth was observed in the greatest width of left premaxilla (k=0.36), followed by the greatest width of pterygoid (k= 0.37) (Table 5).

In males, differences were observed in the stabilization of the asymptotic growth of the variables selected with $r \geq 0.80$. The stabilization of the asymptotic growth of the skull height and length of neurocranium started at 2 years of age (Table 5, Fig. 5a). In zigomatic width, the stabilization of the asymptotic growth started at 2.5 years of age (Table 5, Fig. 5b). However, the stabilization of the condylobasal length, length of rostrum, width of rostrum, distance from tip of rostrum to external nares and greatest postorbital width started at 3 years of age (Table 5, Fig. 5c). In least distance between occipital condyles and length of pterygoid the stabilization started at 4 years of age (Table 5, Fig. 5d). Considering that the median age of all variables selected was 3 years, we suggest that in this study the males attain physical maturity of skull at about 3 years of age.

In females, the stabilization of the asymptotic growth of the condylobasal length began at 4 years of age (Table 5). Unfortunately, in the females it was not possible to estimate the physical maturity of the skull due to small sample size.

On the other hand, it was only possible to estimate the age in 72 skulls (45 males and 27 females) out of 142 skulls. In this situation, it is considered appropriate the use of the asymptotic length attained at 95% of condylobasal length as a criteria of attainment of physical maturity in the skull of *P. spinipinnis*. Thus, the males attain physical maturity when the condylobasal length is ≥ 266 mm, while that the females attain physical maturity when the condylobasal length is ≥ 277mm.

Sexual dimorphism according to the physical development of the skull

Descriptive statistics of the metric characters from physically inmmature skulls of males and females of *P. spinipinnis* is showed in Table 6. In physically immature skulls, the Hotelling T^2 test could not be computed. It this is probably linked to the sample size utilized in this study. The discriminant analysis classified seven characters (height of rostrum at ½ length-HR, greatest width of nasal-GWN, length of upper tooth row-LUR, distance from tip of rostrum to external nares-DLR, width of rostrum-WR, greatest width of frontal-GWF, and distance from maxilar to occipital crest-DMCO) as dimorphic for physically immature skulls of both sexes (Wilks' Lambda=0.09693; F(7,5)=6.6548, P=0.0266). The discriminant functions were 85.71% successful in the classification of sex, with only three males and a single female erroneously classified. The functions by sex for physically immature skull were:

Male = -1059.20 + 25.75(HR) + 89.90(GWN) + 0.72(LUR) + 3.34(DLR) - 36.50(WR) + 5.83(GWF) + 27.72 (DMCO)

Female = -845.86 + 23.75(HR) + 78.15(GNW) + 1.15(LUR) + 2.57(DLR) - 31.49(WR) + 5.09(GWF) + 24.57(DMCO)

In physically mature skulls, the results of the Hotelling T^2 multivariate test showed to be significative ($T^2=118.131$; F(28,29)= 3.4795, P=0.00065). Descriptive statistics of the metric characters from physically mature skulls of males and females of *P. spinipinnis* is showed in Table 7.

The discriminant analysis classified eight characters (length of orbit-LO, greatest width of left premaxilla-GWLPR, length of pterygoid-LPT, greatest preorbital width-GWPRO, height of rostrum at midlength-HR, greatest width of temporal fossa-GTW, greatest width of pterygoid-GWPT, and greatest width of internal nares-(GWNI) as dimorphic for females and males physically mature skulls (Wilks' Lambda=0.37248; F(8,49)=10.319, P=0.0000). The discriminant functions were 95.12% successful in the classification of sex. Two females and two males were erroneously classified. The functions by sex for physically mature skulls were:

Male = - 380.19 + 5.91(LO) - 8.64(GWLPR) + 3.57(LPT) + 0.06(GWPRO) + 6.18(HR) + 4.95(GTW) + 0.88(GWPT) - 2.55(GWNI)

Female = - 420.68 + 6.86(OL) - 11.80(GWLPR) + 4.21(LPT) - 0.37(GWPRO) + 6.74(HR) + 5.45(GWT) -1.25(GWPT) - 2.98(GWNI)

DISCUSSION

Diverse methods have been used for sex determination in marine mammals, including the skull characters that by far are the most common tool used in dolphins and porpoises (e.g., Perrin 1975, Schnell et al. 1985, Perrin et al. 1994), since sex determination can be difficult if not impossible in decomposed animals (Molina-Schiller & Pinedo 2004).

The sexual dimorphisms observed in fourteen cranial characters of *P. spinipinnis* of known sex corroborate the differences in asymptotic growth at 95% of condylobasal length for males and females, where a differentiated development was observed between sexes. However, this result was not coincident with analysis of cranial morphology realized for Burmeister's porpoises from Peru by Reyes & van Waerebeek (1995), because these authors found that condylobasal length is not dimorphic. Probably this differences have relationship with the size of the sample (Males=22 and Females=14), and they used skulls of porpoises sexually mature. The sexual dimorphism observed in physically mature and immature skulls supports the allometric cranial growth in *P. spinipinnis*. In addition, the discriminant functions showed that the height of rostrum at midlength was a dimorphic character present both in physically mature and immature skulls.

The Gompertz growth model showed that the length of rostrum from base in female skull presented an early maturation in relation to the male skull. This character is related to somatic development (feeding apparatus). In males, the condylobasal length showed a faster growth than in females, and this character is related to the neural development (braincaise apparatus). In addition, in males the characters that presented an early maturation are related to neural development (e.g., braincase, visual and hearing apparatus). However, the greatest width of left premaxilla related to feeding apparatus and greatest width of pterygoid related to breathing-sound apparatus had a slower growth.

The sexual dimorphism observed in physically mature skulls of *P. spinipinnis*, with females larger than males supports the differences observed by sex in the body size of *P. spinipinnis* (Brownell & Praderi 1984, Goodall et al. 1995b). Sexual dimorphism has been reported for several species of small odontocetes, where the females are larger than males. Such is the case of franciscana, *Pontoporia blainvillei* (Pinedo 1991, Ramos et al. 2000, Ramos et al. 2002); *P. phocoena* (Read & Gaskin 1990, Read & Tolley 1997); *Phocoena sinus* (Brownell et al. 1987, Hohn et al. 1996, Vidal 1995); *P. dalli* (Amano & Miyasaki 1992, Ferrero & Walker 1999), and *P. spinipinnis*, Brownell and Praderi 1984; Goodal et al. 1995a).

The sexual dimorphism has been associated with a differential investment of energy in growth, reflecting divergent reproductive strategies in the two sexes (Calzada et al. 1997). Maybe in these species the sexual dimorphism has relationship with the reproductive success. Ralls (1977) says that a larger mother may produce a larger calf with greater chances of survival, and may be better at such aspect of maternal care. Other possible selective factor is availability of resources, because this has relation with reduction of inter-sexual competition for food by females (Ralls 1977). Future studies of behavior, feeding, life history and ecology in *P. spinipinnis* will allow to clarify these differences.

The utilization of condylobasal length to estimate the physical maturity of the skull in Burmeister's porpoise was a useful alternative tool in this study because part of the samples kept at museums lack basic data. Its application can allow an increase in sample sizes in studies of population dynamics, geographical variation and taxonomic comparisons. Usually the biological data are scarce, and several skulls are incomplete (e.g., lack of teeth, broken bones) limiting the morphometrics analysis.

Our results suggest that it is important to study growth by analyzing the sexes for each geographic area, because there may be differential growth between sexes. Therefore, the results presented here must be considered more in terms of patterns than for the specific values of the growth parameters. It is highly recommended to develop growth studies of Burmeister's porpoises from three geographic areas (Peru, Chile and Atlantic) including different age-classes for males and females in order to estimate the physical maturity of the skull of *P. spinipinnis* by each geographic area, and to develop a better management of populations subject to differential fishery impacts.

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APPENDIX I

Specimens examined.- The 142 specimens used in his study were obtained from the following collections: Areas Costeras y Recursos Marinos, Pisco, Peru (ACO: 10, 27, 13, 53, 43, 57, 07, 12, 147, 15, 08, 04, 26, 09, N1, 38, 37, 05, 55, 56, 03, 06, 148, 054, 46, 02); personal collection of Julio C. Reyes, Peru (JCR: NN5, nnn 24, NN4, 1457, 69, 1684, 758, 1278, 256, 702, 675, 196, 228, 277, 17, 271, 975, 219, 730, 1334, 1578, 518, 749 1337, 125, 1628, 1627, 657, 747, 1150, 24, 76, 1458, 1484, 01, 04, 117, 48, 46, NN3, ND1, 03, 753, 693, 1604, 728, 724, 1629, 904, JSM 227, JSM 3, AJR 10, AJR 29); Museo Nacional de Historia Natural-Santiago, Chile (MNHN 588); Museo Municipal de Ciencias Naturales y Arqueología de San Antonio, Chile (MMCNASA: 52, 55, 73, 76, 48, 96, 91, 94, 62, 19, 77, 92, JLBM-3); Corporación Terra Australis, Valdivia, Chile (JAO: 06, 17, 99, 01, 02, 75, 03, 04, 05, 07, 08, 09, 10, 11, 96, 12, 13, 14, 15, 16); Museo de Zoología de la Universidad de Concepción, Colecciones Científicas, Concepción, Chile (MZUC-C: 4149, 4148); Universidad de Magallanes, Punta Arenas, Chile (UMA:IPCMC-45, BL-160); CENPAT, Puerto Madryn, Argentina (CENPAT: PS1, PS2, PS4); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN: 3-32, 21864, 20489, 21020, 22221, 20488, 20487, 20484); Fundación Vida Silvestre Argentina, Buenos Aires, Argentina (N91-1, N90-28, N89-4); Universidad Nacional de Mar del Plata**,** Mar del Plata, Argentina (GMM: PS001, PS003); Facultad de Ciencias, Universidad de la República, Montevideo Uruguay (ZVCM 2115); Museo del Mar, Punta del Este, Uruguay (MUSMAR P1); Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul, Brazil (GEMARS0633); Laboratório de Mamíferos Aquáticos da Universidade Federal de Santa Catarina, Florianópolis, Brazil (UFSC 1025).

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Table 1. Descriptive statistics for skull measurements of P. *spinipinnis* from Peru. Data include only specimens of known sex.

Estadística descriptiva para medidas de cráneos de *Phocoena spinipinnis* del Perú. Los datos incluyen sólo ejemplares de sexo conocido.

Measurements (mm)	Males					Females				
	n	Mean	Min	Max	SD	N	Mean	Min	Max	SD
1. Condylobasal length	20	273.43	227.68	296.30	14.15	11	274.35	243.40	287.59	13.00
2. Length of rostrum from base	19	121.98	94.58	134.36	8.23	11	123.76	113.08	128.67	5.19
3. Width of rostrum at base	20	75.74	57.29	82.84	5.89	10	75.26	68.60	83.90	4.55
4. Distance from tip of rostrum to external nares	20	147.07	115.95	157.91	9.21	11	148.92	136.92	160.80	6.59
5. Width of rostrum at midlength	20	50.79	42.82	56.42	3.45	9	50.79	47.03	55.38	2.81
6. Greatest width of left premaxilla	20	12.97	11.39	15.37	1.03	9	12.49	11.59	13.51	0.59
7. Height of rostrum at midlength	19	22.45	17.96	26.60	2.43	11	24.53	21.11	28.96	2.86
8. Greatest width of premaxilla	20	17.37	14.56	21.15	1.67	11	18.16	15.36	21.84	1.68
9. Skull height	20	132.34	114.80	141.33	5.88	11	131.78	126.10	137.65	3.67
10. Greatest preorbital width	19	124.22	105.30	134.50	7.26	11	124.09	113.59	134.42	5.87
11. Greatest postorbital width	20	146.84	115.51	157.08	8.45	10	146.18	135.92	154.84	6.58
12. Zygomatic width	19	146.01	123.05	155.90	7.15	11	146.09	136.02	153.07	6.22
13. Greatest width of frontal	20	122.51	24.60	138.05	23.49	11	125.22	118.18	131.00	3.82
14. Greatest width of internal nares	20	29.38	24.17	34.55	2.78	11	29.55	25.47	33.20	2.72
15. Greatest width of nasal	20	29.56	26.44	32.60	1.51	11	28.72	25.46	32.88	2.43
16. Length of neurocranium	20	159.61	130.40	173.88	10.65	11	160.45	152.61	170.23	6.75
17. Greatest parietal width	20	131.64	118.11	142.00	5.39	11	130.68	123.24	137.40	3.93
18. Least distance between occipital condyles	20	73.77	62.42	84.94	4.71	11	73.49	65.46	81.21	4.97
19. Greatest length of temporal fossa	20	53.94	44.95	63.14	4.17	11	54.57	50.26	59.86	2.55
20. Greatest width of temporal fossa	19	45.91	35.01	49.63	3.57	11	46.18	38.21	52.67	4.03
21. Distance from tip of rostrum to pterygoid hamuli	20	156.43	126.56	173.47	10.45	11	160.54	148.06	170.69	6.72
22. Width of palate at midlength of rostrum	20	44.55	36.62	49.35	3.11	11	44.87	37.65	50.51	3.77
23. Length of orbit	20	52.26	45.07	57.22	2.74	11	53.98	49.20	60.74	3.92
24. Greatest width of pterygoid	19	60.01	49.48	68.15	4.43	10	60.52	53.29	64.63	3.22
25. Length of pterygoid	20	54.70	47.50	59.84	3.41	11	55.87	49.530	63.72	4.13
26. Greatest width of frontal prominence	19	32.91	27.41	41.07	3.70	11	34.14	25.62	38.73	3.39
27. Distance from maxilar to occipital crest	19	13.99	10.38	17.70	2.06	10	12.19	8.15	17.18	2.39
28. Length of upper tooth row	18	74.28	61.14	82.11	5.29	11	81.19	67.49	96.15	7.85

Table 2. Descriptive statistics for skull measurements of *P. spinipinnis* from Chile. Data include only specimens of known sex.

Estadística descriptiva para medidas de cráneos de *Phocoena spinipinnis* de Chile. Los datos incluyen sólo ejemplares de sexo conocido.

Measurements (mm)	Males					Females				
	n	Mean	Min	Max	SD	n	Mean	Min	Max	SD
1. Condylobasal length	3	239.98	210.90	275.26	32.63	2	285.00	284.07	285.93	1.32
2. Length of rostrum from base	3	98.66	81.10	117.53	18.25	2	128.60	125.18	132.02	4.84
3. Width of rostrum at base	4	65.75	53.24	73.67	9.66	3	77.22	74.23	79.84	2.824
4. Distance from tip of rostrum to external nares	3	119.62	101.44	142.31	20.80	2	155.35	151.07	159.56	6.00
5. Width of rostrum at midlength	3	44.99	39.71	54.16	7.97	1	49.89	49.89	49.89	---
6. Greatest width of left premaxilla	3	10.92	10.10	11.55	0.74	1	13.14	13.14	13.14	---
7. Height of rostrum at midlength	3	18.40	15.72	20.02	2.34	2	27.30	24.65	29.95	3.75
8. Greatest width of premaxilla	4	37.39	33.97	42.00	3.44	3	40.42	39.15	42.81	2.07
9. Skull height	4	117.66	103.63	128.75	10.73	3	131.49	127.20	134.97	3.95
10. Greatest preorbital width	3	120.71	114.07	127.01	6.48	3	128.97	120.13	135.57	7.96
11. Greatest postorbital width	4	133.83	112.47	146.89	15.62	3	152.50	143.92	158.07	7.54
12. Zygomatic width	4	137.29	116.99	153.11	15.50	3	155.79	149.51	160.25	5.59
13. Greatest width of frontal	4	118.74	105.08	129.91	10.45	3	134.96	132.25	139.01	3.57
14. Greatest width of internal nares	4	28.66	25.03	31.59	2.72	3	33.08	32.03	33.73	0.92
15. Greatest width of nasal	4	29.10	23.43	35.22	4.91	3	34.39	29.93	38.91	4.49
16. Length of neurocranium	4	148.06	127.96	165.25	17.96	3	165.48	161.80	168.78	3.51
17. Greatest parietal width	4	126.90	116.09	137.43	8.81	3	136.65	135.52	137.85	1.17
18. Least distance between occipital condyles	3	65.11	56.54	73.98	8.72	3	74.81	71.37	78.33	3.48
19. Greatest length of temporal fossa	4	53.45	46.09	62.92	7.16	2	51.28	48.02	54.54	4.61
20. Greatest width of temporal fossa	4	42.56	38.33	45.17	2.99	3	49.94	46.99	53.34	3.19
21. Distance from tip of rostrum to pterygoid hamuli	3	130.28	110.08	154.88	22.72	2	165.23	164.63	165.83	0.85
22. Width of palate at midlength of rostrum	3	42.24	36.02	46.58	5.527	2	47.69	44.11	51.26	5.06
23. Length of orbit	4	46.71	38.72	50.94	5.53	3	53.79	46.72	58.98	6.35
24. Greatest width of pterygoid	4	57.53	50.51	61.18	4.88	3	64.70	59.01	67.99	4.96
25. Length of pterygoid	4	48.19	41.28	56.03	7.64	3	58.43	56.67	60.91	2.21
26. Greatest width of frontal prominence	4	31.27	19.35	39.26	8.88	3	33.29	32.09	34.68	1.30
27. Distance from maxilar to occipital crest	3	11.93	10.16	13.19	1.58	3	10.60	8.20	14.30	3.25
28. Length of upper tooth row	3	54.28	45.51	58.85	7.56	2	71.41	65.90	76.92	7.79

Table 3 Descriptive statistics for skull measurements of *P. spinipinnis* from Atlantic (Argentina, Brazil and Uruguay). Data include only specimens of known sex.

Estadística descriptiva para medidas de cráneos de *Phocoena spinipinnis* del Atlántico (Argentina, Brasil y Uruguay). Los datos incluyen sólo incluyen ejemplares de sexo conocido.

			Males					Females		
Measurements (mm)	n	Mean	Min	Max	SD	n	Mean	Min	Max	SD
1. Condylobasal length	2	276.58	272.96	280.20	5.12	4	278.03	270.26	287.71	8.05
2. Length of rostrum from base	2	112.90	110.03	115.77	4.06	3	119.24	115.76	122.33	3.30
3. Width of rostrum at base	3	80.24	76.15	83.34	3.69	4	78.95	76.43	86.00	4.71
4. Distance from tip of rostrum to external nares	2	142.79	139.08	146.50	5.25	4	147.67	141.76	151.72	4.65
5. Width of rostrum at midlength	2	51.30	48.37	54.22	4.14	3	53.52	52.09	54.73	1.33
6. Greatest width of left premaxilla	2	13.09	12.09	14.09	1.41	3	13.05	12.27	13.56	0.69
7. Height of rostrum at midlength	2	20.16	19.73	20.58	0.60	4	19.16	17.41	20.87	1.51
8. Greatest width of premaxilla	3	39.23	37.25	42.35	2.73	4	39.44	37.61	41.30	1.54
9. Skull height	3	132.64	132.05	133.49	0.76	4	134.13	131.57	140.52	4.28
10. Greatest preorbital width	3	132.76	122.04	143.04	10.51	4	128.49	121.92	136.74	6.48
11. Greatest postorbital width	2	135.14	111.74	158.53	33.09	4	152.88	146.60	158.59	5.00
12. Zygomatic width	1	163.09	163.09	163.09	--	4	156.70	148.17	163.53	6.42
13. Greatest width of frontal	3	135.36	131.37	142.75	6.41	4	137.93	135.02	144.57	4.52
14. Greatest width of internal nares	3	31.88	30.03	34.94	2.67	4	33.47	32.19	35.74	1.66
15. Greatest width of nasal	3	31.95	30.98	33.17	1.12	4	34.11	30.37	38.21	3.23
16. Length of neurocranium	3	164.98	162.21	169.03	3.58	4	166.78	160.31	175.48	6.44
17. Greatest parietal width	3	141.67	139.31	144.72	2.77	4	1 1.16	138.87	143.97	2.18
18. Least distance between occipital condyles	3	76.34	73.56	80.64	3.78	4	77.54	72.53	81.40	4.06
19. Greatest length of temporal fossa	3	53.72	51.52	56.33	2.43	3	56.12	54.04	59.13	2.67
20. Greatest width of temporal fossa	3	50.66	48.47	51.75	1.89	4	51.54	48.57	56.11	3.24
21. Distance from tip of rostrum to pterygoid hamuli	2	159.01	154.46	163.55	6.43	4	162.83	157.41	166.49	3.98
22. Width of palate at midlength of rostrum	2	46.80	42.66	50.94	5.85	4	45.34	41.76	47.14	2.43
23. Length of orbit	3	47.30	42.65	54.81	6.56	4	56.40	53.51	59.48	2.44
24. Greatest width of pterygoid	3	61.38	59.04	64.89	3.10	4	65.06	63.07	68.09	2.14
25. Length of pterygoid	3	61.25	59.73	62.77	1.52	4	59.86	57.75	63.22	2.49
26. Greatest width of frontal prominence	3	30.23	26.73	32.44	3.07	4	36.92	34.86	39.59	2.43
27. Distance from maxilar to occipital crest	3	20.32	17.27	22.06	2.65	3	15.27	14.72	16.24	0.84
28. Length of upper tooth row	2	66.85	65.72	67.97	1.59	4	68.60	61.13	77.52	7.75

TABLE 4. Classification functions for stepwise discriminant analysis of skulls of *Phocoena spinipinnis* with known sex.

Clasificación de las funciones discriminantes por "stepwise" en cráneos de *Phocoena spinipinnis* de sexo conocido

Variables	Male	Female
Length of orbit	3.151	4.765
Greatest width of premaxilla	8.976	4.043
Height of rostrum at midlength	-0.056	1.263
Latitude (sampling site)	-10.488	-10.152
Distance from maxilar to occipital crest	8.486	8.224
Width of rostrum at base	0.722	0.367
Greatest width of temporal fossa	3.151	3.890
Distance from tip of rostrum to external nares	-8.540	-7.424
Condylobasal length	4.994	4.225
Longitude (sampling site)	-2.610	-2.697
Greatest postorbital width	1.143	0.643
Greatest width of pterygoid	-4.190	-3.312
Length of pterygoid	0.144	0.910
Greatest preorbital width	1.904	1.494
Constant	-856.206	-816.497

TABLE 5**.** Parameters of the Gompertz equation for males and females of *Phocoena spinipinnis*.

Parámetros de la ecuación de Gompertz para machos y hembras de *Phocoena spinipinnis*.

	Males							Females						
Measurements (mm)	n	A∞ (mm)	k	t_0	r	Asymptotic length at 95% (mm)	t	n	A∞ (mm)	k	t_0	r	Asymptotic length at 95% (mm)	t
1. Condylobasal length	44	280.27	0.79	-1.345	0.93	266.26	3	27	292.08	0.266	-6.631	0.86	277.47	4
2. Length of rostrum from base	44	124.15	0.96	-0.673	0.91	117.94	3	26	125.48	1.067	-0.272	0.66	119.20	2.5
3. Width of rostrum at base	45	77.53	0.87	-0.911	0.83	73.65	3	NC*						
4. Distance from tip of rostrum to external nares	44	150.88	0.797	-0.899	0.92	143.33	3	NC						
5. Width of rostrum at midlength	43	50.31	54.52	-56.961	0.0	47.79		22	52.98	0.611	-2.911	0.29	50.33	
6. Greatest width of left premaxilla	43	13.77	0.362	-3.087	0.77	13.08		NC						
7. Height of rostrum at midlength	43	23.03	0.76	-1.070	0.58	21.88		22	23.22	2.210	0.937	0.16	22.06	
8. Greatest width of premaxilla	45	21.11	9.00	-2.999	0.0	20.05		27	28.73	0.366	-3.413	0.09	27.29	
9. Skull height	45	134.01	0.97	-1.168	0.88	127.31	2	NC						
10. Greatest preorbital width	43	126.80	0.77	-1.421	0.76	120.46		NC						
11. Greatest postorbital width	42	150.60	0.83	-1.323	0.83	143.07	3	26	150.65	5.745	-44.355	0.00	143.12	
12. Zygomatic width	40	151.88	0.59	-2.446	0.80	144.29	2.5	NC						
13. Greatest width of frontal	NC							NC						
14. Greatest width of internal nares	NC							NC						
15. Greatest width of nasal	45	30.24	0.56	-2.834	0.52	28.73		27	31.20	5.173	-13.589	0.00	29.64	
16. Length of neurocranium	43	163.97	0.78	-1.618	0.87	155.77	2							
17. Greatest parietal width	44	134.44	0.73	-2.512	0.70	127.72		27	134.67	3.128	-5.788	0.00	127.94	
18. Least distance between occipital condyles	45	77.33	0.48	-2.372	0.89	73.46	4	NC						
19. Greatest length of temporal fossa	NC							NC						
20. Greatest width of temporal fossa	42	47.11	0.75	-2.360	0.47	44.76		27	49.50	0.597	-2.218	0.28	47.03	
21. Distance from tip of rostrum to pterygoid hamuli	44	154.01	-2.63	50.617	0.0	146.31		NC						
22. Width of palate at midlength of rostrum	42	44.67	-14.31	12.728	0.0	42.43		27	49.22	0.293	-4.174	0.63	46.76	
23. Length of orbit	43	51.405	35.63	-59.615	0.0	48.83		NC						
24. Greatest width of pterygoid	39	63.34	0.37	-3.978	0.67	60.17		NC						
25. Length of pterygoid	41	57.41	0.53	-2.212	0.80	54.54	4	25	61.81	0.237	-6.773	0.50	58.72	
26. Greatest width of frontal prominence	44	33.99	0.701	-1.016	0.63	32.29		27	34.51	3.864	-7.437	0.00	32.79	
27. Distance from maxilar to occipital crest	NC							25	13.53	0.315	-4.610	0.23	12.85	
28. Length of upper tooth row	NC							NC						

***** NC=did not converge; no converge

TABLE 6. Descriptive statistics of the metric characters (mm) from physically immature skulls of males and females of *Phocoena spinipinnis*.

Estadística descriptiva de los caracteres métricos (mm) de cráneos de machos y hembras de *Phocoena spinipinnis* físicamente jóvenes.

Measurements (mm)	Males						Females					
	n	Mean	Min	Max	SD	CV	n	Mean	Min	Max	SD	CV
1. Condylobasal length	25	248.64	205.66	274.68	18.38	7.39	7	251.87	225.05	264.77	13.84	5.49
2. Length of rostrum from base	25	106.43	81.10	122.96	11.43	10.74	8	107.11	82.79	118.19	12.63	11.79
3. Width of rostrum at base	25	66.71	53.24	79.95	7.21	10.80	7	68.62	62.93	76.05	4.54	6.62
4. Distance from tip of rostrum to external nares	25	127.77	99.79	146.10	13.63	10.66	7	133.18	111.22	142.12	10.11	7.59
5. Width of rostrum at midlength	25	46.88	36.53	54.60	4.28	9.14	7	47.68	43.40	55.70	3.88	8.14
6. Greatest width of left premaxilla	25	11.50	8.82	13.79	1.11	9.68	7	11.89	11.05	13.02	0.81	6.81
7. Height of rostrum at midlength	25	19.77	15.72	26.22	2.44	12.34	7	21.52	18.62	24.34	2.37	11.01
8. Greatest width of premaxilla	25	23.39	13.76	43.91	10.37	44.35	8	23.96	15.35	39.31	10.88	45.41
9. Skull height	25	121.71	94.38	137.41	10.00	8.22	8	124.12	111.48	131.93	6.48	5.22
10. Greatest preorbital width	23	114.85	91.31	130.78	9.61	8.37	8	114.59	103.33	122.08	6.22	5.43
11. Greatest postorbital width	22	133.33	107.90	153.42	12.18	9.13	8	137.92	124.99	155.42	8.65	6.27
12. Zygomatic width	17	132.96	109.46	151.17	9.90	7.44	6	138.19	132.56	154.62	8.21	5.94
13. Greatest width of frontal	25	116.86	24.60	129.44	20.40	17.46	8	122.31	113.46	142.43	8.85	7.24
14. Greatest width of internal nares	25	27.38	22.56	33.07	2.60	9.49	8	28.09	25.11	34.05	3.53	12.57
15. Greatest width of nasal	25	27.99	23.43	33.50	2.48	8.85	8	27.63	23.71	33.49	2.84	10.28
16. Length of neurocranium	24	147.69	121.08	168.08	10.93	7.40	8	149.23	123.64	162.24	13.02	8.72
17. Greatest parietal width	24	127.69	112.97	137.15	6.10	4.77	8	128.73	123.88	136.97	4.99	3.88
18. Least distance between occipital condyles	24	67.23	56.54	76.27	5.07	7.54	8	68.33	63.41	81.14	5.63	8.24
19. Greatest length of temporal fossa	25	50.46	39.60	57.88	4.19	8.29	8	52.76	46.27	56.35	3.47	6.58
20. Greatest width of temporal fossa	23	42.99	35.01	50.26	3.78	8.79	8	45.01	36.85	52.84	5.42	12.04
21. Distance from tip of rostrum to pterygoid hamuli	25	139.87	110.08	160.91	13.68	9.78	7	145.59	124.63	151.29	9.43	6.48
22. Width of palate at midlength of rostrum	25	42.15	32.08	46.58	3.55	8.43	7	40.12	36.44	45.63	3.31	8.25
23. Length of orbit	23	49.01	38.72	55.86	3.88	7.92	8	51.23	43.12	54.91	3.59	7.01
24. Greatest width of pterygoid	18	55.13	45.02	61.34	4.69	8.50	7	58.34	53.00	64.35	4.24	7.27
25. Length of pterygoid	17	48.62	40.66	54.85	4.01	8.24	8	52.60	45.05	57.67	3.83	7.28
26. Greatest width of frontal prominence	24	28.34	19.35	36.01	3.78	13.34	8	30.51	25.62	35.38	3.97	13.01
27. Distance from maxilar to occipital crest	23	15.00	10.16	21.84	2.90	19.31	8	13.22	8.15	17.25	2.84	21.48
28. Length of upper tooth row	23	66.14	45.51	82.53	10.27	15.53	7	63.29	18.22	84.93	22.57	35.66

TABLE 7. Descriptive statistics of the metric characters (mm) in physically mature skulls of males and females of *Phocoena spinipinnis*.

Estadística descriptiva de los caracteres métricos (mm) de cráneos de machos y hembras de *Phocoena spinipinnis* físicamente adultos.

Measurements (mm)	Males						Females					
	n	Mean	Min	Max	SD	CV	n	Mean	Min	Max	SD	CV
1. Condylobasal length	58	277.22	265.76	296.93	7.64	2.69	45	280.59	267.63	294.21	7.29	2.60
2. Length of rostrum from base	58	121.69	110.03	134.36	4.99	4.08	45	123.79	113.04	134.89	4.48	3.62
3. Width of rostrum at base	61	77.41	64.71	88.55	4.44	5.72	47	79.30	68.60	99.05	5.80	7.31
4. Distance from tip of rostrum to external nares	58	148.03	137.25	161.88	5.55	3.70	46	150.94	141.76	160.80	4.73	3.13
5. Width of rostrum at midlength	57	52.02	44.39	60.35	3.45	6.61	41	53.68	43.86	62.45	4.38	8.16
6. Greatest width of left premaxilla	57	13.07	11.10	16.18	1.10	8.33	41	12.68	10.59	14.77	0.93	7.36
7. Height of rostrum at midlength	57	22.25	18.51	28.62	2.43	10.72	46	23.09	17.41	32.08	3.48	15.06
8. Greatest width of premaxilla	61	24.37	14.28	44.36	10.62	43.65	48	30.58	15.36	43.88	11.29	36.93
9. Skull height	61	132.90	107.34	141.33	5.33	3.86	48	134.31	116.33	140.75	4.52	3.37
10. Greatest preorbital width	61	126.68	104.91	143.04	6.59	5.12	46	128.66	109.99	140.53	7.45	5.79
11. Greatest postorbital width	59	149.07	111.74	162.51	7.94	5.22	45	152.33	132.96	163.62	7.21	4.73
12. Zygomatic width	49	150.49	136.50	165.26	7.05	4.64	41	154.25	137.56	171.88	9.08	5.89
13. Greatest width of frontal	61	130.40	118.72	145.24	5.84	4.37	48	133.55	119.27	148.84	7.30	5.46
14. Greatest width of internal nares	61	30.93	26.04	40.88	2.81	8.97	48	31.98	25.81	35.74	2.46	7.69
15. Greatest width of nasal	61	30.37	24.52	35.22	2.31	7.52	48	32.39	24.69	41.75	3.58	11.06
16. Length of neurocranium	60	162.80	153.64	177.16	5.32	3.72	46	163.63	104.36	178.37	11.28	6.89
17. Greatest parietal width	61	134.76	124.46	145.02	4.73	3.42	47	136.51	123.24	147.50	5.69	4.17
18. Least distance between occipital condyles	60	75.08	64.70	85.01	3.85	4.77	47	76.50	65.61	86.68	4.91	6.41
19. Greatest length of temporal fossa	60	55.21	48.06	63.14	3.11	5.57	46	55.36	48.02	64.84	3.63	6.56
20. Greatest width of temporal fossa	60	47.31	41.18	54.24	3.07	6.48	48	48.51	34.60	56.11	4.53	9.34
21. Distance from tip of rostrum to pterygoid hamuli	58	159.44	139.36	173.47	6.04	3.68	45	162.46	128.06	177.36	7.28	4.48
22. Width of palate at midlength of rostrum	56	45.19	38.42	50.94	3.05	6.68	46	46.19	38.42	51.99	3.27	7.08
23. Length of orbit	60	52.28	42.65	60.25	3.24	5.96	48	55.37	42.96	61.34	4.01	7.24
24. Greatest width of pterygoid	56	61.68	54.00	73.74	4.07	6.36	40	64.35	56.90	73.32	4.07	6.33
25. Length of pterygoid	57	56.45	49.50	63.36	3.20	5.47	43	59.23	51.11	69.40	3.72	6.29
26. Greatest width of frontal prominence	61	33.76	22.99	47.30	4.75	13.70	48	35.84	26.92	46.11	3.92	10.95
27. Distance from maxilar to occipital crest	60	14.49	9.91	22.06	3.06	20.68	46	14.34	8.20	22.83	3.31	23.08
28. Length of upper tooth row	56	73.61	58.48	83.52	5.66	7.62	45	74.39	61.13	96.15	7.38	9.93

Fig. 1. Geographical location of *Phocoena spinipinnis* specimens used in the study.

Ubicación geográfica de los especimenes de *Phocoena spinipinnis* usados en el estudio.

Fig. 2. Skull measurements of *Phocoena spinipinnis*. 1. Condylobasal length, 2. Length of rostrum (from base), 3. Width of rostrum (at base), 4. Distance from tip of rostrum to external nares, 5. Width of rostrum (at midlength), 6. Greatest width of left premaxilla, 7. Height of rostrum (at midlength), 8. Greatest width of premaxillae, 9. Skull height (at frontal–nasal suture), 10. Greatest preorbital width, 11. Greatest postorbital width, 12. Zygomatic width, 13. Greatest width of frontal, 14. Greatest width of internal nares, 15. Greatest width of nasal, 16. Length of neurocranium, 17. Greatest parietal width, 18. Least distance between occipital condyles, 19. Greatest length of temporal fossa, 20. Greatest width of temporal fossa, 21. Distance from tip of rostrum to pterygoid hamuli, 22. Width of palate (at midlength of rostrum), 23. Length of orbit, 24. Greatest width of pterygoid, 25. Length of pterygoid, 26. Greatest width of frontal prominence, 27. Distance from maxilar to occipital crest, and 28. Length of upper tooth row.

Medidas del cráneo de *Phocoena spinipinnis.* 1. Longitud condylobasal, 2. Longitud del rostro (desde la base), 3. Ancho del rostro (en la base), 4. Distância desde el tope del rostro al las narinas externas, 5. Ancho del rostro (a la mitad de su longitud), 6. Ancho máximo de la premaxila izquierda, 7. Altura del rostro (en la mitad de su longitud), 8. Ancho máximo de las premaxilas, 9. Altura del cráneo (en la sutura frontal-nasal), 10 Ancho máximo del preorbital, 11. Ancho máximo del postorbital, 12. Ancho del zigomático, 13. Ancho máximo del frontal, 14. Ancho máximo interno del orificio nasal, 15. Ancho máximo del nasal, 16. Longitud del neurocranium, 17. Ancho máximo del parietal, 18. Distância mínima del condilobasal, 19. Longitud máxima de la fosa temporal, 20. Ancho máximo de la fosa temporal, 21. Distância entre la punta del rostro al hámulo del pterigoide, 22. Ancho del palatino (en la longitud media del rostro), 23. Longitud de la orbita, 24. Ancho máximo del pterigoide, 25. Longitud del pterigoide, 26. Ancho máximo de la prominencia frontal, 27. Distância entre el maxilar y la cresta occipital, 28. Longitud de la mandíbula superior.

Fig. 3. Sex frequency of *Phocoena spinipinnis* skulls in the sample: (A) by sex and sampling origin; (B) by sex (known and estimated sex) and origin area.

Frecuencia de edad en la muestra de cráneos de *Phocoena spinipinnis*: (A) por sexo y origen de la muestra (B) por sexo (sexo conocido y estimado) y área de origen

Fig. 4. Frequency of age (GLGs) obtained in males and females of *Phocoena spinipinnis*.

Frecuencia de edad (GLGs) obtenidas en machos y hembras de *Phocoena spinipinnis.*

Fig. 5. Gompertz growth curve for males of *Phocoena spinipinnis*. (A) skull height, (B) zygomatic width (C) condylobasal length and (D) length of pterygoid.

Curvas de crecimiento de Gompertz para machos de *Phocoena spinipinnis*. (A) altura del cráneo, (B) ancho del zigomático, (C) longitud condylobasal y (D) ancho máximo del pterigoide.

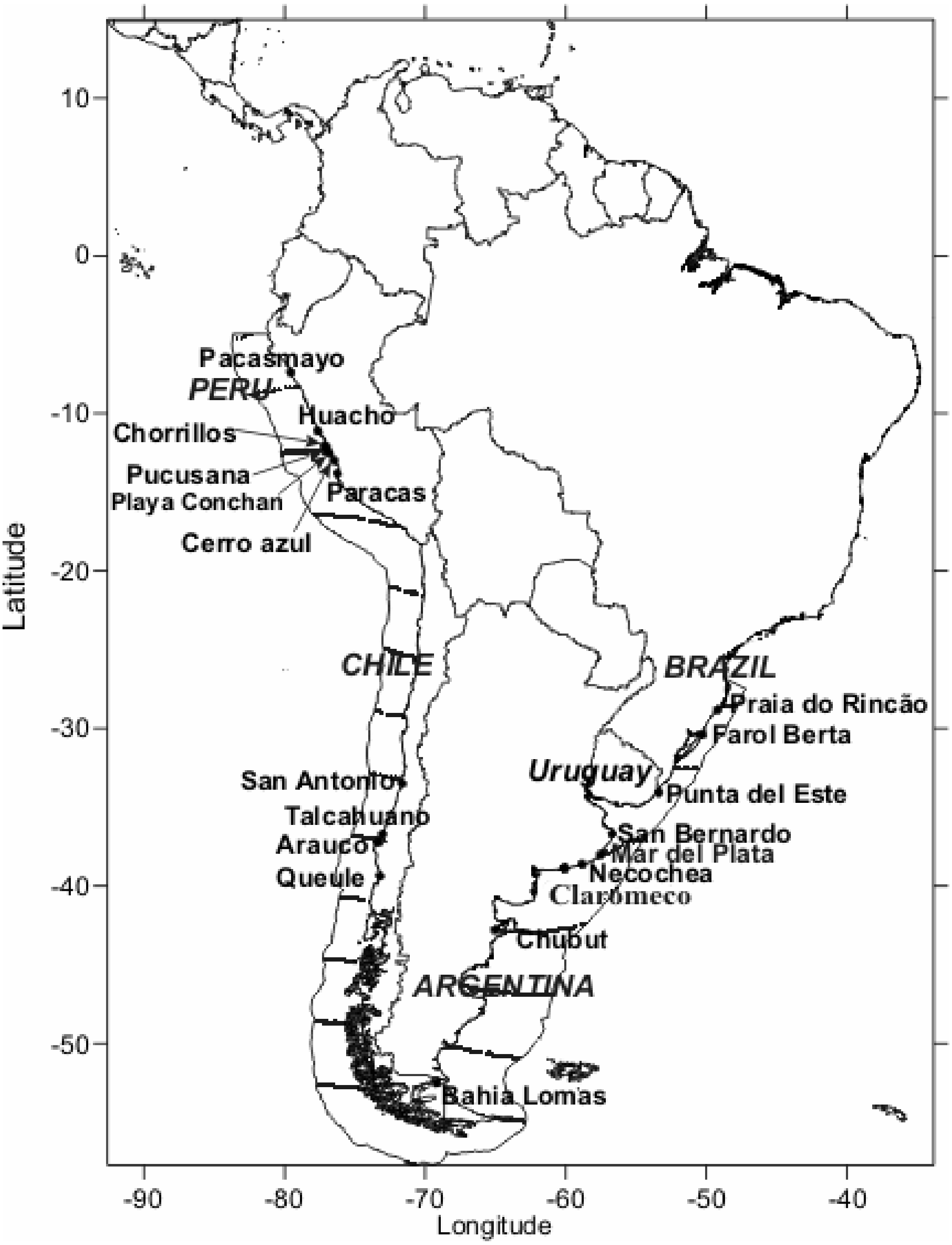

Fig. 1.Geographical location of *Phocoena spinipinnis* specimens used in the study.

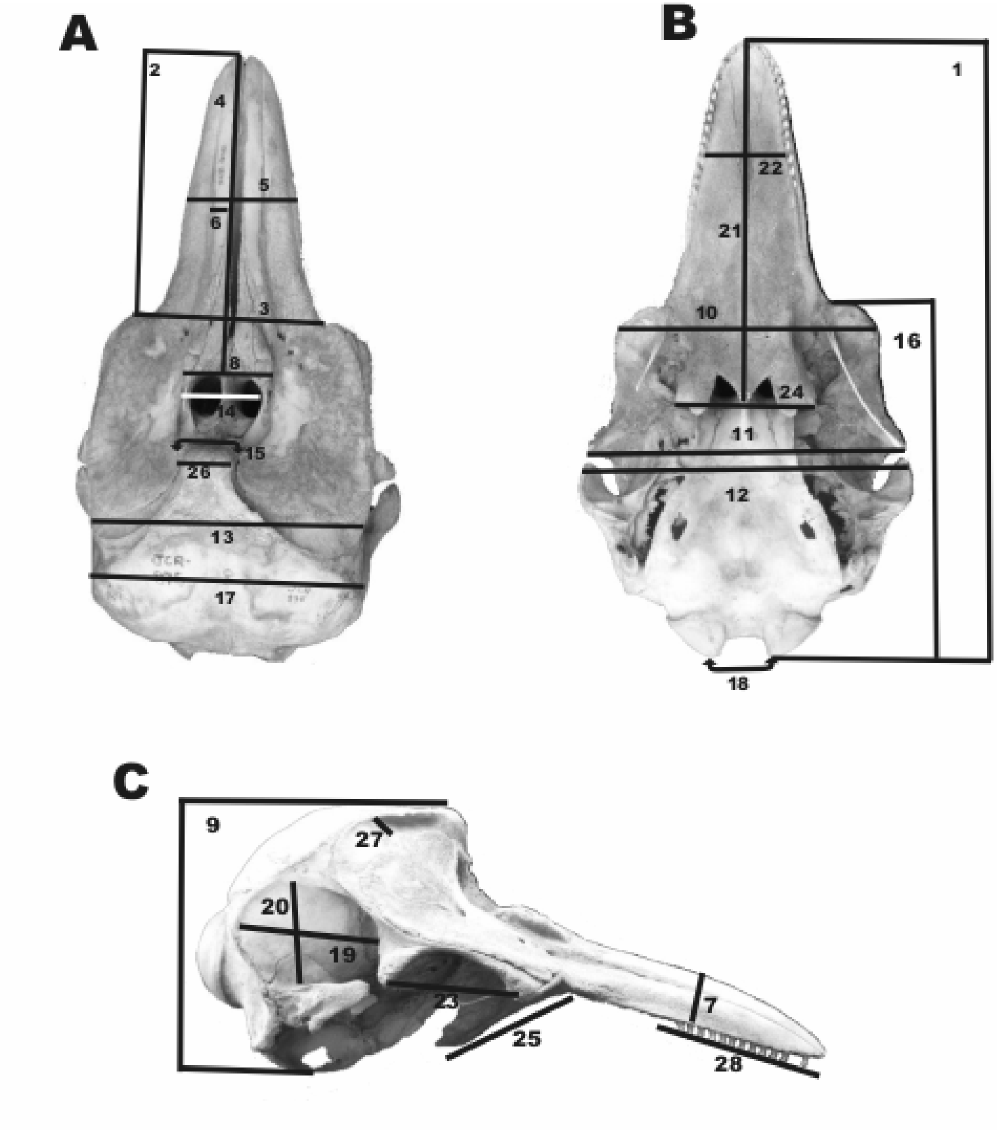

Fig. 2. Skull measurements of *Phocoena spinipinnis*. 1. Condylobasal length, 2. Length of rostrum (from base), 3. Width of rostrum (at base), 4. Distance from tip of rostrum to external nares, 5. Width of rostrum (at midlength), 6. Greatest width of left premaxilla, 7. Height of rostrum (at midlength), 8. Greatest width of premaxillae, 9. Skull height (at frontal–nasal suture), 10. Greatest preorbital width, 11. Greatest postorbital width, 12. Zygomatic width, 13. Greatest width of frontal, 14. Greatest width of internal nares, 15. Greatest width of nasal, 16. Length of neurocranium, 17. Greatest parietal width, 18. Least distance between occipital condyles, 19. Greatest length of temporal fossa, 20. Greatest width of temporal fossa, 21. Distance from tip of rostrum to pterygoid hamuli, 22. Width of palate (at midlength of rostrum), 23. Length of orbit, 24. Greatest width of pterygoid, 25. Length of pterygoid, 26. Greatest width of frontal prominence, 27. Distance from maxilar to occipital crest, and 28. Length of upper tooth row.

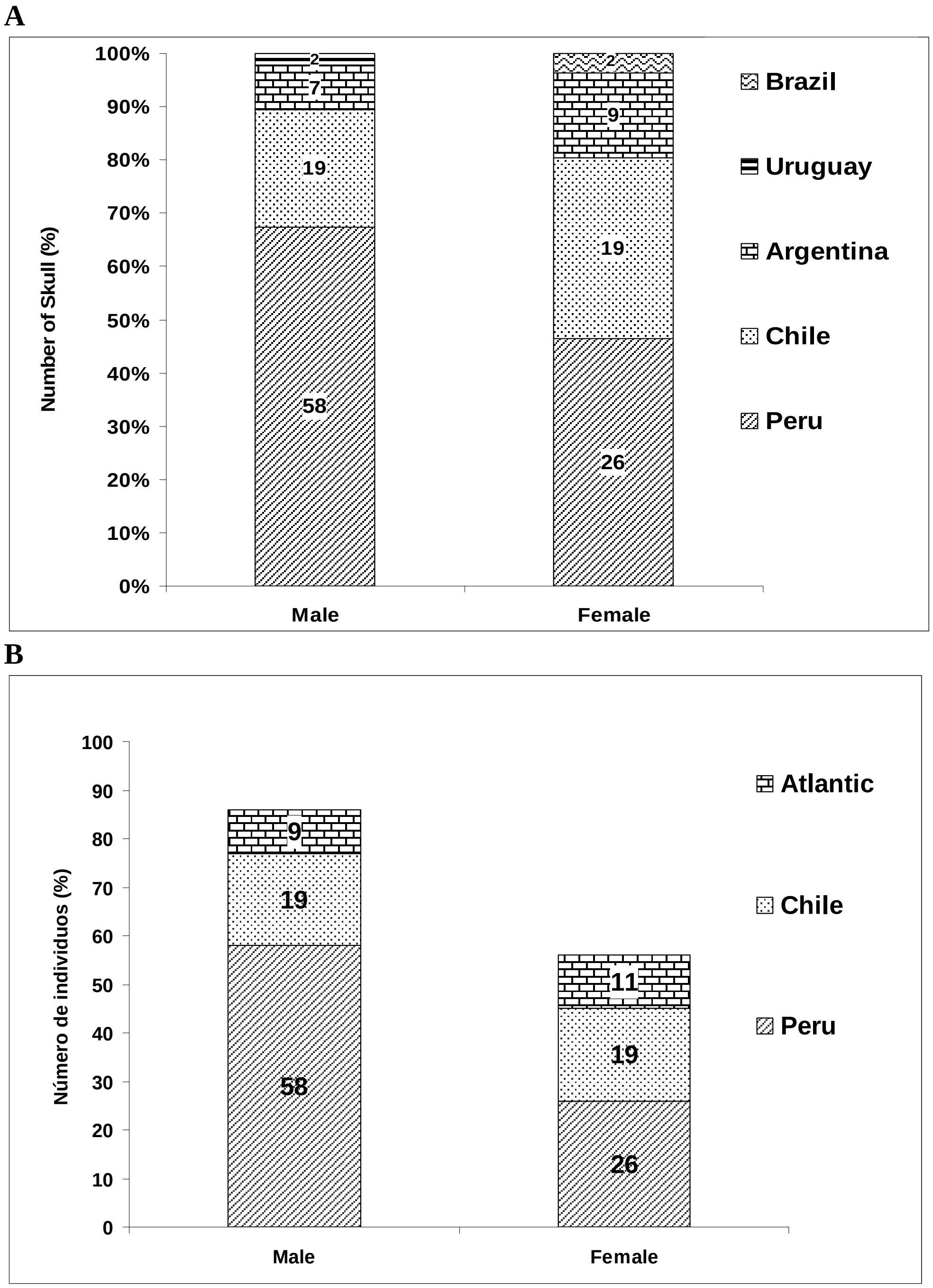

Fig. 3. Sex frequency of *Phocoena spinipinnis* skulls in the sample: (A) by sex and sampling origin; (B) by sex (known and estimated sex) and origin area.

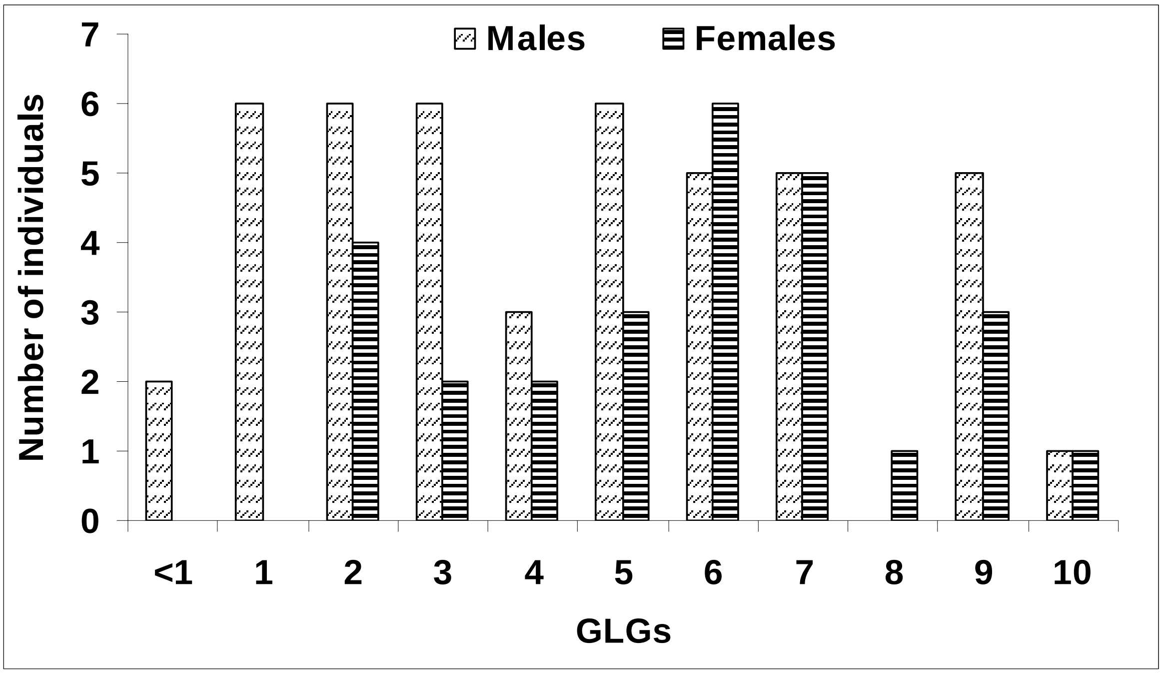

Fig. 4. Frequency of age (GLGs) obtained in males and females of *Phocoena spinipinnis*.

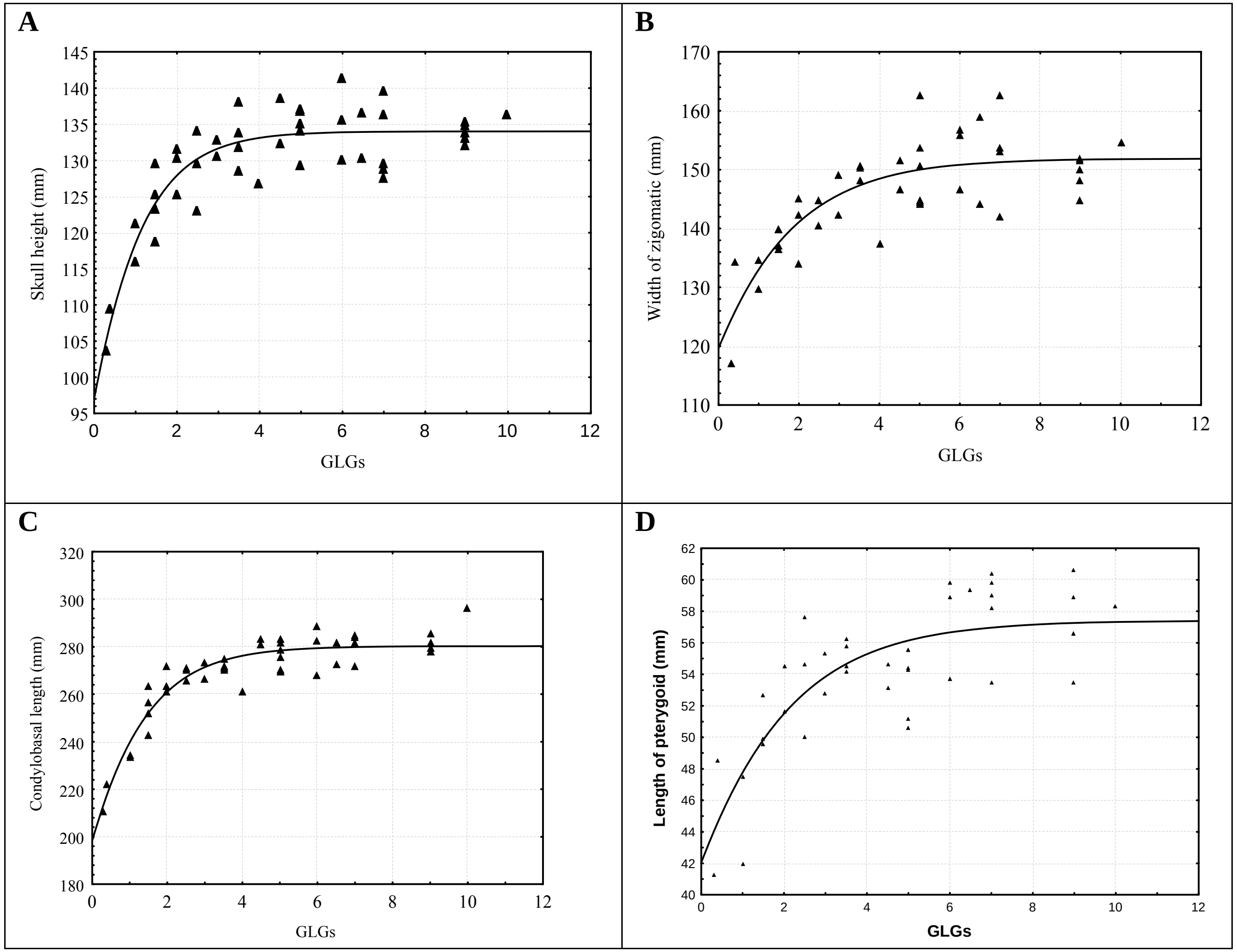

Fig. 5. Gompertz growth curve for males of *Phocoena spinipinnis*. (A) skull height, (B) zygomatic width (C) condylobasal length and (D) length of pterygoid.

CAPITULO 4

CRANIAL SEXUAL DIMORPHISM AND GEOGRAPHIC VARIATION IN *PHOCOENA SPINIPINNIS* (CETACEA: PHOCOENIDAE) USING TRADITIONAL AND GEOMETRIC MORPHOMETRICS

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ABSTRACT– Skulls of 102 *P. spinipinnis* physically mature (61 males and 41 females) were examined to explored the geographical variation in size and shape by traditional and geometric morphometrics. The skulls were obtained from museums and scientific collections from Peru, Chile, Argentina, Uruguay and Brazil. By ANOVA/MANOVA analyses the specimens were separated in three geographic areas: Peru (42 males and 18 females), Chile (13 males and 15 females), and Atlantic (6 males and 8 females). Differences in size and shape of skulls were analyzed by 28 linear measurements. These differences were also investigated applying geometric morphometrics to two-dimensional images of 240 skulls in dorsal, ventral and lateral views. In addition, two-block partial least squares (2B-PLS) method was used to explore the pattern of covariation between variation in shape using partial warp scores and a set of environmental variables (latitude, longitude, temperature, salinity and oxygen at 0 and 50m depth, respectively). Sexual dimorphism in size and shape were observed for skulls of *P. spinipinnis* from three geographical areas, being the females larger than males. The results obtained by linear and geometric morphometrics suggest that geographical variation exists among *P. spinipinnis* from Peru, Chile and Atlantic, with smaller individuals distributed between Pacasmayo, northern Peru (07°24'S) to Paracas, southern Peru (13º50'S), and larger specimens distributed in the Atlantic coast from Chubut, southern Argentina (~42º46'S) to North. Specimens from San Antonio, central Chile (33º30'S) to Strait of Magellan, southern Chile (~52°30'S) showed a size and shape intermediate in relation to porpoises from Peru and Atlantic. Geometric morphometrics was more useful for showing differences between specimens, indicating that males are more variable in skull shape than females; whereas those females from Chile and Atlantic show less difference on skull shape. The differences observed in size and shape in skulls of *P. spinipinnis* from three geographic areas seem to be related to oceanographic pattern associated to their distribution.

Additional investigations (morphometrics and genetics) are needed from central Chile (33ºS) to north to evaluate the differences between porpoises from Chile and Peru.

Key words: Burmeister’s porpoise, sexual dimorphism, geometric morphometrics, geographic variation, *Phocoena spinipinnis*, traditional morphometrics.

INTRODUCTION

Burmeister’s porpoise, *Phocoena spinipinnis,* Burmeister 1865, is endemic to coastal waters of the South American from northern Peru, Paita Bay (05°01’S, 81ºW) southward, round Cape Horn, and northward to southern Brazil (Goodall *et al.* 1995a; Brownell and Clapham 1999). The distribution range to southern Brazil, Santa Catarina, (28°48’S, 49°12’W) is rare, with three know records (Pinedo 1989; Simões-Lopes and Ximenez 1989; GEMARS, record unpublished), associated to the Subtropical Convergence (Molina-Schiller et al. 2005). Information about life history, distribution, movements, abundance, and population structure is limited (Corcuera et al. 1995; Goodall et al. 1995a; Jefferson et al. 1993; Reeves et al. 2003; Reyes and van Waerebeeck 1995; van Waerebeek et al. 2002). Sexual dimorphism has been documented in external traits (Goodall et al. 1995a), and based on skull size using linear measurements (Reyes and van Waerebeeck 1995; Molina-Schiller 2006).

Differences in body size were observed between Burmeister’s porpoises from Peru, Chile, Argentina, and Uruguay (Brownell and Praderi 1984; Corcuera et al. 1995; Goodall et al. 1995b; Reyes and van Waerebeek 1995). Brownell and Praderi (1984) and Corcuera *et al.* (1995), proposed that Pacific and Atlantic Burmeister’s porpoise comprise two different stocks based on differences in body length. On the other hand, recent studies support the genetic differentiation among Burmeister’s porpoises from Peru and Chile-Argentina (Rosa et al. 2005).

Considerable effort has been given globally to managing impacted populations of small cetaceans. The first step in this management is to define the populations involved (e.g., Secchi et al. 2003), and one tool is use geographic variation through morphology analyses (Perrin 1984). Morphometrics techniques using skulls have been use for geographic variations studies in marine mammals using traditional morphometrics (e.g., Amano and Miyazaki 1992; Amano et al. 2002; Beasley et al. 2002; Brunner 2002; Brunner et al. 2002; Jefferson 2002; Perrin et al. 1994; Ramos et al. 2002; Schnell et al. 1986) and geometrics morphometrics (e.g., Drehmer 2005; Higa et al. 2002; Monteiro-Filho et al. 2002; Oliveira et al. 2005; Sanfelice 2003). Considering that morphological structures in an organism have two components (size and shape), and that shape is the most informative for defining biological entities in nature (Atchley et al. 1992; Patton and Brylski 1987), the goal of this study is to explore the geographical variation in size and shape in skulls of *P. spinipinnis*, and whether differences between males and females follow the same patterns along the geographic range studied.

MATERIALS AND METHODS

Samples.— Skulls of 102 *P. spinipinnis* (61 males and 41 females) were examined to explored the geographical variation in size and shape. The skulls were obtained from museums and scientific collections from the following locations and years: In Peru, 60 porpoises (from 7 localities), were a mixture from incidentally, directly-caught or stranded during the period 1984 to 2001, mainly from 1984-1987, and 1998-2001; In Chile, 28 Burmeister’s porpoises from 5 localities were incidentally caught or stranded during the years 1986 to 2004, including two additional individuals collected from central Chile in 1894 and 1967; Argentina samples included 11 individuals from 6 localities collected from incidental catch and stranding events during the period 1975 to 2002, with an additional specimen collected in 1903; the Uruguayan samples comprised two stranded specimens in 2002 and 2004, respectively; and a single Burmeister’s porpoise from Brazil stranded in 1986 (Fig. 1, Appendix 1).

Data analysis.— For analysis of geographical variation in relation to size and shape of Burmeister's porpoise skull, we employed traditional (linear) morphometrics (Marcus 1990) and geometric morphometrics (Bookstein 1991, 1996; Dos Reis et al. 2002a, 2002b; Marcus et al. 1993; Marcus et al. 1996; Monteiro-Filho et al. 2002; Oliveira et al. 2005; Rohlf and Marcus 1993; Sanfelice 2003; Zeldich et al. 2004). We analyzed skulls of physically mature specimens and the samples were grouped by geographic origin following the methodology used by Molina-Schiller (2006.). Based in that study the skulls were separated in three geographic areas (Peru, Chile and Atlantic), because the sample size from the Atlantic coast (Argentina, Brazil and Uruguay) was small (n = 14), and the multivariate analyses indicated no differences between these localities ($P > 0.05$). Therefore, the samples from Atlantic were pooled in a single group named "Atlantic".

Traditional (*linear*) *Morphometrics*.— We took twenty-eight cranial measurements using a 300mm digital caliper (Figs. 2A-C). The characters were based on those taken for *P. spini*pinnis (Brownell and Praderi 1982; Brownell and Praderi 1984; Molina-Schiller 2006.; Pinedo 1989; Reyes and van Waerebeek 1995; Simões-Lopes and Ximenez 1989), *Phocoena phocoena* (Noldus and de Klerk 1984; Stuart and Morejohn 1980; Yurick and Gaskin 1987), Dall's porpoise, *Phocoenoides dalli* (Amano and Miyazaki 1992), spectacled porpoise, *Phocoena dioptrica* (Perrin et al. 2000), *Neophocaena phocaenoides* (Amano et al. 1992; Jefferson 2002). All measurements were taken by DMS, thereby eliminating the potential problem of inter-observer bias. Due to the small number of the mandibles, the associate measures were not included in the analysis. Differences in sample size for each character was due to missing or broken bones in some skulls. The available sample size by sex for geographic origin was as follow: Peru (males = 42 and females = 18), Chile (males = 13 and females = 15), and Atlantic (males = 6 and females = 8).

We employed Student t-test univariate analysis to verify the existence of significant differences between sexes within each geographic area, and the differences between means were tested using Hotelling T^2 multivariate (with casewise MD). Analysis of Variance/ Multivariate Analysis of Variance (ANOVA/MANOVA) were realized using General Liner Models (GLM) to test the effects of sex, geographic area, and interaction between those variables. In addition, we carried out Bonferroni *post hoc* test comparison. A canonical discriminant analysis was applied to identify the subset of variables that, taken in linear combination, shows the greatest degree of geographic variation by sex and geographic area.

In addition, to explore the geographical variation of skulls without the influence of sex, we applied the method of adjusting for sex differences described by Schnell et al. (1985). These authors developed a series of corrections terms to adjust measurements of the larger sex downward and the smaller sex upward, thus producing sex-ajusted or “zwitter” (from a German word for hermaphrodite or hybrid) measurements. These corrections have been employed here so that specimens of the two sexes could be combined for an overall analysis of geographic variation. Characters were standardized so that means were zero and standard deviation one. After conversion to zwitters, means were computed for each character, and these were employed in principal components analysis (PCA), and discriminant analysis.

Canonical correlation analysis (CCA) were realized to explored the correlation among twenty morphological variables (characters that showed significant difference by geographical area in the two-way analysis of variance), and eigth environmental variables (latitude, longitude, temperature at 0m depth, temperature at 50m depth, salinity at 0m depth, salinity at 50m depth, oxygen at 0m, and oxygen at 50m depth). In this analysis, we standardize the data-using LOG10. The environmental variables were obtained from data utilized by Molina-Schiller et al. (2005). We utilized historical average from 1965 to 2000 of the first 5 minute of latitude and longitude of temperature, salinity, and dissolved oxygen (0 and 50m depth) from

Paita, Peru (05°01’S, 81ºW), in the Pacific Ocean to Santa Catarina, Brazil (28°48’S, 49°12’W) in the Atlantic Ocean. All statistical analyses realized in this study were performed using Statistic Program 6.0 for Windows.

Geometric morphometrics.— For this kind of analysis, it is necessary to use specimens with whole and unbroken skulls, so that all landmarks can be digitize in each image. Therefore, we took digital images of 240 skulls in three views: dorsal (40 males and 16 females from Peru; 9 males and 11 females from Chile, and 4 males and 7 females from Atlantic), ventral (35 males and 15 females from Peru; 7 males and 13 females from Chile, and 5 males and 7 females from Atlantic), and lateral (31 males and 15 females from Peru, 7 males and 7 females from Chile, and 4 males and 7 females from Atlantic). The images were obtained with a Sony Cyber-Shot 5.0 mega pixels digital camera with a resolution of 2048 x 1536 pixels, and always included a scale. All images were saved on *JPEG* format. We used TpsUtil 1.2 software (Rohlf 2004) to organize the images. Anatomical landmarks, assumed morphologically and topologically equivalent in all specimens, were selected to describe the variation in skull shape, and were digitized for each specimen (Fig. 2) using TpsDig32 software (Rohlf 2004). For each view, homologous points (landmarks) were identified and defined (Figure 2). The full set of landmarks for each view is referred to as the configuration (Dryden and Mardia 1998). Landmarks were defined as follows:

Dorsal view (Fig. 2D): 1-9 = rostral tip, 2-8 = anterior point of the notch in the maxilla, 3-7 = intersection between the frontal bone and zygomatic process, 4-6 = intersection between supraoccipital suture and posterior-most point on the curve of the parietal, 5 = posterior-most point on the edge of the supraoccipital, 10-11 = posterior-most point of premaxilla at midlength of rostrum, 12-13=posterior-most point on the curve of the premaxillae, 14-15 = posterior-most point on nasal bone,16 = midpoint frontal prominence, 17-18 = intersection between frontal suture and supraoccipital suture.

Ventral view (Fig. 2E): 1-11= rostral tip, 2-8 = anterior point of the notch in the maxilla, 3-9 = anterior point of preorbital, 4-8 = anterior point of postorbital, 5-7 = posterior-most point on the curve of the parietal, 6 = posterior-most point on the edge of the supraoccipital, 12 = midpoint of pterygoid, 13-4 = inferior tip of basioccipital.

Lateral view (Fig. 2F): 1 = rostral tip, 2 = anterior point of the notch in the maxilla, 3 = anterior point of preorbital, 4 = anterior point of postorbital, 5 = intersection between supraoccipital suture and posterior-most point on the curve of the parietal, 6 = posterior-most point on the edge of the supraoccipital, 7 = midpoint frontal prominence, 8 = posterior-most point on the curve of the premaxillae, 9 = posterior-most point of temporal fossa, 10 = anterior-most point of temporal fossa, 11 = superior-most point of length temporal fossa, 12 = intersection between inferior-most point of length temporal fossa and mastoid process, 13 = posterior-most point on nasal bone.

The coordinates and centroid size were calculated using CoordGen (Sheets 2000). Centroid size is the mean square root of distances from each landmark to the centroid (mean of all coordinates) of landmarks (Bookstein 1991). ANOVA/MANOVA were performed on mean centroid sizes between sexes, geographic area, and interaction between sex and geographic area.

To compare shape, the coordinates for each specimen were superimposed on each other by generalized least squares Procustes superimposition (GLS) to create a mean configuration. Generalized least squares superimposes specimens, minimizing the Procustes distance (square root of squared distance between each landmark and its homologue, summed over all landmark) between landmark configurations due to differences in scale, position, and orientation. This removes differences unrelated to shape (Rohlf and Slice 1990; Slice 1996).

To explore patterns change on shape in *P. spinipinnis*, we first explored the relationship between shape and sexual dimorphism using TwoGroupsGen (Sheets 2000). For these data the Goodall's F test was computed to verify difference between sexes on shape using partial Procustes distances (resampling test was computed after 1600 bootstrap iterations). Here the coordinates are superimposed using GLS with the specimens rescaled to unit centroid size. After confirming the sexual dimorphism on skull shape of *P. spinipinnis*, we computed partial warps matrix (including the uniform component) using Regress6c and CVAGen (Sheets 2000). Canonical variates analyses were used to describe differences by geographic area. The differences along the 1st and 2nd canonical variate were computed by regressing shape on canonical variates analysis scores (Rohlf et al. 1996). Partial warp scores were used in ANOVA/MANOVA and ordinal analysis (Rohlf et al. 1996) to test differences by geographic area for the three views. Mahalanobis distances (D^2) from canonical variates scores of males and females for each geographic area was calculated using the *a priori* group assignments. All statistical analyses of ANOVA, MANOVA and multivariate exploratory techniques were performed using software Statistics 6.0 for Windows and IMP program (Sheets 2000).

The two-block partial least squares (2B-PLS) method was used to explore the pattern of covariation between shape variation using partial warp scores (uniform component included) and a set of environmental variables (latitude, longitude, temperature, salinity, and oxygen at 0m and 50m depth, respectively). 2B-PLS constructs pairs of variables that are linear combinations of the variables within each of two sets analysis (Rohlf and Corti 2000; Sampson et al. 1989). NTSYS (Numerical Taxonomy and Multivariate Analysis System, version 2.11V, Rohlf 2002) was used for matrix comparison, and 2B-PLS was computed using TpsPLS (Rohlf 2004). The environmental variables were standardized but the partial warps were not (because they are already in the same units). Scatter plots of the projections of the standardized variables and partial warp scores onto their paired vectors were obtained with $\alpha = 0$ separately for the dorsal, ventral and lateral views. To assess whether covariation is more concentrated into the first few dimensions than would be expected by chance, we use a permutation test (with 999 random permutations). For the ordination of variables, the estimated shape was showed as a thin-plate spline deformation of the reference.

RESULTS

Traditional (*linear*) *morphometrics*

Sexual dimorphism in relation to geographic variation.— Results of the *t*-test indicated sexual dimorphism in skulls of physically mature Burmeister's porpoises from Peru, Chile and Atlantic (Table 1). In samples from Peru, the results of Hotelling T^2 test showed significant differences between sexes ($T^2 = 590.268$, $F = 4.8185$, $P = 0.01298$). The *t*-test showed that the females were significantly larger than males ($P < 0.05$) in five characters (length of rostrum from base, height of rostrum at midlength, length of orbit, greatest width of frontal prominence and length of upper tooth row) (Table 1). In Burmeister's porpoises from Chile, the Hotelling T^2 multivariate test cannot be computed, whereas the *t*-test showed that females were larger than males in four characters (skull height, least distance between occipital condyles, greatest width of temporal fossa and length of pterygoid) ($P < 0.05$) (Table 1). In samples from Atlantic, *t*-test showed that the females were larger than males in ten characters (condylobasal length, length of rostrum from base, width of rostrum at base, distance from tip of rostrum to external nares, skull height, greatest width of internal nares, length of neurocranium, least distance between occipital condyles, distance from tip of rostrum to pterygoid hamuli and greatest width of pterygoid) ($P < 0.05$), while thet distance from maxilar to occipital crest in males was larger than in females ($P < 0.05$) (Table 1). Hotelling T^2 multivariate test cannot be computed.

Multivariate test of significance showed significant differences between sexes (Wilks' Lambda = 0.2294, $F = 2.7592$, $P = 0.0077$); geographic area (Wilks' Lambda = 0.0020, $F =$

17.539, P = 0.0000); and interaction between sex and geographic area (Wilks' Lambda = 0.1081, F = 1.6770, P = 0.03641). On the other hand, Bonferroni *post hoc* test, showed significant differences for sex in eight characters ($P < 0.05$), geographic area in 20 characters ($P < 0.05$), and for the interaction between sex and geographic area in 17 characters ($P < 0.05$).

In females, the discriminant function analysis revealed that three characters (10.7%) (greatest width of premaxillae, length of rostrum from base, and distance from maxilar to occipital crest) best represented the differences among the geographic areas (Wilks' Lambda = 0.0051; F = 76.706, $P < 0.0000$) (Table 2). All specimens from Peru (n = 20) were classified correctly. However, Burmeister's porpoises from Chile (n = 14) presented a 73.33% of successful in predicted classifications, while that porpoises from Atlantic (n = 10) was 66.70%. Females from Chile and Atlantic showed overlap in 7 specimens, three from Chile and four porpoises from Atlantic (Fig. 3A). Evaluation of the standard coefficients of the canonical discriminant analysis indicated that two characters (greatest width of premaxillae and length of rostrum from base) in the first root and distance from maxilar to occipital crest in second root best represent the difference among the geographic areas (Table 2). The squared Mahalanobis distances (D^2) values show a clear separation of Burmeister's porpoises by geographic area, especially among females from Peru and Atlantic (D^2 = 393.40, P = 0.0000), followed by females from Peru-Chile (D^2 = 303.38, P = 0.0000), and finally females from Chile-Atlantic (D^2 = 17.02, P = 0.0004).

In males, the canonical discriminant analysis indicated that fifteen characters (53.6%) best represented the differences among the geographic areas (Wilks' Lambda = 0.00276, F = 43.320, $P < 0.0000$) (Table 3, Fig. 3B). The discriminant function classified correctly all specimens from Peru (n = 35), Chile (n = 9) and Atlantic (n = 5). Evaluation of the standard coefficients of the canonical discriminant analysis indicated that three characters (greatest width of premaxillae, skull height, and greatest parietal width) in the first root and two characters (width of rostrum at midlength, and width of rostrum at base) in second root best represent the difference among the geographic areas (Table 3). No overlap occurred among the three geographic areas (Fig. 3B). The squared Mahalanobis distances (D^2) values show a clear separation of Burmeister's porpoises by geographic area, especially among males from Peru and Chile ($D^2 = 506.08$, $P = 0.0000$), followed by males from Peru-Atlantic ($D^2 = 486.28$; $P = 0.0000$), and males from Chile-Atlantic ($D^2 = 40.38$, $P = 0.0003$).

Geographic variation.— After conversion of males and females to zwitters specimens, and to explore the geographical variation of the skulls without the influence of the sex, means were computed and the results of the *t*-test indicated significant differences in all characters among skulls of Burmeister's porpoises from Peru ($n = 60$) and Chile ($n = 28$) ($T^2 = 225720$, $F = 3430.4$, $P < 0.0000$), and between porpoises from Peru ($n = 60$) and Atlantic ($n = 15$) ($T^2 = 386938$, F=5527.7, $P < 0.0000$). However, two characters were not significant (greatest width of left premaxilla and greatest width of frontal) ($P > 0.05$) among Burmeister's porpoises from Chile (n = 28) and Atlantic ($n = 15$). On the other hand, multivariate tests of significance showed significant differences by geographic area (Wilks' Lambda=0.0000, $F = 3918.07$, $P = 0.0000$), and ($T^2 = 8638.09$, $F = 4164.79$, $P < 0.0000$). In addition, the Bonferroni *post hoc* test, presented significant differences in all characters.

The canonical discriminant analysis revealed that a single character, greatest postorbital width (GPOW) best represented the differences among the geographic areas (Wilks' Lambda = 0.00080; $F = 34486$, $P < 0.0000$). The discriminant function was 100% successful in the classification of the specimens from three geographic areas: Peru ($n = 60$), Chile ($n = 28$), and Atlantic ($n = 15$). The functions by geographic area using zwitter were:

Peru = - 433.701 + 7.820 (GPOW)

Chile = - 775.333 - 10.449 (GPOW)

Atlantic = - 1123.24 - 12.58 (GPOW)

The squared Mahalanobis distances (D^2) values showed a clear geographic separation among specimens from Peru, Chile, and Atlantic (P = 0.0000). The larger distances were observed among porpoises from Peru and Atlantic (D^2 = 6219.16), followed by specimens from Peru-Chile (D^2 = 4987.79), whereas Burmeister's porpoises from Chile-Atlantic showed the smaller distances (D^2 = 67.85).

The first two principal components explained 76.48% and 21.83%, respectively of the total observed variability (Fig. 4). All characters analyzed presented highest loadings. Twenty-three characters showed highest loadings on component I, and in twenty characters the eigenvectors were negative, suggesting that they are correlated with shape, while three characters that were positive (greatest width of left premaxilla, height of rostrum at midlength, and length of upper tooth row) would be correlated with size factor (Table 4, Fig. 4). The component II, showed highest loadings in five characters (greatest length of temporal fossa, greatest width of frontal prominence, length of pterygoid, distance from maxilar to occipital crest, and greatest width of temporal fossa) with eigenvectors positive, suggesting that they are correlated with size factor, whereas that only 1 character (greatest width of frontal prominence) presented eigenvectors negative (Table 4, Fig. 4). Scores of the specimens in the first two components are delineating three groups based on geographic variation (Fig. 4). The PCA also indicates a separation between three geographic areas along the second principal component axis, pointing to the existence of geographic differences in size and shape among these three populations.

Correlation between linear variables and environmental variables.—In canonical correlations analysis, the Chi-Square tests showed that the first canonical root was statistically significant (R^2 = 0.98; χ^2 = 353.14; P = 0.0000). The canonical loadings in the first canonical function showed high correlations in five environmental variables (oxygen at 50m depth, latitude, salinity at 50m depth, longitude, and temperature at 0m depth). The linear variables showed high correlation in three variables (greatest width of premaxillae, greatest width of frontal, and greatest postorbital width) (Table 5). The results showed that these variables are larger for specimens from Chile and Atlantic, associated to high latitudes, in colder, more oxygenated, and less saline waters, whereas that these morphological variables are smaller for Burmeister's porpoises from Peru associated to low latitudes, in warmer, less oxygenated, and more saline waters (Table 5, Fig. 5).

Geometric morphometrics

Size.— The size represented by centroid size for dorsal view were not significant by sex, and for the interaction sex and geographic area ($P > 0.05$). However, the two-way ANOVA showed significative differences by geographic area ($F = 6.903$, *d.f.* = 2, $P = 0.001$), being the Burmeister's porpoises from Atlantic larger than porpoises from Chile, whereas that Peruvian porpoises were smaller than Chilean specimens. In ventral view, the two-way ANOVA by sex, showed significant differences on centroid size ($F = 10.82$, *d.f.* = 1, $P = 0.001$), being the females larger than males. However, these differences were not significative by geographic area, and for the interaction between sex and geographic area ($P > 0.05$). In lateral view, the results of two-way ANOVA were similar to dorsal view, and differences were only observed by geographic area ($F = 10.32$, *d.f* = 2, $P = 0.019$), but the mean centroid size was larger in Burmeister's porpoises from Peru, followed by specimens from Atlantic, and Chile.

Sexual dimorphism on shape.— The Procustes distances between mean shape showed sexual dimorphism in skulls of Burmeister's porpoises for the three views ($P < 0.01$) (Table 6). Diagram with average configuration of skull shape of males and females showed that the sexual dimorphism in shape was more evident for dorsal and lateral views (Fig. 6). For dorsal view, females have in general thinner and longer rostrum compared to males, while the braincase is more compressed in females (Figs. 6A and 6C). Ventral view showed little difference in skull shape (Table 6), and these were related to rostral region (Figs. 6D and 6F). In Lateral view, the differences on shape were similar to observed for dorsal view in rostral region and braincase. The distance between preorbital and postorbital were relatively longer in males, while the midpoint frontal prominence was broader in males than in females (Figs. 6G and 6I).

Geographic variation on shape.— For dorsal view, 32 relative warps showed shape changes associated with the first two canonical axes separating both males and females in three geographic areas (Peru, Chile, and Atlantic). In males, the first two canonical axes in the CVA explained 90% of the observed variation, separating clearly Burmeister's porpoises from Chile, Peru and Atlantic (Fig. 7A). The MANOVA performed on the first axis was highly significant (Wilks' lambda = 0.0192, $\chi^2 = 162.0920$, *d.f.* = 38, $P = 0.0000$), separating males from Chile, while a geographic separation between specimens from Peru and Atlantic was observed along the second axis (Wilks' lambda = 0.3478, $\chi^2 = 43.3017$, *d.f.* = 18, $P = 0.0007$). Males from Peru showed a more compressed rostral region than Atlantic specimens, and braincase region was broader and more compressed compared to Bumeister's porpoises from Chile and Atlantic. Males from Chile were more compressed in rostral region (Fig. 8). In females, on the other hand, the first two canonical axes for dorsal view explained 98% of the observed variation, separating Atlantic specimens along the first axis (Wilks' lambda = 0.0016, $\chi^2 = 135.7029$, *d.f.* = 42, $P = 0.0000$), while Burmeister's porpoises from Chile and Peru presented separation along the second axis (Fig. 7B), but this axis was non-significant ($P = 0.0742$). Females from Chile and Atlantic showed a thinner rostrum than those from Peru, and porpoises from Chile showed a more compressed rostral region than the other specimens. The braincase was broader and more compressed in females from Peru than those from Chile and Atlantic (Fig. 8). The discriminant function based on Mahalanobis distance for dorsal view classified correctly males (Peru = 40, Chile = 9, and Atlantic = 4) (Fig. 7A) and females (Peru = 16, Chile = 11, and Atlantic = 7) (Fig. 7B). Mahalanobis distances (D^2) values showed a clear geographic separation among specimens from Peru, Chile, and Atlantic (P = 0.0001), showing a larger separation among porpoises from Peru-Atlantic (P = 0.0000). However, D^2 value for females from Chile-Atlantic was non-significant (P = 0.2103) (Table 7). This suggests that for dorsal view, males are more variable in skull shape than females, and that Burmeister's porpoises from Chile and Atlantic presented less differences in skull shape, especially between females.

In ventral view, the 24 relative warps showed differences on skull shape and the first two canonical axes explained 91% of the observed variation in males (Fig. 9A) and 86% for females (Fig. 9B). Both males (Wilks' lambda=0.02274, χ^2 = 122.9696, *d.f.* = 48, P = 0.0000) and females (Wilks' lambda = 0.0073, χ^2 = 100.7771, *d.f.* = 48, P = 0.0000) from Chile were separated along the first canonical axis. The second axis separated specimens from Peru and Atlantic, but these differences were not significant for males (P = 0.1199) and females (P = 0.0742). The Chilean specimens presented an intermediate shape between specimens from Peru and Atlantic. The specimens of Peru seem to be smaller than the other porpoises. The rostrum is smaller, and the braincase region was more compressed and the distance between rostral tip to midpoint of pterygoid region, orbital region, and supraorbital were shorter compared to Burmeister's porpoises from Chile and Atlantic. Specimens from Atlantic in general were larger than porpoises from Peru and Chile (Fig. 10). The discriminant function o based on Mahalanobis distance for ventral view classified correctly all males (Peru = 33, Chile = 9, and Atlantic = 5) (Fig. 9A) and females (Peru = 15, Chile = 13, and Atlantic = 7) (Fig. 9B) from the three geographic areas. Mahalanobis distances values showed separation among three geographic areas ($P < 0.05$) similar to obtained for dorsal views (Table 7).

In lateral view, 22 relative warps showed shape changes associated with the first canonical axes for males and females from Peru, Chile, and Atlantic. The first canonical axis explained 59% of the observed variation in males and 76% in females. In both males (Wilks' lambda = 0.0845, $\chi^2 = 67.9637$, *d.f.* = 44, $P = 0.012$) (Fig. 11A) and females (Wilks' lambda = 0.01732, $\chi^2 = 66.92052$, *d.f.* = 44, $P = 0.015$) (Fig. 11B), the first canonical axis separated Chilean specimens, while the second axis was not significant ($P > 0.05$). The differences in shape were similar to dorsal and ventral views. Burmeister's porpoises from Peru have smaller skull in rostral region compared to specimens from Chile and Atlantic, and the braincase was more compressed in males than in females. The orbital and rostral regions were relatively broader in porpoises from Atlantic than in Chilean and Peruvian specimens (Fig. 12). In general, the Chilean specimens presented an intermediate shape between Peru and Atlantic specimens (Fig. 12). The discriminant function on based Mahalanobis distance classified correctly all males (Peru = 31, Chile = 6, and Atlantic = 4) (Fig. 11A) and females (Peru = 15, Chile = 8, and Atlantic = 7) (Fig. 11B). However, the Mahalanobis distances values obtained were not significant among the three geographic areas ($P > 0.05$) (Table 7).

Covariation between shape variation and environmental variables.— For dorsal view, the two-block partial least-squares analysis revealed that skull shape was significantly associated with environmental variables used in this study. The fist two paired latent variables explain 92.47% and 5.33% of the total squared covariance (0.0064) between the two set of variables. The other singular values were much smaller and not statistically significant. In 999 random permutations three singular values (0.30%) were equal to or larger than the observed value for the first dimension. For the other dimensions, all of the random samples yielded greater squared covariances than were found in the observed data. The first pair of latent variables also presented the best correlation (0.85) (Fig. 13B). The other correlations were lower and of little interest (even though were statistically significant) because the corresponding latent variables explained so little of the cross-set covariance (Table 8). The results are largely one-dimensional, because the first dimension explained most of the variance and the other dimensions were not statistically significant, we can expect to interpret only the first dimension in dorsal view. The first dimension has its greatest negative loadings on latitude and oxygen at 50m depth. While that greatest positive loadings were observed on temperature - salinity at 0m of depth, and longitude (Table 8). These gradients show the important of spatial variation on shape of skull. The Figs. 13G and 13F show the shape differences expressed as deformations of the average shape using thin-plate splines, estimating the shapes corresponding to a point at the negative and positive extremes observed for the first pair of variables. For one-dimensional data, the results can be displayed as a pair of shapes representing the observed variation. For point negative extreme, the skull seems to be narrower in rostral region and more compressed in braincase (Fig. 13D), and only two variables (oxygen at 50m of depth and latitude) showed positive loadings (Fig. 13C). On the other hand, for point positive extreme three variables presented negative loadings (Fig. 13E), and the shape changes were observed lightly on rostral region, but the skull seems to be more broader in rostral and braincase region (Fig. 13F).

For ventral view, the 2B-PLS analysis showed that skull shape was significantly associated with environmental variables use is this study. The fist two paired latent variables explain 96.40% and 1.84% of the total squared covariance (0.0022) between the two set of variables. The other singular values were much smaller and nor statistically significant. In 999 random permutations one singular values (0.10%) were equal to or larger than the observed value for the first dimension. For the other dimension, all of the random samples yielded greater squared covariances than were found in the observed data. The first pair of latent variables also presented the best correlation (0.79) (Fig. 14B). The other correlations were lower and of little interest (even though were statistically significant) because the corresponding latent variables explained so little of the cross-set covariance (Table 8). In this cranial view, the results also were one-dimensional. The first dimension has its greatest negative loadings on latitude, and oxygen at 50m depth. While that greatest positive loadings were observed on salinity at 50m depth, and temperature at 0m and 50m depth (Table 8). Shape differences using thin-plate splines for the point negative extreme showed that five variables presented positive loadings (Fig. 14C), and the braincase was more compressed than rostral region (Fig. 14D). For the point positive extreme, only oxygen at 50m depth and latitude showed greatest negative loadings (Fig.14E), and a braincase lightly compressed (Fig. 14F).

For lateral view, the 2B-PLS analysis revealed that skull shape was significantly associated with environmental variables use is this study. The fist two paired latent variables explain 91.41% and 4.57% of the total squared covariance (0.0051) between the two set of variables. The other singular values were much smaller and nor statistically significant. In 999 random permutations forty-three singular values (4.3%) were equal to or larger than the observed value for the first dimension. The first pair of latent variables also presented the best correlation (0.46) (Fig. 15B). The results also were one-dimensional, similar to dorsal and ventral views. The first dimension has its greatest negative loadings on latitude, and oxygen at 50 and 0m depth. The greatest positive loadings were observed on salinity at 50 and 0m of depth, temperature at 0-50m of depth, and longitude (Table 8). For the points negative and positive extremes, the environmental variables presented similar loadings to dorsal view. However, for point negative extreme, the salinity at 50m depth showed greatest negative loadings than for dorsal view (Fig. 15C). Thin-plate splines showed a skull more compressed for the point negative extreme (Fig. 15D) than for point positive extreme (Fig. 15F). This confirmed the differences observed by other views (dorsal and ventral), showing that skulls from high latitudes have rostrum thinner, and the frontal region is more prominent than skulls from low latitudes.

DISCUSSION

We observed sexual dimorphism in skull of physically mature porpoises by traditional and geometric morphometrics analyses, being females larger than males. These methods detected differences concentrated in the rostral and braincase region, and the shape differences were more explicative in dorsal and lateral views. The sexual dimorphism observed in this study corroborates the differences by sex found by Molina-Schiller (2006), but not coincident with the results found by Reyes and van Waerebeek (1995) using cranial measurements. These authors say that skulls of males from Peru are larger than females, but they used skulls of Burmeister's porpoises sexually mature and the sample size was small.

Although the samples used in this study are small (especially from Chile and Atlantic), a clear geographical variation pattern among Burmeister's porpoises from Peru, Chile and Atlantic was detected by traditional and geometric morphometrics methods. In general, males and females from Peru were smaller in several measures (e.g., condylobasal length, zygomatic width, distance from tip of rostrum to external nares, and width of rostrum at midlength, characters associated to braincase and feeding functional apparatus) in relation to Burmeister's porpoises from Chile and Atlantic. This indicates that *P. spinipinnis* from Peru are shorter in rostral region and broader (or robust) in neurocranium than porpoises from Chile and Atlantic. In addition, traditional methods by canonical discriminant analysis showed that greatest width of premaxillae is useful for separate Peruvian specimens of the other geographic areas.

Burmeister's porpoises from Chile presented a size and shape intermediate between Peruvian and Atlantic specimens, whereas that porpoises from Atlantic were relatively longer than Chilean specimens. On the other hand, the orbital region was relatively larger in males and females from Atlantic than Chilean porpoises. Females from Chile and Atlantic showed a rostrum thinner and larger than Peruvian specimens, while that Burmeister's porpoises from Atlantic were larger than females from Chile, mainly related to skull height, orbital region (greatest postorbital width), and rostral region (width of rostrum from base, greatest width pterygoid). These differences were supported by squared Mahalanobis distances, showing a larger separation among porpoises from Peru and Atlantic, while that these differences were smaller between specimens from Chile and Atlantic. These results corroborate the proposed by Corcuera et al. (1995). These authors, based in body size suggested that Burmeister's porpoises from the South Atlantic coast are larger than those from the South Pacific.

Geometric morphometrics was more explicative to show differences between specimens from Chile and Atlantic, especially for dorsal and ventral views, showing that males are more variable in skull shape than females.

The utilization of correction factor for obtained zwitter specimens was very useful for verify the differences in size among Burmeister's porpoises without the influence of the sexual dimorphism. The canonical discriminant analyses distinguish 100% of specimens from Peru, Chile and Atlantic. The analyses corroborate with squared Mahalanobis distances values showing a clear geographic separation among specimens from Peru, Chile, and Atlantic, where the larger distances were observed among porpoises from Peru and Atlantic, and the smaller distances were between Burmeister's porpoises from Chile - Atlantic, corroborating with the observed geometric morphometrics patterns. On the other hand, the canonical discriminant analysis showed that greatest postorbital width is useful for distinguishing specimens from three geographic areas.

Perrin (1984) discussed patterns of geographical variation in small cetaceans, showing that small cetaceans vary sharply over sometimes relatively short distances. Differences in body shape, colorations and skull size were observed between animals in enclosed/open seas (dolphins in enclosed or semi-enclosed tend to be smaller than those of the same species in the open ocean), whereas that differences in size and shape of skull, body length, and colorations were found between dolphins in inshore/offshore waters (offshore forms tend to be larger than inshore specimens). Other examples about geographical variation were observed in small coastal cetaceans with longer distribution, showing differences in size and shape (e.g., *P. blainvillei*, Ramos et al. 2002; *Neophocaena phocaenoides*, Jefferson 2002; *Orcaella brevirostris*, Beasley et al. 2002).

Very few analyses are available that document the association between morphological and environmental variation in marine mammals (e.g., Perrin 1984; Schnell et al. 1986). In Pacific coast, porpoises form Peru and Chile showed a clinal distribution, coincident with Bergmann's Rule (Bergmann 1847). This is a principle that correlates environmental temperature with body mass in warm-blooded animals. It asserts that within a species, the body mass increases with latitude and colder climate. Among mammals and birds, individuals of a particular species in colder areas tend to have greater body mass than individuals in warmer areas (e.g., Mayr 1973; Roberts 1953, 1978; Ruff 1994; Schreider 1950). The correlation between linear variables and environmental variables as covariation between shape variation and environmental variables showed that specimens from Pacasmayo (07°24'S; 79°35'18"W) northern Peru to Paracas (13°50'S; 76°14'W) southern Peru showed a shorter rostrum and a less compressed braincase. These specimens were associated to low latitudes, with more temperate waters, less oxygenated and more saline waters. In addition, it has the influence of the Humboldt Current, which involves upwelling that carries colder water rich in nutrients, and oxygen minimum zone (OMZs) (Escribano et al. 2003; Molina-Schiller et al. 2005; Strub et al. 1998; Tarazona and Arntz 2001).

Burmeister’s porpoises from Chile presented a longer and thinner region rostral and a frontal region more prominent than skulls from low latitudes. Chilean porpoises were associated to high latitudes, austral waters more oxygenated; it has the influence of the

Humboldt Current (influence of upwelling) and downwelling processes, Cape Horn Current, and less saline waters by freshwater contributions from fjords, glaciers and rivers (Blanco et al., 2001; Molina-Schiller et al. 2005; Panella et al. 1991).

On the other hand, in the Atlantic coast the skulls of *P. spinipinnis* were larger than porpoises from Pacific coast, however, the clinal distribution and Bergmann's Rule were not observed. This are is characterized by the confluence of the Brasil Current and Malvinas Current results in complex meso-scale circulation patterns like warm or cold-core rings, eddies, and filaments (Legeckis & Gordon 1982, Olson et al. 1988, Gayoso & Podestá 1996). The distribution ranges of Burmeister’s porpoises from south of the La Plata River, Argentina to Santa Catarina, Brazil should be associated to Subtropical Convergence (Molina-Schiller et al. 2005). These authors suggest that Burmeister’s porpoises present a continuous distribution from Paita, Peru (05°01’S, 81°W) to La Plata River basin, Argentina (~38°S), being able to reach Uruguayan and Brazilian waters under certain oceanographic characteristics (intrusion of colder and less saline waters toward the north associated with the Subtropical Convergence). The zone between 30ºS and 40ºS has a high variability in physical and chemical properties and represents an ecotone of high biological diversity, with freshwater contributions from rivers, the basin of La Plata River, and the estuarine system of Patos Laggon (Calliari et al. 2003; Panella et al. 1991; Piola et al. 2000; Sabatini et al. 2004). In addition, peaks of phytoplankton biomass have been found associated with frontal structures (Gayoso and Podestá 1996). Marine mammal diversification thus could be closely related to nearshore upwelling through primary production and the availability of a variety of prey species (Lipps and Mitchell 1976). Important upwelling zone are found to north of Santa Catarina, Brazil (Matsura 1986; Pereira 1989; Silva et al., 1984).

Morphological differences maybe related to feeding, ecology, perhaps to differing size and toughness of major prey species (Perrin 1975; Ross 1979). The interruption or change in regular feeding habits caused by environmental events can influence the growth of individuals. The Humboldt Current System with its coastal upwelling ecosystem off Peru and Chile is recognized as a highly productive region, sustaining the large fisheries of anchovy and sardine (Alheit and Bernal 1993; Mann and Lazier 1991; Walsh 1991). However, Burmeister's porpoise in the upwelling system might be particularly vulnerable to local depletion as they inhabit a very rich, but unstable environment (e.g., recurrent El Niño events), because El Niño is more intense along the Peruvian coast, than the Chilean coast (Molina-Schiller 2006). These authors recorded three types of anomalies (marker lines, cemental disturbance, dentinal resorption) in teeth of seven individuals from Peru colleted between 1984 to 1998. The marker lines seem to be associated to environmental factors, because the data formation of these marker lines is coincident with events "El Niño".

Changes in size and age structure of population are expected when subjected to fishing effort, usually reducing mean body size and reproductive age (Jennings et al. 2001), and the Burmeister's porpoise from Peru is one the most common smalls cetacean in Peruvian waters, suffers the second highest fishing mortality (Brownell and Praderi 1982; Goodall et al. 1995b; Reyes and van Waerebeeck 1995; van Waerebeeck et al. 2002). The impact of incidental catches on a population may affect recruitment rates and may produce changes in growth rates of the individuals of that population (Gearin et al. 1994). The different body sizes and growth patterns may occur with population stock independent of latitudinal distribution (Ramos et al. 2002). In addition, recent studies support genetic differentiation among Burmeister's porpoises from Peru and Chile-Argentina (Rosa et al. 2005). However, these authors did not observe genetic differences among Burmeister's porpoises from Queule, southern Chile (39°22'S), and Tierra del Fuego, Argentina.

Geographic variation provides a basis for the description of stock units used to assess and manage dolphins (Schnell et al. 1986). Our results based in linear and geometric morphometrics suggest that geographical variation exists among Burmeister's porpoises from Peru, Chile and Atlantic, with smaller individuals distributed between Pacasmayo, northern Peru (07°24'S) to Paracas, southern Peru (13°50'S); larger specimens distributed from Chubut, southern Argentina (~42°46'S) to North, and *P. spinipinnis* with shape and size intermediate distributed from San Antonio, central Chile (33°30'S) to Strait of Magellan, southern Chile (~52°30'S).

A factor that must be considered in the results obtained in this study is the temporal difference between the data collected from the different locations, as well as the sampling type may have an influence on the size of specimens analysed. We recommende further studies to evaluate the differences found in this study. Further investigation on morphological-environmental variation would benefit not only from more and larger samples, but also from accumulation of other types of data. For example, detailed information on reproductive strategies, food habits of Burmeister's porpoises could provide insight concerning the relationship between functional morphology and feeding behavior, as well as a stronger basis for judging the significance of geographic trends in morphology. Genetic studies using teeth of the specimens examined in this study are being carried out, in order to verify the differences detected in this study.

RESUMEN

Cráneos de 102 *P. spinipinnis* físicamente maduros (61 machos y 41 hembras) fueron examinados para explorar la variación geográfica en tamaño y forma a través de morfometria tradicional y geométrica. Los cráneos provienen de museos y colecciones científicas de Perú, Chile, Argentina, Uruguay y Brasil. A través de análisis de ANOVA/MANOVA los especimenes fueron separados en tres áreas geográficas Perú (42 machos y 18 hembras), Chile (13 machos y 15 hembras) y Atlántico (6 machos y 8 hembras). Diferencias en tamaño y forma fueron analizadas usando 28 medidas lineares. Estas diferencias también fueron investigadas a través de morfometria geométrica aplicadas a imágenes bidimensionales de 240 cráneos en las posiciones dorsal, ventral y lateral. Además, el método de cuadrados mínimos de dos block (2B-PLS) fue usado para explorar el patrón de covariación entre la variación de forma usando escores de deformaciones parciales y un set de variables ambientales (latitud, longitud, temperatura, salinidad y oxigeno a 0 y 50m de profundidad, respectivamente). Dimorfismo sexual en tamaño y forma fue observado en cráneos de *P. spinipinnis* de las tres áreas geográficas, con hembras más grandes que los machos. Los resultados obtenidos usando morfometria linear y morfometria geométrica sugieren que existe variación geográfica entre *P. spinipinnis* del Atlántico, Chile y Perú, con individuos más pequeños distribuidos entre Pacasmayo, norte de Perú (07°24'S) hasta Paracas, sur del Perú (13º50'S) y especimenes más grandes distribuidos desde el Chubut, sur de Argentina (~42º46'S) hacia el norte. Especimenes de San Antonio, Chile central (33º30'S) hasta el Estrecho de Magallanes, sur de Chile (~52°30'S) mostraron una forma y tamaño intermedia en relación a las marsopas de Perú y Atlántico. Morfometria geométrica fue más útil para mostrar las diferencias entre los especimenes, mostrando que los machos son más variables en la forma del cráneo que las hembras; mientras que las hembras de Chile y Atlántico presentan

menor diferencia en la forma del cráneo. Las diferencias observadas en tamaño y forma de los cráneos de *P. spinipinnis* de las tres áreas geográficas parecen estar relacionada al patrón oceanográfico asociado en su distribución. Para evaluar las diferencias entre marsopas de Chile y Perú investigaciones adicionales (morfométricas y genéticas) son necesarias desde Chile central (33ºS) al norte.

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APPENDIX I

Specimens examined.– The 102 specimens used in his study were obtained from the following collections: Areas Costeras y Recursos Marinos, Pisco, Peru (ACO: 10, 27, 13, 53, 43, 07, 12, 09, N1, 38, 06, 148, 02); personal collection of Julio C. Reyes, Peru (JCR: NN5, nnn 24, NN4, 1457, 69, 1684, 758, 1278, 256, 702, 675, 196, 228, 17, 271, 975, 219, 730, 1334, 1578, 518, 749 1337, 125, 1628, 1627, 657, 747, 1150, 24, 76, 1458, 1484, 117, 46, NN3, 753, 724, 904, JSM 227, JSM 3, AJR 10, AJR 29); Museo Nacional de Historia Natural- Santiago, Chile (MNHN 588); Museo Municipal de Ciencias Naturales y Arqueología de San Antonio, Chile (MMCNASA: 52, 55, 73, 76, 48, 96, 91, 94, JLBM-3); Corporación Terra Australis, Valdivia, Chile (JAO: 99, 01, 02, 03, 04, 07, 08, 09, 10, 11, 96, 12, 13, 14, 15, 16); Museo de Zoología de la Universidad de Concepción, Colecciones Científicas, Concepción, Chile (MZUC-C:4148); Universidad de Magallanes, Punta Arenas, Chile (UMA: IPCMC-45); CENPAT, Puerto Madryn, Argentina (CENPAT: PS1, PS2, PS4); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN:3-32, 21864, 20489, 21020, 22221); Fundación Vida Silvestre Argentina, Buenos Aires, Argentina (N91-1, N90-28, N89-4); Universidad Nacional de Mar del Plata**,** Mar del Plata, Argentina (GMM: PS001); Facultad de Ciencias, Universidad de la República, Montevideo Uruguay (ZVCM 2115); Museo del Mar, Punta del Este, Uruguay (MUSMAR P1); Laboratório de Mamíferos Aquáticos da Universidade Federal de Santa Catarina, Florianópolis, Brazil (UFSC 1025).

Table 1.— Descriptive statistics of the metric characters (mm) in physically mature skulls of males and females of *Phocoena spinipinnis* from Peru, Chile, and Atlantic.

Characters (mm)	Peru							Chile							Atlantic						
	Males			Females				Males			Females				Males			Females			
	n	mean	*SD*	n	mean	*SD*	*P*	n	mean	*SD*	n	Mean	*SD*	*P*	n	mean	*SD*	n	mean	*SD*	*P*
1. Condylobasal length	42	276.04	7.04	18	279.00	7.16		11	281.59	9.10	12	284.77	5.10		5	277.55	6.94	8	285.48	5.14	*
2. Length of rostrum from base	42	122.79	4.11	18	125.69	4.02	**	11	120.24	6.47	13	123.57	4.16		5	115.63	3.52	8	122.10	3.86	**
3. Width of rostrum at base	42	76.45	4.06	17	75.77	4.24		13	79.34	5.22	15	80.57	3.41		6	79.95	3.29	8	84.69	4.20	*
4. Distance from tip of rostrum to external nares	42	147.84	5.12	18	150.51	4.78		11	150.20	6.92	13	152.75	4.04		5	144.91	4.99	8	153.46	3.42	***
5. Width of rostrum at midlength	41	51.17	2.89	16	51.60	2.63		11	55.52	3.42	12	57.45	4.76		5	51.34	3.57	7	54.43	2.08	
6. Greatest width of left premaxilla	42	12.78	0.86	16	12.57	0.84		10	13.98	1.48	11	13.06	0.79		5	13.67	1.01	7	13.03	0.96	
7. Height of rostrum at midlength	41	22.38	2.31	18	24.64	3.00	***	11	22.10	2.23	13	23.45	3.88		5	21.49	4.03	8	20.47	2.51	
8. Greatest width of premaxillae	42	17.45	1.74	18	18.28	1.81		13	39.60	3.70	15	40.10	2.96		6	39.80	1.97	8	40.86	1.83	
9. Skull height	42	133.79	3.97	18	132.86	5.75		13	129.95	8.53	15	134.98	3.77	*	6	133.01	2.78	8	137.47	2.61	**
10. Greatest preorbital width	42	125.61	6.19	17	123.65	6.84		13	128.52	6.36	14	132.73	4.93		6	130.18	8.76	8	135.68	4.73	
11. Greatest postorbital width	41	148.78	5.45	15	146.34	6.32		13	151.10	7.49	15	155.79	4.90		5	146.16	20.61	8	160.08	3.15	
12. Zygomatic width	36	148.47	5.76	17	147.52	6.41		9	156.01	7.04	11	160.50	4.75		4	156.27	9.58	8	164.06	3.87	
13. Greatest width of frontal	42	128.14	4.10	18	127.01	3.99		13	135.20	5.95	15	139.05	5.47		6	135.87	6.88	8	139.63	5.49	
14. Greatest width of internal nares	42	29.86	1.98	18	29.70	2.00		13	34.14	3.05	15	33.84	1.33		6	31.47	1.87	8	33.83	1.31	**
15. Greatest width of nasal	42	29.48	2.00	18	29.68	2.68		13	32.67	1.69	15	34.66	3.22		6	31.69	1.35	8	33.98	2.98	
16. Length of neurocranium	42	161.22	6.11	17	158.93	15.40		13	165.32	5.68	14	166.99	6.47		6	164.43	4.73	8	170.90	5.08	*
17. Greatest parietal width	42	133.00	3.80	18	131.32	3.59		13	137.81	4.50	15	139.86	3.53		6	140.43	3.58	8	142.57	2.72	
18. Least distance between occipital condyles	42	74.51	4.98	18	74.68	4.50		12	75.25	2.86	14	78.40	4.22	*	6	77.07	2.81	8	80.76	2.99	*
19. Greatest length of temporal fossa	41	55.24	2.81	18	55.52	2.70		13	55.64	4.08	14	57.07	4.79		6	54.02	3.01	7	52.77	0.95	
20. Greatest width of temporal fossa	41	46.74	2.66	18	46.61	4.19		13	47.69	3.75	15	51.00	2.69	**	6	50.38	2.50	8	51.31	2.77	
21. Distance from tip of rostrum to pterygoid hamuli	42	158.80	5.93	18	159.99	9.20		11	162.19	6.83	13	164.46	5.83		5	158.68	4.24	7	167.64	3.45	***
22. Width of palate at midlength of rostrum	40	44.72	2.78	18	45.34	3.05		11	46.20	3.41	13	47.46	2.78		5	46.78	3.96	8	48.50	2.46	
23. Length of orbit	42	52.13	2.71	18	54.28	3.57	**	12	53.59	3.31	15	56.65	5.41		6	50.73	5.66	8	55.28	2.04	
24. Greatest width of pterygoid	38	60.98	3.83	15	61.92	2.20		12	63.78	4.97	13	65.94	3.00		6	61.87	2.34	7	69.42	2.78	***
25. Length of pterygoid	39	55.49	2.76	17	57.13	3.53		12	57.84	3.46	13	61.45	3.52	**	6	59.91	1.97	7	61.72	2.10	
26. Greatest width of frontal prominence	42	32.53	3.63	18	34.62	3.75	*	13	38.22	5.89	15	36.66	4.30		6	32.72	3.59	8	36.48	2.97	
27. Distance from maxilar to occipital crest	41	13.96	2.43	17	13.46	2.83		13	14.31	3.10	15	15.52	4.50		6	18.52	4.27	8	13.54	1.76	**
28. Length of upper tooth row	40	75.68	3.47	18	79.70	6.45	***	11	68.99	7.84	12	71.29	4.66		5	67.20	4.08	8	69.67	5.79	

Results of Student *t*-test, level of significance: *$P \leq 0.05$; ** $P \leq 0.01$; ***$P \leq 0.001$

Table 2.— Classification function and standard coefficients of the canonical discriminant analysis in females of *Phocoena spinipinnis* for three geographic areas, Peru, Chile and Atlantic. The bold values indicate the characters that best showed the differences between geographic areas.

Characters	Classification functions			Standardized coefficients	
	Peru	Chile	Atlantic	Root 1	Root 2
Greatest width of premaxillae	-16.69	-5.180	-3.490	**-1.35083**	-0.031191
Length of rostrum from base	19.29	14.882	13.595	**1.01464**	0.682752
Distance from maxilar to occipital crest	9.91	9.714	8.343	0.14164	**1.028172**
Constant	-1121.84	-906.354	-796.986		
Eigenvalue				86.00058	1.255072
Cumulative proportion				0.98562	1.000000

Table 3.—Classification function and standard coefficients of the canonical discriminant analysis in males of *Phocoena spinipinnis* for three geographic areas: Peru, Chile and Atlantic. The bold values indicate the characters that best showed the differences between geographic areas.

Characters	Classification functions			Standardized coefficients	
	Peru	Chile	Atlantic	Root 1	Root 2
Greatest width of premaxillae	-6.57	8.92	10.51	**-1.70974**	-0.03784
Skull height	0.24	-4.17	-4.66	**1.35016**	-0.01470
Width of rostrum at midlength	-9.35	-7.05	-9.45	-0.18972	**-1.78803**
Width of palate (at midlength of rostrum	2.43	0.73	1.28	0.21871	0.47004
Greatest parietal width	8.03	12.29	13.20	**-0.94648**	0.39431
Length of neurocranium,	1.27	2.48	2.61	-0.63096	-0.01800
Length of upper tooth row	2.75	1.65	1.11	0.37493	-0.50447
Length of pterygoid	2.29	3.38	4.48	-0.23971	0.63454
Width of rostrum at base	1.74	1.83	2.75	-0.10954	**0.83115**
Greatest width of frontal	0.83	-1.59	-2.12	0.62956	-0.27303
Greatest width of frontal prominence	0.44	-1.30	-1.82	0.38723	-0.28024
Greatest length of temporal fossa	9.82	6.21	5.70	0.52805	-0.07083
Greatest width of temporal fossa	-2.36	-0.95	-0.19	-0.25688	0.37513
Least distance between occipital condyles	4.24	2.80	3.03	0.26425	0.31907
Greatest width of internal nares	-2.12	-1.11	-1.82	-0.06830	-0.34593
Constant	-1048.75	-1126.51	-1181.98		
Eigenvalue				94.30730	1.74095
Cumulative proportion				0.98187	1.00000

Table 4.—Eigenvectors from Principal component analysis (PCA) based on zwitter specimens from Peru, Chile, and Atlantic.

Characters	Component I	Component II
1. Condylobasal length	-0.904074	-0.424523
2. Length of rostrum from base	-0.925592	-0.371317
3. Width of rostrum at base	-0.991591	-0.119560
4. Distance from tip of rostrum to external nares	-0.853742	-0.517339
5. Width of rostrum at midlength	-0.997708	-0.015417
6. Greatest width of left premaxilla	0.910275	-0.392415
7. Height of rostrum at midlength	0.959015	0.224444
8. Greatest width of premaxillae	-0.968704	-0.210725
9. Skull height	-0.873550	0.483446
10. Greatest preorbital width	-0.981751	0.183678
11. Greatest postorbital width	-0.994101	-0.102632
12. Zygomatic width	-0.994930	0.094708
13. Greatest width of frontal	-0.921562	0.385417
14. Greatest width of internal nares	-0.852908	-0.520184
15. Greatest width of nasal	-0.965958	0.244049
16. Length of neurocranium	-0.997239	0.032848
17. Greatest parietal width	-0.951648	0.302852
18. Least distance between occipital condyles	-0.967972	0.246084
19. Greatest length of temporal fossa	0.201628	0.976323
20. Greatest width of temporal fossa	-0.685434	0.724951
21. Distance from tip of rostrum to pterygoid hamuli	-0.938059	-0.344826
22. Width of palate at midlength of rostrum	-0.970113	0.156427
23. Length of orbit	-0.973423	-0.192560
24. Greatest width of pterygoid	-0.943141	-0.325769
25. Length of pterygoid	-0.534303	0.836849
26. Greatest width of frontal prominence	0.023974	-0.989970
27. Distance from maxilar to occipital crest	0.510934	0.811254
28. Length of upper tooth row	0.760732	-0.491612

Table 5.— Factor Structure Standardized canonical coefficients for Environmental variables and Morphometric variables. EV (%)=Explained variance.

Environmental variables	Standardized canonical coefficients		Morphometric variables	Standardized canonical coefficients	
	Root 1	EV (%)		Root 1	EV (%)
Latitude	**0.971275**	94	Condylobasal length	0.347019	
Longitude	**-0.726979**	51	Length of rostrum from base	-0.433385	
Temperature 0m depth	**-0.698159**	49	Width of rostrum at base	0.485210	
Temperature 50 depth	-0.561094		Width of rostrum at midlength	0.480026	
Salinity 0m depth	-0.674361		Greatest width of left premaxilla	0.373861	
Salinity 50 depth	**-0.919518**	85	. Greatest width of premaxillae	**0.990089**	98
Oxygen 0m depth	0.601839		Greatest preorbital width	0.418223	
Oxygen 50 depth	**0.989779**	98	Greatest postorbital width	0.537165	
			Zygomatic width	0.635183	
			Greatest width of frontal	**0.740937**	55
			Greatest width of internal nares	0.613191	
			Greatest width of nasal	0.637616	
			Greatest parietal width	**0.684110**	46
			Greatest width of temporal fossa	0.449896	
			Length of orbit	0.466276	
			Greatest width of pterygoid	0.520263	
			Length of pterygoid	0.583518	
			Greatest width of frontal prominence	0.415467	
			Distance from maxilar to occipital crest	0.294431	
			Length of upper tooth row	-0.563130	
Variance extracted	100%		62.71%		
Total redundancy	75.43%		43.78%		

Table 6.—Procustes distances between mean shape showed sexual dimorphism in skulls of *Phocoena spinipinnis* for dorsal, ventral and lateral views.

	Goodall's F test				*Resampling test*			
Views	*F*	*d.f.*	*P*	Distance between sexes	*F*	*P*	range at 95%	*SE*
Dorsal	6.63	32, 2720	0.0000	0.0350	6.63	0.0006	0.0229-0.0521	0.0079
Ventral	3.05	24, 1920	0.0000	0.0178	3.05	0.0144	0.0131-0.0285	0.0040
Lateral	1.92	22, 1518	0.0065	0.0272	3.05	0.0981	0.0223- 0.0473	0.0064

Table 7.—Mahalanobis distance (D^2) (above diagonal) computed among *Phocoena spinipinnis* by sex and geographic area from Peru, Chile, and Atlantic, based on partial warp scores, for dorsal, ventral and lateral views.

View	Mahalanobis distances by sex and geographic area				
	Sex	Geographic area	Peru	Chile	Atlantic
Dorsal	Male	Peru	0	68.19	167.62
		Chile	68.19	0	55.70
		Atlantic	167.62	55.70	0
	Female	Peru	0	609.23	650.89
		Chile	609.23	0	25.34
		Atlantic	650.89	25.34	0
Ventral	Male	Peru	0	88.65	67.29
		Chile	88.65	0	26.59
		Atlantic	67.29	26.59	0
	Female	Peru	0	105.04	125.33
		Chile	105.04	0	31.90
		Atlantic	125.33	31.90	0
Lateral	Male	Peru	0	19.86	30.26
		Chile	19.86	0	35.41
		Atlantic	30.26	35.41	0
	Female	Peru	0	38.93	66.05
		Chile	38.93	0	34.78
		Atlantic	66.05	34.78	0

Table 8.—Results of a partial least-squares analysis of the covariation between the square roots of the environmental variables and the partial warp (shape variable) for skulls of *Phocoena spinipinnis.*

Variable	Dorsal Dimensions		Ventral Dimensions		Lateral Dimensions	
	1	2	1	2	1	2
1. Latitude	-0.96930	0.11902	-0.95346	0.10489	-0.94769	0.29228
2. Longitude	0.71471	-0.38240	0.02731	0.42527	0.61350	-0.08112
3. Temperature at 0m depth	0.77182	0.22096	0.87878	-0.46209	0.81412	-0.13109
4. Temperature at 50m of depth	0.35967	0.25310	0.81101	-0.52893	0.76161	-0.21008
5. Salinity at 0m depth	0.75156	-0.15898	0.72394	0.49280	0.84037	-0.14606
6. Salinity at 50 m of depth	-0.01851	0.60074	0.89122	-0.00756	0.89988	-0.08194
7. Oxygen at 0m of depth	-0.28552	0.66271	0.10067	0.18569	-0.48514	0.93833
8. Oxygen at 50m of depth	-0.93856	0.14633	-0.92667	-0.02278	-0.85505	0.38299
Singular values	0.0769	0.0185	0.0462	0.0064	0.0684	0.0153
Correlations	0.8485	0.2719	0.7901	0.2654	0.45530	0.32576

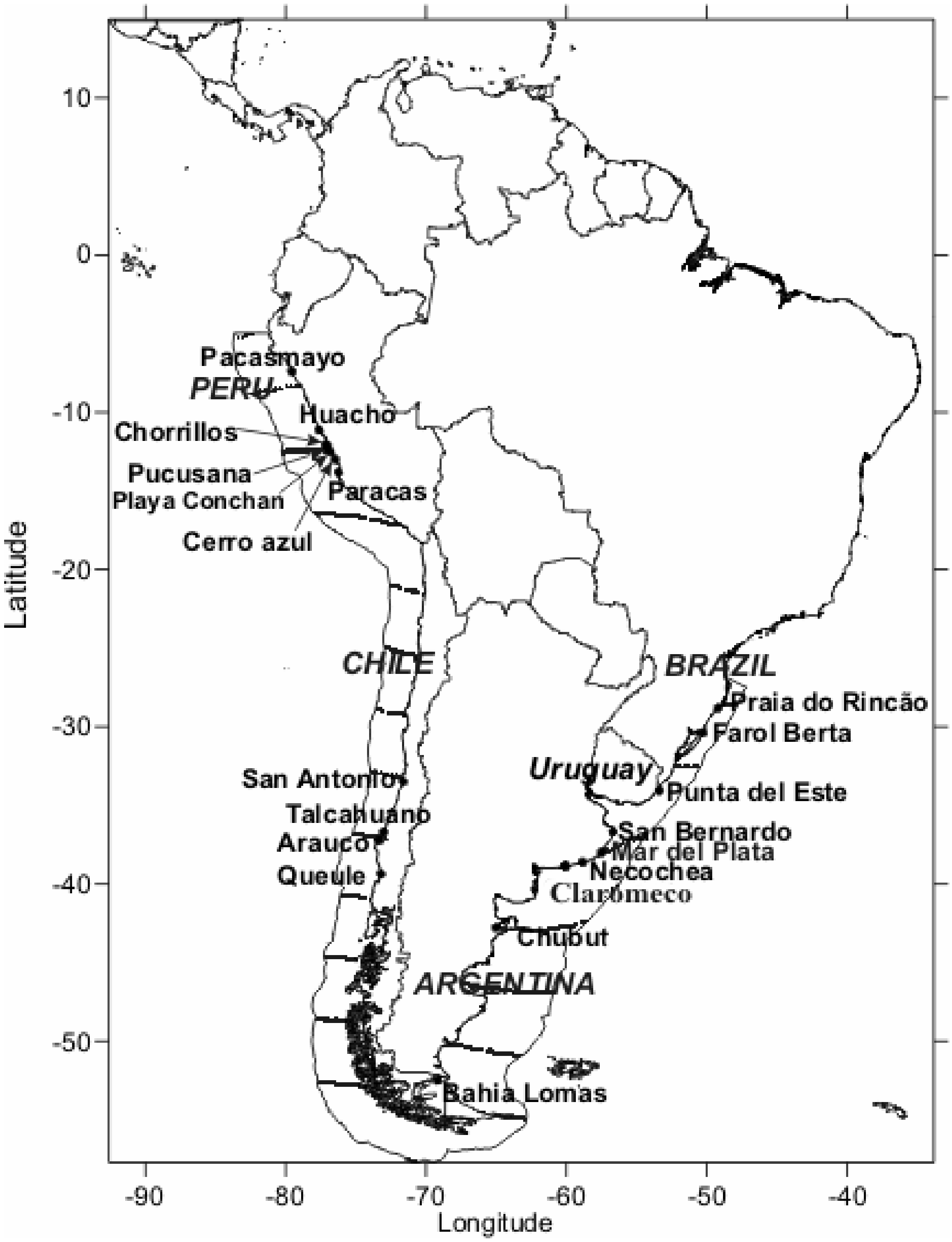


Fig 1.—Geographical location of *Phocoena spinipinnis* specimens used in the study.

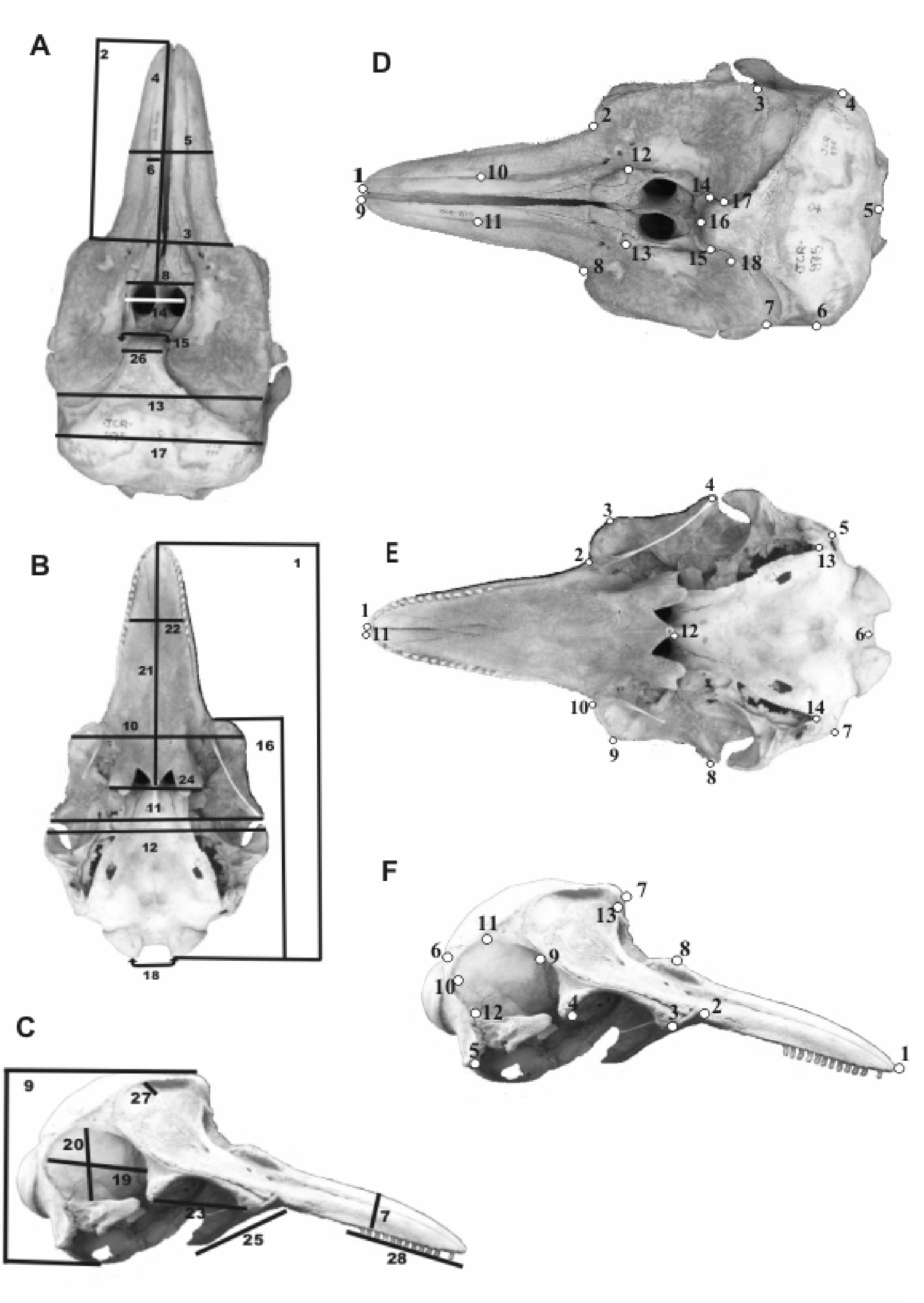


Fig. 2.— Numbered landmarks and linear measurements for each views of the skull of *Phocoena spinipinnis*. 1. Condylobasal length, 2. Length of rostrum (from base), 3. Width of rostrum (at base), 4. Distance from tip of rostrum to external nares, 5. Width of rostrum (at midlength), 6. Greatest width of left premaxilla, 7. Height of rostrum (at midlength), 8. Greatest width of premaxillae, 9. Skull height (at frontal–nasal suture), 10. Greatest preorbital width, 11. Greatest postorbital width, 12. Zygomatic width, 13. Greatest width of frontal, 14. Greatest width of internal nares, 15. Greatest width of nasal, 16. Length of neurocranium, 17. Greatest parietal width, 18. Least distance between occipital condyles, 19. Greatest length of temporal fossa, 20. Greatest width of temporal fossa, 21. Distance from tip of rostrum to pterygoid hamuli, 22. Width of palate (at midlength of rostrum), 23. Length of orbit, 24. Greatest width of pterygoid, 25. Length of pterygoid, 26. Greatest width of frontal prominence, 27. Distance from maxilar to occipital crest, and 28. Length of upper tooth row.

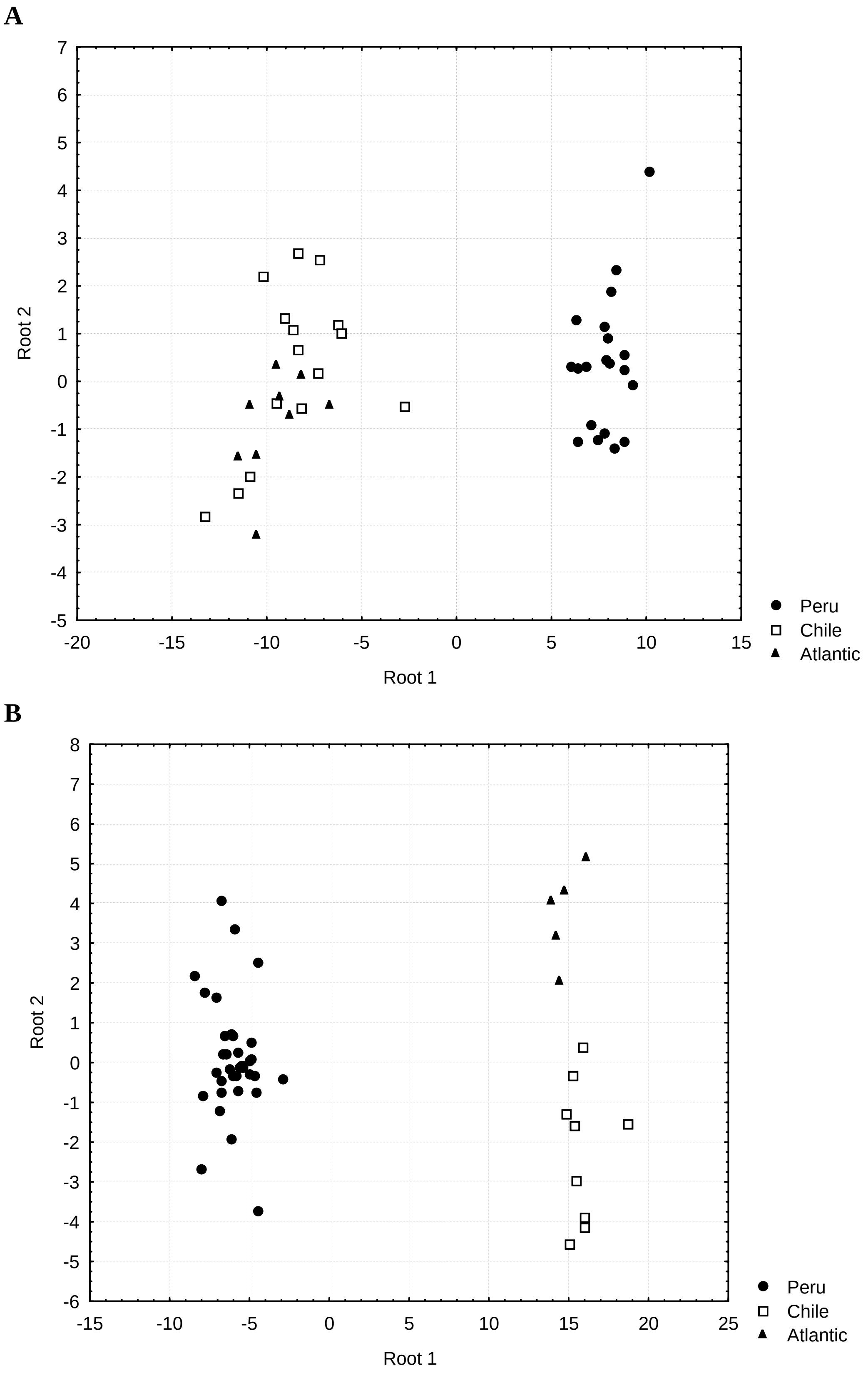


Fig. 3.— Scatterplot of canonical discriminant analysis for cranial metric variables in *Phocoena spinipinnis* from Atlantic, Chile and Peru. (A) Females, (B) Males.

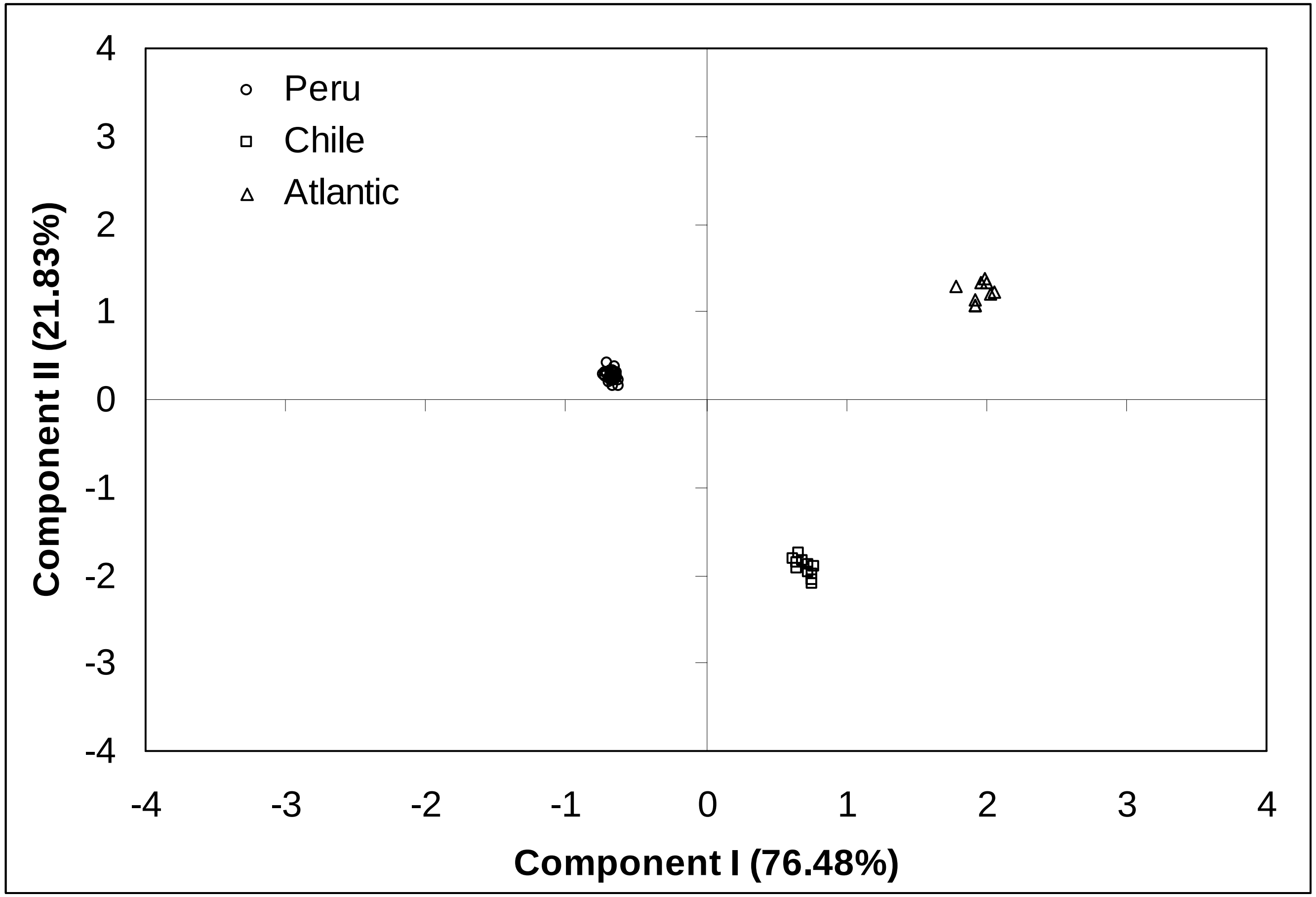


Fig. 4.— Scatterplot of PCA for cranial metric variables in zwitters specimens of *Phocoena spinipinnis* from Atlantic, Chile and Peru.

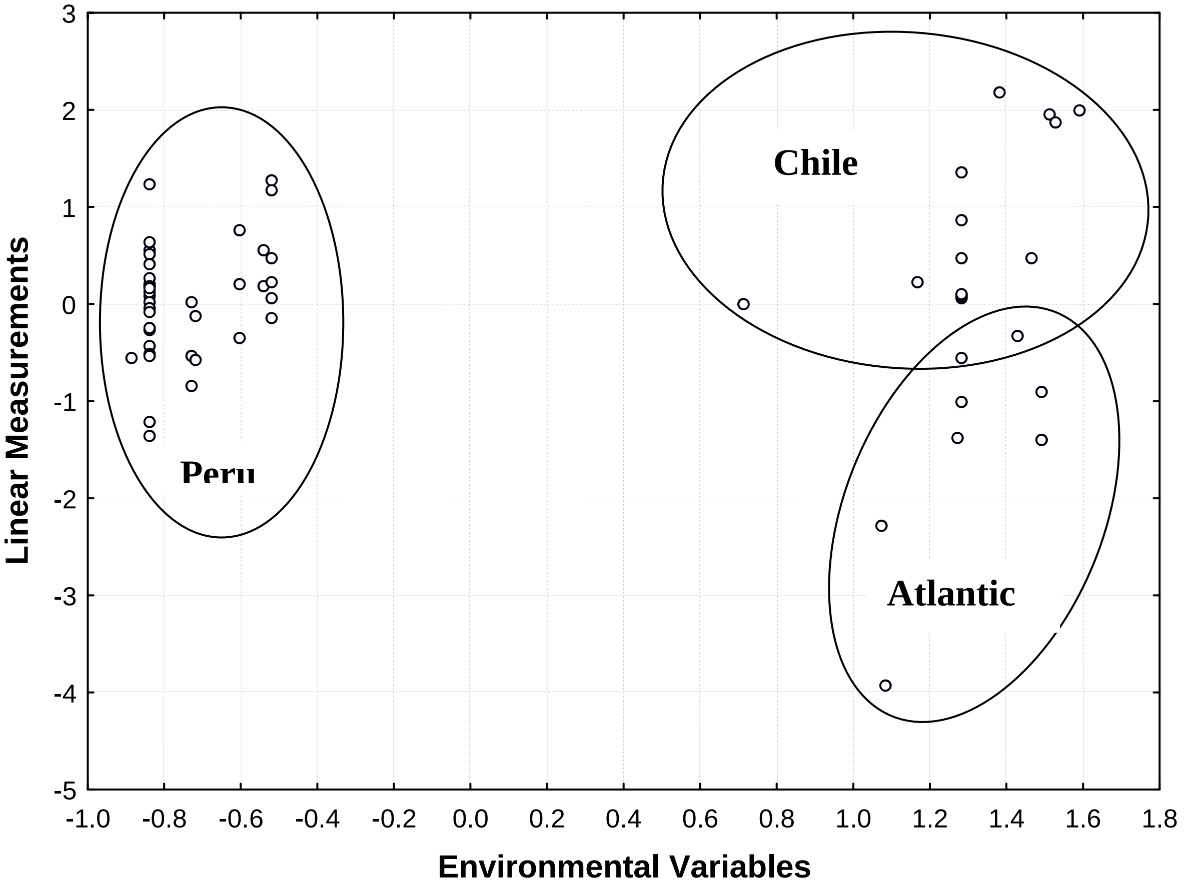


Fig. 5.— Scatterplot of canonical correlation analysis for environmental and cranial variables of *Phocoena spinipinnis* from Atlantic, Chile and Peru.

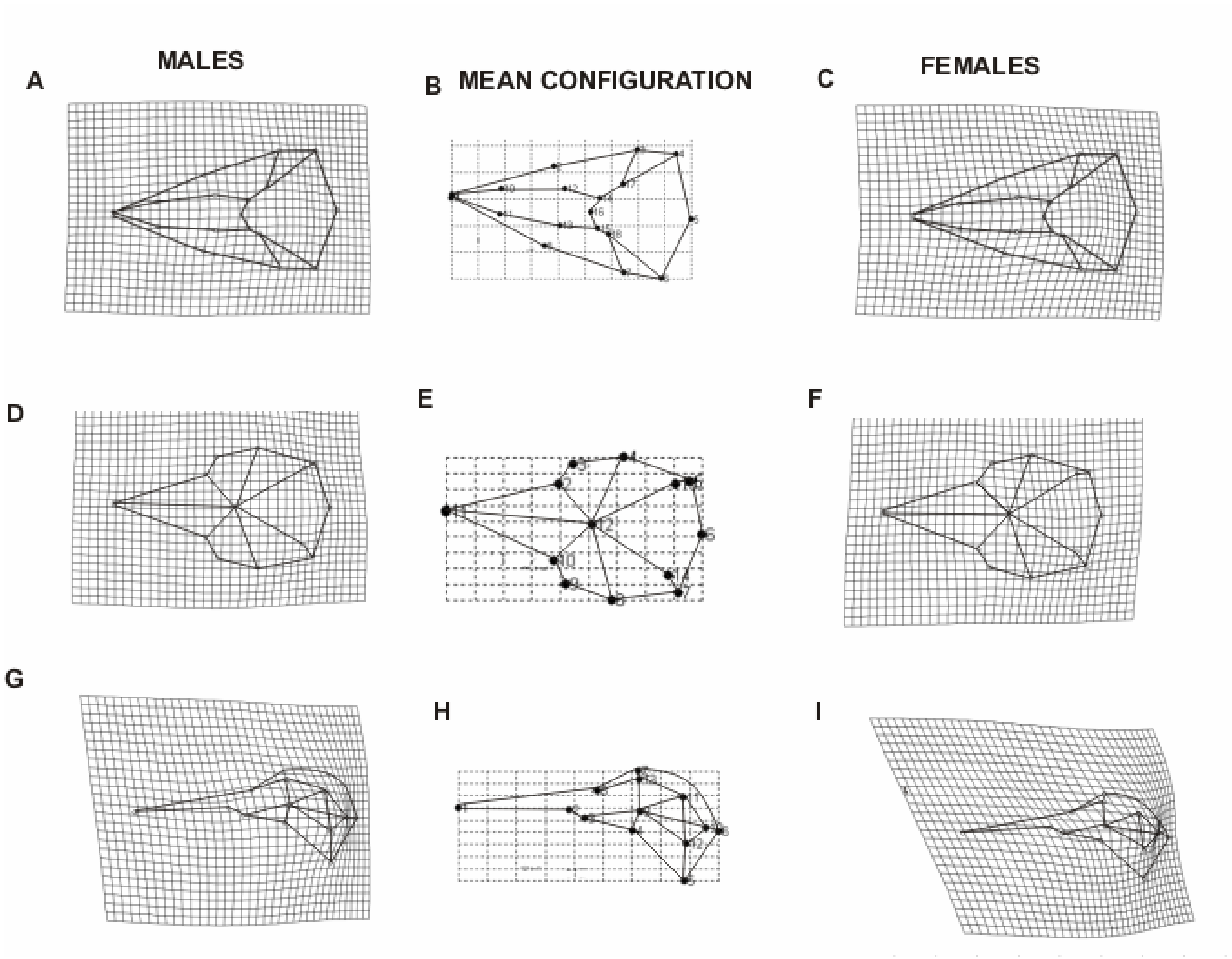


Fig. 6.— Average configuration of males and females from three geographical areas for dorsal, ventral and lateral views.

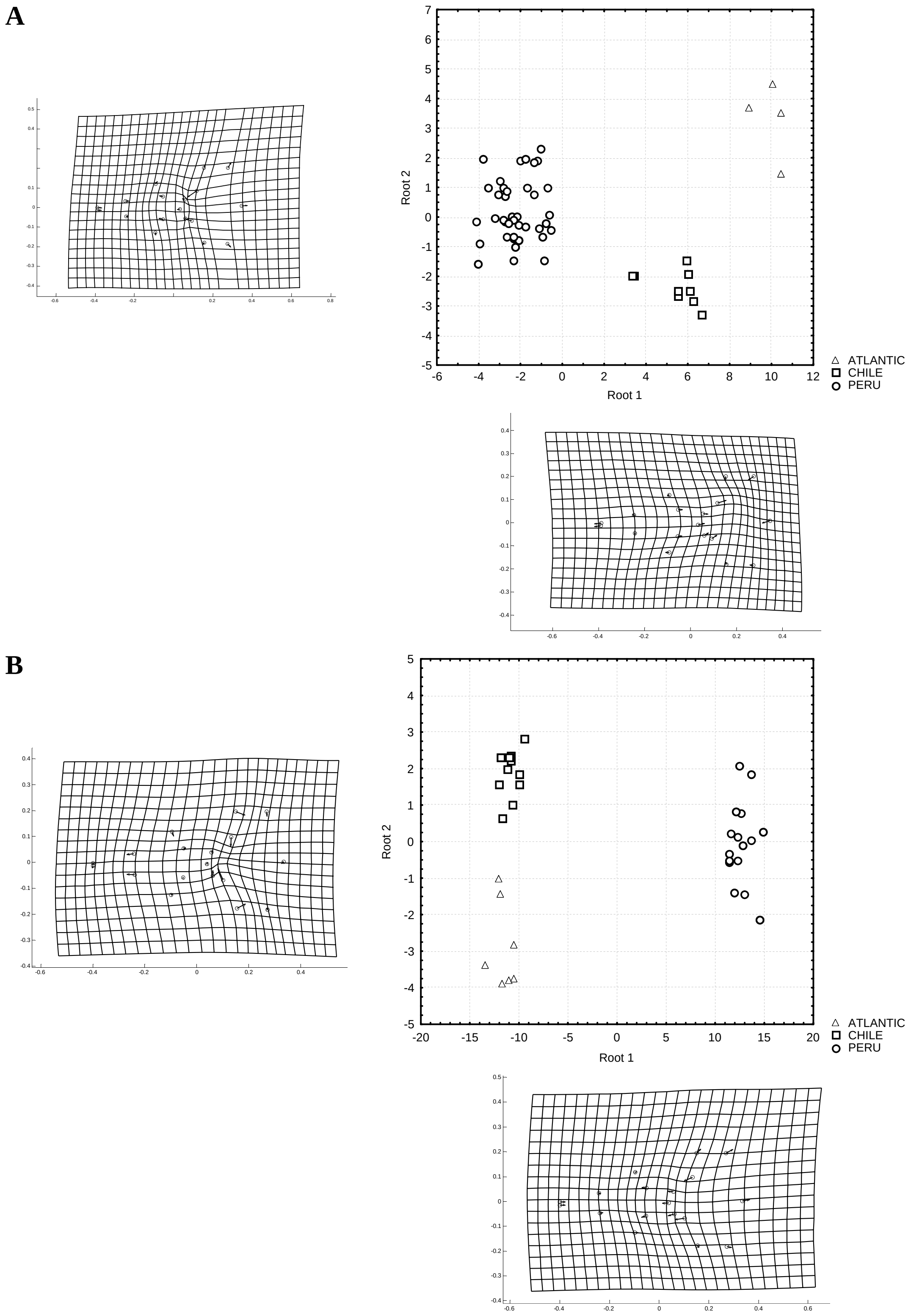


Fig. 7.— Deformation of change along the first two canonical variates of partial warp scores for dorsal view. (A) Males; (B) Females.

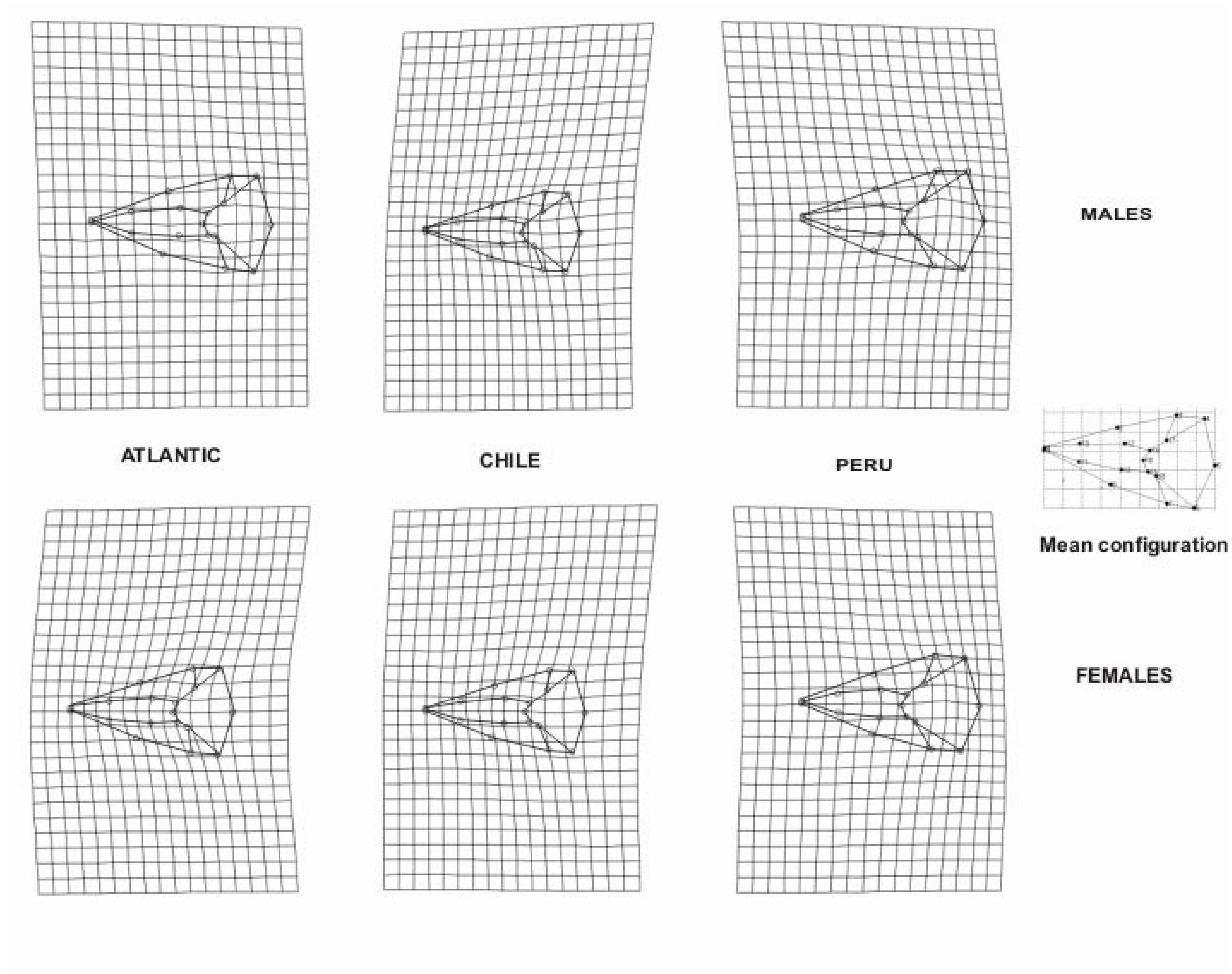


Fig. 8.— Average configuration of males and females from Atlantic, Chile and Peru for dorsal view.

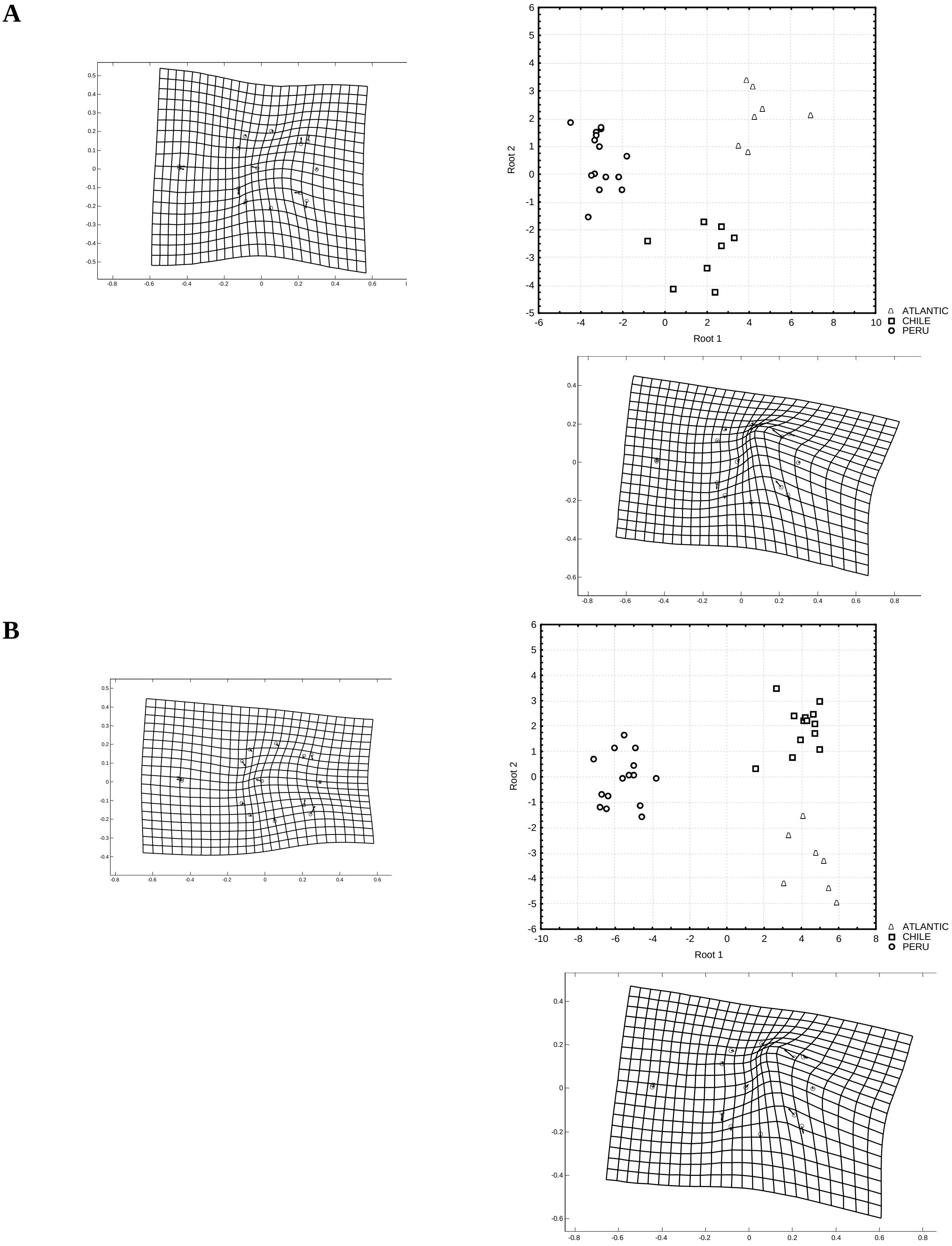


Fig. 9.— Deformation of change along the first two canonical variates of partial warp scores for ventral view. (A) Males; (B) Females.

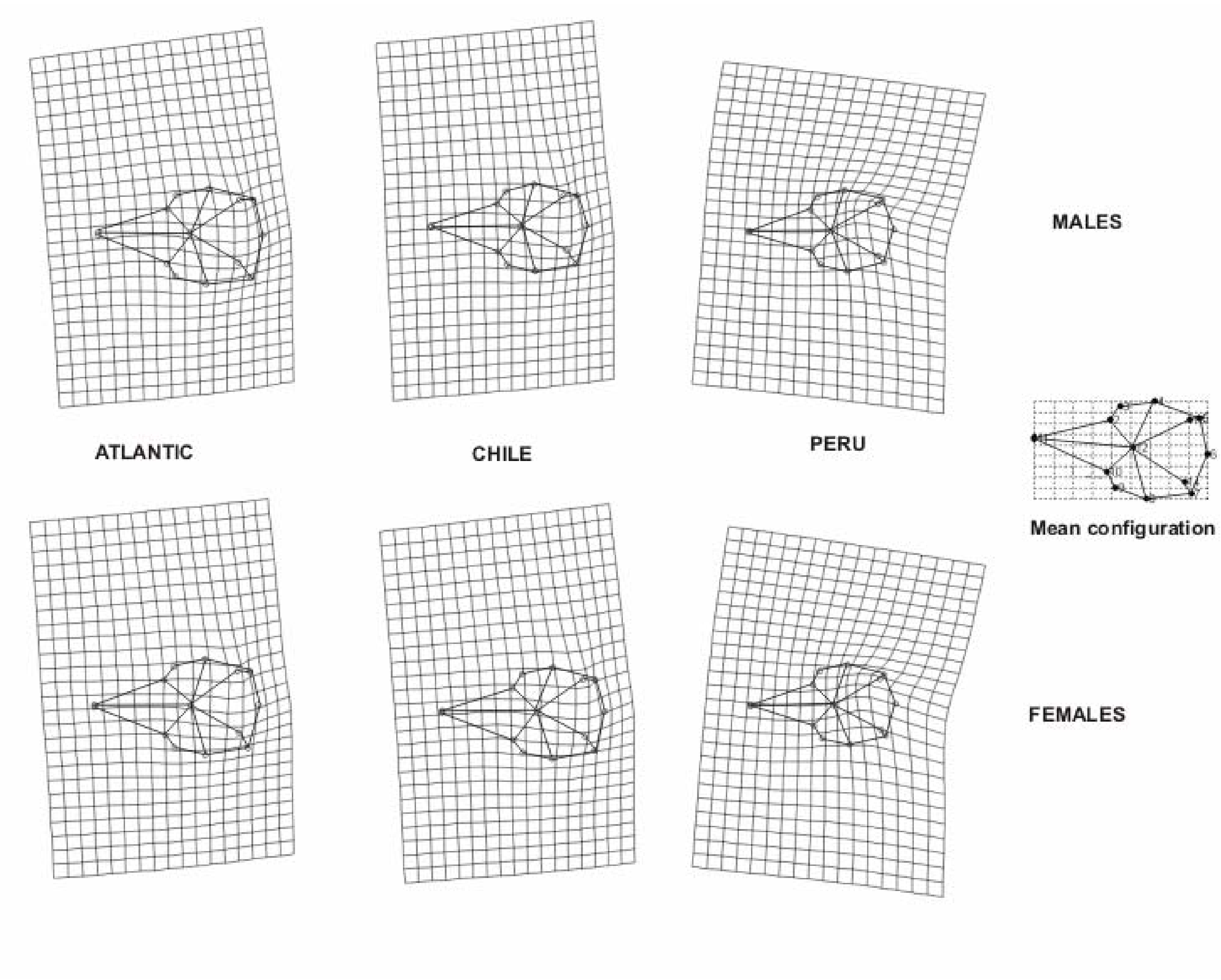


Fig. 10.— Average configuration of males and females from Atlantic, Chile and Peru for ventral view.

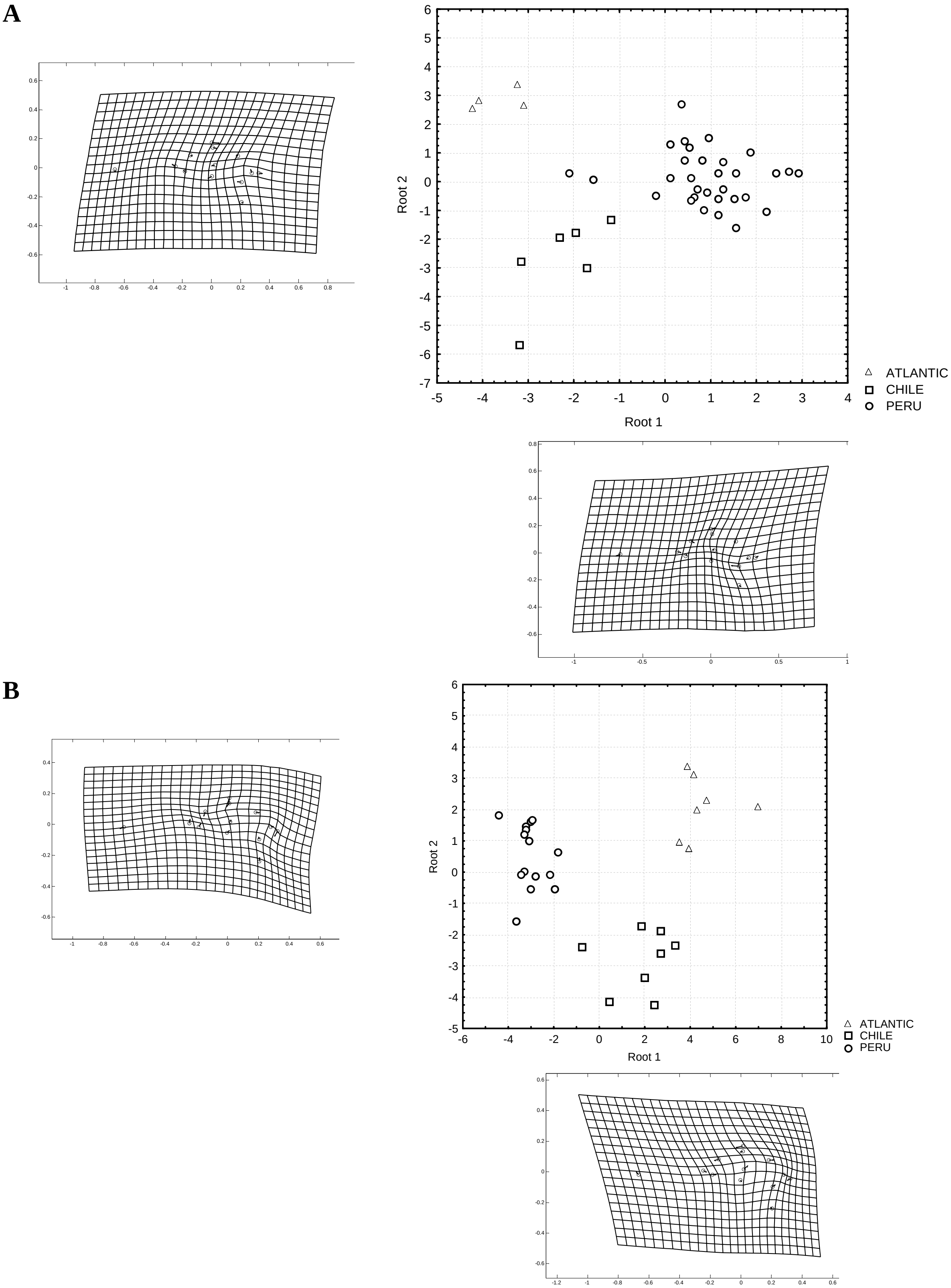


Fig. 11.— Deformation of change along the first two canonical variates of partial warp scores for lateral view. (A) Males; (B) Females.

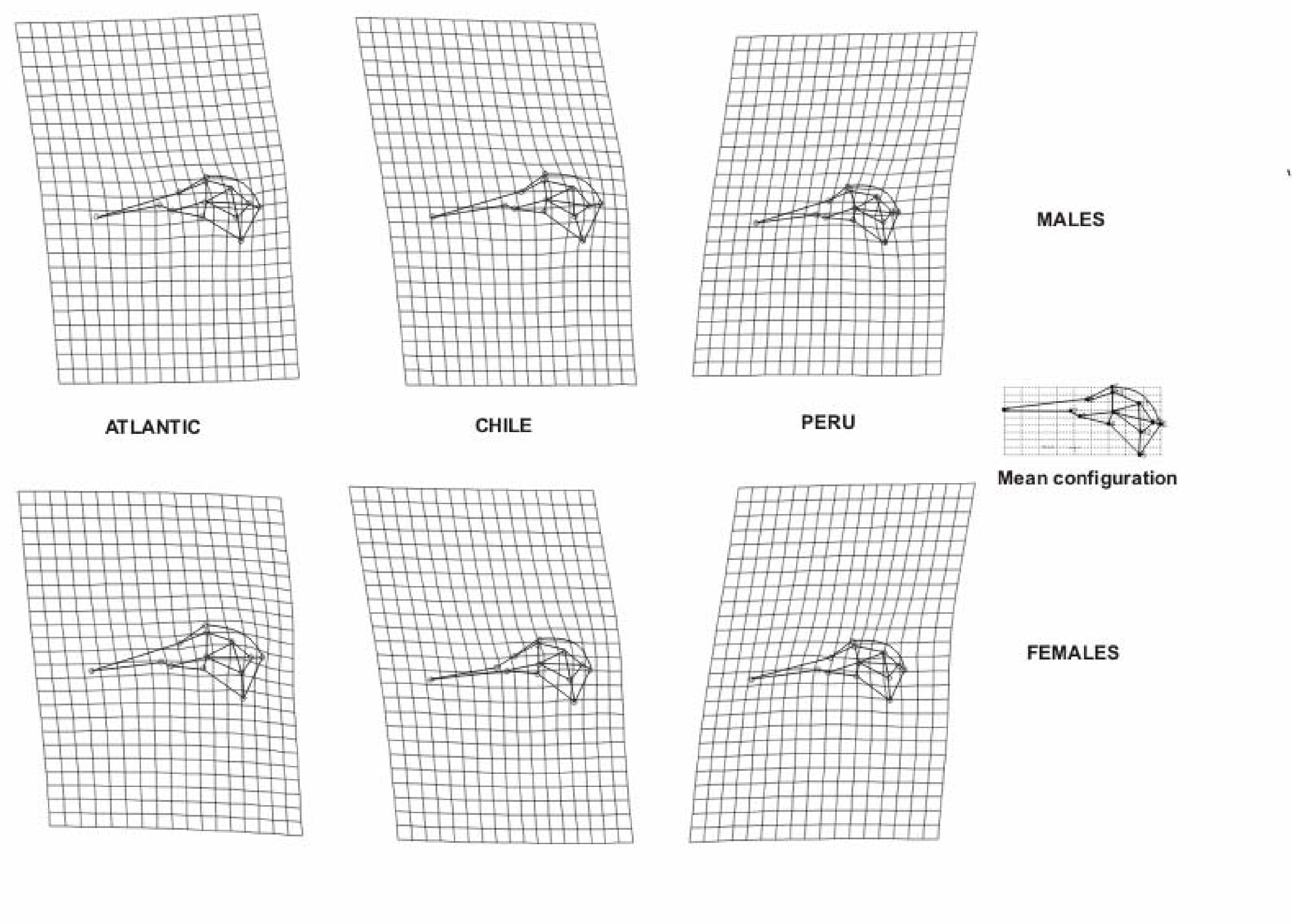
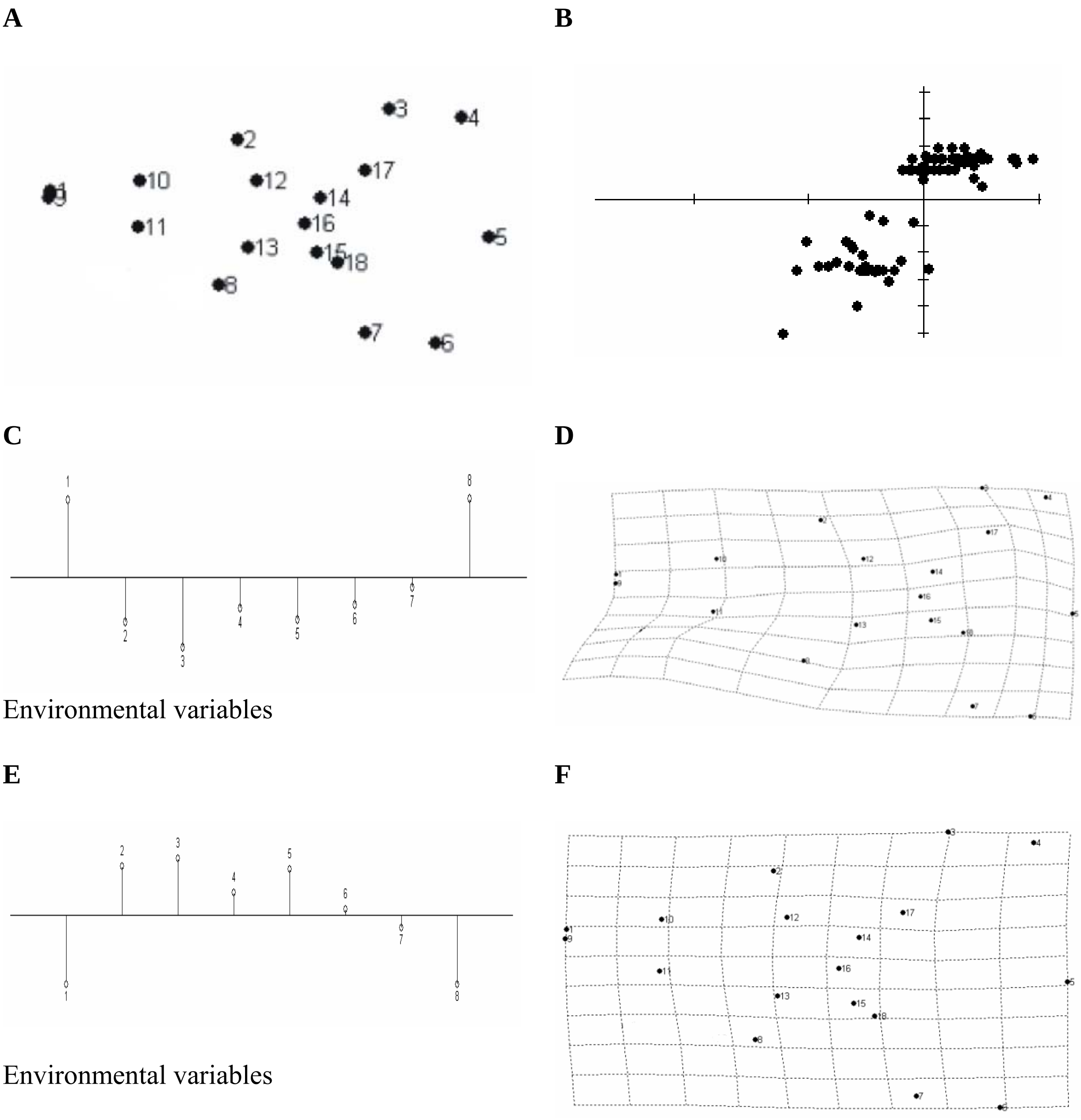


Fig. 12.— Average configuration of males and females from Atlantic, Chile and Peru for lateral view.



Environmental variables

Environmental variables

Fig. 13.— Results of a two-block partial least-squares analysis obtained for the first pair of variables (environmental and shape set variables) for dorsal cranial view of *Phocoena spinipinnis*. (A) Consensus, (B) Display scatter plots of the projections of the standardized environmental variables (along the ordinate) and partial war scores (along abscissa) onto their paired vectors. Correlation is 0.85, (C) environmental variables to a point at the negative extreme, (D) shape corresponding to a point at the negative extreme, (E) environmental variables to a point at the positive extreme, and (F) shape corresponding to a point at the positive extreme. The environmental variables: 1. Latitude, 2. Longitude, 3. Temperature at 0m depth, 4. Temperature at 50m of depth, 5. Salinity at 0m depth, 6. Salinity at 50 m of depth, 7. Oxygen at 0m of depth, 8. Oxygen at 50m of depth.

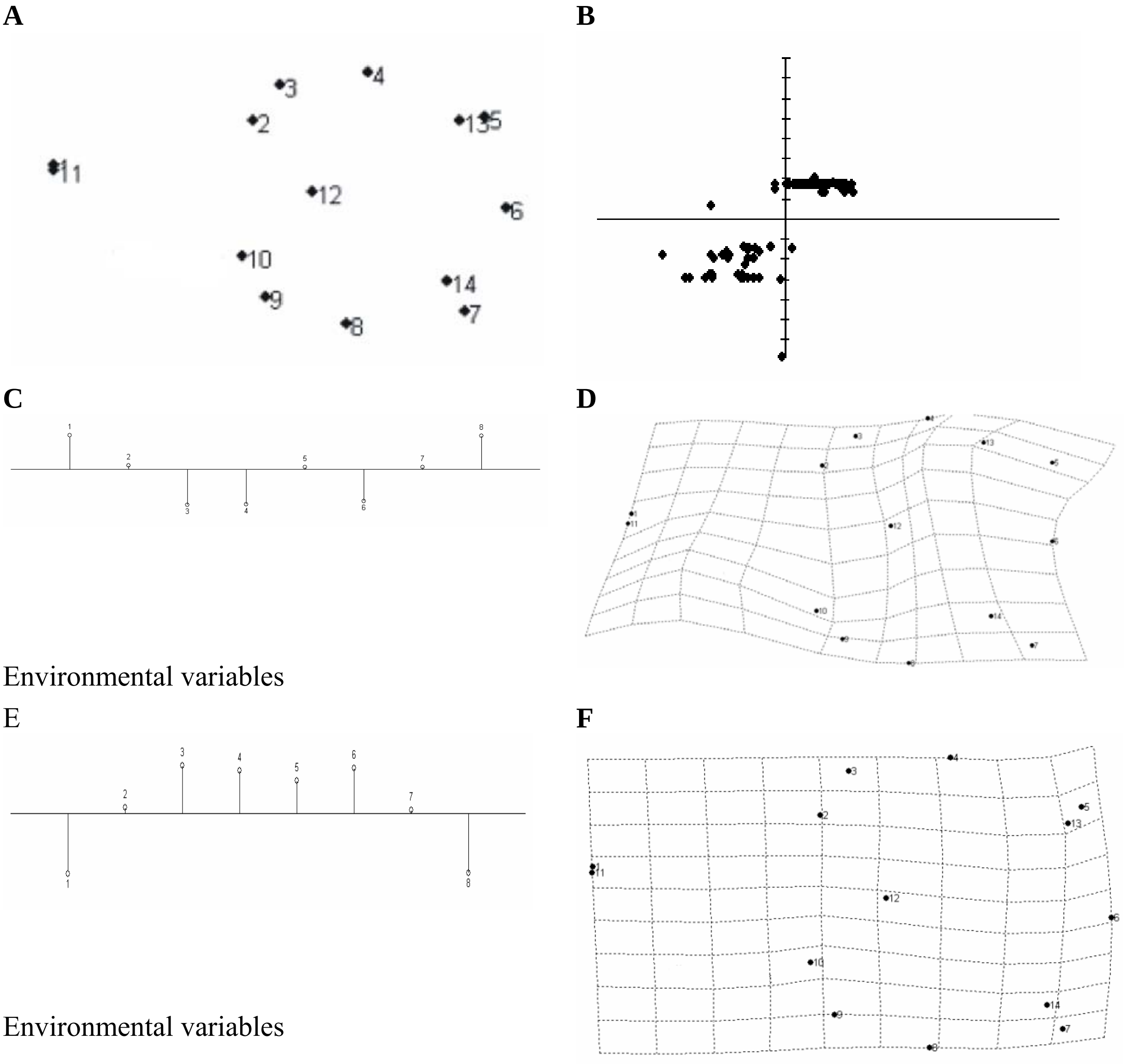
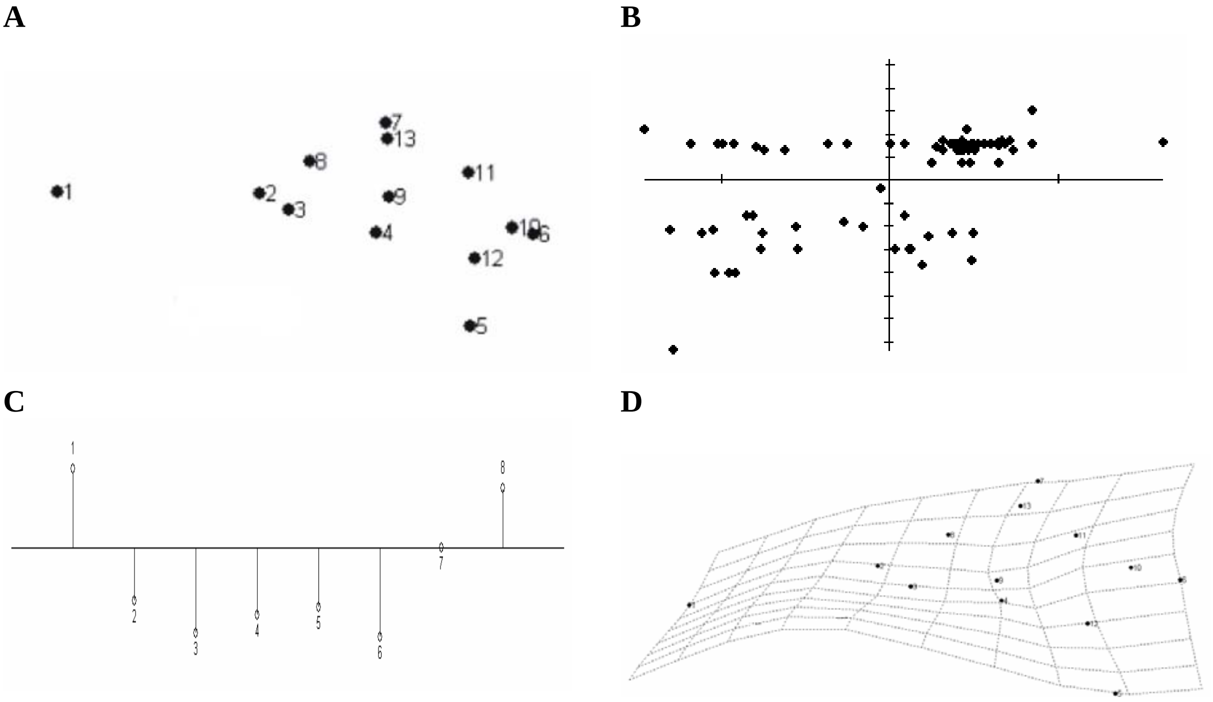
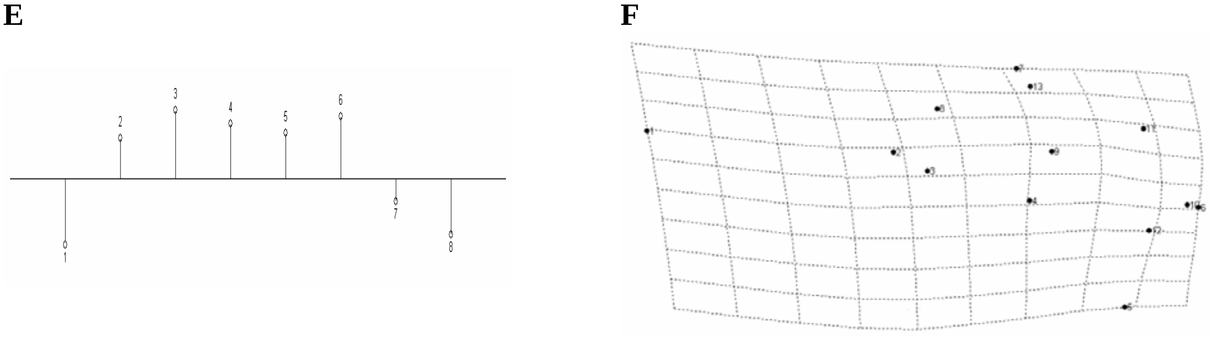


Fig. 14.— Results of a two-block partial least-squares analysis obtained for the first pair of variables (environmental and shape set variables) for ventral cranial view of *Phocoena spinipinnis*. A) Consensus, B) Display scatter plots of the projections of the standardized environmental variables (along the ordinate) and partial war scores (along abscissa) onto their paired vectors. Correlation is 0.79. (C) environmental variables to a point at the negative extreme, (D) shape corresponding to a point at the negative extreme, (E) environmental variables to a point at the positive extreme, and (F) shape corresponding to a point at the positive extreme. The environmental variables: 1. Latitude, 2. Longitude, 3. Temperature at 0m depth, 4. Temperature at 50m of depth, 5. Salinity at 0m depth, 6. Salinity at 50 m of depth, 7. Oxygen at 0m of depth, 8. Oxygen at 50m of depth.



Environmental variables



Environmental variables

Fig. 15.— Results of a two-block partial least-squares analysis obtained for the first pair of variables (environmental and shape set variables) for lateral cranial view of *Phocoena spinipinnis*. A) Consensus, B) Display scatter plots of the projections of the standardized environmental variables (along the ordinate) and partial war scores (along abscissa) onto their paired vectors. Correlation is 0.79. (C) environmental variables to a point at the negative extreme, (D) shape corresponding to a point at the negative extreme, (E) environmental variables to a point at the positive extreme, and (F) shape corresponding to a point at the positive extreme. The environmental variables: 1. Latitude, 2. Longitude, 3. Temperature at 0m depth, 4. Temperature at 50m of depth, 5. Salinity at 0m depth, 6. Salinity at 50 m of depth, 7. Oxygen at 0m of depth, 8. Oxygen at 50m of depth.

CONSIDERAÇÕES FINAIS

Estudos morfométricos, genéticos e ambientais são necessários para conhecer e avaliar padrões de variação geográfica, permitindo assim, estabelecer unidades de manejo (*Management Units* - MUS) (MORITZ, 1994; EIZIRIK, 1996) e unidades evolutivamente significativas (*Evolutionary Significant Units* - ESUs) (RYDER, 1986; WAPLES, 1991, 1995; DIZON *et al*., 1992; MORITZ, 1994). Porém, o conhecimento do tamanho, estrutura e *status* (tendências em abundância e distribuição ao longo do tempo) de populações de cetáceos é indispensável para o estabelecimento de programas de conservação eficientes (REEVES & LEATHERWOOD, 1994).

Os resultados obtidos neste estudo contribuem para o conhecimento da biologia e ecologia do boto-de-Burmeister, *Phocoena spinipinnis* no Atlântico e Pacífico Sul, o que servirá como base para propôr futuros estudos de manejo e conservação a nível local e regional.

Na caracterização ambiental na costa Pacifica e Atlântica realizada (utilizando dados históricos de 1965 a 2000 da temperatura do mar, salinidade e oxigênio dissolvido a 0 e 50m de profundidade) observou-se que a distribuição de *P. spinipinnis* estaria associada a padrões oceanográficos nos dois oceanos. Neste contexto, propõem-se três áreas oceanográficas associadas a sua distribuição: (1) de Paita, Peru (05°01'S, 81ºW) até o sul do golfo de Arauco, Chile (~39°S), que apresenta a influência da corrente de Humboldt (caracterizada pela sistema de *upwelling*, - com águas ricas em nutrientes, frias, salinas) e baixas em oxigênio pela zona do mínimo oxigênio; (2) do sul do golfo de Arauco, até o sul do Rio da Prata (~38°S), caracterizada pela influência das corrente do Cabo de Hornos e a corrente das Malvinas, e que envolve processos de *downwelling* (com aportes de água doce provenientes dos fiordes, glaciais e rios); e (3) do Rio da Prata até Santa Catarina, Brasil (28º48'S; 49°12W), caracterizada pela influência da corrente do Brasil e pelas contribuições da água doce da bacia do Rio da Prata e do sistema estuarino da Laguna dos Patos. Considerando esses resultados propõe-se que *P. spinipinnis* apresenta uma distribuição continua desde Paita, Peru até a bacia do Rio da Prata, Argentina, podendo alcançar águas uruguaias e brasileiras quando segue a pluma da Convergência Subtropical (com águas costeiras mais frias e menos salinas) (SILVA *et al*., 1984; GUERRERO *et al*., 1997; PIMENTA, 2001). A formação de ressurgências, correntes, frentes oceânicas, termoclimas e outros processos oceanográficos possibilitam uma riqueza faunística (BLACKBURN, 1965; LAEVASTU, 1996; LONGHURST *et al.*, 1995). A Convergência Subtropical do Atlântico Sudoeste é um exemplo de caso, influenciando em processos de enriquecimento de águas que acabam concentrando grande quantidade de organismos. Ao norte de Santa Catarina encontram-se importantes zonas de resurgencias (MATSURA, 1986; PEREIRA, 1989; SILVA *et al*., 1984), e a diversidade de mamíferos marinhos esta em estreita relação com a productividade primaria e disponibilidade de peixes associada à upwelling próximo da costa (LIPPS & MITCHELL 1976).

Análises dos dentes através de cortes finos de 25µm revelaram que a dentina apresenta uma ótima resolução para a leitura da idade através dos grupos de camadas de crescimento (GLGs), enquanto que no cimento as GLGs foram ausentes ou apresentaram pouca resolução, não sendo adequadas para as leitura da idade. A largura média da primeira GLG na dentina foi maior nos machos do que nas fêmeas, e também apresentou diferenças geográficas entre botos do Peru e Atlântico (sendo maior nos exemplares do Chile, seguido pelos botos do Peru e Atlântico). Por outro lado, a capa acessória central presente na primeira GLG revelou diferenças entre os exemplares do Chile e Atlântico. Três tipos de anomalias foram registrados (linhas marcadoras, reabsorção dentinal e distúrbios no cimento) em dentes de sete botos-de-Burmeister coletados no

Peru entre 1984 até 1998. As linhas marcadoras parecem estar associadas a fatores ambientais (a data sua formação coincide com o evento *El Niño*.

Análises morfométricas revelaram dimorfismo sexual (através de funções discriminantes) em crânios de *P. spinipinnis*, permitindo não apenas separar machos das fêmeas como determinar o sexo em animais de sexo desconhecido o que possibilitou a utilização de todos os crânios nas análises de crescimento. A idade máxima registrada em machos e fêmeas foi de 10 anos. Contudo, a falta de animais de faixas etárias entre 1-2 anos (principalmente nas fêmeas) foi um fator limitante na determinação da idade de maturidade física dos crânios de *P. spinipinnis*. Por conseguinte, a maturidade física do crânio foi estabelecida quando o comprimento côndilo-basal atingiu 95% do comprimento (ou seja, os crânios foram considerados fisicamente adultos com um comprimento côndilo-basal ≥266mm nos machos e ≥277mm nas fêmeas). Posteriormente, os crânios foram separados em machos, fêmeas, adultos ou jovens, através de uma função discriminante.

O dimorfismo sexual observado nas análises anteriores foi corroborado em crânios de exemplares fisicamente adultos, através de dois métodos: morfometria tradicional e morfometria geométrica, sendo as fêmeas maiores do que os machos, e as diferenças em tamanho e forma concentram-se principalmente na região rostral e no neurocrânio. Contudo, as posições dorsal e lateral evidenciaram melhor o dimorfismo sexual na forma do crânio.

As diferenças morfométricas obtidas nos dois métodos indicam variação geográfica entre botos do Atlântico, Chile e Peru. Em geral, os crânios de *P. spinipinnis* do Peru apresentam um tamanho menor em relação aos botos do Chile e Atlântico no comprimento côndilo-basal, largura do zigomático, distância entre a ponta do rostro até as narinas e na largura do rostro na metade do comprimento. Estes elementos indicam que os espécimes de *P. spinipinnis* do Peru apresentam o rostro mais curto e o neurocrânio ligeiramente mais largo. Os exemplares do Chile apresentam forma e tamanho intermediários entre animais do Peru e do Atlântico, enquanto que os botos do Atlântico são maiores do que os animais do Peru e do Chile, especialmente na região orbital, altura do crânio e região rostral. Os valores obtidos através da distância de Mahalanobis corroboraram as diferenças observadas entre áreas geográficas, indicando que a maior separação ocorre entre *P. spinipinnis* do Peru e Atlântico. Entretanto, a menor distância ocorre entre botos do Chile e Atlântico.

A morfometria geométrica revelou-se como a melhor ferramenta para apresentar as diferenças entre botos do Chile e Atlântico, especialmente nas vistas dorsal e ventral, denotando que a forma dos machos varia mais do que a forma das fêmeas e que os exemplares do Chile e Atlântico (em especial as fêmeas) apresentam diferenças menos significativas na forma.

Os crânios podem ser separados por área geográfica através de funções discriminantes obtidas pelo método tradicional. Quinze caracteres nos machos e três caracteres nas fêmeas separam os crânios das três áreas geográficas. Destacamos também que a largura máxima da pré-maxila é útil para separar animais do Peru das outras áreas geográficas.

Contudo, ao utilizar *zwitter* indivíduos (crânios sem a influência do sexo) a função discriminante separou os crânios do Atlântico, Chile e Peru apenas com um caracter (a largura máxima do pós-orbital).

As correlações entre variáveis ambientais e morfométricas na morfometria tradicional e morfometria geométrica sugerem que as diferenças observadas no tamanho e forma dos crânios teriam uma importante influência espacial, relacionada principalmente a variações na temperatura, salinidade e oxigênio. Assim os espécimes de San Antonio, centro do Chile (33º30'S; 73°13'W) até Santa Catarina, sul do Brasil (28º48'S; 49°12W) estariam associados a águas mais frias, menos salinas e mais oxigenadas, apresentando crânios maiores (maior comprimento do rostro, altura do crânio e região orbital) em relação ao boto-de-Burmeister do Peru (que apresenta um crânio mais curto no comprimento do rostro), e que poderia ser associado a águas mais temperadas, menos oxigenadas e mais salinas.

As diferenças morfométricas observadas neste estudo serão comparadas com estudos genéticos que já se encontram em fase de desenvolvimento. As análises genéticas estão sendo realizadas a partir de DNA extraído dos dentes dos espécimes analisados neste estudo e são de vital importância para o esclarecimento das diferenças geográficas aqui demonstradas e para se determinar se os espécimes de *P. spinipinnis* das três áreas geográficas (Atlântico, Chile e Peru) representam estoques diferentes.

RECOMENDAÇÕES

1) Recomenda-se a realização de estudos de crescimento com um tamanho amostral maior, a fim de estabelecer a maturidade física dos crânios para cada sexo e área geográfica, o que permitirá esclarecer melhor as diferenças observadas neste estudo;

2) Embora diferenças morfométricas na forma e no tamanho tenham sido observadas entre os crânios de *P. spinipinnis* do Chile e Peru, estudos morfométricos e genéticos precisam ser realizados para diferenciar estoques entre os exemplares do Peru e o norte do Chile (30ºS ao norte);

3) Estudos sobre ecologia trófica, reprodução (determinação da idade da maturidade sexual), *status* (tendências em abundância e distribuição no espaço e no tempo) nas diferentes áreas, são de grande importância para se conhecer o padrão de variação geográfica da espécie;

4) Considerando que o boto-de-Burmeister, é uma espécie costeira, as atividades antrópicas (e.g. capturas acidentais e diretas, degradação do habitat pelo tráfego marítimo, poluição, exploração dos recursos) e efeitos ambientais (e.g. *El Niño* Oscilação Sul - ENOS) precisam ser avaliados a escala local e regional, pois tais fatores podem provocar relações denso-dependentes, que regulam os parâmetros populacionais como tamanho populacional, tamanho dos indivíduos e/ou idade da maturidade sexual.

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ANEXO 1

NORMAS PARA O ENVIO DE PUBLICAÇÃO NO PERIÓDICO:
The Latin American Journal of Aquatic Mammals

INSTRUCTIONS FOR AUTHORS

The Scope

The Latin American Journal of Aquatic Mammals (LAJAM) will publish research on aquatic mammals in Latin America, regardless the nationality of the authors. Articles on techniques which the region or nationality of the authors is of no matter will also be accepted.

Language

Manuscripts must be written in either "American" or "British" English; however, authors should be consistent along the text. By using English as its official language, LAJAM will be more readily available, and of greater relevance, to the global aquatic mammal research community. Papers should normally be in the passive voice unless an opinion needs to be clearly attributed to the Authors. The abstract must also be written in English, with an additional version in either Portuguese or Spanish also provided. It is recognized that English may not be the first language for most authors. Therefore, the Editorial Board will work with the authors to ensure that the paper is written in good English.

Types of manuscript

Articles report results of original research. They should normally not exceed 30 pages of text (Title page, Abstract, Keywords, Introduction, Materials and methods, Results, Discussion, Acknowledgements, References).

Notes are brief reports of original research. They should normally not exceed 14 pages of text. They may be organized like articles, with formal headings, or preferably more simply (no headings except for Acknowledgements and References).

Reviews must address topics of general interest or current importance to the Latin American aquatic mammal research community. They should be synthetic in nature (*i.e.* summarize the topic), rather than present large amounts of detailed information. Reviews will be considered for publication only after invitation by, or agreement with, the Managing Editors.

Comments are short critiques of papers previously published in LAJAM. Authors of the original paper being discussed will be invited to reply to these critiques.

Short Communications are brief reports of 1 or 2 paragraphs dedicated to inform about unusual sightings, strandings, incidental captures or other issues. Proof of species identification (such as photographs or detailed sketches of prominent or conspicuous features) must be provided.

Format

Manuscripts should be typed in A4 paper, with double line spacing and all margins set to 2.5cm (1in). All text should be typed using Times New Roman font of size 12. Headings should be in bold (e.g. Introduction). If additional sub-headings are required, these should appear in italics (*e.g. Data analysis*).

Page numbering should start at the Title page, with the page numbers appearing centred at the bottom of each page.

Title page: Should contain a concise and informative title, and a list of authors' names and addresses. The corresponding author should be indicated, and an email address for that author, if available, should also be provided. Keywords (in English) should also be stated.

Abstract page: Should contain an abstract in English, as well as a version in either Portuguese or Spanish. Abstracts should not exceed 350 words.

Body of the manuscript: Should contain the Introduction, Materials and methods, Results, Discussion, Acknowledgements, and References.

Please be brief in the Acknowledgements.

References should be formatted according to the following examples:

DeMaster, D. P., Edwards, E. F., Wade, P. and Sisson, J. E. (1992) Status of dolphin stocks in the eastern tropical Pacific. Pages 1038-1050 *in* McCullough, D. R. and Barrett, R. H. (Eds) *Wildlife 2001: Populations*. Elsevier Science Publishers Ltd., London.

Di Beneditto, A. P., Ramos, R. and Lima, N. R. (2001) *Os golfinhos: Origem, classificação, captura acidental, hábito alimentar*. Editora Cinco Continentes, Porto Alegre, Brazil.

Gerpe, M., Rodríguez, D., Moreno, V.J., Bastida, R.O. and de Moreno, J.E. (2002) Accumulation of heavy metals in the franciscana (*Pontoporia blainvillei*) from Provincia Buenos Aires, Argentina. *The Latin American Journal of Aquatic Mammals* 1 (special issue 1): 95-106.

Palacios, D. M. and Mate, B. R. (1996) Attack by false killer whales (*Pseudorca crassidens*) on sperm whales (*Physeter macrocephalus*) in the Galápagos Islands. *Marine Mammal Science* 12: 582-587.

Important note: abstracts can be quoted (just like personal communications can) and placed in footnotes. The format should be as follows:

Dalla Rosa, L., Secchi, E. R., Kinas, P. G., Santos, M. C. O., Zerbini, A. N. and Bassoi, M. (1999) *Photo-identification and density estimation of humpback whales in Antarctic waters*. Page 43 *in* Abstracts, XIII Biennial Conference on the Biology of Marine Mammals, 28 November - 3 December, Maui, Hawaii.

Only month and year are compulsory for conference dates in the reference. Full date (including days) is preferable if available.

References containing more than two authors should appear in the text as, for example, Di Beneditto *et al.* (2001). When more than one reference is cited at a time, references should appear in chronological order (*e.g.* DeMaster *et al.*, 1992; Palacios and Mate, 1996; Dalla Rosa *et al.*, 1999; Di Beneditto *et al.*, 2001; Gerpe *et al.*, 2002). When citing two or more papers from the same authors, published in the same year, use lower case letters in italics to differentiate between the papers (e.g. Siciliano *et al.*, 2000*a,b*).

TABLES: Each table should be presented on a separate page, with the table caption placed at the top of the page. Tables should be numbered Table 1, Table 2, etc. Authors should try to ensure that as many tables as possible do not exceed 8.5cm in width, when printed in Times Roman 8pt (or similar). The maximum permitted width of any table is 17.5cm.

FIGURES: Each figure should be presented on a separate page, with the figure caption placed at the bottom of the page. Figures should be numbered Figure 1, Figure 2, etc.

Photographs and artwork: The inclusion of photographs in a paper is very expensive. Therefore we only publish photographs that are an essential part of the paper (for example, photographs that would serve to confirm the identification of a species which is extremely difficult to be positively identified at sea). High quality black and white photographs are recommended. Colour print photos will be at the authors' expenses.

Where possible, please submit photographs and/or artwork in an electronic format (*e.g.* .bmp, .tif). Tabulated x,y data files should also be provided for graphs. This will allow, where necessary, graphs to be plotted in our standard style using Excel 8.0. Artwork is expensive. Where possible, single column artwork (width 8.5cm) is preferred. The maximum allowable width is 17.5cm. Lettering should be in Arial, Helvetica or a similar font (10pt).

EQUATIONS: Authors are asked to submit equations created in either Microsoft Equation Editor© (the default supplied with several word-processing packages, including Microsoft Word© and WordPerfect©) or its upgrade called MathType©.

CETACEAN NAMES: Please use approved IWC (International Whaling Commission) common names in the text. For the sake of cultural values, regional names could be used if the international name is referred to at least once. Scientific name must be quoted after the first time the common name is mentioned. Afterwards it should be left up to the authors and at the editor's discretion (for instance, papers on taxonomy may need to quote scientific names several times). Scientific name must be placed in parentheses after the common name.

CAPITALS: examples are given below:

Area (when referring to official Area names - *e.g.* Area I, Franciscana Management Area, etc.), Sector, Division, Antarctic, South Atlantic Ocean, Northern Hemisphere, Scientific Committee, Table 1, Fig. 1, Chairman, Vice-Chairman, Blainville's beaked whale and Commerson's dolphin *(i.e.* where named after a person); but western South Atlantic, sub-committee, sub-Antarctic, humpback whale, bottlenose dolphin, etc.

Numbers, dates, map references: In the text, numbers under 10 should be spelled out fully where used individually. Arabic numerals should be used for a sequence of quantities and in reference to percentages (where % rather than percent is used): *e.g.* three humpback whales but 3% of humpback whales; 1 fin whale, 4 Bryde's whales and 9 southern right whales were observed.

Numbers with four or more figures should have no spaces: *e.g.* 1328; 9369234; 1540.5

Decimal points should be indicated by full stops, not commas. Zeros should be included: *e.g.* 0.86

There should be no space between numbers and abbreviated units: *e.g.* 114cm, 16kg

All units should be metric.

Dates should be in the form: 12 March 1996 not April 14, 1977

Geographic coordinates should be in the form: 32º05'55"S, 52º08'12"W

HYPHENS: should be used in compound adjectives preceding a noun, *e.g.* age-specific survival rates, length-specific model. But not where part of the compound adjective consists of a numeral, *e.g.* 8cm long testis, 35ppm water.

ABBREVIATIONS: Where the last letter of an abbreviation is the same as the last letter of the full word then no full stop is necessary: e.g. Fig. 1 but Figs 1-7

Acronyms or capital abbreviations do not require full stops: *e.g.* IWC, FMA, MSYR, 25°S, CV, SD, SE etc.

Commonly used abbreviations for units have no full stop: *e.g.* 10cm, 15m, 32ft

Generic names (*e.g. Pontoporia blainvillei*) must be originally written in full but may subsequently be abbreviated (*e.g. P. blainvillei*).

If a personal communication is used, abbreviate as 'pers. comm.'.

ITALICS: Should be used for: references to titles of books and periodicals (*e.g. Moby Dick*); names of vessels (*e.g. Ary Rongel*, *Atlântico Sul*); Latin names of plants and animals (*e.g. Coprosma foetidissima*); foreign words not part of everyday English (*e.g. et al., i.e., e.g.*); trade names (*e.g. Serramalte*).

QUOTATIONS: Use single quotation marks. Double quotation marks are only to be used for a quote within a quote. Within a quotation, follow the style and punctuation of the original. If omitting a section, indicate by three full stops '…'. If interpolating a word or phrase *please* use square brackets [my italics].

EQUATIONS, MATHEMATICAL REFERENCES: Ensure that superscripts and subscripts are easily discernible. Clearly distinguish between: the letter l and the number 1 (e.g. by underlining the letter); and the letter O and the number 0. Use italics for letters indicating parameters, *e.g.* $\mathrm{y} = a + b\mathrm{x}$

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The corresponding author of a manuscript submitted to LAJAM should complete a copy of this declaration and enclose it with the submitted manuscript.

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c/o Salvatore Siciliano, Latin American Journal of Aquatic Mammals, Fundação Instituto Oswaldo Cruz - FIOCRUZ/ENSP. Departamento de Endemias, Laboratório de Ecologia, Rua Leopoldo Bulhões 1480 - térreo, Manguinhos Rio de Janeiro, RJ, 21045-900 BRAZIL

Manuscripts will be reviewed by two referees, which will usually, but not necessarily, be members of LAJAM's Editorial Board.

There are no page charges for articles published in LAJAM. Copy of the articles will be available for the authors only in electronic format (e.g. .pdf).

ANEXO 2

NORMAS PARA O ENVIO DE PUBLICAÇÃO NO PERIÓDICO:
Marine Mammal Science

INSTRUCTIONS FOR AUTHORS

MARINE MAMMAL SCIENCE publishes significant new findings on marine mammals resulting from original research on their form and function, evolution, systematics, physiology, biochemistry, behavior, population biology, life history, genetics, ecology and conservation. Range extensions, unusual observations of behavior, and preliminary studies of a few individuals are published only where there is sufficient new information to render the manuscript of general interest. Low priority will be given to confirmatory investigations of local or regional interest.

The Journal endorses the principle that experiments using live animals should be undertaken only for the purpose of advancing knowledge. Consideration should be given to the appropriateness of experimental procedures, species of animals used, and number of animals required. All animal experimentation reported in **MARINE MAMMAL SCIENCE** must be conducted in conformity with the relevant animal care codes of the country of origin. The Editor will refuse manuscripts in which evidence of adherence to such codes is not apparent.

MARINE MAMMAL SCIENCE publishes (1) *Articles:* important original research; (2) *Review articles:* critical appraisals which place recent research in a new conceptual framework; *(3) Notes:* short communications on current research, important preliminary findings or new techniques; (4) *Opinions:* invited contributions on selected topics; (5) *Letters:* a forum for communications in response to papers previously published in **MARINE MAMMAL SCIENCE,** opinion, interpretation, and new information on all topics of interest to marine mammalogists.

Articles, Review articles and *Notes* are subject to peer review. Any *Letter* challenging published results or interpretations is transmitted to the author of the published work with an invitation to respond. The letter and its response are published simultaneously. *Letters* are judged by the Editor on appropriateness of the subject and interest to readers.

MANUSCRIPT PREPARATION

The manuscript should be concise, logical, and unequivocal. Publication is facilitated if authors double-check for typographical and other errors and ensure that manuscripts and figures meet the requirements outlined below. Manuscripts that do not conform will be returned for correction before consideration. If in doubt, consult the Editorial Office. Authors are charged for excessive changes in proof.

A full-length *Article* includes a title page, abstract, keywords, text, acknowledgments, literature citations, tables, figure captions, and figures. *Notes* and *Letters* do not have an abstract and are prepared in narrative form without headings, except for "Literature Cited."

All parts of the manuscript, including footnotes, tables, and figure captions, should be typewritten, double-spaced with margins at least 2.5 cm wide. Underline only when the material is to be set in italics. Use capital letters only when the letters or words are to be capitalized. Do not end a line of text with a hyphen.

TITLE PAGE

The first page should contain only the title and the name, affiliation, and complete address (plus current address, if different) of the author(s). The title should be brief and contain words useful for indexing and information retrieval.

ABSTRACT AND KEY WORDS

The abstract, of not more than 200 words typed on a separate page, should precisely reflect the contents of the paper, and focus attention on the purpose of the study, principal results, conclusions and their significance.

Below the abstract, provide and identify as such three to ten key words or short phrases that will assist in cross-indexing your article.

TEXT

As a general guide, The Chicago Manual of Style is recommended. Spelling should be standard U.S. (not British) to conform to Webster's Third New International Dictionary. Units should conform to the Systeme International d'Unites (SI). Non-standard abbreviations must be defined the first time they appear. Mathematical symbols, Greek letters, and unusual symbols should be identified clearly; superscripts and subscripts should be legible and carefully placed.

STANDARD ABBREVIATIONS

General: s, min, h (hour), d (day), wk, mo, yr, g (gram), mg, kg, Hz, kHz, MHz, km, m (meter), mm, cm, cc, mi (mile), ft, in. (note period), kn (knot), ha, gal, ml, l (liter, spell out when used alone).

Statistics: P (probability), x (mean), SD, SE, CV, SEM, n (sample size), df, r (correlation coefficient), t, F, U, Z (statistical tests); letters in equations are italicized.

Latin words and phrases (always italicized)*: i.e.,* (note comma)*; e.g.,* (note comma)*, ca.; cf; in vivo; in situ; vs.; etc.; per se; et al.; via; sensu; sensu faro; sensu stricto; a priori.*

ACKNOWLEDGMENTS

List all acknowledgments briefly under a single heading at the end of the text on a separate page. If applicable, give the permit number under which the work was conducted.

LITERATURE CITED

References should be cited in the text in the following form: Smith (1982); Smith (1982*a*, *b);* Smith (1983, 1984); Smith and Jones (1984); (Smith 1986); (Smith 1986, Jones 1987); (Smith 1986; Jones 1986, 1987); more than two authors, Smith et *al.* 1987.

References should be double-spaced and listed alphabetically as "Literature Cited" in the following standard form, giving the journal titles in full:

Armstrong, W.A., and C.W. Oliver. 1995. Recent use of fish aggregating devices in the eastern tropical Pacific tuna purse-seine fishery:1990-1994. National Marine Fisheries Service Center Administrative Report LJ-95-14 (unpublished). 47 pp. Available from SWFC, P.O. Box 271, La Jolla, CA 92038.

Gentry, R.L., and J.R. Holt. 1982. Equipment and techniques for handling northern fur seals. U.S. Department of Commerce, NOAA Technical Report NMFS SSRF-758. 15 pp.

Hubbs, C.L., W.F. Perrin and K.C. Balcomb. 1973. *Stenella coeruleoalba* in the eastern and central tropical Pacific. Journal of Mammalogy 54:549-552.

Leatherwood, S., and R.R. Reeves. 1983. The Sierra Club handbook of whales and dolphins. Sierra Club Books, San Francisco, CA.

Murchison, A.E. 1980. Detection range and range resolution of echolocating bottlenose porpoise (*Tursiops truncatus).* Pages 43-70 *in* R.-G. Busnel and J.F. Fish, eds. Animal sonar systems. Plenum Press, New York, NY.

Multiple citations for an author and single co-author are arranged alphabetically according to co-author. If there is more than one co-author, citations are arranged chronologically.

Issue numbers are not used unless page numbering begins at 1 with each issue. The number of pages is not given for books, but should be included for unpublished documents, theses, and "gray literature" (government reports, technical bulletins, *etc.)*

Personal communications and unpublished data are not to be included under "Literature Cited" but may be cited as footnotes, which shall include the complete name and address of the source and the month and year of the communication or notification of the unpublished data. A paper may be cited "in press" only if it has been accepted **IN FINAL FORM** by a journal. Papers "submitted" or "in preparation" may not be cited as such, but information in them may be cited as "personal communication." Any citation of a personal communication, unpublished data, manuscript submitted or in preparation, or unpublished report must be **WITH THE EXPLICIT**

PERMISSION OF THE LEAD AUTHOR OR PERSON WHO PROVIDED THE INFORMATION. Reference to non-refereed documents *(e.g.,* contract reports, environmental impact statements, meeting working papers) is discouraged. Citations of these documents **MUST BE ACCOMPANIED BY THE ADDRESS WHERE THEY CAN BE OBTAINED**. Meeting abstracts should not be cited. Any document bearing a "Do not cite without permission" statement may be cited only **WITH THE EXPLICIT PERMISSION OF THE LEAD AUTHOR**. A statement that all necessary permissions have been obtained must be included in the cover letter accompanying the submitted manuscript. The use of gray literature is DISCOURAGED and should only be cited when there is no primary literature to support important findings or the interpretation of those findings presented in the manuscript. Authors must double-check all literature cited; they are solely responsible for its accuracy.

Taxonomic usage in MARINE MAMMAL SCIENCE in general follows D. W. Rice (1998) “Marine mammals of the world: Systematics and distribution,” Society for Marine Mammalogy Special Publication Number 4. Authors wishing to use a different nomenclature should explain the departure in a footnote.

TABLES

Excessive tabular data are discouraged. Tables should be typed separately and double-spaced. Tables should be numbered with Arabic numerals in the sequence first referenced in the text and have a brief title. Column headings and descriptive footnotes should be brief. Do not use vertical rules.

FIGURES

Figures are costly and should be used with discretion. An illustration is justified only if it clarifies or reduces the text. Figures should be professionally designed. All figures will be published as full page (11.7 cm) width with a maximum length of 17.5 cm.

For further information regarding the preparation of illustrations, the Journal recommends the publication "Steps Toward Better Scientific Illustrations" available from Allen Press, Inc.

SUBMISSION OF MANUSCRIPTS

New manuscripts should be submitted as a single PDF or Word file (text, tables, figures all in one file) with a separate PDF or Word file for the cover letter to mmscience@ucsc.edu. The cover letter must identify a corresponding author--the person (with address, telephone number, fax number, and email address) responsible for negotiations concerning the manuscript. The letter must also state that the same work has not been previously published, nor is it currently under consideration for publication elsewhere; further, that all authors have seen and approved for publication the final manuscript and that any person cited as a source of personal communication or other unpublished information (including abstracts bearing a do-not-cite warning) has approved such citations. Written authorization may be required at the Editor's discretion. The subject of the email should be the lead author's surname. An example is, "Norris". If the corresponding author differs from the lead author, follow the first name with the corresponding author's name in parentheses. An example is, "Norris(Perrin)". A manuscript number will be assigned to each new submission and sent to the corresponding author via return email. In all correspondence beyond the initial submission, please put your assigned manuscript number on the subject line of your email.

The cover letter file should be entitled "Lead author(Corresponding author)Cover.pdf"; *e.g.,* “Norris(Perrin)Cover.pdf”.
The manuscript file should be entitled "Lead author(Corresponding author)Ms.pdf"; *e.g.,* “Norris(Perrin)Ms.pdf”.

In the unusual event that the corresponding author does not have access to email, the cover letter together with three copies of the submitted manuscript should be sent to James A. Estes, Editor, MARINE MAMMAL SCIENCE, Center for Ocean Health, 100 Shaffer Road, Santa Cruz, California, 95060, USA.

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THE F. G. WOOD STUDENT SCHOLARSHIP

Forest G. Wood, a founder of the Society for Marine Mammalogy, was noted for his editorial skills. All students submitting manuscripts accepted for publication in Marine Mammal Science should indicate at the time of submission if they want to be considered for this award. The editor will select the winner from among the accepted manuscripts submitted during the interval between successive Biennial Conferences on the Biology of Marine Mammals. Further details about the award can be found on the Society's web page.

Authors are responsible for page charges of $15.00 (U.S.) per printed page or part thereof. If funds for publication are not supplied by an agency or grant, a waiver of page charges may be applied for, by letter or e-mail to the Editor (James A. Estes, MARINE MAMMAL SCIENCE, Center for Ocean Health, 100 Shaffer Road, Santa Cruz, California, 95060, USA;).

PROOFS AND REPRINTS

Page proofs are sent to the author directly from Allen Press, Inc., together with an order form for reprints. The corrected proof is to be returned in 72 hours to the Assistant Editor and the order for reprints to the Press.

ANEXO 3

NORMAS PARA O ENVIO DE PUBLICAÇÃO NO PERIÓDICO:

Revista Chilena de Historia Natural

INSTRUCIONES A LOS AUTORES

La **Revista Chilena de Historia Natural** (RCHN) publica artículos en las áreas de Ecofisiología, Ecología Conductual, Ecología de Poblaciones y de Comunidades, Ecología del Paisaje y Ecología de Ecosistemas, Oceanografía Biológica, Sistemática, Taxonomía, Evolución Orgánica, Genética de Poblaciones, Biogeografía, Paleobiología, Botánica y Zoología. El énfasis de la Revista son las Ciencias Básicas y, secundariamente, aspectos más aplicados como conservación y manejo de recursos biológicos. En estas temáticas, la Revista enfatiza además artículos que sometan a prueba hipótesis en forma explicita, o que propongan explicaciones novedosas. La Revista publica artículos científicos, revisiones temáticas, conferencias, comentarios, simposios, editoriales, documentos, revisiones de libros y Cartas al Editor, en Español y en Inglés.

Para facilitar la búsqueda de revisores idóneos, los trabajos sobre Morfología, Sistemática y Taxonomía solo serán considerados en inglés. Las contribuciones en estas diferentes categorías son sometidas al juicio crítico del Comité Editorial, el que se hace asesorar por al menos dos revisores. La Revista está abierta tanto a socios como no socios de la Sociedad de Biología de Chile. Los costos de publicación de artículos aceptadod en RCHN son de USD 26,00 por página final impresa. Su aparición es trimestral y cuatro números conforman un volumen. La recepción de trabajos es continua, publicándose en orden de aceptación. Se deja constancia de las respectivas fechas de recepción inicial y de aceptación definitiva de los manuscritos.
Los trabajos que se presenten deben estar escritos en mayúsculas y minúsculas (incluyendo títulos y subtítulos), a doble espacio (incluyendo tablas), en letra tipo“Times New Roman” de 12 puntos, en hojas tamaño carta con márgenes de 2,5 cm y líneas numeradas. Cada página, incluyendo tablas y leyendas de figuras, debe numerarse en forma correlativa y llevar el apellido de los autores en el margen superior derecho (ejemplo: González 21); en caso de múltiple autoría se utiliza la forma et al. a continuación del primer autor. Los manuscritos solo serán sometidos a través de correo electrónico. Para ello, los autores deberán enviar un (1) archivo en formato Word o (de preferencia) PDF con el contenido íntegro del trabajo (incluyendo tablas y figuras si corresponde), más un segundo archivo con la carta de presentación correspondiente a: rchn@genes.bio.puc.cl.

Comience en hoja separada cada una de las siguientes secciones:

(a) Portada, incluyendo título y título acortado del trabajo, nombre de los autores, institución y dirección postal en que se efectuó el trabajo, y nueva afiliación institucional si corresponde. Si hay varios autores, las instituciones respectivas son referidas por números correlativos indicados como superíndice al final de cada nombre.

(b) Resumen.

(c) Abstract.

(d) Texto, incluyendo Introducción, Materiales y Métodos, Resultados, Discusión y Agradecimientos. Dado el caso, se puede fusionar Resultados y Discusión en una sola sección.

(e) Literatura Citada.

(f) Notas a pie de página.

(g) Leyendas de Figuras (que pueden agruparse en una o más páginas).

(h) Cada una de las Tablas, con su correspondiente leyenda. En la sección de Texto, no use sangría en el primer párrafo bajo cada título o subtítulo.

(1) El Título debe ser informativo y preciso en relación al contenido del trabajo (use mayúsculas sólo cuando corresponda). Si es en español, deberá estar seguido de su versión en inglés y viceversa. Proporcione también en la portada un encabezamiento de página (título acortado) de no más de 50 caracteres, incluyendo espacios.

(2) El nombre de los autores (en mayúsculas) se coloca a continuación de los títulos en español e inglés del trabajo. Se usa solamente el nombre y apellido paterno, evitándose título académico o de otra índole. Puede ser apropiado usar la inicial del segundo nombre. Por ejemplo, Juan C. González. Si se desea usar el apellido materno, éste deberá ir unido al paterno por un guión.

(3) Todo trabajo debe contar con un Resumen en español y uno en inglés (Abstract) o viceversa, con precedencia del idioma en que está escrito el texto. Ambos no deben exceder 350 palabras, deben ser comprensibles sin referencia al texto del trabajo y deben presentar sucintamente los hallazgos esenciales. Al pie del Resumen y del Abstract inserte no más de cinco palabras clave.

(4) La Introducción debe exponer el problema y su lugar dentro de un contexto general; no debe ser una revisión exhaustiva del tema, a menos que el artículo sea una Revisión.

(5) La descripción de Materiales y Métodos debe ser concisa, pero con el detalle suficiente para permitir una comprensión cabal de su contenido, además de permitir una comprensión fácil al lector.

(6) Los Resultados se presentan en Tablas, Figuras, o prosa en el texto, dependiendo de qué formato sea el más claro. Las Tablas y Figuras llevan sus leyendas en inglés y español, o

viceversa, con precedencia del idioma en que se encuentra el texto. Indique, mediante notas marginales en el texto, la localización preferida de las Tablas y Figuras.

(7) La Discusión debe ser concisa y referirse a la interpretación de los resultados presentados y a su relación con tópicos similares documentados en la Literatura.

(8) Las citas se indican en el texto por el apellido del autor(es), seguido del año de publicación. Si son dos los autores se separan por el signo &. Si son más de dos autores, se utiliza el apellido del primero seguido de et al. Las citas múltiples en el texto van en orden cronológico.

Ejemplos de citas en el texto:

... como lo confirman varios autores (Valdebenito 1991, Pérez 1992a, 1992b, González 1993)...
... como lo documentan Valdebenito (1987), Pérez (1989a, 1989b) y González (1993)...
... como se especifica en una investigación reciente (González & Pérez 1993)...
... de acuerdo a González & Pérez (1994)...
... discrepando de este modo con Aliaga et al. (1992a, 1992b)...

En la sección Literatura Citada incluya los trabajos citados en el texto en orden alfabético de acuerdo al apellido del primer autor, y luego cronológicamente. Para las referencias con tres o más autores, "et al.", inclúyalas después de aquellas con dos autores, y en forma cronológica (y no alfabética) tal como se aprecia en el siguiente ejemplo:

NESPOLO & ROSENMANN (2002)
NESPOLO, SABAT & ROSENMANN (1994)
NESPOLO, NOVOA & ROSENMANN (1996)
NESPOLO R, L BACIGALUPE, FF NOVOA & M ROSENMANN (2000)

Iniciales y apellido de los autores van en mayúscula. Separe el último de los autores por medio del signo &. Note la ausencia de puntos entre iniciales, año de publicación y título de la referencia. Siempre use el nombre completo de cualquier revista que cite. En el caso de revistas no indexadas, agregue el país de origen de la publicación entre paréntesis y antes del volumen.

Ejemplos de citas de artículos:

MINOKO A & BC KIMURA (1994) A comment on the aggregration of worm holes around Casiopea. Japanese Journal of Astronomy 55: 319-324.

PÉREZ AB (1994) Distribución de kamptozoos saprófitos en un gradiente climático de Chile central. Revista Clásica de Historia Natural 56: 45-46.

PACKARD AB, CD PACKARD & EF BOARDMAN (1994) Water balance of the eggs of a tropical lizard (Iguana antarctica). Proceedings of the Ecology Society of Aucó (Chile) 58: 2051-2058.

Ejemplos de citas de libros:

DIXON WJ (ed) (1975) BMDP biomedical computer programs. University of Califomia Press, Berkeley, California. 214 pp.

FAEGRI GW & L VAN DER PIJL (1979) Principles of pollination ecology. Third edition. Pergamon Press, Oxford, United Kingdom. xvi+280 pp.

HILL D (1994) Soil and sand. Academic Press, New York, New York. xxi+306 pp.

LONG HI & JJ LONGBEARD (eds) (1994)... vi+113 pp.

Ejemplos de citas de capítulos de libros:

PÉREZ J (1994) El culebrón como animal de laboratorio. En: Verón VC & C Capriccio (eds) Los animales de laboratorio: 70-89. Editorial Latina, Ciudad Edén, país.

WHITE CD (1992) Thermoregulation. En: Abs WH (ed) Lizard ecology: 103-142. Cornell University Press, Ithaca, New York, USA.

Use "En"o "In" para citar capítulos de libro si el texto de su artículo está en Español o Inglés, respectivamente.

Ejemplo de cita de artículo en prensa:

ALERTADO JJ & PJ ROCHER (en prensa) Una revolucionaria técnica para el catastro de vegetación. Journal of Controversy.

Para este mismo artículo cite en el texto:...según Alertado & Rocher (en prensa)... Indique en la Literatura Citada la referencia completa, con las palabras "en prensa" entre paréntesis. No indique fecha ni volumen de supuesta publicación.

Ejemplos de citas de Tesis:

ROMARIO-PÉREZ J (1994) Ecología de los murciélagos gigantes de Chile central. Tesis de Licenciatura, Facultad de Ciencias, Universidad de Doñihue, Rancagua, Chile. xxi+108 pp.

Las mayúsculas de nombres y apellidos deben llevar acentos cuando corresponda. No incluya en Literatura Citada los resúmenes de trabajos presentados en congresos, reuniones o simposios. Cítelos en el texto a pie de página (todas las citas a pie de página, referenciadas en el texto, deben llevar una numeración correlativa a lo largo del manuscrito). Tampoco incluya en esta sección los trabajos enviados a publicación. Si es necesario, cítelos en el texto, con el nombre de los autores seguido entre paréntesis por "resultados no publicados". Las comunicaciones personales se citan sólo en el texto, señalando el autor(es), seguido entre paréntesis por "comunicación personal". Deben incluirse los nombres latinos binominales (puestos en cursiva) de todos los animales y plantas que se mencionen. La primera vez que un nombre científico es citado en el texto, debe llevar el nombre de su descriptor.

Ejemplo: ...Sebastodes prognathus (Tortonese, 1942). El trabajo original de descripción, sin embargo, no deberá ser incluido en la Literatura Citada.

Para los efectos de la nomenclatura deben seguirse las reglas establecidas en el International Code of Zoological Nomenclature, el International Code of Botanical Nomenclature o el International Code of Nomen clature of Bacteria. Si decide no citar el descriptor de cada uno de los organismos nombrados en su artículo, debe citar en la sección Materiales y Métodos la fuente bibliográfica que se sigue en el uso de nomenclatura. Por ejemplo: "La nomenclatura sigue a Donoso-Barros (1966) para reptiles y a... para hierbas". Referencias generales de este estilo sí deben ir incluidas en la sección Literatura Citada. Si el título del trabajo incluye nombres científicos, éstos deben ir acompañados de los taxa superiores correspondientes. Ejemplo: Lessonia nigrescens Bory (Phaeophyta: Laminariales).

(9) Las locuciones latinas y griegas (por ejemplo: et al., a posteriori, e.g., i.e., sensu) no deben ir subrayadas ni en cursiva. Sólo use cursiva para los nombres científicos.
(10) Las Tablas se enumeran en arábigo y en forma correlativa, y se presentan con su leyenda en español e inglés (con precedencia del idioma del texto) en la parte superior. Cada tabla debe ir en páginas separadas, y confeccionadas con la herramienta apropiada por Word para tal efecto. Use líneas de separación horizontales para marcar el comienzo y el final de cada Tabla; para separar los encabezados principales, pero no en el cuerpo de la Tabla. Nunca utilice líneas de separación verticales. Las líneas de división deben ser negras sin efectos especiales (e.g., sin subrayar o con relieve). El texto utilizado para los números, para indicar categorías, variables, u otros elementos debe ser idéntico al utilizado en el resto del manuscrito ("Times New Roman"de doce puntos). Las unidades de variables o categorías deben ir entre paréntesis, y abreviadas de acuerdo al Sistema Internacional de Unidades.

(11) Tanto los gráficos, diagramas y fotografías llevan la denominación única de Figura, que se abrevia como Fig. en el texto, y deben estar numeradas correlativamente en arábigo. En el caso de los gráficos, las líneas correspondientes a los ejes deben ser continuas. Las marcas en ambos ejes deben estar orientadas hacia dentro de la figura. El texto utilizado para los números, nombre de los ejes (variables) y sus unidades, leyendas, o cualquier otro elemento escrito debe ser idéntico al utilizado en el resto del manuscrito ("Times New Roman"). Para el nombre de los ejes y sus números se sugiere utilizar texto de 16 y 14 puntos como mínimo, respectivamente. El nombre de cada eje o leyenda debe incluir el uso de mayúsculas (solo la primera letra de la primera palabra) y minúsculas. Las unidades en cada eje deben ir a la derecha del nombre de la variable, entre paréntesis y abreviadas de acuerdo al Sistema Internacional de Unidades. La identificación del estadígrafo de dispersión utilizado puede estar incluida en el texto (i.e., en Materiales y Métodos) y/o en el encabezado de cada Figura, pero no en la Figura (e.g., en los ejes). En el caso de gráficos de barra simples o múltiples, se prefiere el uso de tonos negros, blancos, o achurado diagonal en negro y blanco para el relleno de las barras; no utilice tonos grises. En el caso de gráficos XY de puntos con líneas, se prefiere el uso de símbolos geométricos en blanco y negro, y de líneas negras continuas o segmentadas. Evite el uso de tonos grises.

(12) Uso de números, unidades, y convenciones estadísticas. Los números entre 10 o mayores que 10 deben ir como números excepto al inicio de una oración. Los números entre uno y nueve deben escribirse como texto a menos que sean seguidos por unidades. Los números

correspondientes a años deben ir completos y no abreviados (e.g., 1992- 1998). El uso de unidades y sus abreviaciones en todo el texto debe estar de acuerdo al Sistema Internacional de Unidades. Las medias y sus estimadores de dispersión (e.g., desviación estándar, error estándar), tamaños de muestra, y unidades asociadas deben ir como:

$\bar{X}$ ± DE unidad, n (e.g., 21,7 ± 4,2 g, n =
16)

La descripción de los resultados de cada prueba estadística en el texto debe incluir el nombre de la prueba, el estadístico y su valor, los grados de libertad (o el tamaño de muestra de acuerdo a la convención en cada prueba), y el valor de probabilidad asociado P. Para resultados significativos utilizar valores exactos de P a menos que P sea menor que 0,0001. Para resultados no significativos siempre se debe proporcionar el valor exacto de P.

Por ejemplo: (a) prueba t de Student, $t_{12} = 3,05$; $P = 0,005$; (b) prueba de Kruskal-Wallis, $H_{11} = 287,8$; $P < 0,0001$; (c) correlación por rangos de Spearman, $r_s = 0,80$, $n = 13$; $P = 0,015$; Análisis de varianza, $F_{1,17} = 0,97$; $P = 0,485$. Indicar claramente cuando las pruebas sean de una cola (unilaterales) en lugar de dos colas (bilaterales). Las cifras decimales siempre deben escribirse con un cero a la izquierda de la coma decimal (e.g., 0,82 y no ,82).

Los manuscritos deben enviarse electrónicamente a:

Luis Ebensperger
Editor Jefe
rchn@bio.puc.cl

ANEXO 4

NORMAS PARA O ENVIO DE PUBLICAÇÃO NO PERIÓDICO:

Journal of Mammalogy

INSTRUCTIONS FOR AUTHORS

NOTES:

- Webster's 10th for spellings (follow copy on names of mammals)
- CBE 6th for all style points not on here
- omit word "the" in running text if it's not needed—use discretion

copyeditor: if at all possible, copyedit tables and equations online in electronic files, using word processor characters for any special symbols; otherwise, copyedit tables and mark equations on hard copy; in either case, do not remove original electronic version of tables or equations from online files

- insert a note to pager at beginning of article regarding thin spaces and hair spaces (if used): <Replace X@X with thin space. Replace X#X with hair space.>
- use SGML entities for other characters that aren't available in Word
- OK to use SGML entities for all symbols and special characters

QUERIES:

<AQ> 1. Author: This article has been lightly edited for grammar, style, and usage. Please compare it with your original document and make any corrections on these galleys. Please limit your corrections to substantive changes that affect meaning. If no change is required in response to a question, please write "OK as set" in the margin. Copy editor</AQ>

- stock query is always used as first query; place after the first sentence of abstract or text
- place queries between comment tags near the text to which they refer: <AQ> 2. Please provide title for reference 15. Copy editor </AQ>
- separate query file is created by the typesetter

PDFs and PAPER PROOFS:

- PDFs at 1XO to managing editor
- paper proofs to managing editor
- clean proofs

VOLUME LINE:

Journal of Mammalogy, 81(1):361–374, 2000

- appears in upper left-hand corner of 1st page of article

COPYRIGHT LINE:

© 2003 American Society of Mammalogists
www.mammalogy.org

- appears in lower left-hand corner of first page of article (below corresponding author footnote)

LRH:

- page number to the outside
- JOURNAL OF MAMMALOGY centered
- Vol. 84, No. 2 to the inside
- this head is canned; copyeditor, do not insert

RRH:

- May 2003 to the inside
- HARRIS AND MCMILLAN—SHORT TITLE GENUS SPECIES
- OBITUARY—NAME OF DECEASED
- use et al. for 3 or more authors
- short title should be 40 characters max
- page number to the outside

TITLE:

ALL CAPS BOLD FLUSH LEFT

- common name, genus species, families, kingdoms all permitted in any combination the author uses
- no need to specify genus species with common

name (do not delete; do not query to add)

AUTHOR LINE:

BRUCE D. PATTERSON,* C. L. HOLMES, JR., AND
LINDA PFELT

- space between initials
- asterisk refers to new corresponding author footnote
- corresponding author not necessarily the 1st Autor

AFFILIATION AND PRESENT ADDRESS LINE:

University of Illinois at Chicago, Department of Biological Sciences (M/C 066), 845 West Taylor, Chicago, IL 60607 (BLC)
Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, United Kingdom (MDB)
Present address of JCL: Address starts a new line

- provide complete postal address for everybody
- spell out or query to have author spell out acronyms
- use postal codes
- put addresses in the order the authors are cited
- if everyone is from the same place, no initials appear parenthetically afterward
- For author affiliations, OK to use spelling given by author (Brasil, México)
- For all affiliations, regardless of country: City, State/Province (no comma) Zip, Country (including USA)

CORRESPONDING AUTHOR FOOTNOTE:

* Correspondent: name@world.com

- thin space used after asterisk (use X@X and write note to pager at beginning of article; see NOTES)
- appears in lower left-hand corner of the 1st page of the article (it replaces the old volume line)
- no period after e-mail address
- if e-mail address is not provided, just use

* Correspondent.

SUBMITTED/ACCEPTED LINE:

Submitted 2 March 1999. Accepted 4 August 1999.

- appears just after references

ASSOCIATE EDITOR LINE:

Associate Editor was Edward J. Heske.

- appears as the article's very last line, after submitted/accepted line

ACKNOWLEDGMENTS:

- #1 head used
- use 1st person
- style for grants: National Science Foundation (DEB 97-01057)
- "... grant S1-1274 to M. Aguilera" (note the use of first initial)
- do not abbreviate names of agencies
- reduced type used
- change "We wish to thank" and "We want to thank" to "We thank"

APPENDIX:

APPENDIX II

Description of characters

Paragraph indented run-in #3 head, if used.—Text runs in.

- Use a #2 head if there are 3 levels of head: #2 appendix head is centered, lightface roman, cap and lowercase
- use roman numerals
- set in reduced type
- follow usual stacking of heads; no reverse italic
- follows references, submitted/accepted line, and associate editor
- all appendices are numbered
- table appendices use this same format; if no descriptive #3 head, set table appendix title as roman (not italic)
- specimens examined: abbreviate distance (mi, km, etc.) and directions (E, N, SW, etc.) with no periods
- ♂, ♀, ♂♂, ♀♀ may be used
- use punctuation that is logical; make consistent throughout an appendix
- follow instructions (if given) on hard copy and/or transmittal form

SUMMARY:

- a foreign-language summary may be provided
- it may be a translation of the abstract, or not
- place before the acknowledgments
- title can be RÉSUMÉ, ZUSAMMENFASSUNG, RESUMEN, RESUMO ---follow copy

ABSTRACT:

Flush left abstract that straddles columns. Appears after affiliation line. Only 1 paragraph long. No heading. Should not exceed ca. 5% of the text. Query editor if longer.

KEY WORDS:

Key words: word, comma separators, alphabetical order, no period at end

- use em space before word listing
- reduced typeface
- full rule after key words separates abstract and key words from 2-column text

- spell out ordinals
- ten or fewer key words or phrases---query if >10 are provided

HEADS:
#1 head:
CAP AND SMALL CAP BOLD CENTERED
#2 head:
Cap and Cap Italic Centered
#3 head:
Italic paragraph indent cap then lowercase: lowercase after colon.—Text runs in after an em dash.

- no reverse italic in any head
- most articles move from #1 to #3 heads
- use #2 heads only if there are 3 levels of head
- text after #1 and #2 heads is paragraph indented
- introduction head not used
- text begins with paragraph indentation
- in normal research articles, use heads Materials and Methods (text of this section is set reduced), Results, Discussion, Acknowledgments, Literature Cited, Appendix

SYNONYMIC HEADS:
Family Molossidae
(genus and species indeterminate)
Noctilio lacrimaelunaris, new species
Crocidura fuliginosa (Blyth 1856)
Crocidura horsfieldii Tomes (1856)
Crocidura rapax G. Allen 1923

- these heads are lightface roman
- follow copy on use of punctuation and parens used with taxonomic authorities
- indicate synonymies with a comment tag

SPECIAL ARTICLE TYPES:
“REVIEWS,” “OBITUARIES,” “INFORMATION FOR CONTRIBUTORS,” “BOOKS,” “BOOKS RECEIVED,” MINUTES . . .” “STUDENT PROGRAMS,” “COMMENTS AND NEWS”

- text is same size as regular articles
- level 1 head display flush left, all caps, lightface roman
- level 2 head display flush left, bold roman cap and lowercase
- level 3 head run in, bold roman

INTERNAL STYLE:
General style:

- serial comma; American spelling
- American spelling of country names: Brazil, Mexico
- Follow copy for names of mammals
- ." ," "; ":
- i.e., e.g., et al.
- cf.
- spell out versus always
- ([ ])
- do not allow 2 sets of parens next to each other: ( ) ( ); use (item; item) instead
- Latin is roman; in vivo, in vitro, in situ
- spell out "male" and "female" in text; symbols may be used in tables and appendices
- use a hair space around colons in ratios that use words (use X#X and write note to pager at beginning of article; see NOTES)
- do not use a thin space around colons in ratios of numbers
- day 1, experiment 4, grid 6, site 1
- do not use in-text lists; if it cannot be avoided, follow author for style
- use virgule construction only when modifying a numeral: 6 mice/ha, a few mice per hectare
- do not use virgule in place of punctuation or words, but can be used for and/or
- one of us (BHB)
- percent something, but percentage of something
- do not change “due to,” “above,” “below”
- use quotation marks around section heads used in text: “Materials and Methods”; but for Book Reviews, use italics when referring to sections or chapters of a book
- “pre” and “post” words acceptable, do not change: premating, prehibernation, postreproduction,etc.
- for Book Reviews: use hardbound (not hardcover or cloth) for book information; include author email address with physical address after book review

Sources of materials:

- subcutaneous transponder chip (PIT tag, Indexel, Rhone Merieux, Laupheim, Germany)
- (Sigma Chemical Company, St. Louis, Missouri)
- spell out states in full
- omit symbols for trademark, registered, and copyright (TM, ®, ©)

Hyphenation rules:

- en dashes used in open or hyphenated compounds: Genus species–like
- run together the following prefixes with the word following: ante, anti, bi, co, contra, counter, de, extra, infra, inter, intra, micro, mid, neo, non, over, pre, post, pro, pseudo, re, semi, sub, super, supra, trans, tri, ultra, un, under
- do not permit double vowels or triple consonants with these prefixes; hyphenate these cases, but defer to W10
- retain hyphen if the word that follows is capitalized, is an all-caps abbreviation, or is a

numeral

- retain hyphens for clarity if needed
- use an en dash between 2 units of equal weight
- use normal hyphenation rules for units of measure used adjectivally: a 2-ha plot

Nomenclature:

- Genus species, then G. species. Exception: if 2 genera have the same initial, they could be abbreviated with first 2 letters, such as Ge. species and Ga. species---FOLLOW COPY.
- G. s. subspecies
- do not include authority (author or author and year), except in synonymy
- scientific names of a species used as the subject of a sentence take singular verbs
- spp., sp.; rarely used; follow copy
- follow copy on use of parens around classifiers
- OK to begin a sentence with an abbreviated genus name
- do not begin a paragraph with an abbreviated genus name
- FOLLOW COPY on whether genus name is spelled out in full with each new species

Abbreviations and acronyms:

- Mr., Dr., P.O. Box, St., Ph.D., M.A.
- sentences, but not paragraphs, may begin with an unambiguous abbreviation
- if used 10 or fewer times, do not abbreviate or use acronyms for names of localities, study areas, morphological characteristics, governmental agencies, and physiological parameters.
- abbreviations for museums, standard abbreviations for protein loci, chemical elements, and symbols used in math are acceptable when defined at 1st use
- italic abbreviations for genes are acceptable when defined at 1st use, e.g., cytochrome b (Cytb) or cytochrome-b gene (Cytb).
- abbreviations alone cannot comprise a head
- follow copy for protein loci abbreviations

Time and dates:

- 1950s
- 9 March 1999, 28–30 May 1998
- spell out months in full
- 0700 h
- photoperiod: 14L:10D
- 1972–1973
- 1903–1944

Geography

- latitude and longitude: 10º26'N, 67º50'W
- Always spell out United States
- United Kingdom (spell out always)
- USA never used
- if ZIP code is used, use the postal code: Washington, DC; Waconia, MN
- spell out states in their entirety otherwise: Washington, D.C.; Waconia, Minnesota
- spell out counties: Douglas County, Kansas
- N, E, S, W when giving localities
- legal description for localities: T14N, R10W, SW 1/4 Sec. 2

TECHNICAL STYLE:

Number style:

- 0.01 to 1 to 10 to 1,000 to 10,000
- use leading zero always for decimals
- use numerals for everything: 2 dogs, 3 of 11 patients, 1 ml
- spell out numbers to avoid confusion: three 14-ml samples
- spell out numbers "one" and "two" if they are meant in a nonspecific sense: on the one hand; an example or two
- spell out numerals and any associated units of measure to begin a sentence
- except in key words, use numerals for all ordinals: 1st, 3rd, 10th
- spell out ordinals that appear before a numeral: first 6 mice
- 6-fold; 5.5-fold; 100-fold
- two-thirds (n, adj)

Units of measure:

- s, min, h, day, week, month, year
- for geologic time, use 2.4 × 106 years ago or mya; do not use B.P.
- spell out mya (“million years ago”) at first mention
- non-SI units of measure are not abbreviated: 4 feet
- spell out liter without prefix: 1 liter, 3 liters; however, 3 ml
- do not abbreviate lux
- use standard SI abbreviations
- use slash for 2 units; use space and raise to –1 or whatever for 3 or more units
- magnification: 500×
- centrifuge: 11 × g
- temperature: 11ºC

Statistical style:

- SD, SE, d.f. always abbreviated---need not be defined
- use italics for statistical tests: F, G, H, P, Q, r, R2, t, U, V, W, z, etc.---need not be defined
- spell out mean in running text; use0 (cap italic X with a macron) with values (do not define): we reported mean ± SD, but 0 = 4.6
- spell out chi-square test in running text; use P

2
with values (do not define): using a chi-square test, but P
2 = 260.46

- ANOVA must be defined at 1st use as analysis of variance; thereafter use ANOVA regardless of number of times used
- spell out other statistical acronyms in running text, but abbreviate in statistical situations after defining: e.g., we reported the coefficient of variation (CV)..., and CV = 22.4; we computed the confidence interval (CI)..., and CI = 0.07–0.16
- CI = consistency index, RI = retention index
- FIT FST
- rs
- F-test; z-test
- (n = 409)
- (P < 0.0001)
- Yates’; Wilks’
- Mann--Whitney U-test
- Student's t-test
- a t-test with 4 replications
- (t = 3.76, d.f. = 2, P < 0.04)
- d.f. = 3, 364 (don't run values together)
- if d.f. values are presented as inferior, change to correct style: F6,198 = 0.253, P = 0.618 becomes F = 0.253, d.f. = 6, 198, P = 0.618; G4 = 4.70, P < 0.2 becomes G = 4.70, d.f. = 4, P < 0.2 (note order: primary stat, d.f., P)

Math style:

- superscripts and subscripts are not stacked; sub 1st, super 2nd
- Greek is roman
- all nonstatistical variables are roman: x = 11
- in running text with mathematical operators, space around operators used as verbs: 4 + 8 = 12
- do not space otherwise: a value >11
- equation 3; (see equation 1)
- numbered display equations use flush-right parenthetical numerals; follow author on whether or not they are numbered

Journal-specific style:

- dental formulae: i 1/1, c 0/0, p 1/0, m 3/3, total 18
- vertebral formulae: 7 C, 13 T, 6 L, 2–3 S, 26–31 Ca, total 55–60
- upper teeth use uppercase letters; lower teeth use lowercase letters: P4, m1, m1–3
- chromosome: 2n; FN; X and Y chromosomes
- do not use superscript or subscript numerals to designate upper and lower teeth
- OK to use ranges in running text: 11–40 specimens
- OK to use operators in running text: >40% did this
- do not use "ca." in running text
- use × for arrays, dimensions: 4 × 4 grid; 48 × 16 × 16 cm
- use × to indicate a true hybrid cross (F × G)
- individual animals should not be called by a name, field catalog number, or lab number
- for units of % and ° (degree): 15%, 20%, and 25%; from 21°C to 23°C; 63–100%
- for other units, don't repeat measure: 4, 8, and 11 m
- 9.7 g ± 1.1 SE (or SD or whatever) at 1st use; thereafter, use 9.7 ± 1.1 g
- close all “radio” words: radiotransmitter, radiolocation, radiocollar, radiotrack, radiotelemetry, radiotagged
- live trap (n), livetrap (v), livetrapped, livetrapping
- Neotropic(s), Palearctic, Nearctic
- tropics, tropical, neotropical
- Douglas-fir

TABLE AND FIGURE CITATIONS IN TEXT:

- spell out Figure to begin a paragraph; use Fig. and Figs. otherwise
- items are treated the same inside and outside of parentheses
- Table 1
- (Tables 1 and 2); (Figs. 3 and 8)
- note: Figs. 1a and 1b; (Figs. 3a–d)
- (Figs. 3–5)
- (Table 3; Fig. 8)

IN-TEXT REFERENCES:

- author–year format in alphabetical, then chronological, order
- semicolon separators
- use et al. with $3 authors
- "et al.'s" is always incorrect; recast
- Baker et al. (1989); (Baker et al. 1989)
- Bohlin and Zimmerman (1982); (Bohlin and Zimmerman 1982)
- (Bradley et al. 1991a, 1991b, 1998)
- (Baker et al. 1989; Block and Zimmerman 1991; Bohlin and Zimmerman 1982; Bradley et al. 1991a, 1991b; Tucker and Schmidly 1981; Zykowski, in press)
- if literature citation occurs in the same parenthetical statements as something else (additional info), use an em dash to separate: (Canis mesomelas—Boyer 1987),
(385,000 ha—Koford 1958), (Douglas and Shawnee counties—Jones 1969),
(n = 14—Hall 1980)
- use semicolon to separate figure/table citations: (Scott et al. 1993; Table 2), (additional information; Fig. 4)
- (Cameron 1993:211)

- Jones (1991:1622, table 4); Hafner et al. (1992c:345, figure 4)
- do not capitalize or abbreviate "table" or "figure" when citing others' published work
- (J. J. Lee, pers. comm.); (R. H. Tamarin, in litt.)
- edit spellings and years to match references at end and query OK
- do not use unpubl. data or pers. obs.; use in litt.
- Complete URLs may be given in running text with no corresponding reference list entry; follow author as to whether URL is given in text or in reference list

FIGURE LEGENDS:
FIG. 1.—Text follows, with a) text, b) text, and c) text. Do not use bold parts.
and
FIGS. 3–5.—FIG. 3. Information. FIG. 4. Information. FIG. 5. Information. Etc.
Letter always placed before explanation:
FIG. 1.—A and B) Explanation. C) Explanation.
and
FIG. 2.—Explanation using a) explanation and b) explanation.

- use style a) and b) and a and b)
- spell out everything in the figures; each caption should stand alone, but no need to define statistical tests, ANOVA, SE, SD, CI, CV, d.f. in figure legends
- spell out and include, if appropriate, species, localities, and dates of study, in addition to a description of the content
- OK to let museum acronyms stand in specimen numbers
- match case of in-text citations of figure caption letters (a or A) to figure caption
- for explanations of abbreviations, follow copy for styling; make consistent within an article
- single-line captions are centered

LITERATURE CITED:

- use #1 head: LITERATURE CITED
- reduced typeface
- abstracts of oral presentations delivered at professional meetings and printed separately are not permitted; transfer to text as in litt.
- personal communication, submitted, and under review citations are not permitted; transfer to text as (pers. comm.)
- order strictly alphabetically by author (style change), then chronologically
- style a and b citations as 1992a; the a and b may not appear right next to each other in the literature cited section
- use in press in place of year as needed; delete volume number, and if year is supplied, delete and replace with "In press."
- query for update for all in-press items
- lowercase after colon or em dash for both journal article titles and book titles
- Follow “Appendix III, Pubs. Commonly Cited in JM” title list for journal and publisher names
- periodical names should not begin with “The”; delete if provided by the author

Author rules:

- VAN VOGT, W. A., III but W. A. VAN VOGT III
- PETERSON, L. L., JR. but L. L. PETERSON, JR.
- , AND C. R. LESTER (EDS.).
- PHILLIPPE, J., ET AL.
- leave ET AL. entries in order provided on copy
- use commas with 2 authors
- space between author initials
- use et al. with 7 or more authors; list 1st author, then et al.
- 3 em dash no longer used; repeat authors

Journal article:
BROWN, J. S., AND N. B. PAVLOVIC. 1992a. Evolution in heterogeneous environments: effects of migration on habitat specialization. Evolutionary Ecology 6:360–382.
NEVO, E., V. SIMOSEN, AND A. R. TEMPLETON. In press. Starch gel electrophoresis of enzymes—a compilation of recipes. Biochemical Genetics.

- if not in “Appendix III” list, spell out journal titles in full: Journal of Ecology, Journal of Wildlife Management, Proceedings of the National Academy of Sciences
- delete issue number unless it is clear that each issue is paginated separately
- use italics for Genus species in Mammalian Species references

Book:
ANDERSON, D. A., AND W. A. SMITH. 1976. Forests and forestry. 2nd ed. Interstate Printers and Publishers, Inc., Danville, Illinois 3:1–798.
HALL, E. R. 1981. The mammals of North America. 2nd ed. John Wiley & Sons, Inc., New York 1:1–600 + 90. [OR …2:601–1181 + 90.]
NEAL, E. G., AND C. CHEESEMAN. 1996. Badgers. Poyser Natural History, London, United Kingdom.

- spell out states for all cities except for New York
- provide city, province, Canada; spell out everything
- repeat the city or country if the name is a part of

the publisher or university: University of Chicago Press, Chicago, Illinois; Australian Museum, Sydney, New South Wales, Australia
- do not repeat state in the U.S. if part of the publisher or university: University of Wisconsin, Madison; The University of Kentucky, Lexington
- spell out United Kingdom
- John Wiley & Sons, Inc., New York; University of New South Wales Press, Sydney, New South Wales, Australia
- total number of pages is not provided for a book unless it is part of a series or volume: 3:1–692.

Software:

FELSENSTEIN, J. 1987. PHYLIP (Phylogeny inference package). Version 3.0 manual. University of Washington, Seattle (on disk).

SAS INSTITUTE INC. 1990. SAS/STAT user's guide. Release 6.03. SAS Institute Inc., Cary, North Carolina.

SWOFFORD, D. L. 1999. PAUP*: phylogenetic analysis using parsimony (*and other methods). Version 4. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- note that no comma is used for SAS Institute Inc.

Article in book:

PATTON, J. L., ET AL. 1977. Optimal habitat selection in two-species competitive systems. Pp. 282–293 in Population ecology (U. Halbach and J. Jacobs, eds.). Gustav Fischer Verlag, Stuttgart, West Germany.

Technical report:

GOODWIN, J. G., JR., AND C. R. HUNGERFORD. 1979. Rodent population densities and food habitats in Arizona ponderosa pine forests. United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Research Paper RM-214:1–12.

HENDRIX, P. F. 1996b. Earthworms, biodiversity, and course woody debris in forest ecosystems of the Southeastern U.S.A. Pp. 43–48 in Biodiversity and coarse woody debris in southern forests, proceedings of the workshop on coarse woody debris in southern forests: effects on biodiversity (J. W. McMinn and D. A. Crossley, Jr., eds.). United States Department of Agriculture, Forest Service, General Technical Report SE-94:1–146.

Thesis or dissertation:

STEWART, P. D. 1997. The social behaviour of the European badger, Meles meles. Ph.D. dissertation, University of Oxford, Oxford, United Kingdom.
- use "thesis" for bachelors or masters degrees and "dissertation" for Ph.D

TABLES:

TABLE 3.—Roman text runs in. Multiline titles are paragraph style, and single-line titles are centered. Use
italic for Genus species.
and

TABLE 1.—Continued. [or Extended.]
- spell out units of measure in titles not preceded by a numeral outside parens: weight in grams of the testis;
abbreviate units of measurement in parens: "cranial measurements (mm) of ...."
- column heads: cap then lowercase; % something
- all footnotes are designated
- footnote designators: lowercase letters; asterisks used for probability
- footnote style: ¶a Thin space used, then text that ends in a period.
- probability asterisks (use thin space and paragraph indent): * P < 0.05, ** P < 0.01, *** P < 0.001.
- probability asterisks start their own paragraph under designated footnotes; all will share a single line
- copyeditor, see NOTES section for how to handle thin spaces in electronic file
- spell out and include, if appropriate, species, localities, and dates of study, in addition to a description of the content
- stub: cap then lowercase
- order of footnotes: designated footnotes, asterisks for P values
- style for abbreviations defined: follow copy and make consistent within article; no set style for this;
abbreviations may be defined in table title
- if possible, do not abbreviate months; if space is limited, OK to use 3-letter abbreviations: Jan., Jun., Oct.
- long strings of ± SD (or SE) OK in tables; no need for separate columns

- ×16 single; ×33p6 double; ×49 broadside
- no need to define statistical tests, ANOVA, SE, SD, CI, CV, d.f.
- change mean to0 (put the macron over the cap italic X)

Appendix tables differ from normal tables:

APPENDIX I
Single-line titles should be centered and roman; end with period.

APPENDIX II
Paragraph indent multiline titles. Note that APPENDIX is cap and small cap bold roman and centered.
Appendix tables take roman numerals.

APPENDIX II.—Continued. [or Extended.]