UNIVERSIDADE FEDERAL DO RIO GRANDE
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VARIAÇÕES TEMPORAIS E ESPACIAIS DOS COPÉPODES E DA BIOMASSA ZOOPLANCTÔNICA NA PLATAFORMA CONTINENTAL E TALUDE SUPERIOR DO EXTREMO SUL DO BRASIL

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"... e ao ajuntamento das águas chamou mares.
E viu Deus que isso era bom."
Gênesis 1:10 b

"Eis o mar vasto e imenso, no qual se movem seres sem
conta, grandes e pequenos".
Salmos 104:25

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RESUMO

O zooplâncton é um componente importante dos ecossistemas marinhos por ser elemento chave nas relações tróficas pelágicas. Os copépodes, um dos principais componentes do zooplâncton, são agentes na transformação e transporte da matéria orgânica para as águas profundas, processo importante como fonte de energia para os detritívoros e no ciclo dos compostos orgânicos e inorgânicos nos ecossistemas pelágicos. A região do extremo sul do Brasil apresenta grande produção biológica, não obstante, existe carência de informação sobre este componente-chave. O objetivo deste trabalho foi determinar a distribuição (horizontal e vertical) da biomassa do zooplâncton, em teor de carbono, a composição e abundância dos copépodes retidos pela rede de malha de 150 µm, e suas variações sazonais e fatores relacionados, especialmente massas de água e teor de clorofila *a*. As amostras foram coletadas com rede cilindro-cônica de malha de 150 µm, em arrastos verticais estratificados na região da plataforma e talude superior na região da plataforma continental (31º 40´ S e 33º 45´ S) do Estado do Rio Grande do Sul, em out/1987, set/1988, fev/1990 e jun–jul/1991. A distribuição horizontal e vertical da biomassa zooplanctônica e abundância de copépodes variaram em relação às estações do ano. Os maiores valores ocorreram na região costeira da plataforma continental e no estrato superficial (até 50 m). Os valores altos de biomassa na primavera (33 mg C m^{-3}) e no inverno (11 mg C m^{-3}) estiveram relacionados com a Pluma do Rio da Prata (PRP) e no verão (30 mg C m^{-3}) com a Água Subtropical de Plataforma (ASTP). O maiores valores de clorofila *a* (até 2.56 mg m^{-3}) foram no outono, e relacionados com a PRP, Água Subantártica de Plataforma (ASAP) e a ASTP. A composição em espécies de copépodes foi influenciada pela presença de diferentes massas de água. A abundância de copépodes foi maior no verão, com valor máximo de 34 428 ind, m^{-3}, o máximo valor registrado para copépodes na área. Os maiores valores de densidade foram relacionados com a ASTP no verão, e com a PRP no inverno. Espécies de *Oncaea* apresentaram maior abundância e *Oithona similis* a maior freqüência de ocorrência, indicando a importância de espécies de pequeno tamanho. A produção diária inferida para o zooplâncton (2.36 mg C m^{-3} d^{-1}) corresponde a uma produção anual média de 861 mg C m^{-3} a^{-1} e 44 g C m^{-2} a^{-1}. Desta forma, a biomassa de zooplâncton e a abundância de copépodes, relacionadas principalmente com as águas costeiras e as frias, ricas em nutrientes e com alta biomassa de fitoplâncton, desempenham importante papel no fluxo da matéria e energia, contribuindo para a manutenção dos elevados estoques de recursos pesqueiros na região.

Palavras-chave: Biomassa zooplanctônica; Carbono; Copépodes; Calanoida; Cyclopoida; Massas de água; Atlântico Sul Ocidental.

ABSTRACT

Metabolic activity of zooplankton has important implications for the organic and inorganic compounds in pelagic ecosystems cycles. Copepods are the main agents in the processing and transport of organic matter to the deep waters, an important process as energy source for scavengers. The region of southern Brazil presents large organic production; however, there is lack of information on this key component for the understanding of ecological processes. Therefore, the objective of this study was to determine the distribution (horizontal and vertical) of copepods, their composition and abundance, and the zooplankton biomass (carbon mass) distribution, their seasonal variations and associated factors, especially the water masses and chlorophyll *a*, emphasizing small sized copepod species. Sampling was conducted with cylinder-conical net with 150 µm mesh size, in stratified vertical hauls on the shelf region and upper slope (31º 40' S and 33º 45' S) in the State of Rio Grande do Sul in oct/1987, set/1988, feb/1990 and jun-jul/1991. The horizontal and vertical distribution of zooplankton biomass and copepods species varied in relation to the seasons. The greatest biomass (33 mg C m^{-3}) was related to the coastal region and the surface layer (50 m), and these values were high in spring and winter, related to the Plume Prata Water (PPW) and in summer with the Subtropical Shelf Water (STSW). The values of chlorophyll-*a* (Chl-*a*) showed a pattern opposite to that of the zooplankton biomass, with low values in summer (minimum 0.04 mg m^{-3}) and high in autumn (maximum 2.56 mg m^{-3}). Nevertheless, the highest values of Chl-*a* were related with PPW, Subantarctic Shelf Water (SASW) and STSW, and lower values with Tropical Waters (TW) and South Atlantic Central Water (SACW). The copepod species composition was influenced by the presence of different water masses. The highest copepod value in this region (34 428 ind. m^{-3}) was found in the present study. Species of *Oncaea* and *Oithona similis* were the most important copepods in abundance and in occurrence frequency, respectively. Furthermore, the type of food was related to the community structure of copepods in different seasons. The average daily production inferred for zooplankton (2.36 mg C m^{-3} d^{-1}), corresponded to an average annual production of 861 mg C m^{-3} yr^{-1} and 44 g C m^{-2} yr^{-1}. Thus, the zooplankton biomass and the copepods assemblages, mainly related to the coastal and cold waters, nutrient-rich and with high phytoplankton biomass, plays an important role in the flow of matter and energy, and contributes to maintaining high stocks of fishery resources in region.

Keywords: Zooplankton biomass; Carbon; Copepods; Calanoida; Cyclopoida; Water masses, Southern Brasilian Shelf.

PREFÁCIO

A região de plataforma continental do extremo sul do Brasil é parte de uma das mais ricas da costa brasileira em termos de produção biológica, que sustenta importantes pescarias. O zooplâncton é um componente importante e central nos ecossistemas marinhos, e como elemento chave nas relações tróficas, promove a ligação entre a produção primária fitoplanctônica e os organismos de níveis tróficos superiores. Desta maneira, informações sobre a composição do zooplâncton, sua biomassa e interações tróficas são fundamentais para a compreensão do ecossistema pelágico na costa brasileira e na plataforma continental do Oceano Atlântico Sul – Ocidental.

A presente Tese está estruturada em dois artigos independentes, redigidos em língua inglesa, expostos tal qual foram submetidos às revistas científicas (Anexos I e II), precedidos por uma primeira parte, redigida em língua portuguesa, onde são apresentados uma introdução geral, objetivos, justificativa e hipóteses do estudo, material e métodos, resultados, conclusões e perspectvas futuras, de acordo com normas vigentes no Programa de Pós-Graduação em Oceanografia Biológica.

1. INTRODUÇÃO GERAL

1.1 Importância da comunidade zooplanctônica

O zooplâncton constitui um componente importante e central dos ecossistemas marinhos, como elemento chave nas relações tróficas, promovendo a ligação da produção primária fitoplanctônica com os organismos de níveis tróficos superiores (Skjoldal *et al.* 2000, Karlson 2009).

No zooplâncton existem organismos em posição trófica de consumidores (primários e secundários), de presas e de competidores (por recursos alimentares e espaço), os quais contribuem para a condução da energia e do carbono ao longo da cadeia trófica. O zooplâncton representa uma das principais fontes de alimento para larvas e juvenis de peixes quanto para adultos explorados comercialmente (Schwingel & Castello 1995, Brandini *et al.* 1997, Skjoldal *et al.* 2000). Além dos peixes, alimentam também invertebrados planctônicos, bentônicos e pelágicos (Brandini *et al.* 1997, Skjoldal *et al.* 2000).

O papel do zooplâncton nos ecossistemas pelágicos, sobretudo dos metazoários (metazooplâncton), é de reconhecimento geral, e sua atividade metabólica tem importantes implicações no ciclo dos compostos orgânicos e inorgânicos na coluna d’água (Lopes *et al*. 2006a, 2006b).

O pastejo do zooplâncton determina em grande parte a quantidade e o fluxo vertical de partículas, proporcionando não somente energia para as comunidades bentônicas, mas também exportando carbono da superfície para camadas mais profundas, contribuindo para a remoção do excesso de CO_2 nos oceanos pela sedimentação e soterramento de compostos carbônicos orgânicos e inorgânicos (Lenz 2000, Moriarty *et al.* 2012).

Destes organismos, os copépodes são os principais agentes na transformação e subsequente transporte da matéria orgânica da superfície para o fundo dos oceanos, por meio de suas pelotas fecais, processo de extrema relevância ecológica tanto para a comunidade detritívora, a qual utiliza esta matéria orgânica como fonte de energia (Huys & Boxshall 1991), quanto para o os decompositores (Zervoudaki *et al.* 2007).

1.2 Distribuição da biomassa zooplanctônica e dos copépodes

A distribuição do zooplâncton é determinada pela profundidade local, estado trófico da área e pelo regime de temperatura. Já a diversidade de espécies geralmente depende da temperatura e da idade evolucionária da região do oceano (Lenz 2000). Em regiões tropicais e subtropicais, a diversidade é mais elevada do que em ambientes extremos como as zonas polares e águas salobras. Devido às correntes marinhas, muitas espécies apresentam ampla distribuição, frequentemente global, dentro de seus limites climáticos, o que é verificado de modo mais claro nas águas quentes dos três maiores oceanos, Pacífico, Atlântico e Índico (Raymont 1983, Lenz 2000, Alcaraz *et al.* 2007).

Em menor escala, os gradientes de salinidade e de temperatura podem definir a composição e a estrutura das assembléias zooplanctônicas (Hoffmeyer 2004, Berasategui *et al.* 2006), sua abundância e sua biomassa (Coyle & Pinchuk 2003). Em mesoescala, a estrutura física é altamente dinâmica e as comunidades zooplanctônicas dependem do modo de transferência da matéria e da energia ao longo das cadeias tróficas pelágicas, por sua vez relacionadas com as características qualitativas e quantitativas dos produtores primários (Alcaraz *et al.* 2007).

Quanto à biomassa zooplanctônica, os maiores valores ocorrem em regiões polares durante os picos sazonais de primavera e verão, e os menores em regiões tropicais (Raymont 1983, Valiela 1984). Entretanto, observações recentes mostram que há alta bimassa em uma faixa tropical equatorial (± 5º N) e desta decrescendo até a região subtropical, voltando a crescer em direção aos pólos (Moriarty et al., 2012). As estimativas mostram que a maioria dos valores de biomassa são inferiores a 10 mg C m^{-3}, sendo o valor médio global de 5,52 mg C m^{-3} (Strömberg *et al.* 2009).

Em relação aos organismos e sua distribuição vertical, tem sido verificado que a maioria das espécies mais numerosas, principalmente de copépodes, apresenta um padrão de concentração de indivíduos mais elevado na superfície, sem migração vertical aparente (Wisser *et al*. 2001, Escribano 2006).

Sobre as relações entre distribuição vertical e a alimentação dos organismos, Besiktepe (2001) verificou que esta distribuição parece estar relacionada com a estação do ano, com a espécie, com o seu estágio de desenvolvimento e com a concentração de oxigênio na coluna d’água; já Paffenhöffer & Mazzocchi (2003) sugeriram que a faixa de distribuição vertical de cada espécie estaria relacionada à combinação entre o seu comportamento alimentar, a temperatura do ambiente e a predação exercida sobre ela, sendo esta faixa flexível devido aos efeitos destas variáveis.

Os copépodes (Crustacea, Maxillopoda, Copepoda) são um grupo frequente e numeroso nos mares e oceanos e que, geralmente, apresentam alta biomassa (Bradford-Grieve *et al*. 1999, Thompson *et al.* 2013). Usualmente, esses organismos compõem de 55 a 97% dos metazoários do zooplâncton; a maioria habita ambientes pelágicos marinhos e constituem o grupo de organismos multicelulares mais numerosos da Terra, provavelmente existam mais copépodes do que insetos no mundo (Mauchline 1998, Schminke 2007). Devido seu elevado número, os copépodes são reconhecidos tanto como os principais consumidores primários de praticamente todos os mares e oceanos, quanto como um elo entre o fitoplâncton e os consumidores de níveis tróficos superiores (Raymont 1983, Miyashita *et al*. 2009).

Apesar destes importantes aspectos, espécies de copépodes de menor tamanho são pouco conhecidas, mas parecem ser as mais numerosas e as principais consumidoras de fitoplâncton, e importantes participantes da alça microbiana (*microbial loop),* como predadoras de bacterioplâncton e de protistas heterotróficos, além de presas para o ictioplâncton e outros carnívoros pelágicos (Turner 2004).

A distribuição do zooplâncton e a intensidade da variabilidade temporal e espacial de suas características estruturais e funcionais estão relacionadas com as propriedades físicas das diferentes feições hidrográficas ambientais (Escribano *et al.* 2007).

1.3 Relação entre a comunidade zooplanctônica (biomassa e copépodes) e os fatores abióticos

As condições químicas e físicas da água no Oceano Atlântico Sul variam de acordo com os ventos dominantes, correntes e massas de água (Lima *et al.* 1996, Campos *et al.* 1999, Piola *et al.* 2000, Soares & Möller 2001, Möller *et al*. 2008, Piola *et al.* 2008), que propiciam elevados valores de clorofila *a* e de produção primária, principalmente no final do inverno e da primavera (Teixeira *et al.* 1973, Huboldt 1980a, Ciotti *et al.* 1995, Odebrecht & Garcia 1998, Garcia & Ciotti 2008), Os altos valores de clorofila *a* e de produção primária são relacionados aos nutrientes oriundos das águas subantárticas, aos aportes continentais do Rio da Prata e da Lagoa dos Patos e ao fenômeno de ressurgência na região (Soares & Möller 2001, Möller *et al.* 2008, Piola *et al.* 2008, Muelbert *et al*. 2008).

Gradientes de salinidade e de temperatura podem definir a composição e a estrutura das assembléias de organismos, a abundância e a biomassa do zooplâncton (Coyle & Pinchuk 2003; Hoffmeyer, 2004; Berasategui et al. 2006). Assim, as interações entre a hidrodinâmica e o zooplâncton são frequentemente em nível de comunidade, e relacionadas com a disponibilidade de nutrientes para a produção primária (Alcaraz et al. 2007).

As diferentes combinações entre a salinidade e a tempertura formam cinco massas de água (Piola et al., 2000; Möller et al. 2008) de natureza e origem distintas nesta região no extremo sul do Brasil, que apresentam forte variabiliade relacionada com trocas no regime de ventos e descarga de águas continentais do Rio da Prata e da Laguna dos Patos (Piola et al., 2000) que determinam variações temporais sazonais na biomassa e na estrutura da comunidade zooplanctônica.

1.4 O estado da arte

Na região da plataforma continental do extremo Sul do Brasil, os estudos iniciaram com Gaudy (1963) que abordou a ocorrência e distribuição de copépodes. Björnberg (1963) elaborou o primeiro levantamento, com detalhes de taxonomia e distribuição de copépodes, e continua sendo uma das principais referências no Brasil. Meneghetti (1973, 1975) e Navas-Pereira (1973), descreveram a distribuição de grupos do zooplâncton, incluindo os copépodes.

Ainda, nos atlas editados por Boltovskoy (1981, 1999), vários autores apresentam informações sobre a taxonomia e distribuição de espécies de grupos zooplanctônicos, incluindo os copépodes, para o Oceano Atlântico Sul Ocidental. As espécies de cladóceros, quetógnatos e pterópodes (Resgalla Jr. 1993, 2008, Resgalla & Montú 1993, 1994), taliáceos (Amaral 1994) e os eufausiáceos (Gorri 1995) foram associadas às massas de água predominantes nas diferentes épocas do ano, entre as latitudes de 32° S e 34° S.

Os levantamentos de Montú *et al.* (1998) relacionaram para a região cerca de 150 espécies de copépodes, 85 de cnidários, 39 de tunicados, 26 de eufausiáceos e 20 de quetógnatos, dentre outros grupos.

Recentemente Muelbert *et al*. (2008) verificaram trocas sazonais na comunidade de copépodes na região do farol do Albardão e observaram que a influência de água doce na comunidade é mais forte no inverno do que no verão, e a distribuição e abundância de copépodes estão mais relacionadas com Águas da Pluma do Rio da Prata, do que com a presença da frente oceanográfica.

Bruno (2009) descreveu as variações temporais na distribuição de espécies de copépodes na plataforma do estado do Rio Grande do Sul (RS), Brasil, e relacionou-as com os padrões sazonais das massas de água, sugerindo algumas espécies como bioindicadoras (*Temora stylifera*, águas quentes, e *Calanoides carinatus*, águas frias).

De acordo com os estudos na região, os valores de densidade zooplanctônica são maiores em: (a) áreas costeiras sob a influência de aportes continentais, com altos valores de clorofila *a* e produção primária, (b) ao sul da região, relacionados com a influência de águas subantárticas e aos aportes continentais e (c) na plataforma média e externa, associadas à ressurgência local.

Informações sobre a biomassa e ou biovolume do zooplâncton são importantes para a compreensão da estrutura da comunidade e do fluxo de energia entre os diferentes níveis tróficos (Skjoldal 2000), mas são escassas, tanto em nível mundial, como local, quando comparadas com aquelas sobre a composição e distribuição de organismos. Outrossim, a biomassa pode ser obtida mais rapidamente que as informações sobre a composição e densidade de espécies (Postel *et al.* 2000).

Na região do sul do Brasil, Meneghetti (1973a), Navas-Pereira (1973), Hubolt (1980a, 1980b), Montú *et al.* (1998) e Bruno (2009) verificaram valores elevados de biovolume de zooplâncton total em águas costeiras da região, principalmente ao sul e nos meses mais quentes, período de maior riqueza zooplanctônica. Alguns destes picos foram atribuídos, por Meneghetti (1973b), aos tunicados (Salpidae). Resgalla *et al.* (2001) verificaram relações entre o biovolume do zooplâncton e o transporte de Ekman.

O biovolume de zooplâncton é elevado em águas costeiras e nos meses quentes, período de maior riqueza de espécies (Meneghetti 1973 a; Navas-Pereira 1973, Huboldt 1980a, Huboldt 1980b, Resgalla *et al.* 2001, Bruno 2009). Valores muito elevados de carbono, 8142 mg.C.m^{-3}, foram reportados por Bersano (1994) na zona de arrebentação da praia do Cassino, devido à alta concentração de misídeos. Já Montú *et al.* (1998) registrou um máximo de 98 mg.C.m^{-3} referente ao zooplâncton total da plataforma continental do RS.

A plataforma continental do extremo sul do Brasil é uma das regiões da costa brasileira de maior produção biológica (Castello *et al.*1990, Lopes *et al.* 2006b, Muelbert *et al.* 2008), que apresenta altos valores de clorofila relacionados com os nutrientes provenientes das águas subantárticas, dos aportes continentais e das ressurgências (Huboldt 1980a, 1980b, Ciotti *et al.* 1995, Odebrecht & Garcia 1998, Garcia & Ciotti 2008, Ciotti *et al.* 2010). A elevada produção primária estimula o crescimento das populações zooplanctônicas, e as águas subantárticas aumentam a diversidade de espécies, ambas contribuindo para o aumento da biomassa do zooplâncton na região.

Apesar da importância do zooplâncton no controle da produção fitoplanctônica e na modelagem dos ecossistemas pelágicos (Lenz 2000), aspectos relacionados à sua ecologia necessitam ser melhor compreendidos, especialmente em relação à sua composição, biomassa e às interações tróficas (Brandini *et al.* 1997, Mauchline 1998, Lopes *et al*. 2006b, Lopes 2007).

1.5 Objetivo geral

Determinar a distribuição (horizontal e vertical) da biomassa do zooplâncton, em teor de carbono, e a composição e abundância das espécies de copépodes, com ênfase no conhecimento das espécies retidas pela rede de malha de 150 µm, e verificar suas variações sazonais e fatores relacionados, especialmente as massas de água e o teor de clorofila *a*, a fim avaliar o seu papel nos processos ecológicos nas comunidades do ecossistema pelágico do extremo Sul do Brasil.

1.5.1 Objetivos específicos

- ✓ Determinar a biomassa total do zooplâncton (teor de carbono) em diferentes profundidades e suas prováveis relações com a temperatura, salinidade, massas de água e teor de clorofila *a*;

- ✓ Determinar a composição taxonômica, valores de densidade e o padrão de distribuição horizontal e vertical dos copépodes em diferentes épocas do ano na plataforma continental e talude superior, e verificar as possíveis relações com a temperatura, salinidade, massas de água e teor de clorofila *a*;

- ✓ Verificar o modo de alimentação das principais espécies de copépodes e conhecer a estrutura trófica dos copepodes na região do estudo.

1.6 Justificativa

A região de plataforma continental do extremo sul do Brasil está incluída em uma das mais ricas da costa brasileira em termos de produção biológica, sustentando importantes pescarias (Lopes *et al*. 2006b, Braga *et al*. 2008, Muelbert *et al.* 2008).

Desta maneira, informações sobre a composição do zooplâncton, sua biomassa e interações tróficas são fundamentais para a compreensão do ecossistema pelágico (Brandini *et al.* 1997, Mauchline 1998, Lopes *et al.* 2006b; Lopes 2007).

O estudo sobre a comunidade zooplanctônica no Brasil vem crescendo, não obstante, a maioria dos trabalhos são principalmente descritivos, referindo-se à composição taxonômica das espécies holoplanctônicas e sua distribuição em relação aos principais sistemas de circulação (Brandini *et al.* 1997, Montú *et al*. 1998, Lopes *et al*. 2006b, Lopes 2007). Além disso, a maioria destes trabalhos foi realizada em zonas costeiras, geralmente próximas de portos e estuários (Lopes *et al.* 2006b).

No Brasil, de acordo com Brandini *et al.* (1997), Montú *et al.* (1998), Lopes *et al.* (2006b), Lopes (2007), a composição taxonômica e a diversidade das espécies de invertebrados zooplanctônicos de áreas oceânicas é praticamente desconhecida, não há dados sobre a distribuição horizontal e vertical das espécies mesopelágicas e batipelágicas, e sobre a biomassa do zooplâncton, importantes para compreender a estrutura da comunidade e o fluxo de energia entre os níveis tróficos (Skjoldal 2000).

Conforme Lopes (2007), levantamentos faunísticos devem focalizar os taxa e locais menos conhecidos e, sob o ponto de vista ecológico, é necessário dar prioridade aos estudos de processos voltados ao entendimento dos mecanismos que governam a distribuição, as interações tróficas nas teias alimentares pelágicas e os ciclos de produção do zooplâncton em relação ao ambiente físico.

Existe também a escassez de dados de peso seco, peso seco livre de cinzas e de carbono da comunidade zooplanctônica, que permitam comparações com outras regiões. Com excessação dos estudos de Bersano (1994) e citações em Montú *et al.* (1998), os demais dados disponíveis na literatura referem-se ao biovolume obtido através de diferentes metodologias, impossibilitando comparações diretas.

Cabe ressaltar que, os copépodes correspondem à fração mais significativa do zooplâncton, desta maneira, o seu conhecimento é fundamental para a compreensão dos processos ecológicos nas comunidades pelágicas. Apesar da classe Copepoda ser uma das mais estudas, aqui e mundialmente, há subestimação da importância e do papel das espécies de menor tamanho nos estudos realizados em todo o mundo, uma vez que seu enfoque é nos copépodes da fração mesoplanctônica (0.2-20 mm), isto é, a fração coletada por redes entre 200 e 300 µm, havendo pouca informação sobre a fração menor, normalmente mais numerosa e menos conhecida (Böttger-Schnack 2001, Galliene & Robins 2001, Turner 2004).

Ainda há o potencial de modificação dos resultados de estudos já realizados, podendo ser observadas novas ocorrências ou descobertas novas espécies, como foi com *Oncaea waldemari*, nova espécie descrita no extremo sul do Brasil (Bersano & Boxshall 1994), descoberta nas amostras do projeto ECOPEL (projeto do presente estudo), e um dos principais copépodes epipelágicos em várias áreas do Oceano Atlântico e Mar Mediterrâneo (Böttger-Schnack 2001).

Considerando a importância do zooplâncton e a carência de informações supra citadas, a realização do atual estudo é importante para a compreensão dos processos ecológicos no ambiente pelágico (Lopes *et al.* 2006b, Lopes 2007, Skjoldal 2000) em uma das áreas mais produtivas da costa brasileira e da plataforma continental do Oceano Atlântico Sul – Ocidental. Sendo assim, seguem as hipóteses do atual trabalho:

- ✓ A distribuição horizontal e vertical da biomassa zooplanctônica varia durante o ano, apresentando valores maiores ao sul, em zonas costeiras e no estrato superficial (até 50 m), devido ao enriquecimento dessas águas.

- ✓ A composição em espécies de copépodes é influenciada pela presença de diferentes massas de água, possibilitando reconhecer associações relacionadas com suas águas de origem;

- ✓ A distribuição vertical das espécies dos copépodes apresenta estratificação mais definida nas zonas de maior profundidade;

- ✓ O tipo de alimentação tem relação com a estrutura da comunidade de copépodes em diferentes épocas do ano;

2. MATERIAL E MÉTODOS

2.1 Área de estudo

A área de estudo (31º 40´ S - 34º 45´ S; área aproximada 46.750 km^2) (Fig. 1) faz parte da Plataforma Sul Brasileira que se estende desde o Cabo de Santa Marta (28°40’S) até o Chuí (34°40’S), e integra a Plataforma Continental do Oceano Atlântico Sul - Ocidental. Esta área apresenta baixa declividade com largura da plataforma continental entre 100 e 180 km, e a transição entre a plataforma continental e o talude ocorre em profundidades entre 160 e 190 m (Calliari 1998).

A região de plataforma e talude no extremo sul do Brasil, é uma das mais importantes áreas de pesca do Brasil (Castello *et al.* 1990, Lopes *et al.* 2006a, 2006b, Lopes *et al.* 2007, Braga *et al.* 2008), devido às condições oceanográficas que favorecem alto suprimento de nutrientes. Suas condições químicas e físicas variam com os ventos dominantes, correntes e massas de água (Lima *et al.* 1996, Soares & Möller 2001, Möller *et al.* 2008, Piola *et al.* 2008) que determinam elevados valores de clorofila *a* e de produção primária, principalmente em final de inverno e primavera (Huboldt 1980a, Huboldt 1980b, Ciotti *et al.* 1995, Odebrecht & Garcia 1998, Garcia & Ciotti 2008).

As massas de águas da região são de diferentes origens e características, e apresentam forte variabilidade relacionada com mudanças no regime de ventos e nas descargas de água doce continental do Rio da Prata e da Laguna dos Patos (Piola *et al.* 2000). Os limites termohalinos de acordo com

Piola *et al.* (2000) e Aseff *et al.* (2009), permitem identificar cinco massas de água presentes ao longo do ano: a Pluma do Rio da Plata (PRP), a Água Subantártica de Plataforma (ASAP), a Água Subtropical de Plataforma (ASTP), a Água Central do Atlântico Sul (ACAS) e a Água Tropical (AT). A PRP resulta da mistura da descarga continental das águas do Rio da Prata com as águas da plataforma continental e flui para o norte, na zona costeira; apresenta deslocamento sazonal meridional alcançando latitude 28º S no inverno austral, e 32º S durante o verão. A ASAP, rica em nutrientes, é transportada desde o sul pela Corrente da Patagônia, e alcança maior influência na região de estudo durante inverno e primavera. A AT, quente e salina, e pobre em nutrientes, é transportada para o sul-sudoeste pela Corrente do Brasil sobre o talude, mas pode avançar sobre a plataforma continental, principalmente no verão. A ACAS é formada pela mistura da AT e ASAP na zona da Confluência Brasil-Malvinas (CBM). Desloca-se para o sul em camadas profundas ao longo do talude, abaixo da Corrente do Brasil, entre 200 e 500 m. Embora rica em nutrientes, a radiação solar é insuficiente para estimular a produção primária, todavia eventos de ressurgência que a trazem à superfície podem fertilizar a zona eufótica (Gaeta & Brandini 2006), próximo da quebra de plataforma. A ASTP é o resultado da diluição da ASAP com as águas da plataforma.

Variações sazonais das descargas continentais e a oscilação da Confluência Brasil-Malvinas (CBM) determinam mudanças no transporte das massas de água na região (Lima *et al.* 1996, Möller *et al.* 2008, Piola *et al.* 2008). A combinação entre o transporte dirigido pelo vento e a circulação geostrófica sobre a plataforma produz um fluxo preponderante de águas dirigido para o sul e áreas oceânicas durante o verão (AT, ASTP e ASAP), e para o norte e em direção à costa, no inverno (PRP e ASAP) (Lima *et al.* 1996, Piola *et al.* 2008).

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dirigido para o sul e áreas oceânicas durante o verão (AT, ASTP e ASAP), e para o norte e em direção à costa, no inverno (PRP e ASAP) (Lima *et al.* 1996, Piola *et al.* 2008).

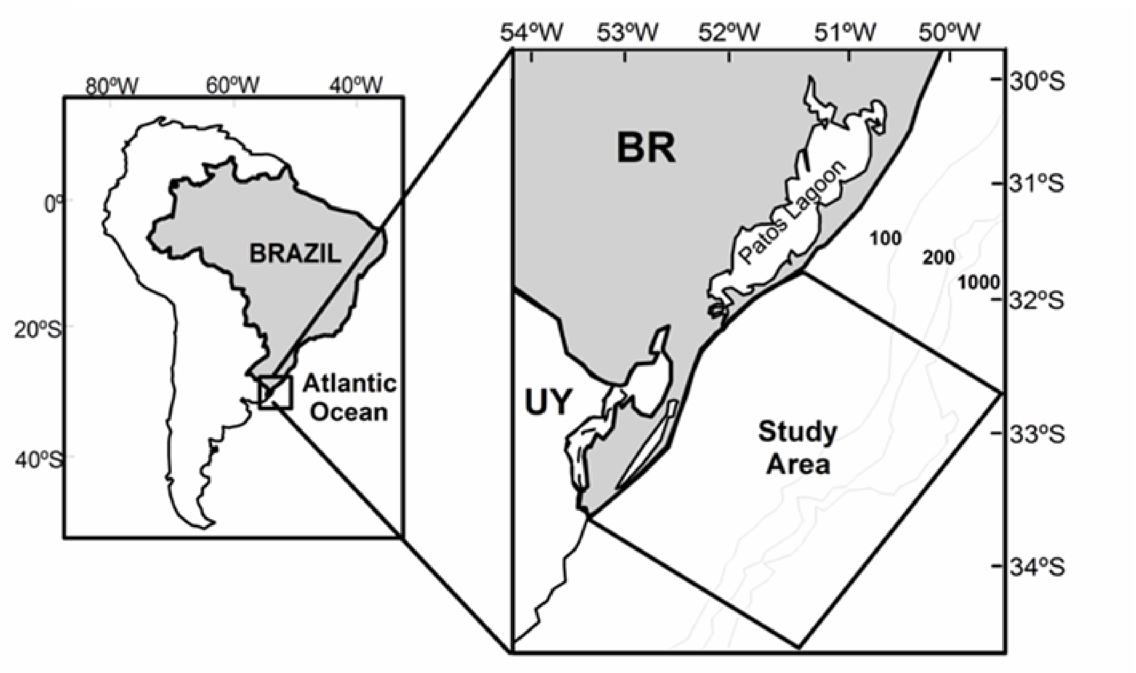

Figura 1. Localização da área de estudo.

As oscilações sazonais da CBM determinam as oscilações da Frente Subtropical de Plataforma (FSTP), que é formada pelo encontro em subsuperfície (~ 50 m) da ASTP (alta temperatura e salinidade) com a ASAP (baixa temperatura e salinidade). Esta frente estende-se entre ~32º S e ~36º S, em direção à quebra de plataforma (Piola *et al.* 2008). Devido às linhas isopicnais, ocorre intensa mistura de águas sobre a plataforma, que dão origem às duas variedades, a quente e a fria, da ASTP (Piola *et al.* 2008).

2.2 Coleta e análise dos dados

Os dados foram obtidos em 94 estações de coleta, localizadas na plataforma continental, entre os faróis da Conceição (31º 40´ S) e Chuí (34º 45´ S), desde a costa (~20 m) até a isóbata de 800 m aproximadamente (Fig. 2), a bordo do NPq Atlântico Sul, no âmbito do Estudo do Ecossistema Pelágico do Extremo Sul do Brasil (ECOPEL). As amostragens foram realizadas na primavera (10 a 17 de outubro de 1987), inverno (07 a 15 de setembro de 1988), verão (06 a 21 de fevereiro de 1990) e outono (18 de junho a 02 de julho de 1991), períodos caracterizados como estações sazonais pelos padrões de distribuição de temperatura e de salinidade (Soares & Möller Jr. 2001).

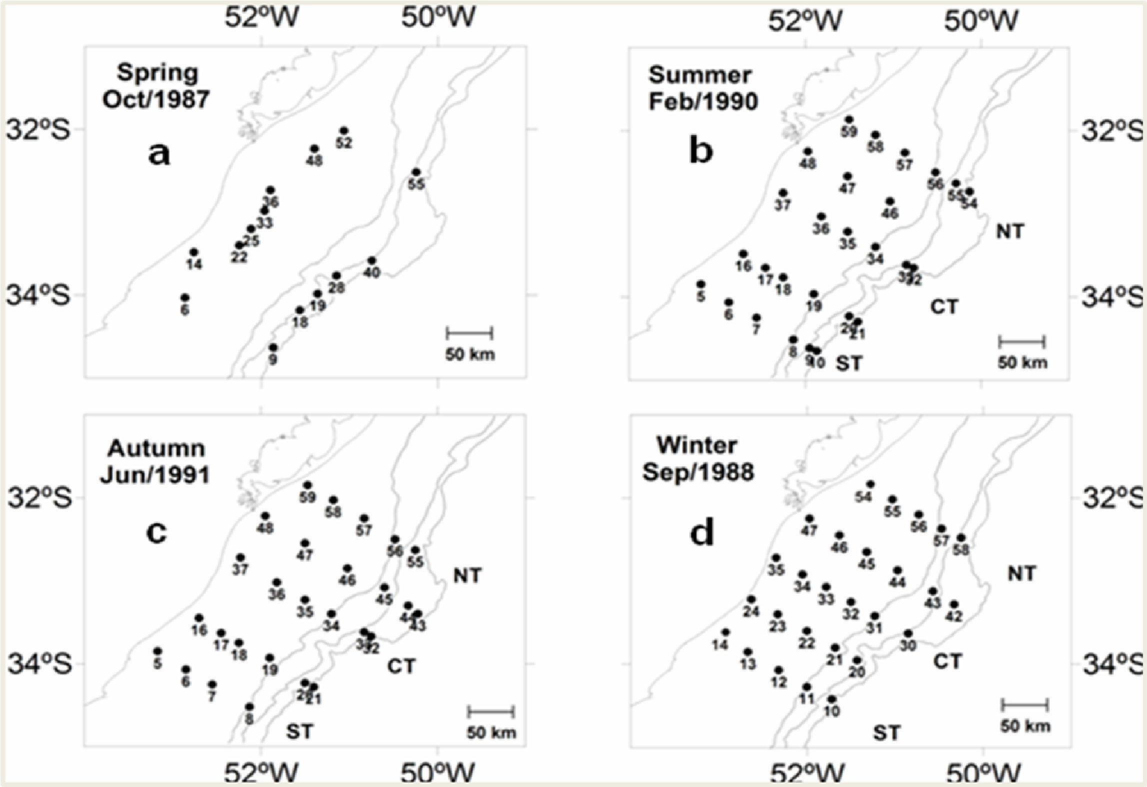

Figura 2. Mapa com a localização geográfica das estações oceanográficas de amostragem de zooplâncton: primavera (10-27/out/1987) (a); verão (06-21/fev/1990) (b); outono (18/jun-02/jul/1991) (c) e inverno (07-15/set/1988) (d).

O termo zooplâncton neste trabalho refere-se aos invertebrados holoplanctônicos coletados com rede cilindro-cônica (tipo WP-2) com malha de 150 µm, 60 cm de diâmetro na boca, equipada com fluxômetro e dispositivo para fechamento. No cruzeiro de primavera, a rede foi arrastada desde próximo ao fundo até a superfície em 14 estações oceanográficas: 08 localizadas entre as isóbatas de 20 e ~ 50 m, e 06 na zona de plataforma externa entre 300 e 800 m, totalizando 14 amostras. As amostras de primavera foram utilizadas somente para as análises de biomassa. Nos cruzeiros de verão, outono e inverno foram amostradas 27 estações de coleta em cada período, totalizando 240 amostras. Nestes cruzeiros, foram realizados arrastos verticais em cinco perfis perpendiculares à costa, nos estratos entre 0-25 m, 25-50 m, 50-100 m (estratos 1, 2 e 3, respectivamente, nas análises), e entre 100-200 m e 200-500 m. Nos dois últimos estratos foi obtida a média dos valores e ambos considerados como um único estrato (>100 m; estrato 4) nas análises e resultados de biomassa e nas análise nMDS da densidade de copépodes.

As amostras de verão, de outono e de inverno foram subdivididas logo após a coleta, 50 % do volume foi fixado em solução aquosa de formaldeído a 4 % neutralizada com bórax (Steedman 1976) para o estudo da composição taxonômica. O volume restante foi fixado com solução aquosa de formaldeído a 3 % neutralizado com glicerofosfato ß de sódio e imediatamente congelado a -20º C (Salonem & Sarvala 1985) para análise da biomassa estimada como massa de carbono (CM). A análise foi realizada após o material ser descongelado e lavado com água destilada e sulfato de sódio para a remoção de sais (Strickland & Parsons 1972), sobre filtros de tela similar à da rede de coleta, previamente limpos, secos e pesados. A massa seca foi obtida após secagem em estufa a 60˚ C por 16 horas (Beers 1976).

Cerca de 5 mg da massa seca foi utilizada para a determinação do conteúdo de carbono orgânico oxidável pelo método de oxidação úmida (Strickland & Parsons 1972). Nas amostras de primavera, após a determinação da massa seca, o material foi incinerado em mufla a 550˚ C por 2 horas (em cadinhos pré-queimados e pesados) e resfriados em dessecadores por 16 horas para a determinação da massa seca livre de cinzas (AFDM) (Beers 1976), após convertida em equivalente em carbono C = 0,6 AFDM (Postel *et al.* 2000). Os valores de CM foram expressos por volume de água (mg m^{-3}) e área (g m^{-2}). Algumas amostras (<3 %) com presença visível de material sestônico não zooplanctônico (diatomáceas e detritos), foram desconsideradas imediatamente após a filtragem.

Dados de temperatura e salinidade foram coletados em profundidades pré-estabelecidas (5, 10, 20, 30, 50, 75, 100, 150, 200, 300, 400 e 500 m) com garrafas de Nansen com termômetro de reversão e sensorer de condutividade, temperatura e salinidade. Amostras de água para análise de clorofila *a* foram obtidas nos mesmos intervalos até 100 m, em superfície com recipientes plásticos e nas demais profundidades com garrafas de Niskin (3 L). As massas d’água foram classificadas de acordo com os índices termohalinos propostos por Piola *et al.* (2000) e adaptados por Assef *et al.* (2009).

O teor de clorofila *a* (Cl-*a*) foi determinado por análise fluorimétrica (ver Ciotti *et al*. 1995). Para comparar os valores de Cl-*a* e de CM nos diferentes estratos, foi utilizada a média dos valores de Cl-*a* das profundidades padrões correspondentes a cada estrato de coleta de zooplâncton. Os valores de CM e Cl-*a* foram integrados para a coluna d’água (g.m^{-2}), através da soma dos valores médios (mg m^{-3}) de cada estrato de profundidade multiplicados pela distância (m; percurso da rede em cada estrato) acima de 100 m para a Cl-*a*, e para toda a coluna de água amostrada (máximo 800 m) para a CM.

A biomassa do zooplâncton (CM) foi analisada como uma função dos fatores sazonais (outono; verão; inverno), massas de água (PRP, ASAP, ASTP, ACAS e AT), distância-da-costa (zona costeira: isóbatas 20-50 m; plataforma intermediária: 50-100 m; e externa: >100 m), período do dia (dia, noite), estratos de profundidade (estrato1: 0-25 m; 2: 25-50 m; 3: 50-100 m e 4: >100

m) e covariáveis quantitativas: latitude, longitude, temperatura, salinidade e concentração de Cl-*a*. Dois grupos de modelos lineares generalizados (GLM) foram testados: i) resposta de variáveis de Cm (=CM) com distribuição Gama e função logarítmica de ligação, e ii) resposta variável log (Cm) com distribuição normal e função identidade de ligação. Em cada família de modelo, diferentes combinações de covariáveis foram propostas e comparadas com critérios de informação de Akaike (AIC), e modelos dos grupos (i) e (ii) foram comparados com "pseudo-R2" (proporção de desvio explicado) (Naglekerke 1991). Isto foi necessário, uma vez que a escala da variável dependente não foi a mesma nos dois grupos.

Dentre o conjunto de modelos propostos, o GLM com melhor ajuste para cada família foi o mesmo, mas ligeiramente melhor para o grupo (i) onde CM apresentou uma distribuição Gama com média,

$$E(CM) = \mu \quad \text{e} \quad \eta = \log \mu = a + \beta_{\mathbf{1}} \cdot sea + \beta_{\mathbf{2}} \cdot wm + \beta_{\mathbf{3}} \cdot depth + \beta_{\mathbf{dc}} \cdot lat$$

Este modelo estima uma intercepção diferente para cada combinação de estação sazonal (sea), massas de água (wm) e estratos de profundidade (depth) e inclui uma função linear de latitude (lat) com coeficientes específicos de distância da costa (dc). A interceptação α estima η para sea = outono, wm = PRP e estratos/profundidade = 1. Os efeitos de outras estações, massas de água e estratos/profundidade são dados pelo βs correspondentes. Os modelos foram ajustados com função GLM do software estatístico R (R Development Core Team 2012).

Os dados de biomassa da primavera não foram considerados na análise GLM, devido às diferenças na metodologia de amostragem do zooplâncton.

Neste caso, foram utilizados testes não-paramétricos de Kruskal-Wallis e de Wilcoxon para comparar os resultados de CM e de Chl-*a* da zona costeira das quatro estações do ano, considerando-se a semelhança de amostragem nesta zona.

A distribuição dos copépodes nas estações do ano, estratos de profundidade e regiões da Plataforma Continental, massas d'água, Clorofila *a* (Cl-*a*), temperatura, salinidade e biomassa zooplanctônica (CM), foi avaliada através de testes estatísticos não paramétricos e técnicas multivariadas, a fim de estabelecer relações entre as espécies (associações), e entre as associações e fatores ambientais.

Os índices individuais lineares de Correlação de Spearman, regressão linear, e suas respectivas significâncias estatísticas foram obtidas utilizando os programas BioEstat e Sigmaplot. O teste de Kruskal- Wallis foi utilizado seguido do teste a posteriori de Dunn (ANOVA não paramétrico) para detectar diferenças significativas entre as médias.

Padrões de distribuição copépodes foram investigados por meio de análise estatística multivariada, utilizando a matriz de similaridade de Bray-Curtis com os dados de densidade (ind. m^{-3}) transformados (raiz quadrada). Análise de ordenação não métrica (nMDS) foi realizada para avaliar os fatores: estação (verão, S; outono, A; inverno, W), regiões da plataforma (região costeira- C, isóbata < 50 m; plataforma intermediária- I, 50 - 100 m de profundidade; plataforma externa- E, > 100 m) e os estratos de profundidade (0-25m, 25-50 m, 50-100 m, >100 m), aplicando o teste ANOSIM ($p < 0,05$) (Clarke & Warwick 1994). Já o teste SIMPER foi utilizado para identificar as espécies que mais contribuiram para as semelhanças dentro dos grupos. A riqueza de espécies e a biodiversidade foram estimadas usando os índices de Simpson e de Shannon-Wiener (Margalef 1995).

3. RESULTADOS

3.1 Temperatura, Salinidade e Massas de água

Os valores de temperatura (mínimo de 4,85 ^{0}C no inverno; máximo de 26,27 ^{0}C no verão) e de salinidade (mínimo de 26,5 na primavera; máximo de 37,05 no verão) e as suas combinações permitiram classificar cinco massas de água: Pluma do Rio da Prata (PRP), Água Subantártica de Plataforma (ASAP), Água Subtropical de Plataforma (ASTP), Água Central do Atlântico Sul (ACAS) e Água Tropical (AT), a maioria presente em todas as estações do ano na área do estudo, porém com freqüências de ocorrência diferentes.

A PRP dominou a maioria das estações e estratos (45 % na primavera; 39 % no outono e 33 % no inverno), exceto durante o verão quando esteve ausente. A ASTP foi dominante durante o verão (49 %), diminuindo sua frequência no outono (25 %), inverno (20 %) e na primavera (12 %). A ACAS apresentou frequência mais elevada no inverno (28 %) e a ACAS foi frequente na primavera (20 %), seguida do verão, outono e inverno. A AT foi frequente no verão (32 %), seguida do outono (22 %), inverno e primavera. No inverno a PRP e a ASAP (32 %) foram mais frequentes, seguidas da ASTP (16 %), ACAS e AT (10 % cada uma).

Considerando as estações do ano, na primavera a PRP foi a massa mais comum ao longo da área do estudo e ocorreu muito próxima da costa. A ACAS ocupou grande parte da plataforma, algumas vezes até cerca de 100 m, principalmente ao sul, diminuindo sua influência em direção ao norte, onde esteve presente a ASTP. A AT ocorreu somente após a quebra de plataforma no sul, e avançou sobre a plataforma externa ao norte. Durante o verão a ASTP dominou a plataforma continental. A ASAP ocorreu somente próxima da quebra de plataforma ao sul, enquanto a AT foi registrada sobre a quebra de plataforma ao sul, aumentou sua influência em direção ao norte e avançou sobre a plataforma externa. No outono a PRP esteve presente ao longo de toda a zona costeira, a ASAP na plataforma intermediária e externa ao sul, e a ASTP ao norte, em toda a coluna d'água. A AT ocorreu ao longo da área e teve maior influência ao norte, onde se aproximou da quebra de plataforma. No inverno a ASAP esteve presente na maior parte da plataforma no sul, e afastou-se da costa em direção ao norte enquanto a PRP avançou sobre a plataforma. A ASTP esteve sobre a plataforma ao norte, e a AT não ocorreu no sul. A ACAS ocorreu em todas as estações do ano sobre o talude, em profundidades abaixo de 200 m, com exceção do inverno quando esteve mais próxima da superfície, a partir dos 100 m de profundidade.

3.2 Biomassa de zooplâncton e clorofila *a* integrados na coluna d'água

(Vide Anexo I)

A biomassa de zooplâncton (CM) integrada por área (m^{-2}) em cada estação de amostragem variou entre 0,01 e 1,36 g m^{-2} e os valores de Cl-*a* entre 0,01 e 0,07 g m^{-2}. Altos valores de CM ocorreram no verão (0,15 - 1,36 g m^{-2}) e coincidiram com os menores valores de Cl-*a* (0,01 a 0,03 g m^{-2}). No outono, foram encontrados a menor CM (até 0,12 g m^{-2}) e os maiores valores de Cla-a (0,02 a 0,07 g.m^{-2}). Os valores de CM foram intermediários no inverno

(0.06 - 1,04 g m^{-2}) e na primavera (0.13 - 0,82 g.m^{-2}), enquanto os de Cl-*a* foram relativamente altos na primavera (0,01 - 0,07 g m^{-2}), seguidos do inverno (0,01 - 0,05 g m^{-2}).

A distribuição da CM por área, na primavera, foi mais alta ao sul na zona costeira e ao norte afastado da costa, para a Cl-*a*, os valores mais altos foram observados desde o sul até a latitude de ~31ºS, aproximando-se gradativamente da costa. No verão, os maiores valores de CM ocorreram nas estações da plataforma externa (isóbata >100 m) em latitude próxima de ~31º S, enquanto a distribuição de Cl-*a* foi relativamente homogênea. No outono os valores de CM foram muito baixos, a Cl-*a* foi elevada na maior parte da área, com valores máximos na zona costeira e plataforma intermediária ao norte. No inverno, os máximos de CM ocorreram ao sul, na zona intermediária e externa da plataforma, e os de Chl-*a* em uma faixa desde o sul na zona intermediária da plataforma até o norte, em direção à costa. Os valores integrados por área referem-se a 0-100 m para a Chl-*a*, enquanto para a CM até 600-800 m. Este fato está relacionado com os altos valores de CM em certos locais distantes da costa (verão e inverno).

Considerando os valores médios de CM e Cl-*a* por área, verifica-se que: CM (g.m^{-2}): Verão (0,52) > Primavera (0,43) > Inverno (0,28) > Outono (0,05), Chl-*a* (g.m^{-2}): Primavera (0,04) > Outono (0,03) > Inverno (0,02) > Verão (0,01).

3.3 Biomassa de zooplâncton e clorofila *a* nos estratos de profundidade

Os valores de CM e de Cl-*a* nos estratos de profundidade apresentaram variações entre as estações do ano, e na mesma estação do ano. No primeiro estrato (0-25 m), os valores de CM e de Cl-*a* foram mais altos, até o dobro ou mais, comparados ao segundo (25-50 m) e demais estratos. A CM variou entre valores mínimos (0,01 e 0,05 mg.m^{-3}) no outono e inverno nos estratos >50 m, e máximos (29,95 e 27,23 mg.m^{-3}) no verão entre 0-25 m e 25-50 m, respectivamente. Valores intermediários (~11 mg.m^{-3}) foram frequentes entre 0-25 m durante o inverno, e ocorreram também até cerca de 100 m, em poucas estações amostrais, provavelmente relacionados com as águas subtatárticas ricas (ASAP). Em profundidades maiores que 100 m os valores sempre foram baixos (0,04 - 1,65 mg.m^{-3}). A Cl-*a* variou entre valores mínimos (0,04 - 0,05 mg.m^{-3}) no verão em todos os estratos, e máximos (2,56 mg.m^{-3}) no outono entre 0-25 m. Abaixo (25-50 m) os valores foram elevados no outono (1,56 mg.m^{-3}) e inverno (1,83 mg.m^{-3}).

Altos valores de CM (>10 mg.m^{-3}) foram observados até a profundidade de cerca de 70 m no verão, sobretudo na zona costeira, e em direção ao talude na latitude ~ 31º (transversal central, CT). Valores altos de Chl-*a* ocorreram somente na zona costeira, havendo em geral uma relação negativa entre CM e Cl-*a* nas estações da plataforma intermediária e externa. Durante o outono, foram encontrados os mais baixos valores de CM (<5 mg m^{-3}) de toda a área, e os mais altos de Cl-a (>1,5 mg m^{-3}), sobretudo na zona costeira ao norte da desembocadura da Lagoa dos Patos, sob influência de seu deságue, onde foi também verificado o máximo valor de CM (4,76 $mg.m^{-3}$). No inverno, o padrão de distribuição da CM e de Cl-*a* apresentou certa semelhança, com os maiores valores na zona costeira ao sul da desembocadura da Lagoa dos Patos e na zona intermediária da plataforma ao sul (máximos CM 24,87 mg m^{-3}; Cl-*a* 1,86 mg m^{-3}).

A comparação dos valores CM e Cl-*a* na zona costeira, nas quatro estações do ano mostra que houve grande amplitude de valores de CM durante o verão, pequena amplitude na primavera e inverno, e mínima no outono. A CM foi maior no verão e primavera, e menor no inverno e no outono, mostrando diferenças significativas ($H = 27{,}4$; gl=3; $p = 0{,}47x10^{-5}$) entre as estações do ano, exceto entre o verão e primavera, quando os valores das medianas foram próximos (13 e 15 mg m^{-3}). No verão, a distribuição dos valores de biomassa foi ampla, enquanto na primavera os valores estiveram mais próximos da mediana. A análise para a Cl-*a* mostrou grande amplitude de valores na primavera e no verão, e pequena amplitude no outono e inverno. Os valores baixos no verão e inverno foram significativamente diferentes do outono ($H = 10{,}5$; gl=3; $p = 0{,}01$). No verão e inverno ocorreram as menores medianas (0,6 e 1,0 $mg.m^{-3}$, respectivamente), na primavera e outono as maiores (2,2 e 1,6 mg m^{-3}, respectivamente). Entretanto, não houve diferenças no teste *a posteriori* e a primavera foi semelhante ao outono, verão e inverno, devido à grande amplitude de variação dos valores da Chl-*a* na primavera. Já os valores no verão foram significativamente menores que no outono (mediana 1,6 $mg.m^{-3}$), quase o triplo do verão. Não foram verificadas diferenças entre o verão e o inverno, mas o inverno foi significativamente diferente do outono, com maior valor de mediana.

3.4 Relação entre a biomassa de zooplâncton e fatores ambientais

Os valores altos na primavera e no inverno estiveram relacionados com as águas da PRP e, no verão com a ASTP. Valores intermediários no inverno nos estratos 0-25 m e 25-50 m foram associados com a presença da ASAP.

De acordo com a análise estatística GLM, os parâmetros mais importantes para explicar a CM foram a estação do ano, estrato de profundidade e massas de água. O verão e o inverno (altos valores de CM) não apresentaram diferenças entre si, mas foram significativamente diferentes ($p<0,001$) do outono (baixos valores), da mesma forma o estrato 1 (0-25 m), com maior biomassa, foi significativamente diferente ($p<0,001$) dos demais estratos. As massas de água relacionadas com os maiores valores de CM foram a PRP e a ASTP, que não apresentaram diferenças significativas entre si ($p<0,1$), enquanto a AT apresentou os menores valores de CM e foi significativamente diferente da PRP ($p<0,01$); a ASAP e a ACAS foram diferentes da PRP ($p<0,05$). Quanto à distância da costa, a zona costeira, até a isóbata de 50 m, e a plataforma intermediária (entre isóbatas de 50 e 100 m) apresentaram maiores valores de CM comparadas com a zona de plataforma, além da isóbata de 100 m, porém sem diferença significativa. Os valores de CM observados durante o dia e noite não foram significativamente diferentes. O teor de Cl-*a* não mostrou, estatisticamente, relação com as variações da CM. Apesar do padrão sazonal distinto da CM e da Cl-*a*, os maiores valores de Cl-*a* também estiveram relacionados com a PRP, a ASTP e a ASAP, e os menores com a ACAS e TW.

Com base no pseudo-R2, o modelo GLM explicou aproximadamente 65 % da variação da biomassa do zooplâncton. Os resíduos do desvio (deviance) entre -2,66 e 2,56 indicam que não houve discrepâncias restantes e que o modelo se ajustou aos dados. A qualificação do modelo é visualizada comparando o log (CM) observado contra os valores estimados e a correlação é linear, r = 0,814, indicando uma adequação aceitável do modelo.

3.5 Composição de copépodes e sua abundância (vide Anexo II).

Os copépodes representaram entre 63 e 100 % do zooplâncton. Percentuais superiores a 82 % foram os mais frequentes. Estes valores aumentaram do verão para o inverno, quando atingiram cerca de 100 %, geralmente nos estratos >100 m, em todas as massas de água, com exceção da PRP.

Os demais grupos do metazooplâncton presentes nas amostras foram desde cnidários (Siphonophora e Hydromedusae) até vertebrados, representados pelas larvas de peixes. Destes grupos foram mais representados em densidade de organismos e F.O.; em ordem decrescente: Pteropoda, Larvacea, Chaetognatha e Cladocera, no verão; Cladocera, Chaetognatha, Larvacea e larvas de Gastropoda e Bivalvia (meroplâncton) no outono; e larvas de Gastropoda e Bivalvia, Pteropoda, Larvacea e Cladocera, no inverno.

Foram registradas 115 espécies de copépodes na região do estudo, destas 91, 68 e 60 espécies ocorreram, respectivamente, no verão, outono e inverno. Muitas espécies tiveram ampla distribuição na área, e estiveram presentes em todas as épocas do ano e poucas espécies foram restritas a apenas uma das estações do ano.

A maioria das espécies encontradas pertence à ordem Calanoida (70) e Cyclopoida (36) e poucas à ordem Harpacticoida (09). Apesar de Cyclopoida apresentar menor número de espécies, os valores de densidade foram superiores (max. 15 059 ind.m^{-3}, verão) aos de Calanoida no verão e no outono, e Calanoida superou a densidade de Cyclopoida no inverno (max. 4 011 ind. m^{-3}).

As espécies de copépodes com maior freqüência de ocorrência (F.O. >60 %) no verão foram *Oithona similis*, *O. nana*, *O. plumifera*, *Oncaea* spp., *Calocalanus pavoninus*, *Clausocalanus furcatus* e *Temora stylifera*. Com F.O. em torno de 50 % foram *Acartia danae*, *Corycaeus giesbrechti*, *Farranula gracilis*, *Mecynocera clausi* e *Microsetella rosea*. No outono foram *O. similis* e *Oncaea* spp. (F.O. >60 %). Já no inverno foram *O. similis* e *Calanoides carinatus* (F.O. >60 %), enquanto *O. nana*, *O. plumifera*, *Paracalanus quasimodo* e *Ctenocalanus citer* com cerca de 50 % F.O.. Estas espécies são as que apresentaram, em geral, os maiores valores de densidade média. *O. similis* foi a espécie com a maior F.O. em todas as estações do ano (79, 83 e 88 %, em verão, outono e inverno, respectivamente). *Oncaea* spp. apresentou a maior densidade de organismos (10 824 ind.m^{-3}) no verão na zona costeira (#59). A densidade média total dos copépodes diminuiu cerca de cem vezes do primeiro estrato (0-25 m) até o quinto (>200 m), enquanto o número de espécies diminuiu cerca de duas vezes.

O número de espécies foi maior na plataforma continental externa, principalmente no verão, e na ASTP e AT também no verão, e foi menor na ASAP no outono.

Os copepoditos apresentaram F.O. igual a 100 % no verão e inverno, e 95 % no outono, e altos valores de densidade.

Os nauplios de copépodes tiveram F.O. de 85 % no verão, de 7 e 1,5 %, no outono e inverno, respectivamente, e valores de densidade muito baixos. Isto foi devido à malha da rede, superior ao ideal para coletar esses organismos adequadamente. Quanto aos copepoditos, provavelmente os primeiros estágios de desenvolvimento e aqueles das espécies de pequeno tamanho, também tenham sido subamostrados, apesar da sua densidade elevada.

Em relação ao número de espécies e sua freqüência de ocorrência (F.O.) nas diferentes épocas do ano e massas de água, no verão, um grande número de espécies teve F.O. até 50 %, a maioria apresentou F.O. inferior a 10 %. A massa de água com menor representação de espécies foi a ASAP. No outono e inverno a representação das espécies até 50 % predominou, com pouca diferença em cada categoria. A ASTP, ASAP e PRP tiveram maior contribuição no inverno, enquanto a ASAP e a ACAS foram as massas com menor número de espécies no outono.

3.6 Biodiversidade de copépodes

Os valores de diversidade foram opostos aos da abundância, como é geralmente observado na maioria dos ambientes marinhos. Os valores de diversidade de copépodes foram relacionados com as massas de água em cada estação do ano, sendo que os maiores valores de diversidade coincidiram com as massas de água, estratos de profundidade e as regiões da plataforma onde os valores de densidade de organismos foram os menores.

A diversidade de Shannon–Wiener (*H*') variou de 3,05 a 3,82 e o Índice de Simpson de 0,62 a 0,77 nas estações. Entretanto, considerando a massa de água, o estrato de coleta e a região da plataforma, estes limites foram inferiores (*H*'= 2,02, AT, inverno) ou superiores (*H*'= 4,18, cinco estratos, >200 m, verão), como também para o Índice de Simpson. Valores elevados de diversidade ocorreram no outono e no verão e baixos no inverno. Quanto às massas de água, alta diversidade foi encontrada em ACAS no verão, em AT no outono, e PRP e ASAP no inverno. Os indices na ASAP não mostraram diferença significativa entre as estações do ano.

Nos estratos de profundidade os valores de diversidade foram crescentes com a profundidade no verão, provavelmente relacionado com a ACAS e altos no segundo estrato (25-50 m) no outono e inverno, associados com a ASAP. De acordo com as regiões da plataforma, os maiores valores foram observados na plataforma externa e intermediária no verão, na plataforma intermediária no outono, e na costeira e intermediária no inverno. Este padrão mostra relação como a influência das massas de água em cada estação do ano, na área do estudo.

3.7 Alimentação dos copépodes

A alimentação da maioria das espécies presentes na área do estudo é através da microfagia. Neste modo de obtenção de alimento predominam os organismos de hábitos herbívoro e onívoro. A maioria das espécies de Calanoida encontrados está na base da cadeia alimentar, como consumidores de microalgas. Poucas espécies são macrófagas, e foram pouco frequentes e numerosas no inverno (espécies de *Heterorabdus*, *Pleurommama*, *Euaetideus giesbrechti* e *Metridia gerlachei*), e no verão (espécies de *Lubbockia*, *Lucicutia*, *Candacia curta*), nos estratos de profundidades >100 m.

A maioria dos gêneros e espécies de Cyclopoida são macrófagos (carnívoros) como as de *Corycaeus* e *Oncaea*, entretanto, espécies de *Oithona* são micrófagas. Estes três gêneros são os principais desta ordem em termos de número de espécies (riqueza), densidade de organismos (abundância) e frequência de ocorrência. A maioria dos Harpacticoida é macrófaga, porém há pouco conhecimento sobre o modo de alimentação e hábitos alimentares neste grupo.

3.8 Copépodes e fatores ambientais

Uma análise de correlação (Spearman) entre a densidade dos copépodes e fatores bióticos (teor de Cl-*a*, biomassa zooplantônica) e fatores abióticos (temperatura, salinidade, profundidade local e de coleta, latitude e longitude) resultou em relações significativas ($p<0,0001$; $R^2=0.3801$) com a profundidade local ($R^2=0,1198$), estrato de coleta ($R^2=0,125$) e longitude ($R^2=0,1721$), os quais foram os mais relevantes para explicar os valores de densidade. Não foram verificadas relações significativas com a temperatura, salinidade, latitude e Cl-*a*. Foi verificada correlação significativa ($p<0,0001$) entre os valores de densidades de náuplios, copepoditos e copépodes adultos, sendo maior entre os copepoditos e os adultos ($R^2=0,7319$).

Os valores de densidade dos copépodes (adultos, copepoditos e nauplios) e a biomassa zooplanctônica (CM) foram analisados por uma análise de regressão linear múltipla, que mostrou uma relação altamente significativa ($p<0,0001$; $R^2=0,5625$), indicando que em geral, os copépodes compreenderam mais de 56 % da biomassa do zooplâncton.

Uma análise de Correlação Canônica, considerando de um lado as variáveis abióticas, incluindo a Cl-*a*, e do outro lado a densidade de copépodes, copepoditos e náuplius, e a biomassa em carbono do zooplâncton resultou em uma relação altamente significativa, com um R canônico de 0,686 ($R^2=0,4706$, $p=0,0001$). Isto significa que cerca de 50 % da variação dos copépodes e da biomassa da qual eles compõem uma grande parcela, foi explicada por esses fatores ambientais e Cl-*a*.

A Análise de Variância não paramétrica, ANOVA (Kuskal-Wallis - posteriori de Dun) apontou como altamente significativo ($p<0,001$) o efeito do estrato sobre a densidade total ou das espécies de copépodes na coluna de água. As maiores densidades foram encontradas em geral no primeiro (0-25 m) ou segundo (25-50 m) estratos, dependendo da região da plataforma e época do ano. Também a região da plataforma (costeira, intermediária e externa) mostrou relação significativa ($p<0,001$) com a densidade de copépodes, exceto no inverno.

3.9 Assembleia de copépodes

A análise de ordenação das amostras em uma Escala Multidimensional não-métrica (nMDS), mostrou que, em cada estação do ano, nas diferentes regiões da plataforma, e entre alguns estratos de profundidade, em cada estação do ano (verão, S; outono, A; inverno, W) grupos ecológicos foram distinguidos com base nas semelhanças taxonômicas entre as estações. Os grupos foram significativamente diferentes (ANOSIM, p <0,05).

As estações do ano verão (S), outono (A) e inverno (W) apresentaram diferença significativa (Global R =0.409; p =0.001) quando comparadas em pares. As espécies que mais contribuíram para essas diferenças (p<0.05) entre verão e outono (89% de dissimilaridade média, SIMPER) foram *Oncaea* spp. (18.4%), *Oithona similis* (8.5%) e *Clausocalanus furcatus* (5.8%); entre verão e inverno (90.89% de dissimilaridade média, SIMPER) foram *O. similis* (14.5%), *Oncaea* spp. (14.2%) e *O. nana* (6.3%); e entre outono e inverno (86.16 de dissimilaridade média), *O. similis* (25%), *Oncaea* spp. (7.1%) e *Paracalanus quasimodo* (5.3%). As espécies que mais contribuiram para a similaridade entre as estações do ano, além de *O. similis* e *Oncaea* spp comuns a todas as épocas, foram *C. furcatus, O. nana, T. stylifera* e *C. giesbrechti*, durante o verão; *Paracalanus* spp. e *C. vanus* no outono, e *P. quasimodo, O. plumifera, O. nana*, *C. brevipes* e *C. carinatus* no inverno.

Analisando cada estação do ano separadamente, verificou-se diferença significativa (p<0.05) entre as regiões da plataforma continental (costeira, intermediária e externa da plataforma continental). No verão (Global R = 0.2729; p=0.001) as espécies que mais contribuíram para as diferenças entre as zonas costeira e externa (82% de dissimilaridade média, SIMPER) foram *Oncaea* spp. (12.18%), *O. nana* (7.7%), *O. waldemari* (5.6%) e *Corycaeus giesbrechti* (5.0%); entre as zonas costeira e intermediária (68% de dissimilaridade média) foram *Oncaea* spp. (14.5%), *O. nana* (6.4%), *O. waldemari* (6.2%), *P. quasimodo* (5.0%), e entre externa e intermediária (74% de dissimilaridade média) *Oncaea* spp. (10.3%), *O. nana* (6.8%), *C. furcatus* (5.2%) e *Temora stylifera* (5.0%). As espécies que mais contribuíram para as associações características de cada região foram na zona costeira: *O. nana, Oncaea* spp. e *T. stylifera*; na zona intermediária: *Oncaea* spp., *O. similis* e O. *nana*, na zona externa: *C. furcatus, O. similis* e *Oncaea* spp. Os estratos de profundidade também apresentaram diferença (p<0.05, SIMPER) entre o primeiro (0-25 m) e os segundo (25-50 m), terceiro (50-100 m), e quarto (>100 m), e entre o segundo e o quarto estratos.

No outono (Global R = 0.297; p=0.001) as espécies que mais contribuíram para explicar as diferenças (p<0.05) entre a zona costeira e a intermediária (76%de dissimilaridade média, SIMPER) foram *Oncaea* spp. (19.3%), *O. similis* (13.4%), *Paracalanus spp* (9.8%), *Ctenocalanus vanus* (8.3%); entre costeira e externa (90.3% de dissimilaridade média) foram *Oncaea* spp. (19.3%), *O. similis* (12.4%), *Paracalanus spp* (9.4%); entre a intermediária e externa (84.9% de dissimilaridade média) foram *O. similis* (18.5%), *Oncaea* spp. (13.3%) e *Ctenocalanus vanus* (11.7%). As espécies que mais contribuíram para a similaridade na zona costeira foram *O. similis, E. acutifrons* e *Oncaea* spp.; na intermediária *O. similis, Oncaea* spp. e *C. vanus*; na externa *Oncaea* spp., *O.*

similis e *M. clausi*. Entre os estratos de profundidade foi verificada diferença ($p<0.05$, SIMPER) entre o primeiro (0-25 m) e o terceiro (50-100 m), primeiro e o quarto (>100 m), e entre o segundo e o quarto estratos.

No inverno (Global R = 0.379; p=0.001) as espécies que mais contribuíram na explicação das diferenças ($p<0.05$) entre as zonas costeira e intermediária (73% de dissimilaridade média, SIMPER) foram *Euterpina acutifrons* (11.6%), *O. similis* (11.0%), e *O. nana* (9.5%); entre costeira e externa (85% de dissimilaridade média), *E. acutifrons* (12.8%), *O. nana* (9.5%) e *P. quasimodo* (9.2%); entre externa e intermediária (69% de dissimilaridade média), *O. similis* (14.6%), *C. brevipes* (8.7%) e *P. quasimodo* (8.2%). As espécies que mais contribuíram para a similaridade na zona costeira foram *E. acutifrons, O. nana* e *O. similis;* na zona intermediária foram *O. similis, P. quasimodo* e *C. brevipes*; na externa *O. similes, O. plumifera* e *C. pergens*. Os primeiro, segundo e terceiro estratos apresentaram composição específica semelhante quando comparados aos pares, mas havendo diferença entre o primeiro e o quarto (p=0.001) e entre o segundo e o quarto (p=0.037).

4. CONCLUSÃO

Em relação à biomassa zooplanctônica verificou-se que sua distribuição horizontal e vertical foi diferente nas estações do ano (alta no verão e baixa no outono). Os maiores valores ocorreram na zona costeira e nos estratos superficiais (até 25 ou 50 m), e foram associados com águas frias do sul (PRP e ASAP) e com águas subtropicais (ASTP). *(Desta forma, a Hipótese I foi aceita).*

Quanto à estrutura da comunidade em relação às variações temporais sazonais e a influência das massas de água na composição das espécies de copépodes, foi possível confimar que cada estação do ano pode ser caracterizada por associações de diferentes espécies, e a composição de copépodes é influenciada pela presença de diferentes massas de água, possibilitando reconhecer associações relacionadas com suas águas de origem *(Desta forma, a Hipótese II foi aceita).*

A distribuição vertical das espécies de copépodes apresentou estratificação mais definida nas zonas de maior profundidade. Isto foi verificado, sobretudo no inverno, onde espécies de águas profundas como *Metridia gerlachei* e *Racovitzanus antarticus* estiveram presentes entre 200 e 500 m de profundidade, enquanto no outono e verão as espécies presentes foram as mesmas presentes nos estratos mais superficiais. *(Desta forma, a Hipótese III foi aceita).*

O tipo de alimentação das espécies de copépodes mostrou predomínio de espécies micrófagas (herbívoras/onívoras) da ordem Calanoida, e espécies do gênero *Oithona* (Cyclopoida) no inverno e no outono, relacionadas com as massas de águas frias do sul (ASAP e PRP). No verão houve predomínio de espécies macrófagas (carnívoras) do gênero *Oncaea* (Cyclopida), associadas com águas subtropicais (ASTP) e tropicais (AT). *(Desta forma, a Hipótese IV foi aceita).*

Apesar de algumas diferenças significativas entre alguns estratos (nMDS) em relação à composição de espécies de copépodes, ressalta-se que muitas espécies ocorreram até cerca e 100 m, e desta forma acredita-se que não seria necessário um esforço maior para realizar amostragem estratificada. Os arrastos oblíquos desde 200 m ou 100 m de profundidade, forneceriam informações adequadas e suficientes na região da plataforma continental.

5. PERSPECTIVAS FUTURAS

Os resultados do presente estudo denotam a necessidade de se obter maiores informações sobre as espécies de menor tamanho do mezooplâncton (0,2 - 20 mm), sobretudo das famílias Oncaeidae e Oithonidae, e do microplâncton (20 – 200 µm), que inclui espécies ainda menores, os copepoditos e os náuplios. Aspectos taxonômicos e a distribuição, assim como estimativas de produção e de biomassa dos organismos, são fundamentais para conhecer o papel do zooplâncton nos processos ecológicos e na modelagem dos ecossistemas pelágicos marinhos.

6. REFERÊNCIAS BIBLIOGRÁFICAS

ALCARAZ, M, A CALBET, M ESTRADA, C MARRASÉ, E SAIZ & TREPAT, I. 2007. Physical control of zooplankton communities in the Catalan Sea. Progr. in Oceanogr. 74: 294-312.

AMARAL, WJA, 1994. Salpidae (Thaliacea) da Plataforma Continental do Extremo Sul do Brasil: Composição, Distribuição e Abundância. (Verão de 1990). Monografia de Conclusão de Curso. Univ. Fed. do Rio Grande. 46p.

ASEFF, CRC, GARCIA, VMT, MÖLLER JR, OO, 2009. Estudo da variação sazonal na composição físico-química das massas de água da Plataforma Continental do Atlântico Sudoeste entre Mar del Plata (AR, 38º S) e Itajaí (BR, 26º S). M. Sc. Thesis. Universidade Federal do Rio Grande, 100p.

BEERS, JR. 1976. Determination of zooplankton biomass. In ; STEEDMAN, HF (ed) Zooplankton fixation and preservation. UNESCO, Paris. p 35-86.

BERSANO, JG.1994. Zooplâncton da zona de arrebentação de praias arenosas, situadas ao sul de Rio Grande, RS. Primavera de 1990, Verão de 1991. Tese de Mestrado. Univ. Fed. do Rio Grande. 163p.

BERSANO, JGF & GA BOXSHALL 1994. Planktonic Copepods of Oncaea Philippi (Poecilostomatoida: Oncaeidae) from the waters off Southern Brazil. Nauplius 2: 29-41.

BERASATEGUI, AD, MENU MARQUE, S, GÓMEZ-ERACHE, M, RAMIREZ, FC, MIANZAN, HW & EM ACHA, 2006. Copepod in a highly complex hydrography región. Estuarine, Coastal and Shelf Science, 66: 483-492 BESIKTEPE, S. 2001. Diel vertical distribution, and herbivory of copepods in the south-western part of the Black Sea. Jour. Mar.Syst., 28:281–301.

BESIKTEPE, S. 2001. Diel vertical distribution, and herbivory of copepods in the south-western part of the Black Sea. Jour. Mar.Syst., 28:281–301.

BJÖRNBERG, TKS. 1963. On the marine free-living copepods off Brazil. Bolm. Inst. Oceanogr., São Paulo 13(1):3-142.

BOLTOVSKOY, D. (ed).1981. Atlas del Zooplankton del Atlantico Sudoccidental y Métodos de Trabajo con el Zooplancton Marino. Mar del Plata, INIDEP. 933p.

BOLTOVSKOY, D. (ed). 1999. South Atlantic Zooplankton. Backhuys Publishers, Leiden, The Netherlands. Vol.1 e 2. 1705p.

BÖTTGER-SCHNACK, R. 2001. Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea. II. Seven species of *Oncaea* s.str. Bull. nat. His. Mus. Lond. (Zool.) 67 (1): 25-84.

BRADFORD-GRIEVE, JM, MARKHASEVA, EL, ROCHA, CEF, ABIAHY, B. 1999. Copepoda. *In*: D. Boltovskoy (Ed.). South Atlantic Zooplankton. Leiden, Backhuys Publishers, 2: 869-1098.

BRAGA, ES, VC CHIOZZINI, GBB BERBEL, JCC MALUF, VMC AGUIAR, M CHARO, D MOLLINA, SI ROMERO, BB.EICHLER. 2008. Nutrient distributions over the Southwestern South Atlantic continental shelf from Mar del Plata (Argentina) to Itajaí (Brazil): Winter– Summer aspects. Cont. Shelf Res. 28: 1649– 1661.

BRANDINI, FP, RM LOPES, KS GUTSEIT, HL SPACH, & R SASSI, 1997. Planctonologia na plataforma continental do Brasil - Diagnose e revisão bibliográfica. FEMAR, Rio de Janeiro. 196p.

BRUNO, MA. 2009. Mesozooplâncton do extremo sul do Brasil com ênfase em Copepoda Calanoida de 1987 a 2007. Tese de Doutorado. Univ. Fed. do Rio Grande, 106 p.

CALLIARI, J, 1998. O ambiente e a biota do Estuário da Lagoa dos Patos: Características geológicas, in: Seeliger U., Odebretch, C., Castello, J.P. (Eds.), Os Ecossistemas Costeiro e Marinho do Extremo Sul do Brasil. Ecoscientia, Rio Grande, pp 13-18.

CAMPOS, E., A. BUSALACHI, S.GARZOLI, J.LUTJEHARMS, R.MARANO, P.NOBRE, D.OLSON, A.PIOLA, C.TANAJURA & I.WAINER. 1999. The South Atlantic and the Climate. Proc. Inter. Conf. of the Ocean Observing system for climate.St.Raphael, France.http: /www.bom.gov.au/OceanObs99/Papers/Campos.pdf.

CASTELLO, JP, DUARTE, A, MÖLLER, O, NIENCHESKI, F, ODEBRECHT, C, WEISS, G, HABIAGA, R, BELLOTTO, V, KITZMANN, D, SOUTO, C,

SOUZA, R, CIOTTI, A, FILLMANN, G, SCHWINGELL, P, BERSANO, J, CIRANO, M, FREIRE, K, LIMA, I, MELLO, R, MONTEIRO, A, RESGALLA, C, SOARES, I, SUZUKI, M, 1990. On the importance of coastal and subantartic waters for the shelf ecosystems off Rio Grande do Sul. II Simpósio de Ecossistemas da Costa Sul e Sudeste Brasileira: Estrutura, Função e Manejo, ACIESP, São Paulo, Brasil, pp 112–119.

CIOTTI, AM., C ODEBRECHT, G FILLMAN & OO MÖLLER JR. 1995. Freshwater outflow and Subtropical Convergence influence on phytoplankton biomass on the southern Brazilian continental shelf. Cont. Shelf Res. 15(14): 1737-1756.

CIOTTI, AM, GARCIA, CAE & JORGE, DSF, 2010. Temporal and meridional variability of Satellite-estimates of surface chlorophyll concentration. Pan-American Journal of Aquatic Sciences, 5(2), 236-253.

CLARKE, KR & RM WARWICK, 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth. 144p.

COYLE, KO & AI PINCHUK, 2003. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. Fish. Oceanogr. 12(4/5), 327-338.

ESCRIBANO, R. 2006. Zooplankton interactions with the oxygen minimum zone in the eastern south Pacific. Supl. Gayana 70:19-21.

ESCRIBANO, R, HIDALGO, P, GONZÁLEZ, H, GIESECKE, R, RIQUELME-

BUGUENO, R, MANRÍQUEZ, K, 2007. Seasonal and inter-annual variation of mesozooplankton in the coastal upwelling zone off central-southern Chile. Progress in Oceanography 75, 470–485.

GAETA, SA, BRANDINI, FP, 2006. Produção primária do fitoplâncton na região entre o Cabo de São Tomé (RJ) e o Chuí (RS), in: WONGTSCHOWSKI, CLDB, MADUREIRA, LSP (Eds.), O ambiente oceanográfico da Plataforma Continental e do Talude na região Sudeste-Sul do Brasil. EDUSP, São Paulo, pp 219-264

GAALLIENE, CP, ROBINS, DB. 2001. Is *Oithona* the most important copepod e=in the world’s oceans? Journal of Plakton Research, Vol. 23(12): 1421-1432.

GARCIA, VMT & CIOTTI, A, 2008. Primary production in the SWAOM region. http//www.skio.peachnet.edu/ meeting/ Primary_Production_SWAOM. Pdf.

GAUDY, R. 1963. Campagne de navière océanographique dans les eaux cotière du Brésil (Janvier-Fevrier 1962) copépodes pélagiques. Rec. Trav. Sta. Mar. Endoume 45:15-42.

GORRI, C.1995. Distribuição espaço-temporal e estrutura populacional de Euphausiacea (Crustacea) na região do extremo sul do Brasil (31º 40´S - 33º 40´S). Tese de Mestrado Univ. do Rio Grande. 124p.

HOFFMEYER, MS 2004. Decadal change in zooplankton seasonal succession in the Bahía Blanca estuary, Argentina, following introduction of two zooplankton species. J. Plankton Res. 26(2):181-189.

HUBOLT, G. 1980a. Hidrography and plankton off southern Brazil and Rio de La Plata. August-November 1977. Atlântica, 4: 1-22.

HUBOLT, G. 1980b. Second report on hidrography and plankton off southern Brazil and Rio de La Plata. Autumn cruise: April-June 1978. Atlântica, 4: 23-42.

HUYS, R. & GA BOXSHALL. 1991. Copepod Evolution. The Ray Society, London, 468p.

KARLSON, B. 2009. Observational approaches to community structure, from microbes to zooplankton. In: Workshop on Ocean Biology Observatories. Mestre, Italy, 12p.

LENZ, J. 2000. Introduction. In: HARRIS, RP, PH WIEBE, J LENZ, HR SKJOLDAL, M HUNTLEY (eds). ICES - Zooplankton Metodology Manual. Academic Press. Chap.1:1-32.

LIMA, I. D., CA. GARCIA, E. & OO. MÖLLER, Jr., 1996. Ocean surface processes on the southern Brazilian shelf: characterization and seasonal variability. Cont. Shelf Res.16 (10):1307-1317.

LOPES, RM., M KATSURAGAWA, J DIAS, MA MONTÚ, JH MUELBERT, C GORRI, & F BRANDINI, 2006 *a*. Zooplankton and ichtyoplankton distribution on the southern Brasilian shelf: an overview. Sci. Mar. 70 (2): 189-202.

LOPES, RM, MA MONTÚ, C GORRI, E MUXAGATA, LK MIYASHITA. & LP OLIVEIRA. 2006 *b*. O zooplâncton marinho na região entre o Cabo de São Tomé (RJ) e Chuí (RS). In: WONGTSCHOWSKI CL & L MADUREIRA. (eds). O Ambiente Oceanográfico da Plataforma Continental e do Talude na Região Sudeste-Sul do Brasil. EDUSP, São Paulo. Cap. 5: 265-358.

LOPES, R. 2007. Marine zooplankton studies in Brazil – A brief evaluation and perspective. Anais da Academia Brasileira de Ciências 79(3): 369-379. .

MARGALEF, R. 1995; Ecologia. Ediciones Omega, S.A. Barcelona

MAUCHLINE, J. 1998. The biology of Calanoid copepods. Academic Press, 710p.

MENEGHETTI, JO. 1973 *a*. Zooplankton from southern Brazil. 1-Quantitative aspects. Iheringia 43: 60-74.

MENEGHETTI, JO. 1973 *b*. Zooplankton from southern Brazil–2. Its composition, distribution and density in space and time. Iheringia 43: 100-125.

MENEGHETTI, JO. 1975. Zooplankton from southern Brazil-3. Quantitative aspects and seasonal fluctuations of some copepods. Iheringia 47: 47-66.

MIYASHITA, LK, M MELO JR & RM LOPES. 2009. Estuarine and oceanic influences on copepod abundance and production of a subtropical coastal area. J. Plankton Res. 31(8):815-826.

MÖLLER JR, OO, AR PIOLA., AC FREITAS & EJD CAMPOS. 2008. The effects of river discharge and seasonal winds on the shelf off southeastern South America. Cont. Shelf Res. 28: 1607-1624.

MONTÚ, M, I M GLOEDEN, A K DUARTE & C RESGALLA JR. 1998. Ambientes Costeiros e Marinhos e sua Biota: Zooplâncton. In: SEELIGER, U; C ODEBRECHT & JP CASTELLO (eds), Os Ecossistemas Costeiro e Marinho do Extermo Sul do Brasil. Ecoscientia, Rio Grande, Cap 6.9:123-134.

MORIARTY, R, BUITENHUIS, ET, LE QUÉRÉR, C, GOSSELIN, MP. 2012. Distribution of known macrozooplankton abundance and biomass in the global ocean. Earth System Science. Data Discuss: 5,187–220.

MUELBERT, JH, M ACHA, H MIANZAN, R GUERRERO, R RETA , ES BRAGA, VMT GARCIA, A BERASATEGUI, M GOMEZ-ERACHE & F RAMIREZ. 2008. Biological, physical, and chemical properties at the Subtropical Shelf Front Zone in the SW Atlantic Continental Shelf. Cont. Shelf Res., 28: 1662-1673.

NEGLEKERKE, N. 1991. A note on a general definition of the coefficient of determination. Biometrika, 78, 691-692.

NAVAS-PEREIRA, D. 1973. Análise qualitativa e quantitativa do zooplâncton. entre Torres e Maldonado (Lat. 29ºS - 35ºS). Inst. Oceanogr. Univ. São Paulo. Publ. Esp. 3(1): 29-92.

ODEBRECHT, C & VMT GARCIA 1998. Ambientes Costeiros e Marinhos e sua Biota: Fitoplâncton. In: SEELIGER,U, C ODEBRECHT & JP CASTELLO (eds), Os Ecossistemas Costeiro e Marinho do Extermo Sul do Brasil. Ecoscientia, Rio Grande, Cap. 6.7:117-121.

PAFFENHÖFER, GA & M G MAZZOCCHI. 2003. Vertical distribution of subtropical epiplanktonic copepods. J. Plankton Res., 25 (9): 1139-1156.

PIOLA, A.R., CAMPOS, E.J.D., MOLLER, O.O., CHARO, M. & C. MARTINEZ, 2000, Subtropical shelf front off eastern South America, J*ournal of Geophysical Research,* 105, C3, 6566-6578.

PIOLA, AR, OO MÖLLER JR, RA GUERRERO & EJD CAMPOS. 2008. Variability of the subtropical shelf front off Eastern South America: Winter 2003 and summer 2004. Cont. Shelf Res. 28: 1639-1648.

POSTEL, L.; H. FOCK & W. HAGEN. 2000. Biomass and abundance. In: ICES -Zooplankton methodology manual (ed) HARRIS, RP, PH WIEBE, J LENZ, HR SKJOLDAL & M HUNTLEY. Chap. 4:83-192.

RAYMONT, J.E. G.1983. Plankton and productivity in the ocean. Pergamon Press. 824p.

RESGALLA JR., C.1993. Influência das massas de água na distribuição espaço-temporal de Pteropoda, Cladocera e Chaetognatha na plataforma do sul do Brasil (31º 40´S - 33º 40´S). Rio Grande, Tese de Mestrado. Univ. do Rio Grande. 134 p.

RESGALLA JR., C.2008. Pteropoda, cladocera and chaetognatha associations as hydrological indicators in the southern Brasilian Shelf. Lat. Am. J. Aquat. Res. 36 (2): 271-282.

RESGALLA JR., C. & M MONTÙ, 1993. Cladóceros marinhos da plataforma continental do Rio Grande do Sul, Brasil. Nauplius 1: 63-79.

RESGALLA JR., C & M MONTÚ. 1994. Distribuição espacial e temporal de Pteropoda Euthecosomata (Mollusca, Gastropoda) na plataforma do sul do Brasil. Atlântica 6: 23-29.

RESGALLA JR, C, CL ROCHA & MA MONTÚ. 2001. The influence of Ekman transport on zooplankton biomass variability off southern Brazil. J. Plankton Res., 23(6): 641-650.

SCHMINKE, H K. 2007. Entomology for the copepodologist. J.Plankton Res.29: 49-62.

SALONEM, K & J SARVALA, 1985. Combination of freezing and aldehyde fixation. A superior preservation method for biomass determination of aquatic invertebrates. Arch. Hydrobiol. 103(2):217-230.

SCHWINGEL, PR & CASTELLO, JP. 1995. Alimentación de la anchoita (Engraulis anchoita) en el sur de Brasil. Frente Marítimo (Montevideo), v. 15, SEC. A, 67-85.

SKJOLDAL, HR, PH WIEBE, & KG FOOTE. 2000. Sampling and experimental design. In: HARRIS, RP, PH WIEBE, J LENZ, HR SKJOLDAL, M HUNTLEY. (eds). ICES-Zooplankton Methodology Manual. Academic Press.Chap2: 33-49.

SOARES, I. & MÖLLER JR. OO. 2001. Low-frequancy currents and water mass spatial distribution on the southern Brazilian shelf. Cont. Shelf. Res. 21: 1785-1814.

STEEDMAN, H F. (Ed). 1976. Zooplankton Sampling. UNESCO. Paris. 160p

STRICKLAND, JDH & TR PARSONS. 1972. A practical handbook of seawater analysis. Fisheries Research Board of Canada, Bulletin 167, Ottawa, Canada. 203p.

STRÖMBERG, KHP, SMYTH, TJ, ALLEN, JI, PITOIS, S, O'BRIEN, TD, 2009. Estimation of global zooplankton biomass from satellite ocean color. Journal of Marine Systems, 78, 18–27.

TEIXEIRA, C, E AIDAR, & RM FERNANDEZ. 1973. Estudo preliminar sobre a distribuição de clorofila-a e potencial de produção primária. Relatórios sobre a segunda pesquisa oceanográfica e pesqueira no Atlântico Sul entre Torres e Maldonado (Lat. 29ºS - 35ºS). Inst. Oceanogr. Univ. São Paulo. Publ. Esp. 3(1):1-27.

THOMPSON, GA, DINOFRIO, EO, ALDER, VA. 2013. Structure, Abundance And Biomass Size Spectra Of Copepods And Other Zooplankton Communities In Upper Waters Of The Southwestern Atlantic Ocean During Summer. J. Plankton Res. 35(3): 610–629. First Published online February 26, 2013

TURNER, JT. 2004. The Importance of Small Planktonic Copepods and Their Roles in Pelagic Marine Food Webs. *Zoological Studies* 43(2): 255-266.

VALIELA, I 1984. Marine ecology processes. New York. Springer-Verlag. 546p.

WISSER, AW, H SAITO, E SAIZ & T KIORBOE. 2001. Observations on copepod feeding and vertical distribution under natural turbulent conditions in the Noth Sea. Mar. Biol. 138:1011-1019.

ZERVOUDAKI, S, CHRISTOU, ED, NIELSEN, TG, SIOKOU-FRANGOU, I, ASSIMAKOPOULOU, G, GIANNAKOUROU, A, MAAR, M, KRASAKOPOLOU, E, CHRISTAKI, U, MORAITOU-APOSTOLOPOULOU, M. 2007. The Importance Of Small Sized Copepods In A Frontal Area Of The Aegean Sea. J. Plankton Res., Vol. 29 No. 4, P. 317-338

ANEXO I

Zooplankton biomass distribution in the Subtropical Southwestern Atlantic Ocean: relationships with environmental factors and chlorophyll *a*.

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Abstract

Zooplankton is a vital element in pelagic trophic links in marine ecosystems. The zooplankton vertical flow of particles provides energy to benthic organisms and contributes to the removal of excess CO_2 in the oceans. Its abundance and biomass are indicators of climate impacts on marine ecosystems. Despite its importance in controlling phytoplankton production and in modeling pelagic ecosystems, several aspects of zooplankton ecology are still not fully understood, especially regarding its biomass and trophic interactions. The present study assessed the distribution of zooplankton biomass (as carbon mass, CM), its seasonal variations and relationship to water masses and chlorophyll-a in the extreme south of Brazil. This region is one of the most productive of the Brazilian coast and of the entire continental shelf of the Southwestern Atlantic Ocean. The values of zooplankton biomass ranged between 0.01 and 32.89 mg C m^{-3}, and were higher in spring and summer, a little lower in winter and significantly lower in autumn. The high values in spring and winter were related to Plata Plume Water (PPW), in summer to Subtropical Shelf Water (STSW), and intermediate values in winter were related to Subantarctic Shelf Water (SASW). The values of chlorophyll-*a* (Chl-*a*) showed a pattern opposite to that of the CM, with low values in summer (minimum 0.04 mg m^{-3}) and high in autumn (maximum 2.56 mg m^{-3}). Nevertheless, the higher values of Chl-*a* were also related to PPW, SASW and STSW, and the lower values to Tropical Water (TW) and South Atlantic Central Water (SACW). The average daily production inferred for zooplankton (2.36 mg C m^{-3} d^{-1}), corresponded to an average annual production of 861 mg C m^{-3} yr^{-1} and 44 g C m^{-2} yr^{-1}. The zooplankton biomass, mainly related to the coastal and cold waters in southern Brazil, rich in nutrients and with a high phytoplankton biomass, plays an important role in the flow of matter and energy, and contributes to the maintenance of large fish stocks in the region.

Keywords: zooplankton, carbon, continental shelf, water masses, depth strata, seasonal variations.

1. Introduction

Zooplankton is an important component in pelagic trophic links in marine ecosystems. Their organisms can be predators, prey and competitors that contribute to the transfer of energy and carbon through the food chains, connecting phytoplankton primary production and organisms of higher trophic levels (Skjoldal et al., 2000; Escribano, 2006). Zooplankton is the main food source of several species of fish (larvae, juveniles and adults), many of them commercially important (Schwingel and Castello, 1995; Brandini et al., 1997; Skjoldal et al., 2000). Zooplankton grazing determines to a large extent the amount and vertical flow of particles, providing energy to benthic communities, exporting carbon from the surface to deeper layers, and contributing to the removal of excess CO2 in the oceans through sedimentation and burial of organic and inorganic carbon compounds (Lenz, 2000; Moriarty et al, 2012). The abundance and biomass of zooplankton are useful parameters in studies of climate impacts on marine ecosystems (Dvoretsky and Dvoretsky, 2013). Despite the importance of zooplankton in controlling phytoplankton production and in modeling pelagic ecosystems (Lenz, 2000), some aspects of its ecology are still not fully understood, especially regarding its composition, biomass and trophic interactions (Brandini et al., 1997; Mauchline 1998; Lopes et al., 2006a; Lopes, 2007). Zooplankton global distribution and the intensity of the temporal and spatial variability of its structural and functional characteristics are related to the different environmental hydrographic aspects (Escribano et al., 2007). Globally, the trend is toward a high biomass in the tropics, decreasing until the subtropical regions and slightly increasing toward the poles (Moriarty et al., 2012). Estimates show that most values are lower than 10 mg C m^{-3}, and the overall average value is 5.52 mg C m^{-3} (Strömberg et al., 2009). At mesoscale, the physical structure of the water column is highly dynamic, making zooplankton communities more dependent on the mode of transfer of matter and energy throughout the pelagic trophic food chains, which in turn are related to the qualitative and quantitative characteristics of primary producers (Alcaraz et al., 2007). At this scale, the gradients of salinity and temperature may define the composition and structure of zooplankton assemblages (Hoffmeyer, 2004; Berasategui et al., 2006), and together with primary producers influence their abundance and biomass (Coyle and Pinchuk, 2003). Thus, interactions between hydrodynamics and zooplankton occur often at the community level and are related to the availability of nutrients for primary production (Alcaraz et al., 2007).

In Brazil, knowledge about the taxonomic composition and diversity of species of zooplankton invertebrates, and their distribution in relation to the main systems of ocean circulation is restricted (Brandini et al., 1997; Montú et al., 1997; Lopes et al., 2006b; Lopes, 2007). Most studies were conducted in coastal zones and close to ports and estuaries, mainly in the south and southeast regions, where the relationship between zooplankton associations and the water masses, are known. There is little information on biomass and vertical distribution of zooplankton (Lopes et al. 2006a), despite its importance for the understanding of the community structure and the flow of energy between trophic levels (Skjoldal, 2000). Among the few data on zooplankton biomass in the extreme south of the country, in the summer a high value in the coastal zone of the shelf (~ 34º S; 98 mg C m^{-3}; Montú et al., 1997), and an extremely high value in the surf zone (~ 33º S; 8,142 mg C m^{-3}; Bersano, 1994) were recorded. The biovolume of zooplankton is high in coastal waters and in the warm months, the period of greatest species richness (Meneghetti 1973; Navas-Pereira 1973; Huboldt 1980a, b; Resgalla et al., 2001; Bruno, 2009).

The continental shelf of the extreme south of Brazil is one of the regions with the highest biological production of the Brazilian coast (Castello et al., 1990; Lopes et al, 2006b; Muelbert et al., 2008), presenting high amount of chlorophyll *a* related to nutrients from subantarctic waters, continental waters and upwellings (Huboldt, 1980a; Ciotti et al., 1995; Odebrecht and Garcia, 1997; Ciotti et al., 2010). The high primary production stimulates the growth of zooplankton populations, and the various water masses increase the diversity of species, contributing to the increase in zooplankton biomass in the region. This study aims to determine the horizontal and vertical distribution of zooplankton biomass (in carbon content), its seasonal variations and related factors, especially the water masses and chlorophyll-*a*, in the extreme south of Brazil. Considering the importance of zooplankton and the lack of information on the distribution of its biomass, this study is essential for understanding the ecological processes in the pelagic environments.

2. Material and Methods

2.1. Study area

The study area (31º 40´ S - 34º 45´ S; approximate area 46 750 km^2) (Fig.1) in Southern Brazil extends from Santa Marta Grande Cape (28°40’S) to Chuí (34°40’S), as part of the Southwestern Atlantic Ocean Continental Shelf. This area has a slow slope; the continental shelf varies between 100 and 180 km wide, and the shelf break depth between 160 and 190 m (Calliari, 1998).

This region is one of the most important fishing areas of the country (Castello et al., 1990; Lopes et al., 2006b; 2007; Braga et al., 2008) due to ocean conditions that favor high nutrient supply. Its chemical and physical conditions vary with the prevailing winds, currents and water masses (Lima et al., 1996; Soares and Möller, 2001; Möller et al., 2008; Piola et al., 2008) that determine high values of chlorophyll-*a* and primary production, especially in late winter and spring (Huboldt, 1980a, b; Ciotti et al., 1995; Odebrecht and Garcia, 1997).

The water masses are from different sources and present strong variability related to changes in wind regime and in continental freshwater discharges of the La Plata River and the Patos Lagoon (Piola et al., 2000). The thermohaline limits, according to Piola et al. (2000) and Aseff et al. (2009), allow the identification of five water masses present throughout the year: the Plata Plume Water (PPW), the Subantarctic Shelf Water (SASW), the Subtropical Shelf Water (STSW), the South Atlantic Central Water (SACW) and the Tropical Water (TW).

According to the previous studies (Ciotti et al., 1995; Piola et al. 2000; Soares and Möller Jr, 2001; Möller et al., 2008; Piola et al., 2008), the PPW is a coastal water mass, rich in nutrients, that results from the mixture of the continental discharge of the La Plata River with the waters from the continental shelf, and flows to the north. It has seasonal meridional displacement reaching latitude 28º S in winter and 32º S in summer, in the extreme south of Brazil. It is frequent in spring, autumn and winter. The SASW, rich in nutrients, is transported from the south by the Patagonian Current, and is stronger during winter and spring, particularly in the south. The TW, warm, saline and poor in nutrients, is transported to the south/southwest by the Brazil Current on the continental slope, in all the seasons. It is more frequent in summer when it can move forward the continental shelf. The SACW is formed by the mixture of TW e Subantarctic Water (SAW) in the zone of the Brazil Malvines Confluence (BMC). It moves south on deep layers along the slope, between 200 and 500 m, below the Brazil Current. Although rich in nutrients, solar radiation at these depths is insufficient to stimulate primary production. Upwelling events may bring it to the surface fertilizing the euphotic zone (Gaeta and Brandini, 2006), close to the shelf break. The STSW results from the dilution of the SACW with shelf waters. It is present in all seasons of the year, particularly to the north of the region. However, it dominates the continental shelf during summer.

Seasonal variations in continental discharges and the oscillation of the Brazil Malvinas Confluence (BMC) cause changes in the transport of water masses in the region (Lima et al., 1996; Möller et al., 2008, Piola et al., 2008). The combination of transport driven by the wind and the geostrophic circulation over the shelf, produces a stream of water directed predominantly to the south and the oceanic areas during summer (TW, STSW and SACW), and to the north and towards the coast in winter (PPW and SASW) (Lima et al., 1996; Piola et al., 2008).

The seasonal variations of the BMC determine the oscillations of the Subtropical Shelf Front (STSF), which is formed in the subsurface (~ 50m) when the STSW (of high temperature and salinity) meet the SASW (low temperature and salinity). This front extends between ~32º S and ~36º S, towards the shelf break (Piola et al., 2008). Because of the constant density lines (isopycnals) there is intense mixture of water masses upon the shelf that form two varieties of waters, warm and cold, of the STSW (Piola et al., 2008).

2.2. Collection and data analysis

Data were obtained from 94 oceanographyc stations located in the continental shelf, between the lighthouses of Conceição (31º 40´ S) and Chuí (34º45´S), from the coast (~20m) to the approximately 800 m isobath (Fig. 1), aboard the R V Atlântico Sul, within the scope of the ECOPEL (Study of the Pelagic Ecosystem of the Extreme South of Brazil) project. Samples were collected between October 10 and 17, 1987, September 07 and 15, 1988, February 06 and 21, 1990, and June 18 -July 02, 1991, periods that characterize the spring, winter, summer and autumn seasons, respectively, according to the distribution patterns of temperature and salinity (Soares and Möller Jr., 2001).

The zooplankton, in this study, concerns the holoplanktonic invertebrates collected with a WP-2 net fitted with 150 µm mesh size, 60 cm diameter at the mouth, equipped with a flow meter and closing device. In the spring, the net was towed from the bottom to the surface in 14 stations: 08 located between the 20 and ~ 50m isobaths, and

06 in the zone of the external shelf between 300 and maximum 600m, totaling 14 samples. In the summer, autumn and winter cruises, 27, 27 and 26 sampling stations, were respectively performed, totaling 240 samples (73, 99 and 68 samples, respectively). In these cruises, tows were vertical in five onshore-offshore transects, in the 0-25m, 25-50m, 50-100m, 100-200m and 200-500m strata. In the last two strata, the average of the values was obtained, and both were considered as one single stratum (>100m) in analyzes and results, because of the very low values of biomass and reduced number of stations.

Summer, autumn and winter samples were subdivided soon after collection. 50% of the volume of the samples was preserved in 4% formaldehyde-seawater solution buffered with borax (Steedman, 1976) for the study of the taxonomic composition. The remaining volume was preserved in 3% formaldehyde-seawater solution buffered with ß sodium glycerophosphate and immediately frozen at -20ºC (Salonem and Sarvala, 1985) for biomass analysis, estimated as carbon mass (CM). The analysis was performed after the material was thawed and washed with distilled water and sodium sulfate to remove salts (Strickland and Parsons, 1972), on previously cleaned, dried and weighed screen filters similar to those of the net used in sample collection. The dry mass was obtained according Beers (1976), and about 5 mg of this was used to determine the content of oxidizable organic carbon by wet oxidation method (Strickland and Parsons, 1972). In spring samples, following determination of dry mass, the material was incinerated to determine the ash-free dry mass, AFDM, (Beers, 1976) and then converted in carbon equivalent, C = 0.6 AFDM (Postel et al., 2000). The CM values were expressed by water volume (mg m^{-3}) and area (g m^{-2}). Some samples (< 3%) with the presence of non-zooplankton sestonic material (diatoms and debris), were disregarded immediately after filtering.

Salinity and temperature data were obtained at predetermined depths (5, 10, 20, 30, 50, 75, 100, 150, 200, 300, 400 and 500m) *in situ* by a Sensordata CTD (model

200), and reversing thermometers attached to Nansen sample bottles and KAHLSICO salinometer. Water samples for analysis of chlorophyll-*a* were obtained at the same intervals up to 100 m, with plastic containers on surface and with Niskin bottles (3 L) at the other depths. The water masses were classified according to thermohaline indexes proposed by Piola et al. (2000), adapted by Assef et al. (2009). The calculation of the frequency of occurrence of the water masses, considered the presence of each water mass within each depth stratum of all stations collected every season. The chlorophyll-*a* (Chl-*a*) content was determined by fluorimetric analysis (see Ciotti et al., 1995). For comparison of Chl-*a* and CM values in the different strata, the mean values of Chl-*a* at the standard depths corresponding to each stratum of zooplankton collection were used. CM and Chl-*a* values were integrated to the water column (g m^{-2}), through the sum of the average values (mg m^{-3}) of each depth stratum, multiplied by the path (m) traveled by the net in each stratum, above 100m for Chl-*a*, and for the entire sampled water column (maximum 600 m) for CM.

Zooplankton biomass (CM) was modeled as a function of factors season (autumn, summer, winter), water masses (PPW, SASW, STSW, TW), distance-from-coast (the coastal zone: defined by the range between 20-50m isobaths; the internal shelf: the range between 50-100m isobaths, and the external shelf >100m), day period (day, night), depth *s*trata (0-25m; 25-50m; 50-100m and >100m), and quantitative covariates latitude, longitude, temperature, salinity and Chl-a. The data of biomass in spring time was not considered in this analysis due to differences in zooplankton sampling methodology.

Two groups of generalized linear models (GLM) were proposed: i) response variable CM with Gamma distribution and logarithmic link function; and ii) response variable log (CM) with Normal distribution and identity link function. Within each model family, different covariate combinations were proposed and compared with Akaike

Information Criteria (AIC); comparisons of models from group (i) and (ii) were done with "pseudo-R^2" (proportion of deviance explained, Naglekerke, 1991).

Among the set of proposed models, the GLM with best fit within each family was the same but slightly better for group (i) when CM has a Gamma distribution with mean

$$E(CM) = \mu \qquad \text{and} \qquad \eta = \log \mu = a + \beta_{\mathbf{1}} \cdot sea + \beta_{\mathbf{2}} \cdot wm + \beta_{\mathbf{3}} \cdot depth + \beta_{\mathbf{dc}} \cdot lat$$

This model estimates a different intercept for each combination of season (*sea*), water mass (*wm*) and depth strata (*depth*) and includes a linear function of latitude (*lat*) with distance-from-coast specific (*dc*) coefficients. The intercept α estimates η for *sea* = autumn, *wm* = PPW and *depth stratum* = 0-25 m. The effects of other seasons, water masses and depth strata are given by the correspondent βs.

The models were adjusted with function *glm ()* of the statistical software R (R Development Core Team, 2012).

Nonparametric Kruskal-Wallis and Wilcoxon tests were used to compare CM and Chl-*a* results in the coastal zone in the four seasons of the year, considering the similarity of sampling in this area.

3. Results

3.1. Water masses

The temperature (minimum of 4.85 ^{0}C in winter, maximum of 26.27 ^{0}C in summer) and salinity (minimum of 26.5 in spring, maximum of 37.05 in summer) values and its combinations (Table 1), allowed to classify five water masses: Plata Plume Water (PPW), Subantarctic Shelf Water (SASW), Subtropical Shelf Water (STSW), South Atlantic Central Water (SACW) and Tropical Water (TW). These were present in all the seasons in the study area (Fig. 2), however with different frequencies of occurrence.

The PPW dominated most stations and depth strata (45% in spring, 39% in autumn and 33% in winter), except in summer when it was absent. The STSW was dominant during summer (49%), reducing its frequency in autumn (25%), winter (20%) and spring (12%). The SASW showed higher frequency in winter (28%) and the SACW was frequent in spring (20%), followed by summer, autumn and winter. TW was frequent in summer (32%), followed by autumn (22%), winter and spring.

Regarding the seasons (Fig. 2), in spring, PPW was the most frequent water mass in the study area. The SASW occupied most of the water column, sometimes up to 100 m in the south, reducing its influence towards the north. During summer, the STSW dominated the continental shelf, while the TW occurred near the shelf break from the north, advancing on the shelf up to the south. In autumn PPW was present along the entire coastal zone, the SASW was present in the intermediate and external shelf in the south, and the STSW was present along the entire water column to the north. In winter the SASW occurred in most of the shelf to the south, moved away from the coast towards the north, while the PPW advanced over the shelf. The STSW was limited to the north, and the TW did not occur in the south. The SACW occurred in all seasons and the TW was present along the area, with greater influence to the north.

3.2. Zooplankton biomass and chlorophyll-*a* integrated in the water column

The zooplankton biomass (CM) integrated by area (m^{-2}) at each station varied between 0.01 and 1.36 g m^{-2} and the values of Chl-*a* between 0.01 and 0.07 g m^{-2} (Table 2). High CM values occurred in the summer (0.15 - 1.36 g m^{-2}) and coincided with the lowest Chl-*a* values (0.01 - 0.03 g m^{-2}). In autumn the lowest CM value (maximum 0.12 g m^{-2}), and the highest Chl-*a* values (0.02 - 0.07 g m^{-2}) were found. CM values were intermediate in winter (0.06 - 1.04 g m^{-2}) and in spring (0.13 - 0.82 g m^{-2}), while Chl-*a* values were relatively high in spring (0.01 - 0.07 g m^{-2}), followed by winter (0.01 - 0.05 g m^{-2}).

In spring CM distribution by area (Fig. 3a) showed higher values in the south and on the slope in the north, and lower values in the coastal zone. Chl-*a* values (Fig. 3e) were higher to the south and in ~33ºS close to the coast. In the summer (Fig. 3b), the highest CM values occurred in the stations of the external shelf (isobath >100 m) in latitude near ~32ºS and to the south, and in the coastal zone in the north. Chl-*a* values (Fig. 3f) were homogeneously low, with slightly higher values in the coastal zone between 32ºS and 33ºS, and in the south. In autumn (Fig. 3c), CM values were lowest, while Chl-*a* (Fig. 3g) was high in most of the area, with maximum values in the coastal zone and in the internal shelf in the north. In winter, the maximum CM (Fig. 3d) values occurred in the south, in the intermediate and external zone of the shelf, and the maximum Chl-*a* (Fig. 3h) values occurred in a strip from the south in the intermediate zone of the shelf to the north, towards the coast. Considering the mean values of CM and Chl-*a* by area, it is found that:

CM (g m^{-2}): Summer (0.52) > Spring (0.43) > Winter (0,28) > Autumn (0,05),
Chl-*a* (g m^{-2}): Spring (0.04) > Autumn (0.03) > Winter (0.02) > Summer (0.01).

3.3. Zooplankton biomass and chlorophyll-*a* in depth strata

The values of CM and Chl-*a* in the depth strata showed variations among the seasons and in the same season of the year (Table 2). In the first stratum (0-25 m), CM and Chl-*a* values were higher, even double or more, compared to the second (25-50 m) and the other strata (Figs. 4 and 5).

CM ranged from minimum values (0.01 and 0.05 mg m^{-3}) in the autumn and winter at depths >50m, and maximum in the summer (29.95 and 27.23 mg m^{-3}) between 0-25 m and 25-50 m, respectively. Intermediate values (~11 mg m^{-3}) were frequent between 0-25 m, and sometimes up to 100 m, during winter. The values were always low (0.04 -1.65 mg m^{-3}) at depths beyond 100 m.

Chl-*a* ranged between minimum values (0.04 - 0.05 mg m^{3}) in the summer in all strata, and maximum (2.56 mg m^{3}) in the autumn, between 0-25 m. Below (25-50 m) the values were high in the autumn (1.56 mg m^{-3}) and winter (1.83 mg m^{-3}).

During the summer, CM values >10 mg m^{-3} were observed up to the depth of approximately 70 m, mainly in the coastal zone, and towards the slope at latitudes >33ºS (Central and North Transects, CT; Figs. 1b, 4a and 5a, b). High Chl-*a* values occurred only in the coastal zone in the south and in the north (Figs. 4d and 5d, e, f). During the autumn (Fig. 4b), the lowest CM values (<5 mg m^{-3}) of the whole area were obtained, and the highest Chl-*a* values (>1.5 mg m^{-3}) particularly in the coastal area in the north of the mouth of the Patos Lagoon (Fig. 4e), under the influence of its outflow, where the maximum CM value (Fig. 4b) was also found (4.76 mg m^{-3}, not visible in the figure due to the scale). In winter, the distribution pattern of the CM and Chl-*a* showed some similarity (Fig. 4c, f), the higher values occurred in the coastal zone to the south of the mouth of the Patos Lagoon, and in the intermediate zone of the shelf to the south (maxima: CM 24.87 mg m^{-3}; Chl-*a* 1.86 mg m^{-3}) (Figs. 4c, f, and 5m, n, o/ p, q, r,).

Comparison of CM and Chl-*a* values in the coastal zone (stations up to the 50 m isobath), in the seasons of the year (Kruskal-Wallis and Wilcoxon tests; Fig. 6; Table 3), shows that there was a large range of CM values during summer, small range during spring and winter and minimum range in autumn. CM was higher in the summer and spring, and lower in winter and autumn, with significant differences (H =27.4; gl=3; p=0.47x10^{-5}) between the seasons, except between summer and spring (median values 13 and 15 mg m^{-3}; Table 3a). In summer, the distribution of biomass values was wide, while in spring the values were close to the median. The maximum CM values in spring (32.89 mg m^{-3}) and summer (29.95 mg m^{-3}) were similar. However, in spring the maximum value was out of the distribution. The same occurred with the maximum value (24.83 mg m^{-3}) in winter (Fig. 6a). Analysis of Chl-*a* (Fig. 6b) showed a high range of values in spring and summer, and a low range in autumn and winter. The low values in summer and winter were significantly different from those in the autumn (H=10.5; gl=3; p=0.01), (Table 3b). The lowest medians were observed in summer and winter (0.6 and 1.0 mg m^{-3}, respectively); the highest in spring and autum (2.2 and 1.6 mg m^{-3}, respectively). However, there were no differentes in the *a posteriori* test, and spring was similar to autumn, summer and winter, due to the high range of Chl-*a* values in spring. In summer, in turn, the values were significantly lower than in autumn (median 1.6 mg m^{-3}), almost triple the values of summer. No differences were found between summer and winter, but winter was significantly different than autumn, with a higher median value.

3.4. Relationship between zooplankton biomass and environmental factors

The high values found in spring and winter, were related to the Plata Plume Water (PPW), and in summer with the Subtropical Shelf Water (STSW). Intermediate values in winter in the 0-25 m and 25-50 m strata were associated to the Subantarctic Shelf Water (SASW) (Fig. 7).

The CM values were explained by the season of the year, stratum depth and water masses (Table 4). There were no difference between summer and winter values (high CM values) but they were significantly different ($p<0.001$) from those in autumn (low values). Likewise, the 0-25 m stratum, with greater biomass, was significantly different ($p<0.001$) from the other strata. The water masses related to the higher CM values were PPW and STSW, which did not show significant differences between each other ($p<0.1$), while the Tropical Water (TW) showed the lowest CM values and was significantly different from PPW ($p<0.01$); SASW and SACW (South Atlantic Central Water) were different from PPW ($p<0.05$). Regarding the distance from the coast, the coastal zone (up to the 50 m isobath) and the intermediate shelf (between 50 and 100 m isobaths) showed higher CM values compared to the zone of the external shelf (beyond the 100 m isobath), however without significant differences. There were no differences between CM values observed during daytime and nighttime; and Chl-*a* content did not statistically explain CM changes. Despite the distinct seasonal pattern of CM and Chl-*a*, the higher Chl-*a* values were also related to the PPW, STSW and SASW, and the lower values with SACW and TW.

Based on pseudo-R^2, the data in the model GLM, explained approximately 65% of the variation in CM. Deviance residuals between -2.66 and 2.56 indicate that there were no remaining outliers and that the model fits the data. The qualification of the fitted model (Fig. 8) can be visualized comparing observed log (CM) against estimate values η. A perfect fit would imply that all points are on the drawn line. The observed linear correlation is $r = 0.814$ indicating an acceptable model fit.

4. Discussion

The zooplankton biomass (CM) in the extreme south of Brazil was associated with the seasons of the year, the water masses and the depth of the water column. The highest CM values occurred in spring and summer, which was probably related to the growth of zooplankton populations, stimulated by the presence of rich waters and high temperature that favor the reproduction and development of organisms. High densities of meroplanktonic larvae occur in this period (Montú et al., 1997), which may account for the higher values. Intermediate and high values were observed in winter, which although it is not a typical reproduction period for most species has a predominance of crustaceans (Montú et al., 1997), which have a high carbon content (Postel et al., 2000). Lavaniegos and Ohman (2007) found that crustaceans and chaetognaths may account for up to 90% of carbon biomass in Southern California (USA).

The water masses associated with the higher CM values were the Plata Plume Water (PPW) in spring, winter and autumn, and the Subtropical Shelf Water (STSW) in summer. The distribution pattern of zooplankton biomass and the relationships with the water masses observed in the present study are similar to the reported distribution of biovolume in this area (Meneghetti, 1973; Navas-Pereira, 1973; Huboldt, 1980a, b;

Bruno, 2009). The high biovolume reported for autumn in the region (Resgalla et al., 2001) was due to the presence of tunicates, organisms with high water content, but low carbon content (Postel et al., 2000).

There are few reports in the literature on the zooplankton biomass estimated as carbon content by area (g C m^{-2}), particularly in latitudes similar to those in the present study. The comparison of the values for summer in this region to those of the Barrents Sea shelf, Arctic, one of the most productive regions of the world (0.74 - 3.72 g C m^{-2}; Dvoretsky and Dvoretsky, 2013), and to those of Bransfield Strait, Antarctic (0.23 g C m^{-2} for crustaceans and 14.71 g C m^{-2} for salps; Alcaraz et al., 1998), shows that they are lower here (0.15 -1.36 g C m^{-2}), but indicate the importance of zooplankton in the local pelagic production.

Globally, estimates of zooplankton biomass were obtained based on the color of the ocean by SeaWiFS satellite and parametric models that related the transfer of energy from primary production to zooplankton biomass with *in situ* data (Strömberg et al., 2009). In the Atlantic Ocean, the estimated biomass of zooplankton is higher (7.35 mg C m^{-3}; S.D. 8.62) than the global average value (5.52 mg C m^{-3}; S.D. 8.94). The average value in the present study (6.54 mg C m^{-3}; S.D. 6.03) is intermediate to the values mentioned. On the map of global distribution of zooplankton biomass presented by the authors, the values for the extreme south of Brazil to the south of Argentina reach 20-30 mg C m^{-3}, consistent with the values found in this study, and are higher in the mouth of Rio de La Plata, indicating the positive influence of these waters for the entire region. In the Gulf of Trieste (NE Mediterranean) the average biomass (7.14 mg C $m^{-3;}$ S.D. 4.3; Kamburska and Fonda-Umani, 2009) was slightly higher than the value found in our study. Moriarty et al. (2012) found a global average biomass of 8.4 mg C m^{-3} (S.D. 63.46), though for the macrozooplankton, a zooplankton fraction, which is larger than in the present study and in studies of the other cited authors. In Brazil, the biomass of zooplankton reaches higher values in the upwelling region of Cabo Frio (~23^0S, around

88 mg C m^{-3} based on its dry mass 220 mg m^{-3}; Valentin, 2001). Nevertheless, in the coastal estuarine zone of the litoral of São Paulo, the average values (2.55 and 3.45 mg C m^{-3}; Miyashita et al., 1999) were low compared to those in the region of this study and in the other referred regions. A very high value (98 mg C m^{-3}) was reported in the summer, in a coastal area south of the study area by Montú et al. (1997), which was probably overestimated by the high level of suspended material (45 mg l^{-1}) and organic matter (18 mg l^{-1}) (Muelbert et al., 2008). On the other hand, the concentration of mysids in the surf zone of Cassino beach (32ºS) yielded an extreme value, one of the highest in the literature (8,142 mg C m^{-3}; Bersano, 1994).

A decreasing gradient, from the coast to the ocean, in the density of zooplankton has been observed in the Brazilian south region previously (Lopes et al., 2006; Muelbert et al., 2008). However, no significant differences were reported in this study among the three zones regarding biomass, although the highest values occurred more frequently in the coastal zone. Also, the biomass did not show a latitudinal pattern, despite the presence of two groups during the summer: a group of high values (>20 mg C m^{-3}) to the north of the study area (31ºS a 33ºS), and another group with lower values (< 15 mg C m^{-3}) to the south of the area (latitude > 33ºS). This may be related to the position of the Subtropical Shelf Front (STSF) between 32ºS and 36ºS (Piola et al, 2008). The daily vertical migration did not significantly influence the results of this study, since, regardless of the time of collection, CM values were higher in the surface layer (0-25 m).

The relatively high phytoplankton biomass in the region is related to the enrichment of the area with nutrients obtained from water inflows of the Patos Lagoon and La Plata River, of the subantarctic waters and upwellings (Huboldt, 1980a; Ciotti et al., 1995; Odebrecht and Garcia, 1997). These inflows occur mainly in spring, autumn and winter, leading to the highest average values of Chl-*a* of the entire Brazilian coast (Ciotti et al., 2010). The distribution of phytoplankton biomass is directly related to the spatial and temporal variability of water masses (Odebrecht and Garcia, 1997), which along with other physical processes, such as changes in the wind and rainfall regime influence the growth and distribution of the phytoplankton. The results of this and other studies in the region show that the stock of Chl-*a* may exceed the values recorded in the upwelling of Cabo Frio (0.5 - 6.0 mg m^{-3}; 23ºS, RJ; Valentim, 2001). This abundance of chlorophyll in much of the year probably stimulates the development of zooplankton populations, leading to the high biomass values found in the present study.

The low Chl-*a* values observed in the summer are consistent with previous records in the region (Muelbert et al., 2008; Ciotti et al., 2010). In winter, the first authors found relatively high values in the coastal zone (0.43 to 8.0 mg m^{-3}), associated to the enrichment of the waters of La Plata River (PPW). The analysis of a greater number of stations in the same winter and spring by Ciotti et al. (1995) resulted in higher values (<0.5-8.0 mg m^{-3} and >0.5-4.3 mg m^{-3}, respectively) close to the mouth of the Patos Lagoon. The influence of the Patos Lagoon has been pointed out by several authors. Abreu et al. (1995) found chlorophyll values >5 mg m^{-3} in the region that coincided with the values from images of ocean color obtained by satellite (Gaeta and Brandini, 2006). Further south, at the mouth of La Plata River, even higher chlorophyll values (15 and 23 mg m^{-3}) were reported (Carreto et al., 2008; Ferrari 2008). In the Patagonian shelf (Argentina) values up to 9 mg m^{-3}, and an extreme value > 64 mg m^{-3} were observed in the shelf break zone between high latitudes (~ 51^0 S - 53^0 S; Romero et al. (2006). These data reinforce the idea that the inflows of he PPW and the Patos Lagoon increase the amount of chlorophyll in the region, which should benefit the zooplankton.

There was no statistical relationship between the concentration of Chl-*a* and CM in the study area. The CM showed high values in spring and summer, and very low values in the autumn, a period in which the Chl-*a* was significantly higher. Unlike the CM, the Chl-*a* was lower in the summer, which was also reported by Ciotti et al. (2010). Aseff et al. (2009) found that the lowest nitrate values occur in the summer and the highest in autumn, winter and spring. These observations could explain the low Chl-*a* values in the summer, as well as the grazing of zooplankton. The population growth of most zooplankton species usually begins in the spring, reaches its peak in the summer, controlling the growth of the phytoplankton populations that are limited by the lower supply of nutrients. After reaching its peak, the zooplankton would decline in the autumn, with minimum grazing pressure, which would release the grazing pressure and allow the growth and maintenance of phytoplankton populations. Therefore, a seasonal relationship between primary producers and zooplankton biomass apparently exist with a time lag, since the development of zooplankton is slower. Chlorophyll and zooplankton are frequently inversely related, and the low values of Chl-*a* may result from the consumption by copepods (Muelbert et al., 2008) and other zooplankton organisms, characterizing a top down control. However, in winter the distribution of Chl-*a* and CM suggests some direct relation in some locations as well, particularly in the coastal zone (Fig. 4c, f) dominated by the Plata Plume Water (PPW), and in the central and southern zone between 0-50 m (Fig. 5n, k / o, r) under the influence of the Subantarctic Shelf Water (SASW). An important relationship between the different pelagic components was observed in the winter between the south (ST) and central (CT) transects (Figs. 1b and 5n, k / o, r), area under the influence of the SASW, where high Chl-*a* and CM values coincided with high abundance (>100 t km^{-2}) of zooplanktivorous fish (*Engraulis anchoita*) (Lima and Castello, 1995).

Despite the distinct seasonal pattern between CM and Chl-*a*, the highest values of the latter were also related to PPW, SASW and STSW, and the lowest values with TW and SACW. In the autumn, despite the low CM values (<5 mg m^{-3}), the highest values (3.0 and 4.8) coincided with the highest values of Chl-*a*, close to the coast, to the north of the mouth of the Patos Lagoon (33 ^{0} S) (Fig. 4b, e).

Cycles of warm and cold events of the ENSO (*El Niño*-Southern Oscillation) phenomenon determine rainy and dry periods, respectively, in the south of South

America (Brazil, Uruguay and Argentina), changin the hydrographic characteristics, particularly the flow of freshwater in the region (Ciotti et al., 1995; Möller et al., 2008). Strong and moderate *El Niño* phenomena occurred in the spring of 1987 and autumn of 1990, respectively (http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml) periods with high Chl-*a* values, probably influenced by the higher inflows of continental waters (Ciotti et al., 1995). However, there was no apparent influence of these events on zooplankton biomass (CM).

The results of GLM analysis indicate that the factors season of the year, water mass and depth, explained approximately 65% of the zooplankton biomass variability. Biological aspects probably accounted for the remaining 35% of the changes. In addition to the physical characteristics, the life cycle of the species (reproduction and development), nutrition, competition and predation influence zooplankton composition and biomass (Pepin et al., 2011).

Although the Chl-*a* did not explain the changes of CM in the GLM analysis, in Fig. 9 it is shown that a possible exponential increase in CM depending on the Chl-*a* is expected mainly in the summer. This forecast points to the importance of chlorophyll in the formation of zooplankton biomass in the study area. During the austral spring and summer, the percentage of winds that favor upwelling is high in the region (Soares and Möller Jr., 2001), a phenomenon that would favor the development of phytoplankton, and, thus, zooplankton.

The biomass of zooplankton also increased from spring to the early autumn further south, on the continental shelf of Argentina, with high values in coastal zone and close to the shelf break, while the main peak of Chl-*a* occurred in spring, followed by a second one in the autumn (Sabatini and Colombo, 2001). In the Chile South Pacific region, the increase in carbon content of zooplankton was related to the high concentration of diatoms (Escribano et al., 2007). Kamburska and Fonda-Umani, 2009 found that the changes were related with the taxonomic composition of phytoplankton, demonstrating the relationship between these two pelagic components However, Escribano et al. (2007) did not find a significant relationship between zooplankton biomass and chlorophyll, assigning that the heterotrophic components provide continuous food supply to the zooplankton. They suggested that perhaps Chl-*a* alone may not be a reliable index to assess the availability of food for zooplankton and the general lack of a relationship between CM and Chl-*a* in the present study confirm this idea.

Given the values of the average standard stocks of CM and Chl-*a* found in this study (Table 2), we related them in terms of production (phytoplankton) and consumption (zooplankton). Based on these values, we could infer that the consumption of zooplankton was approximately equivalent to the production of organic matter by the phytoplankton in spring and winter, being higher in the summer and lower in autumn.

In marine ecosystems, the efficient transfer from producers to herbivores is estimated in around 20% (Lalli and Parsons, 1996). Given the average values of Chl-*a* (Table 2), and equating them to their carbon content (C/Chl-a = 40; Parsons et al., 1984), we would obtain the average values of autotrophic biomass by area: spring 1.6 g C m^{-2}, autumn 1.2 g C m^{-2}, winter 0.8 g C m^{-2}, and summer 0.4 g C m^{-2}. Based on these values and on zooplankton carbon content values by area in the same periods (Table 2) a transfer efficiency can be inferred of 27% in spring and 35% in winter (percentages higher than the estimates), of 3% in autumn, when there was apparently no consumption, and 130% in the summer, when consumption was apparently higher than the available autotrophic biomass, or as fast as its production. In this period, the zooplankton probably fed on other items, for its biomass measurement (CM) refers to the entire community and not only herbivores.

Based on zooplankton biomass data, one can infer the production by relating these values to instantaneous growth rates of the organisms, as proposed by Hirst et al.

(2003), and the zooplankton production deduced according to the equation P = B *g* (P = instantaneous production rate, B = zooplankton biomass, *g* = instantaneous growth rate; Riegler and Downing, 1984). (*g* concerns the daily increase in the mass, Mauchline,1998). Thus, according to the main species of copepods present in each period of the year (Duarte et al., in prep.) and the intervals of temperature during these periods, *g* 0.42 was assumed for spring and summer and *g* 0.18 for autumn and winter. The annual average zooplankton production inferred would be 2.36 mg C m^{-3} d^{-1} (Table 5), which corresponds to an average annual production of 861 mg C m^{-3} yr^{-1}. According to the production values in different locations (Table 5), this value is high, even if compared to estuaries, which are well-known as highly productive environments (ex: Patos Lagoon, 146 and 1,333 mg C m^{-3} yr^{-1}**,** Muxagata et al., 2012).

The high production rate found here ensures the large fish stocks in this major Brazilian fishing region (Castello et al., 1990; Brandini, 2006). Among the various resources (pelagic and demersal fish and squid), it is worth mentioning the abundant planktivorous engraulidae *E. anchoita* (600 thousand to 4.5 million t), (Madureira et al., 2009). Its diet consists of more than 90% of zooplankton (copepods, hyperiids and euphausiids; Schwingel and Castello, 1995).

We can also infer zooplankton production per area (Table 5), whose daily average value would be 0.12 g C m^{-2} d^{-1}, resulting in a secondary annual production of 44 g C m^{-2} yr^{-1}, which corresponds to 28% of the estimated average primary production in this region (160 g C m^{-2} yr^{-1}; Odebrecht and Garcia, 1997). This percentage is consistent with the transfer efficiency (20%) estimated between these two trophic levels. Considering the total study area (~ 46 750 km^2), the zooplankton would produce about 2 x 10^6 t of carbon, and 7.5 x 10^6 t of carbon would be generated by the primary producers in the area per year. These values indicate the region as a highly productive zone of the ocean, considering the estimate of 45-50 Gt C yr^{-1} of global primary net production, which corresponds to 125-139 g C m^{-2} yr^{-1} for the global ocean (Longhurst et al., 1995). Thus, it can be concluded that zooplankton and phytoplankton in the extreme south of Brazil play an important role in the carbon cycle and CO_2 balance.

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References

Abreu, P.C., Granéli, H.W., Odebrecht, C., 1995. Produção fitoplanctônica e bacteriana na região da pluma estuarina da Lagoa dos Patos, RS, Brasil. Atlântica, Rio Grande, 17, 35-52.

Alcaraz, M., Saiz, E., Fernandez, J.A., Trepat, I., Figueiras, F., Calbet, A., 1998. Antarctic zooplankton metabolism: carbon requirements and ammonium excretion of salps and crustaceans zooplankton in the vicinity of Bransfield Strait during January 1994. Journal of Marine Systems, 17, 347-359.

Alcaraz, M., Calbet, A., Estrada, M., Marrasé, C., Saiz, E. Trepat, I., 2007. Physical control of zooplankton communities in the Catalan Sea. Progress in Oceanography, 74, 294-312.

Ara, K., 2004. Temporal variability and production of the planktonic copepod community in the Cananéia Lagoon Estuarine System, São Paulo, Brazil. Zoological Studies 43(2), 179 -186.

Avila, T.R., Machado, A.A.S., Bianchini, A., 2012. Estimation of zooplankton secondary production in estuarine waters: comparison between the enzymatic (chitobiase) method and mathematical models using crustaceans. Journal of Experimental Marine Biology and Ecology, vol. 416-417, 144-152.

Aseff, C.R.C., Garcia, V.M.T., Möller Jr, O. O., 2009. Estudo da variação sazonal na composição físico-química das massas de água da Plataforma Continental do Atlântico Sudoeste entre Mar del Plata (AR, 38º S) e Itajaí (BR, 26º S). M. Sc. Thesis. Universidade Federal do Rio Grande, 100p.

Beers, J.R., 1976. Determination of zooplankton biomass. In : Steedman, H.F. (ed) Zooplankton fixation and preservation. UNESCO, Paris, p 35-86.

Bersano, J.G.,1994. Zooplâncton da zona de arrebentação de praias arenosas situadas ao sul de Rio Grande, RS. Primavera de 1990 e Verão de 1991. M. Sc. Thesis. Universidade Federal do Rio Grande. 163p.

Berasategui, A., Menu Marque, S., Gomez Erache, M., Ramırez, F.C., Mianzan, H.W., Acha, E.M., 2006. Copepod assemblages in a highly complex hydrographic region. Estuarine, Coastal and Shelf Science 66, 483-492.

Braga, E.S., Chiozzini, V.C., Berbel, G.B.B., Maluf, J.C.C., Aguiar, V.M.C., Charo, M., Mollina, D., Romero, S.I., Eichler, B.B.,. 2008. Nutrient distributions over the Southwestern South Atlantic continental shelf from Mar del Plata (Argentina) to Itajaí (Brazil): Winter–Summer aspects. Continental Shelf Research, 28, 1649-1661.

Brandini, F.P., Lopes R.M., Gutseit K.S., Spach H.L., Sassi R., 1997. Planctonologia na plataforma continental do Brasil - Diagnose e revisão bibliográfica. FEMAR, Rio de Janeiro. 196p.

Bruno, M.A., 2009. Mesozooplâncton do extremo sul do Brasil com ênfase em Copepoda Calanoida de 1987 a 2007. Ph. D. Thesis. Universidade Federal do Rio Grande, 106 p.

Calliari, J., 1998. O ambiente e a biota do Estuário da Lagoa dos Patos: Características geológicas, in: Seeliger U., Odebretch, C., Castello, J.P. (Eds.), Os Ecossistemas Costeiro e Marinho do Extremo Sul do Brasil. Ecoscientia, Rio Grande, pp 13-18.

Carreto, J.I., Montoya, N., Akselman, R., Carignan, M.O.,Silva, R.I Colleoni, D.A.C., 2008. Algal pigment patterns and phytoplankton assemblages in different water masses of the Rio de la Plata maritime front. Continental Shelf Research 28, 1589-1606.

Castello, J.P., Duarte, A., Möller, O., Niencheski, F., Odebrecht, C., Weiss, G., Habiaga, R., Bellotto, V., Kitzmann, D., Souto, C., Souza, R., Ciotti, A., Fillmann, G., Schwingell, P., Bersano, J., Cirano, M., Freire, K., Lima, I., Mello, R., Monteiro, A., Resgalla, C., Soares, I., Suzuki, M., 1990. On the importance of coastal and subantartic waters for the shelf ecosystems off Rio Grande do Sul. II Simpósio de Ecossistemas da Costa Sul e Sudeste Brasileira: Estrutura, Função e Manejo, ACIESP, São Paulo, Brasil, pp 112–119.

Ciotti, A.M., Odebrecht, C., Fillmann, G., Möller Jr.,O.O.,1995. Freshwater outflow and subtropical convergence influence on phytoplankton biomass on the southern Brazilian continental shelf. Continental Shelf Research 15, 1737-1756.

Ciotti, A.M., Garcia, C.A.E. Jorge, D.S.F., 2010. Temporal and meridional variability of Satellite-estimates of surface chlorophyll concentration. Pan-American Journal of Aquatic Sciences, 5(2), 236-253.

Coyle, K.O., Pinchuk, A.I. 2003. Annual cycle of zooplankton abundance, biomass and production on the northern Gulf of Alaska shelf, October 1997 through October 2000. Fisheries Oceanography, 12(4/5), 327-338.

Dvoretsky, V.G., Dvoretsky, A.G., 2013. Epiplankton in the Barents Sea: Summer variations of mesozooplankton biomass, community structure and diversity. Continental Shelf Research, 52, 1-11.

Escribano, R., 2006. Zooplankton interactions with the oxygen minimum zone in the Eastern South Pacific. Suplemento Gayana 70, 19-22.

Escribano, R., Hidalgo, P., González, H., Giesecke, R., Riquelme-Bugueno, R., Manríquez, K., 2007. Seasonal and inter-annual variation of mesozooplankton in the coastal upwelling zone off central-southern Chile. Progress in Oceanography 75, 470–485.

Ferrari Ciancio, G., 2008. Relación del fitoplancton con las masas de agua del Río de La Plata y su frente oceánico. M.Sc. Thesis. Universidad de la República, Uruguay, 108p.

Gaeta, S.A., Brandini, F.P., 2006. Produção primária do fitoplâncton na região entre o

Cabo de São Tomé (RJ) e o Chuí (RS), in: Wongtschowski, C.L.D.B., Madureira, L.S.P (Eds.), O ambiente oceanográfico da Plataforma Continental e do Talude na região Sudeste-Sul do Brasil. EDUSP, São Paulo, pp 219-264.

Hirst, A.G., Sheader, M., Williams, J.A. 1999. Annual pattern of calanoid copepod abundance, prosome length and minor role in pelagic carbon flux in the Solent, UK. Marine Ecology Progress Series, 177: 133–146.

Hirst, A.G., Roff, J.C., Lampitt, R.S., 2003. A synthesis of growth rates in marine epipelagic invertebrate zooplankton, in: Southward, A.J., Tyler, P.A., Young, P.S., Fuiman, L.A., (Eds.), Advances in Marine Biology. Academic Press, Amsterdam, pp 1-142.

Hoffmeyer, M.S. 2004. Decadal change in zooplankton seasonal succession in the Bahía Blanca estuary, Argentina, following introduction of two zooplankton species. Journal of Plankton Research, 26(2), 181-189.

Hubolt, G. 1980a. Hidrography and plankton off southern Brazil and Rio de La Plata. August-November 1977. Atlântica, 4,1-22.

Hubolt, G. 1980b. Second report on hidrography and plankton off southern Brazil and Rio de La Plata. Autumn cruise: April-June 1978. Atlântica, 4, 23-42.

Kamburska, L., Fonda-Umani, S. 2009. From seasonal to decadal inter-annual variability of mesozooplankton biomass in the Northern Adriatic Sea (Gulf of Trieste). Journal of Marine Systems 78, 490–504.

Lalli, C.M., Parsons, T.R., 1996. Biological Oceanography: An introduction. Butterwoth-Heinemann, Oxford.

Lavaniegos, B.E., Ohman, M.D., 2007. Coherence of long-term variations of zooplankton in two sectors of the California Current System. Progress in Oceanography, 75, 42–69.

Lenz, J. 2000. Introduction, in: Harris, R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M., (Eds.), ICES, Zooplankton Metodology Manual. Academic Press, San Diego, pp 1-32.

Liang, D., Uye, S., 1996. Population dynamics and production of the planctonic copepods in a eutrophic inlet of the Inland Sea of Japan, III. Paracalanus sp., Marine Biology, 127, 219-227.

Lima, I.D., Castello, J.P., 1995 Distribution and abundance of South-west Atlantic anchovy spawners (Engraulis anchoita) in relation to oceanographic process in the southern Brazilian shelf. Fisheries Oceanography, 4(1), 1-16.

Lima, I.D., Garcia, C.A.E., Möller, Jr.,O.O.,1996. Ocean surface processes on the southern Brazilian shelf: characterization and seasonal variability. Continental Shelf Research, 16 (10), 1307-1317.

Longhurst, A., Sathyendranath, S., Platt, T., Caverhill, C., 1995. An estimate of global primary production in the ocean from satellite radiometer data. Journal of Plankton Research, 17, 1245-1271.

Lopes, R.M., Katsuragawa, M, Dias, J., Montú, M.A., Muelbert, J.H., Gorri, C., Brandini, F., 2006a. Zooplankton and ichtyoplankton distribution on the southern Brasilian shelf: an overview. Sciencia Marina. 70 (2): 189-202.

Lopes, R.M., Montú, M.A, Gorri, C., Muxagata, E., Miyashita, L.K., Oliveira, L.P., 2006b. O zooplâncton marinho na região entre o Cabo de São Tomé (RJ) e Chuí (RS), in: Wongtschowski C.L., Madureira, L., (Eds.), O Ambiente Oceanográfico da Plataforma Continental e do Talude na Região Sudeste-Sul do Brasil. EDUSP, São Paulo, pp 265-358.

Lopes, R., 2007. Marine zooplankton studies in Brazil – A brief evaluation and perspective. Anais da Academia Brasileira de Ciências 79(3), 369-379.

Madureira, L.A.S.P., Castello, J.P., Hernández, C.P., Queiroz, M.I, Santo M.L.P.E., Ruiz, W.A.,Abdallah, P.R.., Hansen, J., Bertolotti, M.I., Manca, E. ; Yeannes, M. I. ; Avdalov, N., , Amorín, S.F. 2009. Current and potential alternative food uses of the

Argentine anchoita (Engraulis anchoita) in Argentina, Uruguay and Brazil. FAO Fisheries and Aquaculture Technical Paper, v. 518, pp 269-287,

Mauchline, J., 1998.The biology of calanoid copepods, in: Southward, A.J., Tyler, P.A., Young, P.S., Fuiman, L.A., (Eds.), Advances in Marine Biology. Academic Press, San Diego, pp 297-346.

Meneghetti, J.O., 1973 Zooplankton from southern Brazil. 1- Quantitative aspects. Iheringia, 43, 60-74.

Miyashita, L.K., Melo, J.R.M., Lopes, R.M., 2009. Estuarine and oceanic influences on copepod abundance and production of a subtropical coastal area. Jounal of Plankton Research, 31(8), 815-826.

Möller Jr., O.O., Piola, A.R., Freitas, A.C., Campos, E.J.D., 2008. The effects of river discharge and seasonal winds on the shelf off Southeastern South America. Continental Shelf Research, 28, 1607-1624.

Montú, M., Gloeden, I. M., Duarte, A. K., Resgalla, Jr., C., 1997. Coastal and marine environmental and their biota: Zooplankton, in: Seeliger, U., Odebrecht, C., Castello, J.P. (Eds.), Subtropical Convergence Environments. The Coast and Sea in the Southwestern Atlantic, Springer, Berlin- Heidelberg, pp.123-134.

Moriarty, R., Buitenhuis, E.T., Le Quérér, C., Gosselin, M.P. 2012. Distribution of known macrozooplankton abundance and biomass in the global ocean. Earth System Science. Data Discuss: 5,187–220.

Muelbert, J.H., Acha, M, Mianzan H, Guerrero, R., Reta R, Braga E.S., Garcia, V.M.T.,Berasategui, A., Gomez-Erache, M., Ramirez., 2008. Biological, physical, and chemical properties at the Subtropical Shelf Front Zone in the SW Atlantic Continental Shelf. Continental Shelf Research, 28, 1662-1673.

Muxagata, E., Amaral, W.J.A., Barbosa, C.N., 2012. Acartia tonsa production in the Patos Lagoon estuary, Brazil. ICES Journal of Marine Science 69(3), 475-482.

Navas-Pereira, D., 1973. Análise qualitativa e quantitativa do zooplâncton entre Torres e Maldonado (Lat. 29ºS - 35ºS). Instituto Oceanográfico, Universidade São Paulo. Publicação Especial, 3(1), 29-92.

Neglekerke, N. 1991. A note on a general definition of the coefficient of determination. Biometrika, 78, 691-692.

Odebrecht, C., Garcia V.M.T., 1997. Coastal and marine environmental and their biota: Phytoplakton. In: Seeliger, U., Odebrecht, C., Castello, J.P. (Eds.), Subtropical Convergence Environments. The Coast and Sea in the Southwestern Atlantic. Springer, Berlin Heidelberg, pp 117-121.

Parsons, T.R., Takahashi, M., Hargrave, B., 1984. Biological Oceanographic Processes. Pergamon Press, Oxford.

Pepin, P., Colbourne, E., Maillet, G., 2011. Seasonal patterns in zooplankton community structure on the Newfoundland and Labrador Shelf. Progress in Oceanography, 91, 273-285.

Piola, A.R., Campos, E.J.D., Möller Jr., O.O., Charo, M., Martinez, C.M., 2000. Subtropical shelf front off eastern South America. Journal of Geophysical Research 105 (C3), 6566–6578.

Piola, A.R., Möller Jr., O.O., Guerrero, R.A., Campos, E.J.D., 2008. Variability of the Subtropical Shelf front off eastern South America: winter 2003 and summer 2004. Continental Shelf Research, 28, 1639-1648.

Postel, L., Fock, H., Hagen, W., 2000. Biomass and abundance, in: Harris, R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M., (Eds.), ICES, Zooplankton Metodology Manual. Academic Press, San Diego, pp 83-192.

R Development Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Resgalla Jr, C., Rocha, C.L., Montú, M.A. 2001. The influence of Ekman transport on zooplankton biomass variability off southern Brazil. Journal of Plankton Research, 23(6): 641-650.

Rigler, F. H., Downing, J. A., 1984. The calculation of secondary productivity, in: Downing, J. A., Rigler, F. H., (Eds.), A Manual on methods for the assessment of secondary productivity in fresh waters. Blackwell Scientific, London, pp19-58.

Romero, A.I., Piola, A.R., Charo, M., Garcia, C.A.E., 2006. Chlorophyll-a variability off Patagonia based on SeaWiFS data. Journal of Geophysical Research, vol. 111, C05021.

Sabatini, M.E., Colombo, G.L.A., 2001. Seasonal pattern of zooplankton biomass in the Argentinian shelf off Southern Patagonia (45–551S). Scientia Marina, 65, 21–31.

Salonem, K., Sarvala, J., 1985. Combination of freezing and aldehyde fixation. A superior preservation method for biomass determination of aquatic invertebrates. Archieves of Hydrobiology, 103(2), 217-230.

Schwingel, P.R., J.P., Castello. 1995. Alimentación de la anchoita (Engraulis anchoita) en el sur de Brasil. Frente Marítimo (Montevideo), v. 15, SEC. A, 67-85.

Skjoldal, H.R., Wiebe, P.H., Foote, K.G., 2000. Sampling and experimental design, in: Harris, R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M. (Eds.), ICES-Zooplankton Methodology Manual. Academic Press, San Diego, pp 33-49.

Soares, I., Möller, J.R.O., 2001. Low-frequancy currents and water mass spatial distribution on the southern Brazilian shelf. Continental Shelf Research, 21, 1785-1814.

Steedman, H. F. 1976. Zooplankton Sampling. UNESCO, Paris.

Strickland, J.D.H., Parsons, T.R., 1972. A practical handbook of seawater analysis. Fisheries Research Board of Canada, Bulletin 167, Ottawa, Canada.

Strömberg, K.H. P., Smyth, T.J., Allen, J. I., Pitois, S., O'Brien, T.D., 2009. Estimation of global zooplankton biomass from satellite ocean color. Journal of Marine Systems, 78, 18–27.

Valentin, J.L., 2001. The Cabo Frio upwelling system, Brazil, in: Seeliger, U., Kjierfve, B., (Eds.), Coastal Marine Ecosystems of Latin America, Ecological Studies, vol. 144, pp 97-117.

Uye, S., Iwai, Y., Kasahara, S., 1983. Growth and production of the inshore marine copepod Pseudodiaptomus marinus in the central part of the Inland Sea of Japan. Marine Biology, 73, 91-98.

Uye, S., Nagano, N., Shimazu, T., 2000. Abundance biomass, production and trophic roles of micro-and net-zooplankton in Ise Bay, Central Japan, in winter. Journal of Oceanography, 56, 389-398.

http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml (Accessed on 03/06/2013).

Table 1
Termohalines indexes for water masses in spring, summer, autumn and winter according Piola (2000) and Assef et al., (2009). PPW: Plata Plume Water, SASW: Subantartic Shelf Water, STSW: Subtropical Shelf Water, SACW: South Atlantic Central Water and TW: Tropical Water

	PPW	SASW	STSW	SACW	TW
Spring	$S \leq 33.5$ $T \geq 10$	$33.5 < S < 34.2$ $T \leq 17$	$33.5 < S < 35.3$; $T > 17$; $35.3 \leq S < 36$; $T \geq 18.5$	$S \geq 35.3$ $T < 18.5$	$S \geq 36$ $T \geq 18.5$
Summer	$S \leq 33.5$ $T \geq 10$	$33.5 < S < 34.2$ $T \leq 21$	$33.5 < S < 35.3$; $T > 21$; $35.3 \leq S < 36$; $T \geq 20$	$S \geq 35.3$ $T < 20$	$S \geq 36$ $T \geq 20$
Autumn	$S \leq 33.5$ $T \geq 10$	$33.5 < S < 34.2$ $T \leq 17$	$33.5 < S < 35.3$; $T > 17$; $35.3 \leq S < 36$; $T \geq 18.5$	$S \geq 35.3$ $T < 18.5$	$S \geq 36$ $T \geq 18.5$
Winter	$S \leq 33.5$ $T \geq 10$	$33.5 < S < 34.2$ $T \leq 14$	$33.5 < S < 35.3$; $T > 14$; $35.3 \leq S < 36$; $T \geq 18.5$	$S \geq 35.3$ $T < 18.5$	$S \geq 36$ $T \geq 18.5$

Table 2.
Averaged zooplankton biomass (CM) and chrorophyll (Chl-*a*) with maximum and minimum values of CM and Chl-*a* per strata (mg m^{-3}). Also are shown the values of CM and Chl-*a* per unit of area (g m^{-2}) by integrating all strata sampled. Max =maximum, Min =minimum, S.D. = Standard Deviation, — indicates no data available.

	0 - 25 m	**25 - 50 m**	**50 - 100 m**	**> 100 m**	**depth integrated**
		(mg m^{-3})			**(g m^{-2})**
Spring					
MC					
Max / Min	32.89 / 0.93	—	—	—	0.82 / 0.13
Mean/ S.D.	9.23 / 9.14	—	—	—	0.43 / 0.20
Chl- *a*					
Max / Min	4.34 / 0.12	—	—	—	0.07 / 0.01
Mean/ S.D.	1.44 / 1.19	—	—	—	0.04 / 0.02
Summer					
MC					
Max / Min	29.95 / 2.55	27.23 / 0.11	3.58 / 0,80	1.66 / 0,09	1.36 / 0.15
Mean/ S.D.	14.00 / 8.68	5.46 / 6.12	1.94 / 0.94	0.71/ 0.60	0.52 / 0.35
Chl-*a*					
Max / Min	2.36 / 0.05	0.58 / 0.05	0.44 / 0.04	—	0.03 / 0.00
Mean/ S.D.	0.43 / 0.58	0.23 / 0.15	0.14 / 0.10	—	0.01 / 0.01
Autumn					
MC					
Max / Min	4.76 / 0.31	2.82 / 0.08	1.67 / 0.01	0.20 / 0.05	0.12 / 0.01
Mean/ S.D.	1.19 /1.04	0.73/0.63	0.38 / 0.47	0.10 / 0 06	0.05 / 0.03
Chl-*a*					
Max / Min	2.56 / 0.26	1.55 / 0.28	0.63 / 0.21	—	0.07 / 0.02
Mean/ S.D.	1.10 / 0.60	0.61 / 0.27	0.34 / 0.13	—	0.03 / 0.01
Winter					
MC					
Max / Min	24.87 / 0.07	10.99 / 0.24	11.82 / 0.02	1.27 / 0.05	1.4 / 0.06
Mean/ S.D.	6.44 / 5.66	2.92 / 3.08	2.93 / 4.00	0.51 / 0.46	0.28 / 0.24
Chl-*a*					
Max / Min	1.86 / 0.21	1.83 / 0.14	0,19 / 0.05	—	0.05 / 0.01
Mean/ S.D.	0.77 / 0.49	0.55 / 0.49	0.11 / 0.05	—	0.03 / 0.01

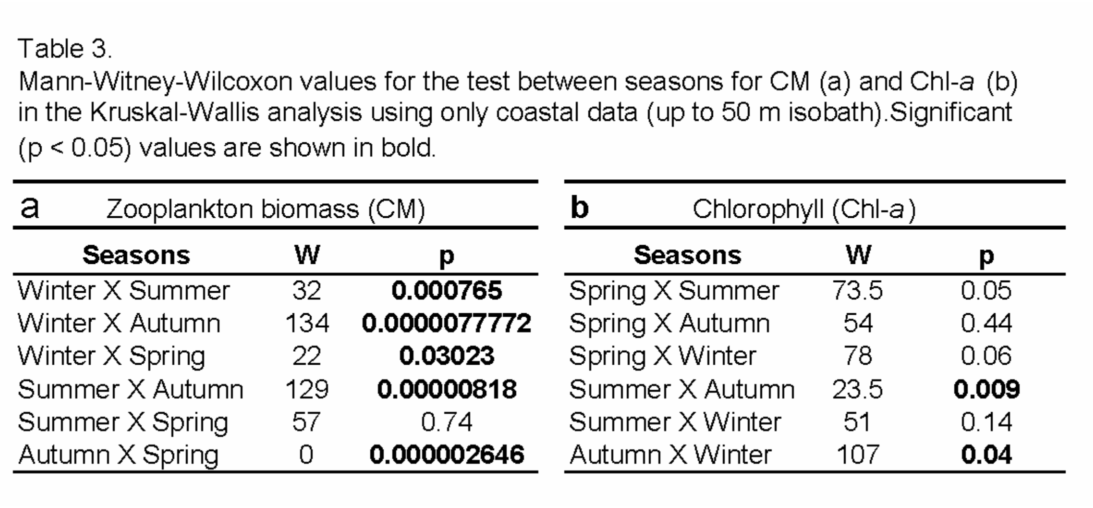

Table 3.
Mann-Witney-Wilcoxon values for the test between seasons for CM (a) and Chl-*a* (b) in the Kruskal-Wallis analysis using only coastal data (up to 50 m isobath).Significant ($p < 0.05$) values are shown in bold.

a Zooplankton biomass (CM)

Seasons	**W**	**p**
Winter X Summer	32	**0.000765**
Winter X Autumn	134	**0.0000077772**
Winter X Spring	22	**0.03023**
Summer X Autumn	129	**0.00000818**
Summer X Spring	57	0.74
Autumn X Spring	0	**0.000002646**

b Chlorophyll (Chl-*a*)

Seasons	**W**	**p**
Spring X Summer	73.5	0.05
Spring X Autumn	54	0.44
Spring X Winter	78	0.06
Summer X Autumn	23.5	**0.009**
Summer X Winter	51	0.14
Autumn X Winter	107	**0.04**

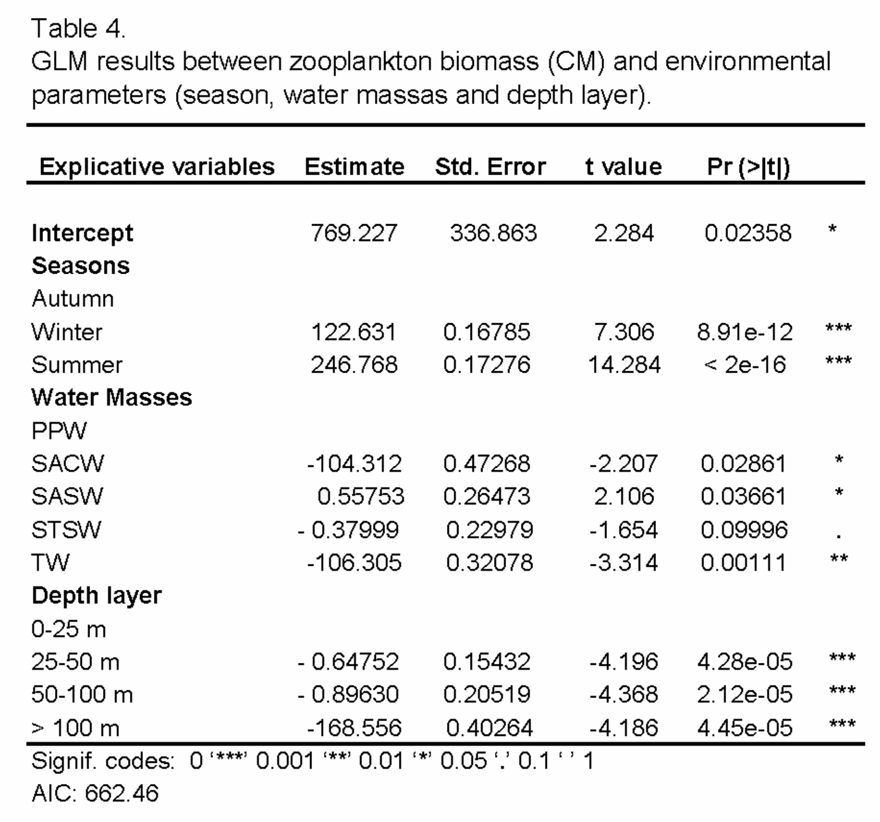

Table 4.
GLM results between zooplankton biomass (CM) and environmental parameters (season, water massas and depth layer).

Explicative variables	Estimate	Std. Error	t value	Pr (>|t|)	
Intercept	769.227	336.863	2.284	0.02358	*
Seasons					
Autumn					
Winter	122.631	0.16785	7.306	8.91e-12	***
Summer	246.768	0.17276	14.284	< 2e-16	***
Water Masses					
PPW					
SACW	-104.312	0.47268	-2.207	0.02861	*
SASW	0.55753	0.26473	2.106	0.03661	*
STSW	- 0.37999	0.22979	-1.654	0.09996	.
TW	-106.305	0.32078	-3.314	0.00111	**
Depth layer					
0-25 m					
25-50 m	- 0.64752	0.15432	-4.196	4.28e-05	***
50-100 m	- 0.89630	0.20519	-4.368	2.12e-05	***
> 100 m	-168.556	0.40264	-4.186	4.45e-05	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

AIC: 662.46

Table 5
Annual and seasonal zooplankton production and daily rates growth from different locations.

Taxa group/species	Region	Study Period	Daily Rate (mg C m^{-3} d^{-1})	Production (mg C m^{-3})	Daily Rate (g C m^{-2} d^{-1})	Production (g C m^{-2})	Source
Pseudodiaptomus marinus	Inland Sea of Japan	Annual	0.057	21	—	—	Uye et al., 1983
Paracalanus sp	Inland Sea of Japan	Annual	—	734	—	5.5	Liang and Uye, 1996
Acartia spp (four species)	Southampton Water, UK	Annual	—	20	—	—	Hirst et al., 1999
Copepods	Cananeia Lagoon Estuary, BR	Spring	0.75 - 1.84	68 - 166[1]	—	—	Miyashita et al., 1999
		Summer	2.09 - 4.73	188 - 426[1]	—	—	
Zooplankton	Ise Bay, Central Sea, Japan	Winter	1.87	168[1]	0.04	3.6[1]	Uye et al., 2000
Copepods	Cananeia Lagoon Estuary, BR	Annual	5.23	1 909	—	—	Ara, 2004
Zooplankton (copepods and cladocerans)	Patos Lagoon Estuary, BR	Spring	2.07	186[1]	—	—	Ávila et al., 2012
		Winter	3.84	346[1]	—	—	
Acartia tonsa (copepodtes and adults)	Patos Lagoon Estuary, BR						
	inner estuary	Annual	0.40	146	—	0.73[2]	Muxagata et al., 2012
	channel	Annual	3.65	1 333	—	6.67[2]	
Zooplankton	Continental shelf of Southern Brazil	Spring	4.03	363	0.18	16	This study
		Summer	4.24	382	0.22	20	
		Autumn	0.18	16	0.01	0.9	
		Winter	0.98	88	0.05	4.6	
		Annual	2.36	861	0.12	44	

— Not available

[1] Values obtained by multiplying the daily rates for 90 days (study period).

[2] Values obtained considering 5m local depth.

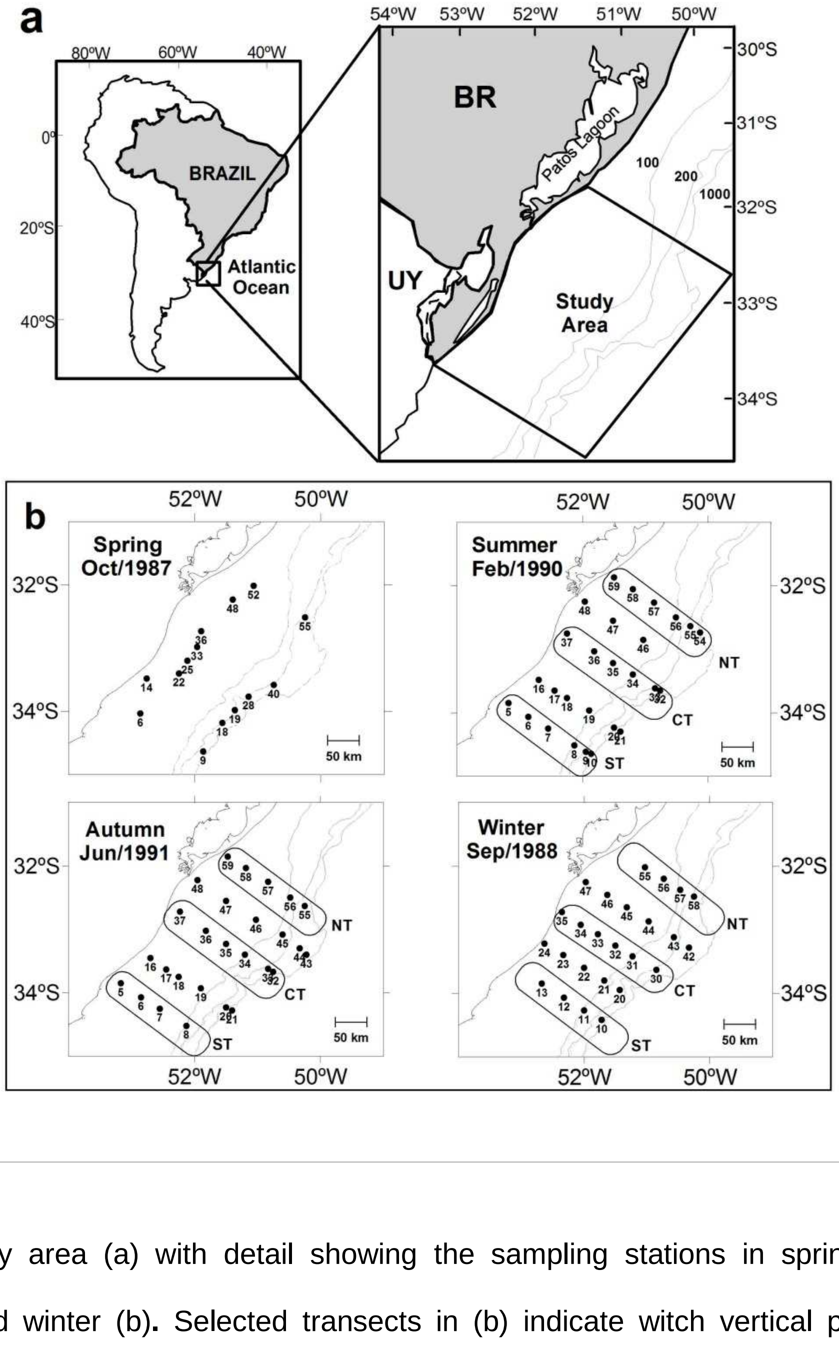

Fig.1. Study area (a) with detail showing the sampling stations in spring, summer, autumn and winter (b). Selected transects in (b) indicate witch vertical profiles were chosen to represent the distribution of zooplankton biomass (CM) and chlorophyll (Chl-*a*) in Fig. 5. (NT: Northern Transect, CT: Central Transect and ST: Southern Transect; isobaths in meters).

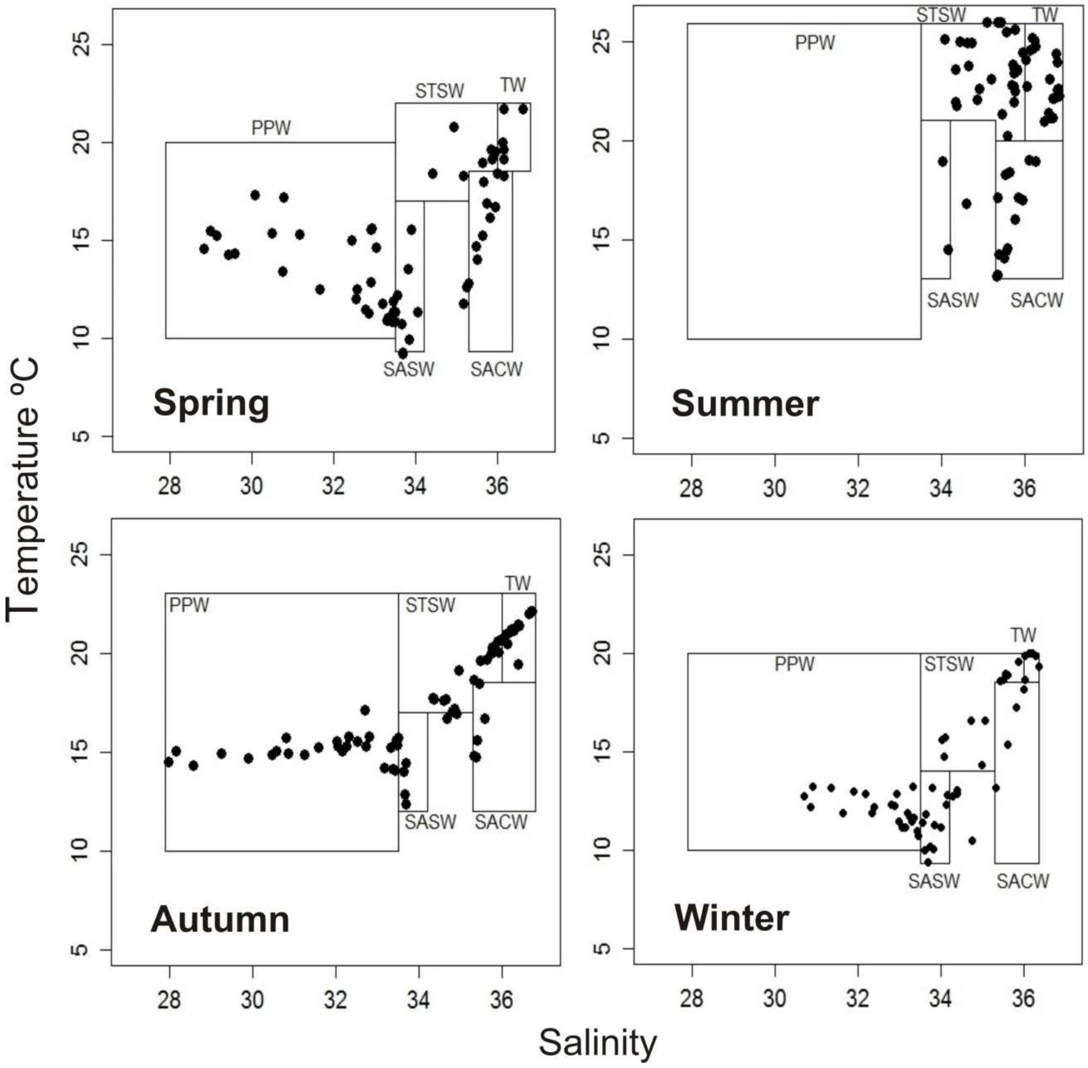

Fig.2. Temperature and salinity (TS) diagrams for spring, summer, autumn and winter during the sampling periods. On each season the different water masses present are shown by rectangles delimited by each seasonal termohaline indexes (Table 1). PPW: Plata Plume Water, SASW: Subantartic Shelf Water, STSW: Subtropical Shelf Water, SACW: South Atlantic Central Water and TW: Tropical Water.

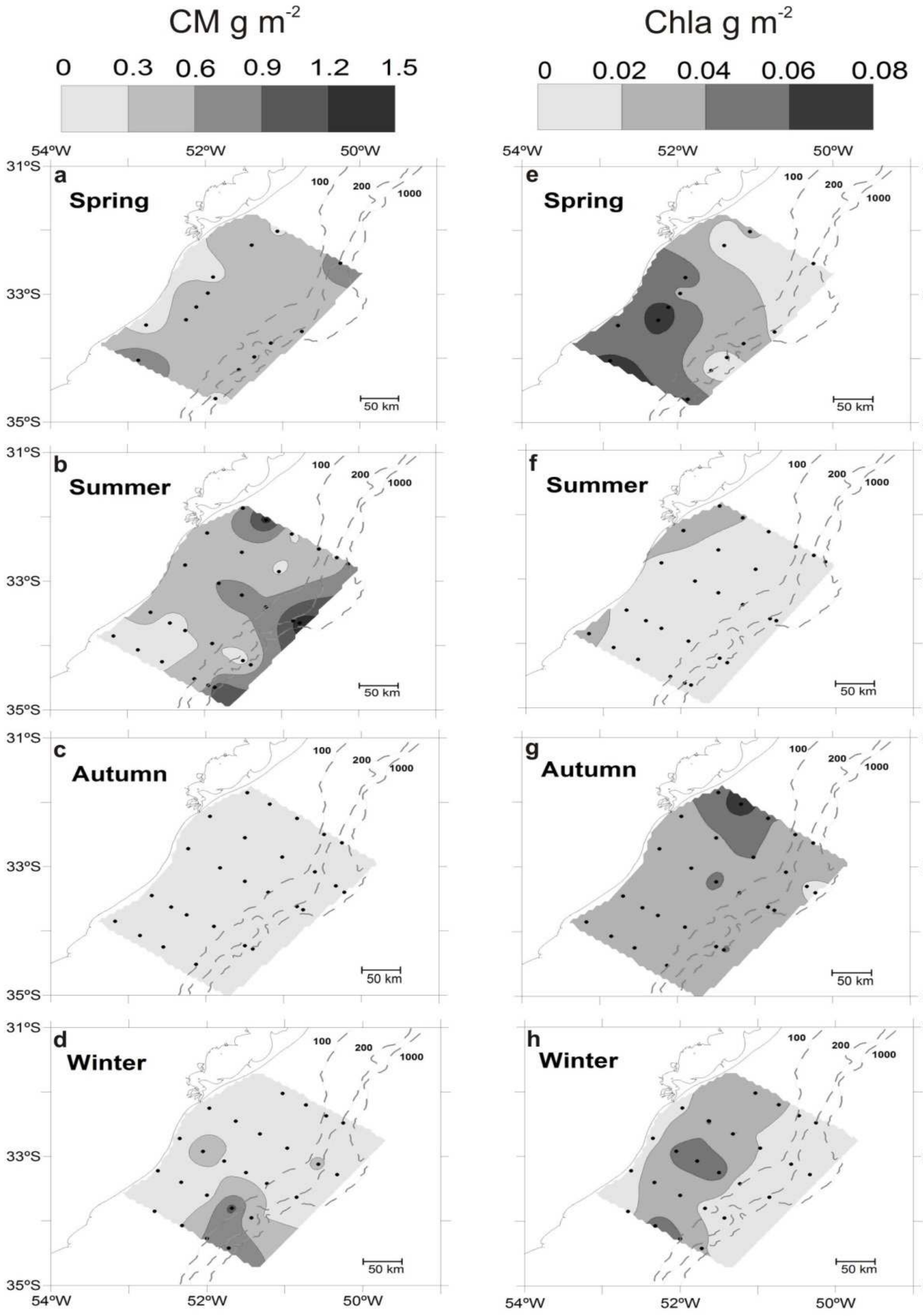

Fig.3. Zooplankton biomass (CM) (a, b, c, d) and chlorophyll (Cla-*a*) (e, f, g, h) distribution per unit of area (g m^{-2}) in spring, summer, autumn and winter.(Isobaths in meters).

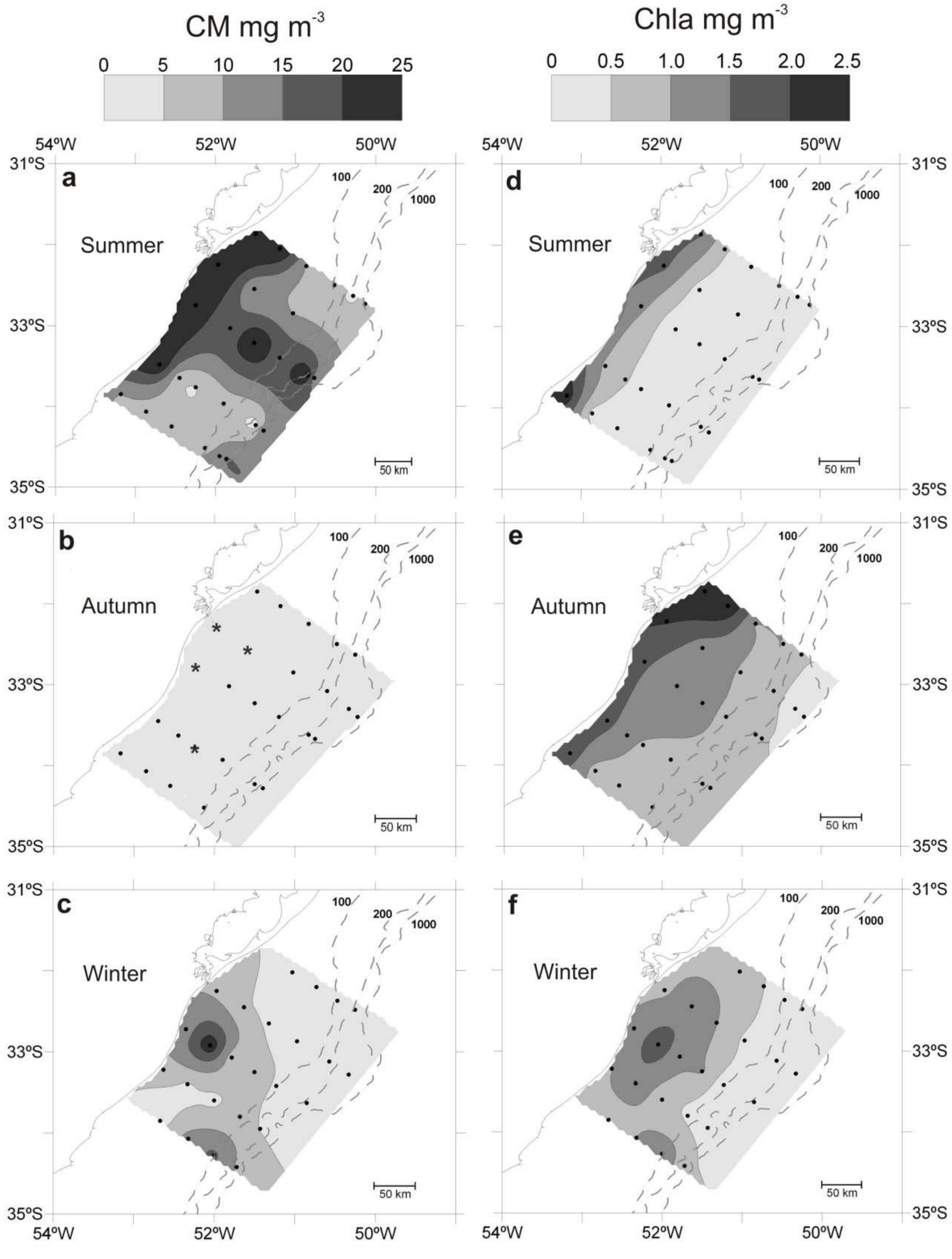

Fig.4. Horizontal distribution (0-25 m) of zooplankton biomass (CM) (a, b, c) and chlorophyll (Chl-*a*) (c, d, e) in summer, autumn and winter. Star sign (*) in the autumn (b) shows the sampling stations where the highest CM values (3 to 4.8 mg C m^{-3}) were found.(Isobaths in meters).

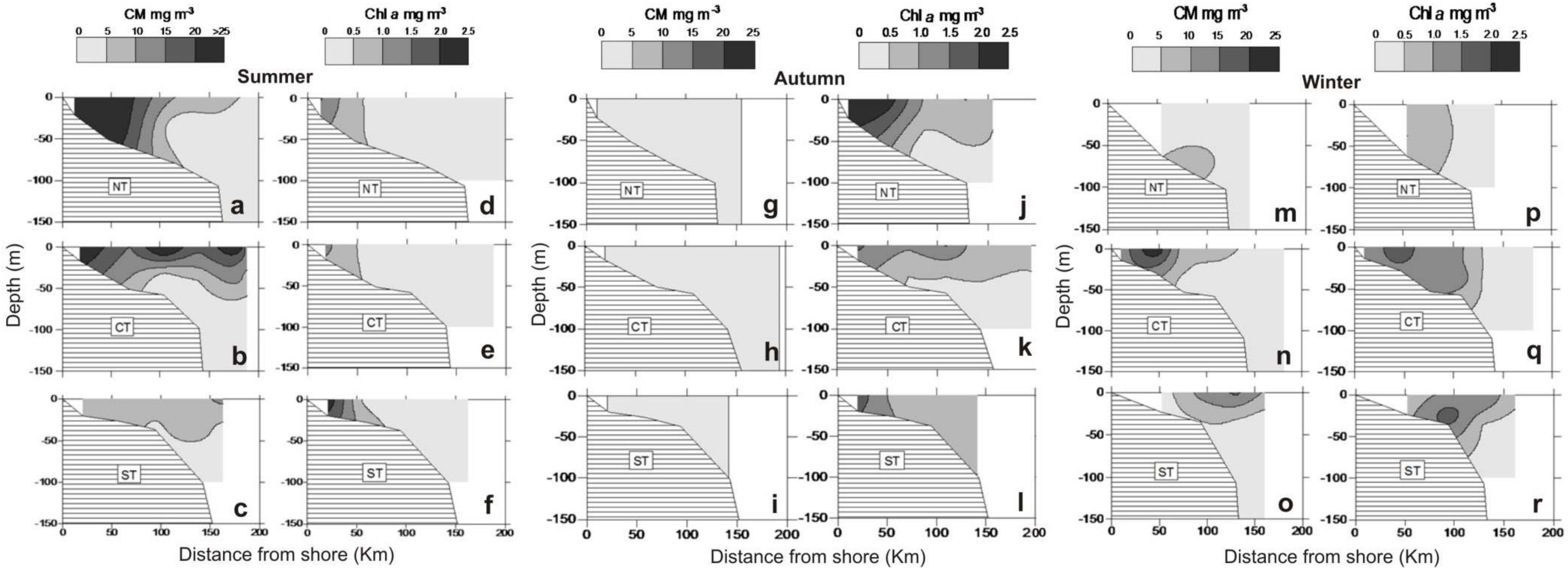

Fig.5. North (NT), Central (CT) and South (ST) onshore-offshore transects of zooplankton biomass (CM) and chlorophyll (Chl-*a*), respectively, in summer (a, b, c / d, e, f), autumn (g, h, i / j, k, l) and winter (m, n, o / p, q, r).

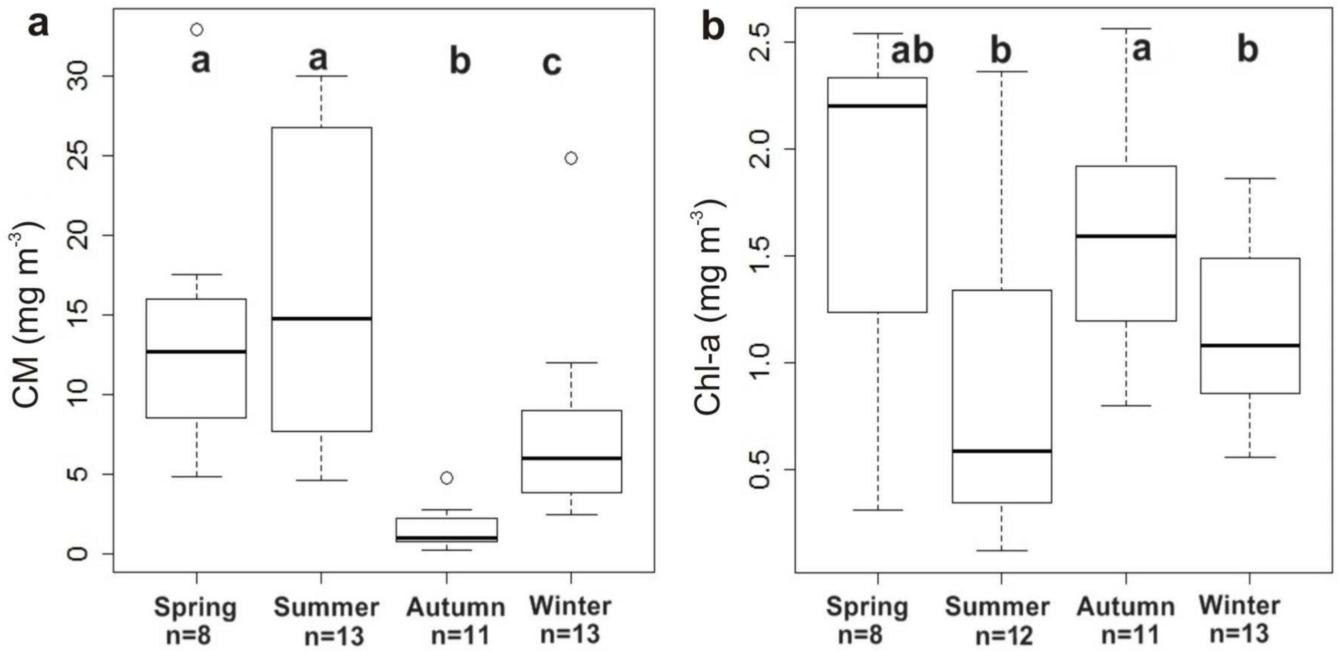

Fig.6. Box-plot of the Kruskal-Wallis test for values of CM (a) and Chl-a (b) in the coastal zone in the four seasons. The boundaries of the rectangles indicate the 25th and 75th percentiles, and the horizontal bars indicate the median. The dotted vertical bars indicate upper and lower distribution limits. The circles in (a) are extreme values, outside the distribution (outliers).

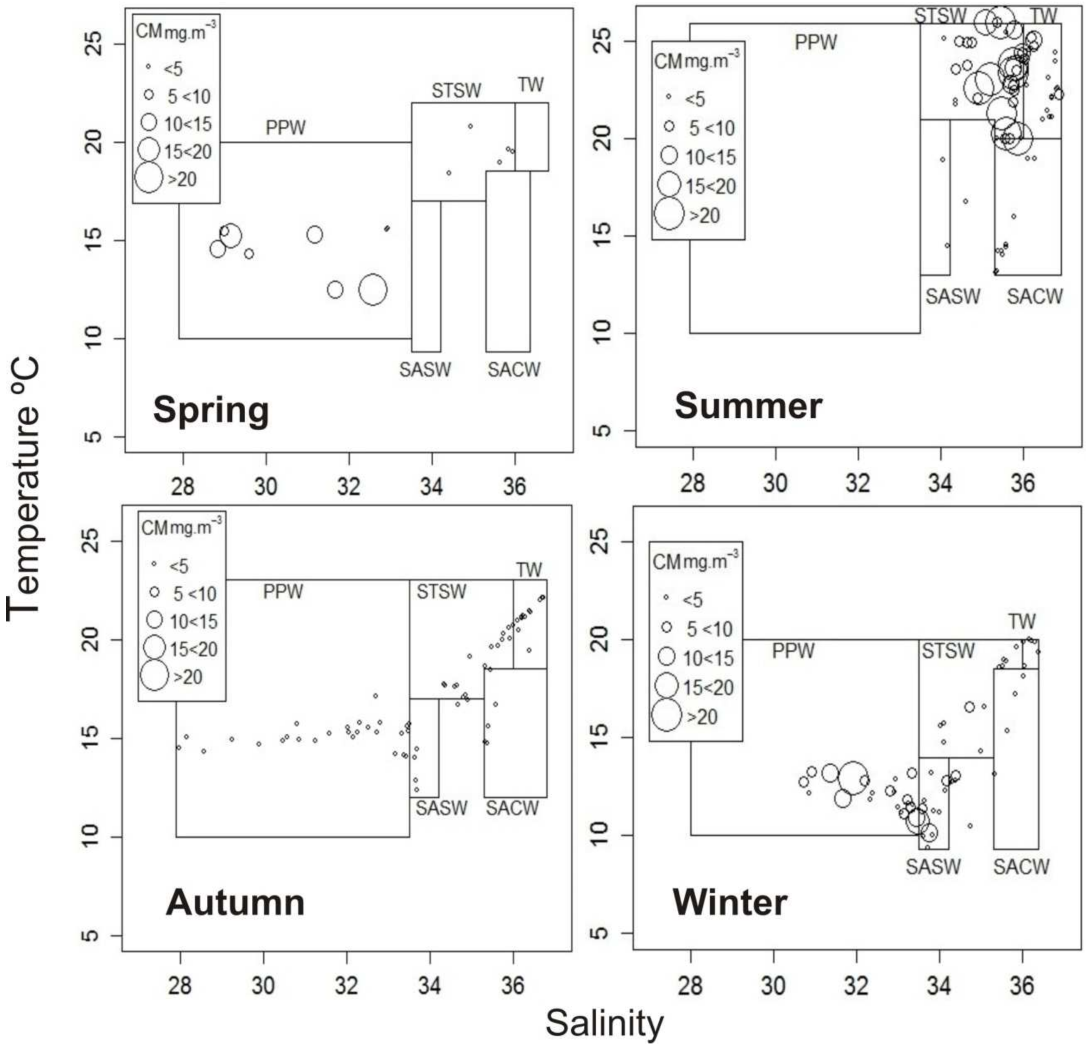

Fig.7. Temperature, salinity and zooplankton biomass diagrams (TSZ) for spring, summer, autumn and winter. Rectangles indicate each water mass according termohaline indexes on Table 1. PPW: Plata Plume Water, SASW: Subantartic Shelf Water, STSW: Subtropical Shelf Water, SACW: South Atlantic Central Water and TW : Tropical Water.

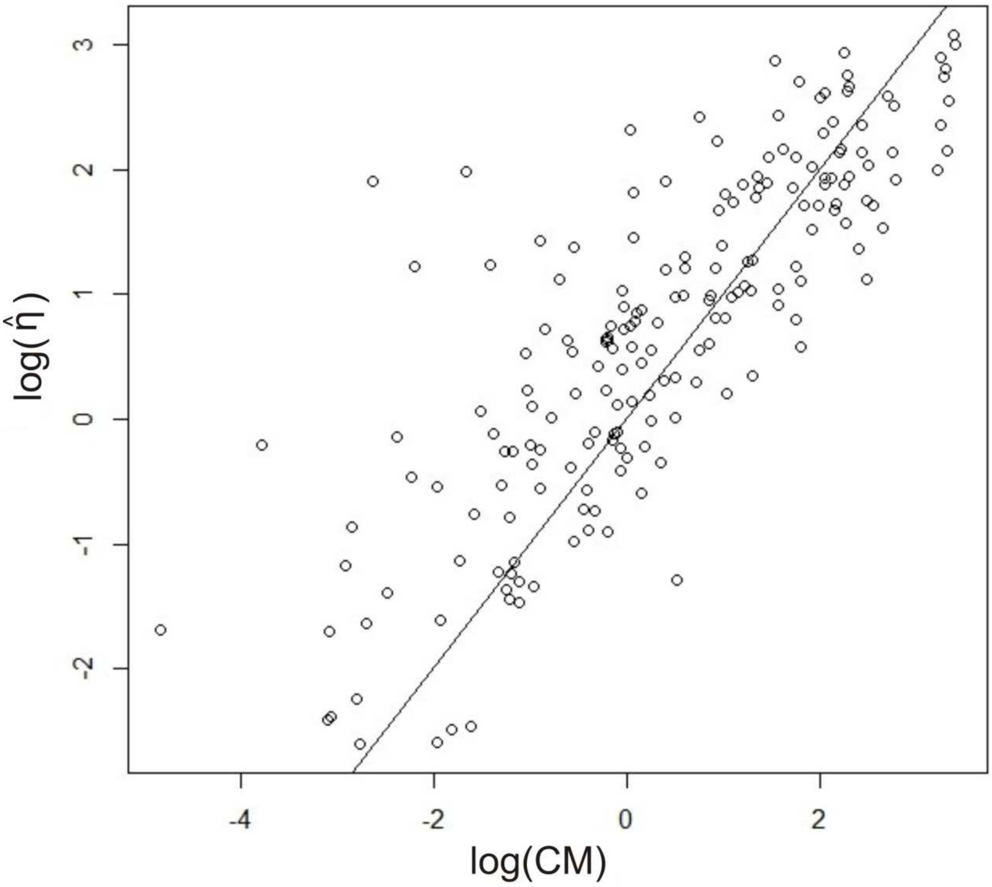

Fig.8. Fitted model that compares the log (CM) observed with the values estimated in the GLM analysis. The correlation is linear, r = 0.814.

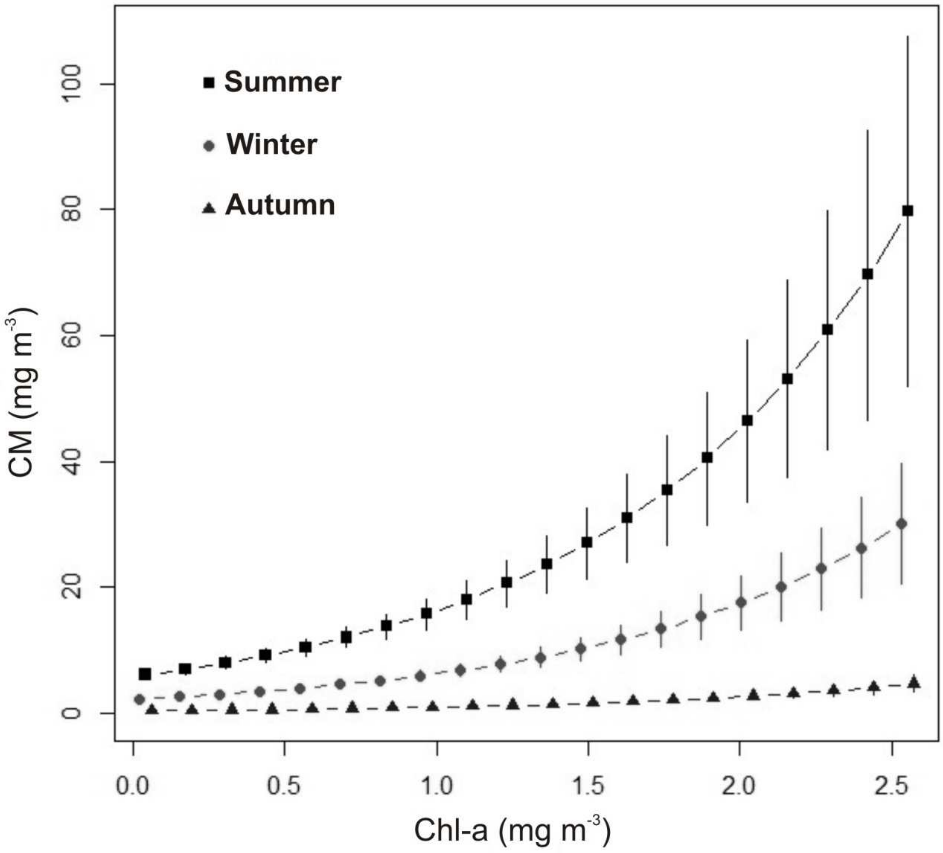

Fig.9. Predictive model indicating the possible effects of increased Chl-*a* over CM values in summer, winter and autumn, according to the GLM analysis. Vertical lines are the prediction intervals of 95% for the mean value of response (y) for each value specified on the axis (x).

ANEXO II

Copepod assemblage in a subtropical shelf region of the Southwestern Atlantic Ocean and relationships with environmental factors.

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Abstract

Copepods are frequent and abundant organisms in the seas and oceans. They present variable sizes, and the abundance and composition of the small sized species are generally underestimated. The Oncaeidae and Oithonidae families constitute numerous and diversified groups of marine microcopepods, that appear to be the main consumers of phytoplankton, and major participants in the microbial loop. Considering the importance of the copepods, and the lack of knowledge about small sized species, the purpose of the present study is to evaluate horizontal and vertical distribution, abundance and influence of the different water masses on the composition and associations of species smaller than 150 µm and their feeding, in order to establish their role in the ecological processes of the pelagic ecosystem in the south of Brazil. The data were obtained in the continental shelf (31º 40´ S and 34º 45´S), and the zooplankton samples were collected with a WP-2 net fitted with 150 µm mesh size. One hundred and fifteen copepod species were found in this region, comprising 63 to 100% of the zooplankton. Many species were widely distributed and were present at all times of the year. During summer, we observed a higher number of species and abundance (about 34 000 ind. m^{-3}). The small species of *Oncaea* and *Oithona*, were numerous in summer, and species of Calanoida in winter. Copepodits were present and abundant in all seasons. The highest of abundance occurred in coastal and superficial waters, generally related with coastal and cold waters. The copepods were abundant in Southern Brazilian Shelf, and they play an important role in the flow of matter and energy, contributing to the maintenance of large fish stocks in this region.

Key words: copepods, Calanoida, Cyclopoida, abundance, continental shelf, water masses, vertical distribution.

Introduction

Copepods (Crustacea, Maxillopoda) are frequent and abundant organisms in the seas and oceans comprising a large amount of biomass, between 55 and 97% of the metazoan plankton (Bradford-Grieve et al., 1999, Thompson et al., 2013), They are the most numerous multicellular organisms on Earth and there are probably more of them than insects worldwide (Mauchline, 1998; Huys and Boxshall, 1999; Schminke, 2007). Copepods are recognized as the main primary consumers in the seas (Raymont, 1983; Skjoldal *et al.*, 2000**;** Miyashita *et al*, 2009), and they are vital in the initial feeding phases of fish larvae (Lenz 2000; Skjoldal *et al.*, 2000). Besides fishes, they feed planktonic, benthic and pelagic invertebrates (Brandini *et al.*, 1997; Skjoldal *et al.*, 2000), and are efficient agents transforming and transporting organic matter into deep waters through their fecal pellets, a relevant process as a source of energy for detritivores (Huys and Boxshall, 1991) and decomposers (Zervoudaki et al., 2007).

The abundance and composition of the smaller sized species are generally underestimated, since the plankton nets used in most studies, with a mesh between 200 and 300 µm, select the larger fraction of zooplankton, while the smaller fraction is less known (Böttger-Schnack, 2001; Gallienne and Robins, 2001; Turner, 2004). The Oncaeidae family, constitutes one of the most numerous and diversified groups of marine microcopepods, recent studies have revealed new species (Böttger-Schnack, 1999, 2001, Böttger-Schnack et al., 2001). The small copepods appear to be the most numerous and main consumers of phytoplankton, and major participants in the microbial loop as predators of bacterioplankton and heterotrophic protists, besides being the prey of the ichthyoplankton and other pelagic carnivores (Turner, 2004; Zervoudaki et al., 2007).

Gallienne and Robins (2001) estimated that < 10% of the mesozooplankton (0.2-20 mm) is captured with conventional 200 µm mesh nets, which would lead to serious implications for the estimates of biomass, secondary production, fluxes of matter and modeling the ecosystem dynamics. These authors suggest that the genus *Oithona* species are the most important copepods of all oceans. In the Western South Atlantic Ocean in Argentine waters, this genus contributes over 73% of the total biomass and it is more important in oceanic waters. (Thompson et al., 2013).

The distribution and diversity of the copepod species are related to the local depth, the trophic state of the area and temperature regime (Lenz, 2000). In tropical and subtropical regions, there is greater diversity than in the extreme environments such as polar zones and brackish coastal waters. Due to the marine currents, many species present a broad geographic distribution within the climate boundaries. Regionally, salinity and temperature gradients related to the water masses also define the composition and abundance of the species and zooplankton assemblages (Hoffmeyer, 2004; Berasategui *et al.,* 2006). Many copepod species present a vertical distribution related to the season of the year and stage of development (Besiktepe, 2001). Paffenhöffer and Mazzocchi (2003) suggested that the vertical distribution of each species is related to the combination of its dietary behavior, environmental temperature and predation, but this zone is flexible due to the combined effects of these variables. However, the most numerous species present a higher concentration of individuals on the surface without apparent vertical migration (Wisser et al., 2001; Escribano, 2006).

In the continental shelf region, in the extreme South of Brazil, except for foreign expeditions that collected a few samples, studies on the occurrence and distribution of copepods began with Gaudy (1963). The first distribution survey with taxonomic details on the copepods was presented by Björnberg (1963), Meneghetti (1973; 1975) and Navas-Pereira (1973), who described the distribution of zooplankton groups including copepods. In the atlas on zooplankton (Boltovskoy (1981; 1999), there is information on the taxonomy and distribution of copepods on the entire Atlantic coast of South America and Africa, including the South of Brazil and the Antarctic.

Montú *et al.* (1997) listed about 150 copepod species in the extreme South of Brazil, a much greater number than those of the other zooplankton groups. Other studies have revealed new occurrences and new species such as *Oncaea waldemari* (Bersano and Boxshall, 1994), one of the main epipelagic copepods in several areas of the Atlantic Ocean and the Mediterranean Sea (Böttger-Schnack, 2001).

Most studies on copepods in southern Brazilian waters were performed based on collection using 300 µm mesh plankton nets. With this type of net, it was found that the composition and density of copepods vary throughout the year in the region where this study was performed, and the influence of fresh water from the Plate Plume Water is stronger during the wintertime than in summer (Muelbert *et al*., 2008). The presence and distribution of Calanoida copepods was related to the seasonal patterns of the water masses, suggesting a few bioindicator species (Bruno, 2009) such as *Temora stylifera* and *Clausocalanus furcatus* in warm waters, and *Calanoides carinatus* and *Ctenocalanus vanus* in cold waters.

According to Lopes (2007), the fauna surveys in Brazil should be directed at the less well known taxa and sites, and, to the study of processes involved in understanding of mechanisms that rule the distribution of the organisms and interactions with the physical environment. As regards pelagic environments, discernment of water masses and current distribution, fronts and upwelling is necessary to interpret plankton distribution patterns (Boltovskoy, 1999). In the Southwest Atlantic Ocean, marine fronts are common and cover different space and time scales due to freshwater discharges, ocean currents and the action of wind (Soares and Möller, 2001; Acha et al., 2004).

Considering the importance of the copepods as one of the main components of zooplankton, and that the small size fraction is not well known, the purpose of the present study is to evaluate horizontal and vertical distribution, abundance and influence of the different water masses on the composition and associations of species captured by nets with 150 µm, and also their feeding, in order to establish their role in the ecological processes of the pelagic ecosystem in the south of Brazil.

Material and Methods

Data

The data in this study were obtained from 81 oceanographic stations located on the continental shelf of the Southern Brazilian Shelf between 31º 40´ S and 34º 45´S from the coast (~20m depth) approximately to the 1 000 m isobath (Fig. 1), aboard the R\V Atlântico Sul, within the scope of the Study of the Pelagic Ecosystem of the Extreme South of Brazil (ECOPEL project). Samples were collected between September 07 and 15, 1988; February 06 and 21, 1990; and June 18 – July 02, 1991. These periods characterize the winter, summer and autumn seasons, respectively, according to the distribution patterns of temperature and salinity (Soares and Möller Jr., 2001).

The zooplankton samples were collected with a WP-2 net fitted with 150 µm mesh size, 60 cm diameter at the mouth, equipped with a flow meter and closing device. A total of 27 stations were sampled each season and comprised 72, 69 and 68 samples in summer, autumn and winter, respectively, The tows were vertical in five onshore-offshore transects, in the 0-25m, 25-50m, 50-100m, 100-200m and 200-500m strata. The last two strata (>100m) presented low organism density, and the average values were considered in nMDS analyses (see below).

After collection, 50% of the sample volume was preserved in 4% formaldehyde-seawater solution buffered with borax (Steedman, 1976) for the taxonomic composition study. The remaining volume was preserved for carbon analysis as described by Duarte et al. (subm.) Subsamples of 2.5–25% of the original sample were counted and organisms identified according to the main groups. Adult copepods were identified to the lowest possible taxonomic level following Björnberg (1981) and Bradford-Grieve et al. (1999). The type of feeding was determined according to Mauchline (1998) and Bämstedt *et al.* (2000).

The temperature and salinity data were obtained *in situ* at standard depths (5, 10, 20, 30, 50, 75, 100, 150, 200, 300, 400 and 500m) by a Sensordata CTD (model 200), and reversing thermometers attached to Nansen sample bottles and KAHLSICO salinometer. Water samples were obtained for chlorophyll-*a* (Chl-*a*) analysis at the same intervals up to 100 m, with plastic containers on the surface and Niskin bottles (3 L) at different depths. The Chl-*a* content was determined by fluorimetric analysis (see details in Ciotti et al., 1995). The water masses were classified according to thermohaline indexes (Piola et al., 2000; Assef et al., 2009) and the frequency of occurrence of each water mass was estimated, considering their presence at each depth stratum.

Biodiversity Indexes

The richness of species and biodiversity were estimated using Simpson and Shannon-Wiener indexes (Margalef, 1995).

In brief, the Simpson biodiversity index 1 - *l'*, and $l'=\sum_{i=1}^{z}\left(\frac{N_i}{N}\right)^2$ where N_i= number of individuals of the species in the sample and N= number of individuals in the sample. The Shannon-Wiener biodiversity index (*H'*) is noted as $H=-\sum p_i \log_2 p_i$, where $\sum p_i = 1$, p_i= the number of individuals of the species in all samples divided by total of individuals of each species and in all samples.

Statistical Analysis

Relationships between density and distribution of copepods, with the seasons, depth strata and regions of the continental shelf, and with the Chl-a content, temperature, salinity, water masses and zooplankton biomass (CM) were evaluated using nonparametric statistical tests and multivariate techniques to establish the possible influence of environmental factors on species associations.

The individual linear Spearman correlation indices, linear regressions, and respective statistical significance were obtained in BioEstat and Sigmaplot.The Kruskal-Wallis test with Dunn's posteriori (non-parametric ANOVA) was employed to detect significant differences among averages. All additional analyses were performed in Excel, R, BioEstat or Sigmaplot software.

The correspondence analysis, a non-hierarchical model of differences and similarities, was based on a matrix of log transformed organism density [Log (density+1)] at each sample for those species with occurrence frequency higher than 10% in, at least, one of season, and for nauplius and copepodits. The correspondence analysis was completed with the function 'ca' available in the R software library (Nenadic and Greenacre, 2007).

Copepod distribution patterns were investigated using multivariate statistics analysis by means of a similarity matrix (Bray-Curtis) of density data (ind. m^{-3}) transformed into square root. The non-metric Ordination Analysis (nMDS - Multi Dimensional Scaling) aimed to evaluate the following factors: season (summer, S; autumn, A; winter, W), shelf regions (coastal shelf, C, isobath < 50m; intermediate shelf, I, 50 - 100 m depth; external shelf, E, > 100 m), and depth strata (0-25m, 25-50m, 50-100m, > 100 m), by Analysis of Similarities, ANOSIM ($p < 0.05$) (Clarke and Warwick, 1994). This technique has been proved appropriate for designing groups with a distinct community structure in a large number of ecological studies (Clarke and Warwick, 1994).

The SIMPER test (similarity percentages) was used to identify the species that most contributed to similarities within groups.

Results

Temperature, salinity and water masses

Water temperature ranged between the minimum of 4.85 ^{0}C in winter and maximum of 26.27 ^{0}C in summer; salinity presented a minimum of 26.5 in spring, and maximum of 37.05 in summer. Thermohaline indexes allowed classifying five water masses: Plata Plume Water (PPW), Subantarctic Shelf Water (SASW), Subtropical Shelf Water (STSW), South Atlantic Central Water (SACW) and Tropical Water (TW), present in all seasons but with different occurrence frequencies.

In summer the STSW was dominant (48%), followed by the TW (29%) and the SACW (20%); SASW was restricted to 3% of samples and PPW was not present. In autumn the PPW was the most frequent (36%) followed by STSW and TW (25%, each), whereas in winter PPW and SASW (32%) were most frequent, STSW (16%) and SACW and TW (10% each).

Species composition and abundance

The copepods comprised between 63 and 100% of the zooplankton, generally more than 82%, increasing from summer to winter, when they reached almost 100% in the strata >100 m, in all water masses, except for PPW. Other groups included all the way from cnidaries (Siphonophora and Hydromedusae) to vertebrates such as fish larvae, and the most represented in decreasing order of density and density and occurrence frequency (O.F.) were: Pteropoda, Larvacea, Chaetognatha and Cladocera in summer; Cladocera, Chaetognatha, Larvacea and larvae of Gastropoda and Bivalvia (meroplankton) in autumn, and Gastropoda and Bivalvia, Pteropoda, Larvacea and Cladocera larvae in winter.

One hundred and fifteen copepod species were found in the region of the study (Table 1). A total of 91, 68 and 60 species occurred respectively in summer, autumn and winter. Many species were widely distributed and were present at all times of the year, and some occurred only during one of the seasons.

Most of the species found belong to the Calanoida (70) and Cyclopoida (36) orders, and a few to Harpacticoida (09). Despite the smaller number of the Cyclopoida species, they were more abundant than the Calanoida in summer and autumn (max. 15 059 ind. m^{-3}, summer); in winter Calanoida presented higher density (max. 4011 ind. m^{-3}) (Table 2; Fig. 2). The percentage of Cyclopoida contribution was lower in winter (12%) compared to summer (40%) and autumn (39%), while Calanoida increased from summer (11%) to winter and autumn (20%) (Fig.3). Harpacticoida was not much represented, between 0.5% in summer and 6% in winter. The larvae (copepodits and nauplii) dominated in density in summer and autumn, and percentagewise in winter, with a greater contribution of copepodits.

In summer the most frequent species (O.F. >60 %) (Table 1) were O*ithona similis, O. nana, O. plumifera, Oncaea* spp., *Calocalanus pavoninus, Clausocalanus furcatus* and *Temora stylifera*, followed (O.F. ±50 %) by *Acartia danae, Corycaeus giesbrechti, Farranula gracilis, Mecynocera clausi* and *Microsetella rosea*. In autumn, O*ithona similis* and *Oncaea* spp. were most frequent (O.F. >60 %) and in winter O*ithona similis* and *Calanoides carinatus* (O.F. >60 %), and *O. nana, O. plumifera, Paracalanus quasimodo* and *Ctenocalanus citer* (O.F. ± 50 %) (Table 1). These species also presented in general the highest density values. O*. similis* was the species with the highest O.F. in all seasons of the year (79, 83 and 88%, in summer, autumn and winter, respectively) and *Oncaea* spp. presented the highest density or organisms (10 824 ind. m^{-3}) in summer in the coastal area (#59). The mean density of the copepods diminished about one hundred times from the surface (0-25 m) to the fifth stratum (> 200 m) (Table 2), while the number of species diminished about two-fold (Table 3). There was a greater number of species on the external shelf, especially in summer in STSW and TW, and smaller in SASW in autumn (Table 2).

The copepodits were present at a high density in 100% of the summer samples (max. 15 096 ind. m^{-3}) in STSW, and in winter (max. 10 877 ind. m^{-3}) in PPW, and in 95 % of samples in autumn on the contrary of nauplii, with low density values and occurrence frequencies (O.F.: 85 % in summer; 7 and 1.5 %, in autumn and winter, respectively) (Table 1). Therefore, it is clear that the net mesh size (150 µm) was large to collect nauplii and probably also the first copepodits stages.

As to the number of species and their occurrence frequencies (O.F.) at the different times of year and in the water masses (Fig. 4), in summer a large number of species presented an O.F. of up to 50%, but most were less than 10%. The water masses with highest species numbers were STSW and TW, and lower in SASW. In autumn and winter most species were present up to 50%, with little difference in each category. STSW, SASW and PPW were the masses with the highest contribution in winter, while SASW and SACW presented the smallest species numbers in autumn.

Copepod diversity

As expected, the copepod diversity trend was opposed to that of abundance, and the highest values coincided with water masses, depth strata and continental shelf areas where the density of organisms was smallest. The Shannon–Wiener diversity (*H*') varied from 3.05 to 3.82 and the Simpson index from 0.62 to 0.77 in the seasons (Fig. 5; Table 4), with higher values in autumn and summer, and lower in winter. However, considering the mass of water, depth strata and shelf region, these values were lower (*H*'= 2.02, TW, winter) or higher (*H*'= 4.18, fifth stratum (>200 m, summer). High diversity was found in

SACW in summer, in TW in autumn, and PPW and SASW in winter. The diversity increased with depth during summer, with the highest values in the strata >200 m, related to SACW, and high in autumn and winter in the second stratum (25-50 m), associated with SASW. The highest values were observed on the external and intermediate shelf in summer, on the intermediate shelf in summer, and on the coastal and intermediate shelf in winter.

Copepods feeding

Most of the species present in the study area feed by microphagy, which comprises herbivory and omnivory. However, considering the copepods density, the macrophage individuals predominated in summer and autumn and the microphages in winter, when the Calanoida and microphage copepodits were dominant. Few species of Calanoida are macrophages (carnivores) and occurred in winter (*Euaetideus giesbrechti*, *Metridia gerlachei* and species of *Heterorabdus* and *Pleurommama*) and in summer (C*andacia curta* and species of *Lubbockia* and *Lucicutia*) at a depth of >100 m. Among the Cyclopoida, the *Corycaeus* and *Oncaea* species are macrophages and the *Oithona* are microphages. These three genera were the main Cyclopoida in terms of species number, density of organisms. The occurrence frequency of macrophage individuals in summer and autumn was due to the dominance of Cyclopoida, above all *Oncaea* spp. Most of the Harpacticoida appear to be macrophages, but their dietary aspects are less well known.

Copepods and environmental factors

The correlation analysis (Spearman) between copepod density and biotic (Chl-a content, zooplankton biomass) and abiotic factors (temperature, salinity, local and collection depth, latitude and longitude) resulted in significant relations ($p<0.0001$; $R^2= 0.3801$) with the local depth ($R^2= 0.\ 1198$), depth stratum ($R^2= 0.125$) and longitude ($R^2= 0.1721$), which most contributed to explain the density values. No significant relations were found with temperature, salinity, latitude or Chl-a. A significant correlation was found ($p<0.0001$) between the nauplii, copepodits and adult copepod density values, which was greater between the copepodits and the adults ($R^2= 0.7319$). The density values of the copepods and zooplankton biomass (CM) were correlated and the multiple linear regression analysis between these values found a highly significant relationship ($p<0.0001$; $R^2 = 0.5625$), indicating that, generally, the copepods comprised more than 56% of the zooplankton biomass.

The Canonical Correlation analysis, considering the abiotic variables + Chl-a, and the density of copepods, copepodits, nauplii, and the zooplankton carbon biomass, resulted in a highly significant relationship with a canonical R of 0.686 ($R^2= 0.4706$, $p=0.0001$), indicating that about 50% of the variation of the copepods and of the biomass of which they comprise the largest part, were explained by abiotic environmental factors and Chl-a.

The nonparametric Analysis of Variance, ANOVA (Kruskal-Wallis – Dun a posteriori) pointed out as highly significant ($p<0.001$) the effect of depth on the total density of copepods in the water column. The highest densities were generally found in the first (0-25 m) or second (25- 50 m) stratum, depending on the region of the shelf and time of the year. Moreover, the shelf region (coastal, intermediate and external) showed a significant relationship ($p< 0.001$) with copepod density, except in winter.

The influence of water masses on the copepod density was evident, with differences in the density values of the adult copepods (p< 0.001), copepodits (p = 0.004), and *nauplii* (p <0.001) in the different water masses. According to this analysis, there are similarities between the PPW, SASW and STSW water masses, which are different from the TW and SACW.

The influence of the water masses on the composition of copepod species was found through the Analysis of Correspondence (Fig.6). The water masses that were most similar in terms of density and occurrence frequency of the species are plotted closer together, enabling to distinguish the species associated with certain water masses from those that transit freely between two or more masses. It is also possible to observe the association, by proximity, between species and between water masses (Fig. 6; Table 5). In summer, *T*. stylifera was strongly associated with STSW, as well as *P. aculeatus, U. vulgaris* and *O. hebes*; while *O. venusta, A. negligens, F. gracilis*, and *M. clausi* were associated with TW. *C. australis*, from cold waters, was related to SASW. In autumn, with the increased influence of cold waters, *C. carinatus, E. acutifrons, P. parvus, C. velificatus, C. vanus, C. citer* and *P. parvus* were associated with PPW and SASW. Some species that were common in summer were associated with warm waters (STSW and TW). During winter, *C. carinatus, P. quasimodo, P. parvus, O. nana,* and *E. acutifrons,* were associated with PPW; and *C. australis, C. carinatus, O. similis, C. parapergens*, *P. parvus* and *P. quasimodo* with SASW. The warm waters of the external shelf region were associated as follows: *M. rosea* with TW,and *O. plumifera, M. clausi, C. pavoninus* with SACW (Table 6).

A few associations are noteworthy, such as between *P. parvus* and *P. quasimodo* and between *C. australis* and *C. vanus*, strongly associated with each other and with STSW in summer. The cold water PPW and SASW were associated by sharing species, as well as the warm waters TW and SACW. STSW shows an association with TW and SACW only in autumn.

Copepod assemblages

The ordination analysis of samples with a non-metric Multidimensional Scaling (nMDS) distinguished ecological groups based on taxonomical similarities in each season of the year, regions of the shelf and depth strata (ANOSIM, $p<0.05$) (Fig. 7 a, b, c, d, e). The characteristic species in each season in the shelf regions and depth strata are recorded in Table 6.

The seasons, summer (S), autumn (A) and winter (W) presented a significant difference (Global R =0.409; p =0.001) when compared in pairs. The species that contributed most to these differences (($p<0.05$) between summer and autumn (average dissimilarity 89%, SIMPER) were *Oncaea* spp. (18.4%), *Oithona similis* (8.5%) and *Clausocalanus furcatus* (5.8%); between summer and winter (average dissimilarity 90.89%, SIMPER) were *O. similis* (14.5%), *Oncaea* spp. (14.2%) and *O. nana* (6.3%); and between autumn and winter (average dissimilarity 86.16), *O. similis* (25%), *Oncaea* spp. (7.1%) and *Paracalanus quasimodo* (5.3%). The species that most contributed to the similarity between seasons, besides those common to all seasons, *O. similis* and *Oncaea* spp., were *C. furcatus, O. nana, T. stylifera* and *C. giesbrechti*, during the summer; *Paracalanus* spp. and *C. vanus* in autumn, and *P. quasimodo, O. plumifera, O. nana*, *C. brevipes* and *C. carinatus* in winter (Table 6).

Analyzing each season separately a significant difference was found ($p<0.05$) between the regions of the continental shelf (coastal, intermediate and external shelf). In summer (Global R = 0.2729; p=0.001) the species that contributed most to the difference between the coastal and external shelf ((average dissimilarity 82%, SIMPER) were *Oncaea* spp. (12.18%), *O. nana* (7.7%), *O. waldemari* (5.6%) and *Corycaeus giesbrechti* (5.0%); between the coastal and intermediate shelf (average dissimilarity 68%), were *Oncaea* spp. (14.5%), *O. nana* (6.4%), *O. waldemari* (6.2%), *P. quasimodo* (5.0%); and between the external and intermediate shelf (average dissimilarity 74%), *Oncaea* spp. (10.3%), *O. nana* (6.8%), *C. furcatus* (5.2%) and *Temora stylifera* (5.0%). The species that contributed most to the characteristic associations of each region were: in the coastal shelf *O. nana, Oncaea* spp. and *T. stylifera*; in the intermediate shelf, *Oncaea* spp., *O. similis* and O. *nana*, and in the external shelf, *C. furcatus, O. similis* and *Oncaea* spp. (Table 6). The depth strata were also different (p<0.05, SIMPER) between the first (0-25 m) and the second (25-50 m), third (50-100 m), and fourth (>100 m), and between the second and fourth stratum.

In autumn (Global R = 0.297; p=0.001) the species that contributed most to explain the differences (p<0.05) between coastal and intermediate shelf (average dissimilarity 76%, SIMPER) were *Oncaea* spp. (19.3%), *O. similis* (13.4%), *Paracalanus spp* (9.8%), *Ctenocalanus vanus* (8.3%); between coastal and external shelf (average dissimilarity 90.3%) were *Oncaea* spp. (19.3%), *O. similis* (12.4%), *Paracalanus spp* (9.4%); between intermediate and external shelf (average dissimilarity 84.9%) were *O. similis* (18.5%), *Oncaea* spp. (13.3%) and *Ctenocalanus vanus* (11.7%). The species that contributed most to similarity in the coastal shelf were *O. similis, E. acutifrons* and *Oncaea* spp.; in the intermediate shelf, *O. similis, Oncaea* spp.and *C. vanus*; in the external shelf *Oncaea* spp*., O. similis and M. clausi*. A difference was found (p<0.05, SIMPER) in the depth strata between the first (0-25 m) and the third (50-100m), the first and the fourth (>100 m), and between the second and fourth stratum.

In winter (Global R = 0.379; p=0.001) the species that contributed most to explaining the differences (p<0.05) between coastal and intermediate shelf (average dissimilarity 73%, SIMPER) were *Euterpina acutifrons* (11.6%), *O. similis* (11.0%), and *O. nana* (9.5%); between coastal and external shelf (average dissimilarity 85%), *E. acutifrons* (12.8%), *O. nana* (9.5%) and *P. quasimodo* (9.2%); between external and intermediate shelf (average dissimilarity 69%), *O. similis* (14.6%), *C. brevipes* (8.7%) and *P. quasimodo* (8.2%). The species that contributed most to similarity in the coastal shelf were *E. acutifrons O. nana* and *O. similis;* in the intermediate shelf, *O. similis, P. quasimodo* and *C. brevipes*; in the external shelf*, O. similes, O. plumifera* and *C. pergens*. The first, second and third strata presented a similar composition when compared to the pairs, but different between the first and the fourth (p=0.001) and between the second and the fourth (p=0.037).

In general, a large number of species occurred up to about 100 m but the same species were responsible for the differences due to the different percentages of contribution in each stratum.

Discussion

The species that formed the groups or assemblages of copepods varied according to season, and were related to the predominant water masses, characteristics of the seasonal changes in the Southwest Atlantic Ocean region (warm oceanic/humid subtropical climate). In pelagic environments, discernment of water masses and currents is essential to interpret plankton distribution patterns (Boltovskoy, 1999). The changes in the water masses cause temporal and spatial changes of species, since, due to their planktonic character, the copepods are transported by the ocean current and their distribution is related to the pattern of distribution of the water masses. In the study region five water masses (PPW, SASW, STSW, TW and SACW) occurred in different proportions at the seasons, influencing the species present, their frequency, density and associations. This was found for *E. acutifrons* and *O. nana* regarding PPW, *C. velificatus* and *C. vanus* for PPW and SASW; *C. carinatus, C. australis, P. parvus* and *P. quasimodo* for SASW; *T. stylifera* and *P. aculeatus* for STSW; *O. venusta* and *F. gracilis* for TW and *O. plumifera* and *M. clausi* for SACW.

These species were frequent and numerous at the times of year when the masses with which they are associated were dominant, although they may also be present in another period. For instance *C. carinatus* and *C. simillimus* are characteristic of Antarctic waters, which occur even in summer in the area of this study, transported by SASW.

Bruno (2009) found a similar relation between some species (e.g. *C. vanus, C. carinatus, C. furcatus, T. stylifera)* with water masses and seasons (summer and winter). A consistent relationship between the species and the water masses was found in the Southern Hemisphere in Argentine waters (Berasategui et al., 2006), and further south in the Antarctic zone (Thompson, 2013), and in a high latitude in the Northern Hemisphere NH, in the continental Labrador Shelf (Pepin et al. 2010). Bjönberg (1981) indicated *C. carinatus* as neritic specie in Argentina and upwelling waters in Brazil. In the southeast region of Brazill, Valentin (1989), Lopes et al. (1999) and Esquinazi-Sant'Anna and Björnberg (2006) related the dominant species *C. carinatus* to the upwelling of SACW. Also the main warm water species *T. stylifera, P. aculeatus, C. giesbrechti* and other cold water ones reported by these authors were common further south in the region of the current study. According to Bjönberg (1981), *T. stylifera* and *C. furcatus* are common species in warm oligothrophic waters from coastal and continental shelf.

A significant relationship between the spatial distribution pattern of the species and that of the water masses is observed for species associated with TW more frequent on the external shelf (e.g. *M. clausi*), on the contrary of the coastal ones associated with PPW (e.g. *E. acutifrons, A. tonsa*). The same occurred regarding depth: species associated with STSW (*T. stylifera*) occurred up to a depth of 50 m, while those associated with TW (*O. venusta* and *O. plumifera*) occurred up to about 100-200 m, and with SACW (*M. rosea*) below 200 m. The copepod associations were confirmed in the analyses of ordination nMDS and correspondence, that resulted in differences between seasons (summer, autumn and winter) shelf regions (coastal, intermediate and external shelf), and depth strata, mainly between the surface and the deeper ones. Environmental factors and Chl-*a* contributed about 50% to the variation of copepod density values. Meneghetti (1973) observed a relation between distribution patterns, temporal changes and abundancy, influenced by physical process and reproduction of species.

The wealth of copepod species found (115) was lower than the number reported (149) by Montú et al. (1997) who compiled all the records available until then in the literature. Muelbert et al. (2008) found 25 species and Bruno (2009) 93 Calanoida species for the same region where this study was performed, while, Berasategui et al. (2006) recorded 113 species, further south in Argentine waters. The species diversity increased from the coast to the external shelf and to the deepest stratum as expected for neritic regions, and the values found in this study (3.05 e 3.82) were higher than previously reported by Bruno (2009), between 0.2 and 2.38, and max. 1.8 slightly north of this area (Ávila et al. 2009). The area studied by Muelbert et al. (2008) and Ávila et al. (2009), were smaller than in this study and with fewer sampling stations, which may have influenced the results, since these indexes trend to vary nonlinearly with sample size. The diversity of species in the marine environments is often estimated as between 1 and 4 (Margalef, 1983), and therefore it can be said that this is a region with high diversity. The increasing diversity gradient from the coast to the ocean was the contrary of that found for density, with high and low values in the coastal zone and external shelf, respectively (Fig. 2), similarly as recorded by Muelbert et al. (2008) and Lopes et al. (2006).

The percentage of copepods observed (63 to 100%) is in accordance with the pattern in marine environments (55 a 97%), as well as the fact that most of the species were Calanoida (91) (Raymont, 1983; Mauchline, 1998; Huys and Boxshall, 1991). However, in the present study, the high density of individuals (> 34 000 ind. m^{-3}) must be underlined, the highest copepod value ever recorded in the region had a great contribution from copepodits (max. 15 096 ind. m^{-3}) and *Oncaea* spp. (Cyclopoida; 10 824 ind. m^{-3}). The closest value (21 964 ind. m^{-3}; Bersano, 1994) was reported in a surf zone of Cassino Beach, while other values did not exceed 2 000 ind. m^{-3} (Montú et al., 1997; Muelbert et al., 2008). Mauchline (1998) cited values between 1 000 and 10 000 ind. m^{-3}, the largest for limited periods in certain coastal regions. This significant difference in values may be explained by the mesh of the nets used, between 200 and 300 µm, i.e., up to double what was used in this study. The high density of *Oncaea* spp. and copepodits, the wealth of species of genus *Oithona* and the high frequency of occurrence of *O. similis*, all of them small organisms, result from the collection method used and they are generally underestimated (Böttger-Schnack, 2001; Gallienne and Robins, 2001; Turner, 2004). Gallienne and Robins (2001) suggest that species of *Oithona* are the most important and numerous of the marine ecosystems worldwide, and Thompson et al (2013) also recorded *O. similis* as the species with the greatest occurrence in Antarctic waters in the south of Argentina.

Several small individuals that presented morphological similarities and were difficult to identify were grouped as *Oncaea* spp.*, Corycaeus* spp. and *Oithona* spp, These may include species that have not yet been described, or whose distribution is unknown, such as the small Calanoida *Parvocalanus crassirostris,* recorded for the first time in ECOPEL samples. Also in the Aegean Sea, the small copepods are important (Zervoudaki et al., 2007) and the potential significance of such small copepods in the oceans' pelagic communities and biogeochemical cycles, has been recognized (Paffenhöfer 2001).

The alternance of modes of feeding observed during the seasons of the year, may be related to the type of food available. Most of the species observed are microphages, a habit that predominated in winter because of the abundance of Calanoida. In summer high density macrophage organisms predominate, like *Oncaea* spp. interestingly, because when the carnivores predominated (summer), the percentage of Calanoida and copepodits was lower. According to Mauchline (1998) *Oncaea* species may be predatory to the Calanoida and copepodits species.

The region of the study is favored by the enrichment of nutrients from the continental contributions (Rio de La Plata, Lagoa dos Patos), and from the subantarctic waters (Piola *et al.* 2000; Soares and Möller 2001; Möller *et al.*, 2008; Muelbert *et al*., 2008; Piola *et al.,* 2008), which determine high values of chlorophyll -a and primary production, especially at the end of winter and spring. (Ciotti et al., 1995; Odebrecht and Garcia, 1997; Garcia and Ciotti, 2008). In summer the Chl-a content is low in the region (<4.0 mg m^{-3}) (Odebrecht and Garcia, 1997; Muelbert et al., 2008; Duarte et al., subm.), probably due to the smaller contribution of nutrients during this period (Braga et al., 2008), and to the consumption carried out by the copepods in spring and in the beginning of summer (Muelbert et al., 2008), exercising top down control. The absence of a significant relationship between copepod density and Chl-a does not mean that this is irrelevant, as observed with the presence of many microphage species, preferably herbivores. On the other hand, it may be due to the result of high consumption and of the different timing of microalgae and copepod population development, which makes a direct relationship between these two components difficult to observe. Calbet and Landry (2004) estimated that 67 % of the daily phytoplankton production can be consumed by the microzooplankton, which calls attention to the role of the small species.

Chlorophyll and zooplankton are frequently inversely related (Escribano et al, 2007), and thus, in summer, when there is less phytoplankton available, macrophage species (carnivores) developed their populations possibly by feeding on larvae from benthic organisms and ichthyoplankton, which are numerous at this time of the year in the region (Montú et al., 1997) and on zooplankton itself. In deeper waters (>100 m), the presence of few species of Calanoida and the greater presence of macrophages

(*Oncaea* spp.), coincides with strata that do not have much phytoplankton available. Wisser et al. (2001) and Escribano (2006), emphasize that most of the more numerous species are concentrated on the surface.

The high copepods number found support their major role in pelagic ecosystems, and as important food for several fishing resources, including commercially important fish species. In addition, the high zooplankton biomass, especially in spring and in summer in the study area, is due to its high density of small copepods, which were underestimated in previous studies. Greater effort is needed for the small species to be adequately analyzed and thus to correctly evaluate the role of copepods in the carbon flux.

Copepods are not randomly distributed in the marine environments, but their distributions are related to the water masses on small and large scales. These distribution patterns form assemblages on several simultaneous scales, which are observed in the region of the present study. On a temporal scale they form characteristic summer, autumn and winter associations, while at each season the associations are related to distance from the coast and depth, and these associations are always closely related to the water masses.

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REFERÊNCES

Acha, M., Mianzan, H., Guerrero, R., Favero, M., Bava, J., 2004. Marine fronts at the continental shelves of austral South America. Physical and ecological processes. Journal of Marine Systems 44, 83–105.

Aseff, C.R.C., Garcia, V.M.T., Möller Jr, O. O., 2009. Estudo da variação sazonal na composição físico-química das massas de água da Plataforma Continental do Atlântico Sudoeste entre Mar del Plata (AR, 38º S) e Itajaí (BR, 26º S). M. Sc. Thesis. Universidade Federal do Rio Grande, 100p.

Ávila, T.R., Pedrozo, C.S., Bersano, J.G. 2009. Variação temporal do zooplâncton da Praia de Tramandaí, Rio Grande do Sul, com ênfase em Copepoda. Iheringia, Sér. Zool., Porto Alegre, 99(1):18-26

Bämstedt, U., Gifford, D.J., Irigoien, X., Atkinson, A., Roman, M. 2000. Feeding In: HARRIS, RP, PH WIEBE, J LENZ, HR SKJOLDAL, M HUNTLEY (eds). ICES - Zooplankton Metodology Manual. Academic Press. Chap.8:297-399.

Bersano, J.G.1994. Zooplâncton da zona de arrebentação de praias arenosas, situadas ao sul de Rio Grande, RS. Primavera de 1990, Verão de 1991. Tese de Mestrado. Univ. Fed. do Rio Grande. 163p.

Bersano, J.G.F., Boxshall, G.A. 1994. Planktonic Copepods of Oncaea Philippi (Poecilostomatoida: Oncaeidae) from the waters off Southern Brazil. Nauplius 2: 29-41.

Berasategui, A.D., Menu Marque, S., Gómez-Erache, M., Ramirez, F.C., Mianzan, H.W., Acha, E.M. 2006. Copepod in a highly complex hydrography región. Estuarine, Coastal and Shelf Science, 66: 483-492 BESIKTEPE, S. 2001. Diel vertical distribution, and herbivory of copepods in the south-western part of the Black Sea. Jour. Mar.Syst.., 28:281–301.

Besiktepe, S. 2001. Diel vertical distribution, and herbivory of copepods in the south-western part of the Black Sea. Jour. Mar.Syst.., 28:281–301.

Björnberg, T.K.S. 1963. On the marine free-living copepods off Brazil. Bolm. Inst. Oceanogr., São Paulo 13(1):3-142.

Björnberg, T.K.S. 1981. Copepoda in: Boltovskoy, E. 1981. Atlas del zooplancton del atlantico sudoccidental y métodos de trabajo con el zooplankton marino pp 760-791.

Boltovskoy, D. (ed).1981. Atlas del Zooplankton del Atlantico Sudoccidental y Métodos de Trabajo con el Zooplancton Marino. Mar del Plata, INIDEP. 933p.

Boltovskoy, D. (ed). 1999. South Atlantic Zooplankton. Backhuys Publishers, Leiden, The Netherlands. Vol.1 e 2. 1705p.

Böttger-Schnack, R. 1999. Taxonomy of Oncaeidae (Copepoda: Poecilosttomatoida) from the Red Sea. – I. Eleven species of *Triconia* gen. nov. and a redescription of T. similis Sars from Norweigian waters. Mitt. Hamb. Zool. Mus. Inst. 96:37-128.

Böttger-Schnack, R. 2001. Taxonomy of Oncaeidae (Copepoda, Poecilostomatoida) from the Red Sea. II. Seven species of *Oncaea* s.str. Bull. Nat. His. Mus. Lond. (Zool.) 67 (1): 25-84.

Böttger-Schnack, R., Hagen, W., Schnack-Schiel, S.B. 2001. The microcopepod fauna in the Gulf of Aqaba, Northern Red Sea: Species Diversity And Distribution Of Oncaeidea. Journal Of Plankton Research. Vol. 23(9): 1029-1035.

Bradford-Grieve, J.M., Markhaseva, E.L., Rocha, C.E.F., Abiahy, B. 1999. Copepoda. *In*: D. Boltovskoy (Ed.). South Atlantic Zooplankton. Leiden, Backhuys Publishers, 2: 869-1098.

Braga, E.S., Chiozzini, V.C., Berbel, G.B.B., Maluf, J.C.C., Aguiar, V.M.C., Charo, M., Mollina, D., Romero, S.I., Eichler, B.B.,. 2008. Nutrient distributions over the South western South Atlantic continental shelf from Mar del Plata (Argentina) to Itajaí

Brandini, F.P., Lopes R.M., Gutseit K.S., Spach H.L., Sassi R., 1997. Planctonologia na plataforma continental do Brasil - Diagnose e revisão bibliográfica. FEMAR, Rio de Janeiro. 196p.

Bruno, M.A. 2009. Mesozooplâncton do extremo sul do Brasil com ênfase em Copepoda Calanoida de 1987 a 2007. Tese de Doutorado. Univ. Fed. do Rio Grande, 106 p.

Calbet, A., Landry, M.R. 2004. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. Limnol. Oceanogr 1; 49:51-57.

Ciotti, A.M., Odebrecht, C., Fillman, C., Möller, O.O. 1995. Freshwater outflow and Subtropical Convergence influence on phytoplankton biomass on the southern Brazilian continental shelf. Cont. Shelf Res. 15(14): 1737-1756.

Clarke, K.R., Warwick, R.M.. 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth. 144p.

Escribano, R. 2006. Zooplankton interactions with the oxygen minimum zone in the eastern south Pacific. Supl. Gayana 70:19-21.

Escribano, R., Hidalgo, P., González, H., Giesecke, R., Riquelme-Bugueno, R., Manríquez, K., 2007. Seasonal and inter-annual variation of mesozooplankton in the coastal upwelling zone off central-southern Chile. Progress in Oceanography 75, 470–485.

Esquinazi-Sant'anna, E.M.E., Bjönberg, T.K.S. 2006. Seasonal dynamics of mesozooplankton in Brazilian coastal waters. Hydrobiologia 563:253-268

Gaalliene, C.P., Robins, D.B. 2001. Is *Oithona* the most important copepod e=in the world's oceans? Journal of Plakton Research, Vol. 23(12): 1421-1432.

Garcia, V.M.T., Ciotti, A. 2008. Primary production in the SWAOM region. http//www.skio.peachnet.edu/ meeting/ Primary_Production_SWAOP. Pdf.

Gaudy, R. 1963. Campagne de navière océanographique dans les eaux cotière du Brésil (Janvier-Fevrier 1962) copépodes pélagiques. Rec. Trav. Sta. Mar. Endoume 45:15-42.

Hoffmeyer, M.S. 2004. Decadal change in zooplankton seasonal succession in the Bahía Blanca estuary, Argentina, following introduction of two zooplankton species. J. Plankton Res. 26(2):181-189.

Huys, R., Boxshall. G.A. 1991. Copepod Evolution. The Ray Society, London, 468p.

Lenz, J. 2000. Introduction. In: Harris, R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M. (eds). ICES - Zooplankton Metodology Manual. Academic Press. Chap.1:1-32.

Lopes R.M., Brandini F.P., Gaeta, S.A. 1999. Distributional Patterns Of Epipelagic Copepods Off Rio De Janeiro State, Southeastern Brazil. Hydrobiol 411: 161–174

Lopes, R.M., Montú, M.A., Gorri, C., Muxagata, E., Miyashita, L.K., Oliveira, L.P. 2006 . O zooplâncton marinho na região entre o Cabo de São Tomé (RJ) e Chuí (RS). In: Wongtschowski, C.I., Madureira, L. (Eds). O Ambiente Oceanográfico da Plataforma Continental e do Talude na Região Sudeste-Sul do Brasil. EDUSP, São Paulo. Cap. 5: 265-358.

Lopes, R. 2007. Marine zooplankton studies in Brazil – A brief evaluation and perspective. Anais da Academia Brasileira de Ciências 79(3): 369-379.

Margalef R. 1983. *Limnología*. Omega, S.A. Barcelona.

Margalef, R. 1995; Ecologia. Ediciones Omega, S.A. Barcelona

Mauchline, J. 1998. The biology of Calanoid copepods. Academic Press, 710p.

Meneghetti, J.O. 1973. Zooplankton from southern Brazil–2. Its composition, distribution and density in space and time. Iheringia 43: 100-125.

Meneghetti, J.O. 1975. Zooplankton from southern Brazil-3. Quantitative aspects and seasonal fluctuations of some copepods. Iheringia 47: 47-66.

Miyashita, L.K., Melo, M., Lopes, R.M. 2009. Estuarine and oceanic influences on copepod abundance and production of a subtropical coastal area. J. Plankton Res. 31(8):815-826.

Möller Jr, O.O., Piola. A.R., Freitas, A.C., Campos, E.J.D. 2008. The effects of river discharge and seasonal winds on the shelf off southeastern South America. Cont. Shelf Res. 28: 1607-1624.

Montú, M., Gloeden, I. M., Duarte, A. K., Resgalla, Jr., C., 1997. Coastal and marine environmental and their biota: Zooplankton, in: Seeliger, U., Odebrecht, C., Castello, J.P. (Eds.), Subtropical Convergence Environments. The Coast and Sea in the Southwestern Atlantic, Springer, Berlin- Heidelberg, pp.123-134.

Muelbert, J.H., Acha, M., Mianzan, H., Guerrero, R., Reta, R., Braga, E.S., Garcia, V.M.T., Berasategui, A., Gomez-Erache, M., Ramirez, F.. 2008. Biological, physical, and chemical properties at the Subtropical Shelf Front Zone in the SW Atlantic Continental Shelf. Cont. Shelf Res., 28: 1662-1673.

Navas-Pereira, D. 1973. Análise qualitativa e quantitativa do zooplâncton. entre Torres e Maldonado (Lat. 29ºS - 35ºS). Inst. Oceanogr. Univ. São Paulo. Publ. Esp. 3(1): 29-92.

Nenadic, O., Greenacre, M., 2007. Correspondence analysis in R, with two- and three-dimensional graphics: The ‘ca’ package. Journal of Statistical Software, 20 (3), available at http://www.jstatsoft.org/v20/i03/

Odebrecht, C., Garcia V.M.T., 1997. Coastal and marine environmental and their biota: Phytoplakton. In: Seeliger, U., Odebrecht, C., Castello, J.P. (Eds.), Subtropical Convergence Environments. The Coast and Sea in the Southwestern Atlantic. Springer, Berlin Heidelberg, pp 117-121.

Paffenhöfer, G. A. 2001. Future marine zooplankton research - a perspective. Marine Zooplankton Colloquium 2. MZC 2. Mar. Ecol. Prog. Ser. 222: 297–308.

Paffenhöfer, G.A., Mazzocchi, M.G. 2003. Vertical distribution of subtropical epiplanktonic copepods. J. Plankton Res., 25 (9): 1139-1156.

Pepin, P., Colbourne, E., Maillet, G., 2011. Seasonal patterns in zooplankton community structure on the Newfoundland and Labrador Shelf. Progress in Oceanography, 91, 273-285.

Piola, A.R., Campos, E.J.D., Moller, O.O., Charo, M.,Martinez, C. 2000, Subtropical shelf front off eastern South America, J*ournal of Geophysical Research,* 105, C3, 6566-6578.

Piola, Ar, Moller, O.O., Guerrero, R.A., Campos, E.J.D. 2008. Variability of the subtropical shelf front off Eastern South America: Winter 2003 and summer 2004. Cont. Shelf Res. 28: 1639-1648.

Raymont, J.E. G.1983. Plankton and productivity in the ocean. Pergamon Press. 824p.

Sartori, L.P., Lopes, R.M. Seasonal variability of pelagic copepod assemblages on the Inner shelf off Paraná, Brazil. Nauplius, 2000, vol. 8, no. 1, p. 79-88.

Schminke, H.K. 2007. Entomology for the copepodologist. J.Plankton Res.29: 49-62.

Skjoldal, H.R., Wiebe, P.H., Foote, K.G. 2000. Sampling and experimental design. In: Harris, R.P., P.H. Wiebe, J. Lenz, H.R. Skjoldal, M. Huntley. (eds). ICES-Zooplankton Methodology Manual. Academic Press.Chap2: 33-49.

Soares, I., Möller J.R. Oo. 2001. Low-frequancy currents and water mass spatial distribution on the southern Brazilian shelf. Cont. Shelf. Res. 21: 1785-1814.

Steedman, H F. (Ed). 1976. Zooplankton Sampling. UNESCO. Paris. 160p

Thompson, G.A., Dinofrio, E.O., Alder, V.A. 2013. Structure, Abundance And Biomass Size Spectra Of Copepods And Other Zooplankton Communities In Upper Waters Of The Southwestern Atlantic Ocean During Summer. J. Plankton Res. 35(3): 610–629. First Published online February 26, 2013

Turner, J.T. 2004. The Importance of Small Planktonic Copepods and Their Roles in Pelagic Marine Food Webs. *Zoological Studies* 43(2): 255-266.

Valentin, J.L. 1989. A Dinâmica do Plâncton na Ressurgência de Cabo Frio – RJ. In: Brandini, F.P. (org.). Memórias do III Encontro Brasileiro de Plâncton. Caiobá, Universidade Federal do Paraná, pp.26-35.

Wisser, A.W., Saito, H., Saiz, E., Kiorboe, T. 2001. Observations on copepod feeding and vertical distribution under natural turbulent conditions in the Noth Sea. Mar. Biol. 138:1011-1019.

Zervoudaki, S., Christou, E.D., Nielsen, T.G., Siokou-Frangou, I., Assimakopoulou, G., Giannakourou, A., Maar, M., Krasakopolou, E., Christaki, U., Moraitou-Apostolopoulou, M. 2007. The Importance Of Small Sized Copepods In A Frontal Area Of The Aegean Sea. J. Plankton Res., Vol. 29 No. 4, P. 317-338

Table 1. Composition of copepods during Summer, Autumn and Winter. Feeding Categories (F.C.) of species (M- macrophages; m- microphages). Average density (A.D.- ind. m^{-3}), Standard Deviation (S.D.- ind. m^{-3}), Maximum value (MAX- ind. m^{-3}), Relative Abundance (R.A. %) and Occurrence Frequency (O.F.). The gray rectangles have shown the species which occurred in only one season.

		Summer					**Autumn**					**Winter**				
Species	**F.C.**	**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**	**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**	**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**
Calanoida																
Acartia danae Giesbrecht, 1889	m	3	6	36	0.14	45.83	<1	1	9	0.09	8.70	1	2	12	0.04	14.71
Acartia negligens Dana, 1849	m	<1	<1	2	0.00	1.39	2	6	37	0.61	26.09	0	3	27	0.04	4.41
Acartia tonsa Dana, 1849	m						4	19	156	0.99	17.39	5	26	195	0.45	8.82
Acrocalanus gracilis Giesbrecht, 1888	m	<1	<1	2	0.00	1.39						<1	<1	<1	0.00	1.47
Acrocalanus longicornis Giesbrecht, 1888	m	1	4	32	0.03	5.56										
Calanoides carinatus (Kroyer, 1849)	m	1	3	15	0.03	9.72	1	2	10	0.17	18.84	42	247	2022	3.47	60.29
Calanus australis Brodsky, 1959	m	1	3	20	0.02	6.94	<1	<1	2	0.01	1.45	11	41	321	0.87	47.06
Calanus propinquus Brady, 1883	m											<1	<1	3	0.00	1.47
Calanus similimus Giesbrecht, 1902	m	<1	<1	4	0.00	1.39						3	13	100	0.22	17.65
Calocalanus pavo (Dana, 1849)	m	3	15	117	0.12	19.44										
Calocalanus pavoninus Farran, 1926	m	17	27	123	0.73	66.67	1	4	20	0.35	20.29	1	3	18	0.06	17.65
Calocalanus styliremis Giesbrecht, 1888	m	<1	<1	4	0.00	1.39										
Candacia curta (Dana, 1849)	M	<1	<1	4	0.00	2.78										
Candacia longimana Claus, 1863	M						<1	<1	1	0.00	1.45					
Centropages brachyatus (Dana, 1849)	m	1	7	62	0.05	6.94						3	7	38	0.22	29.41
Centropages bradyi Wheeler, 1899	m											<1	<1	1	0.00	1.47
Centropages velificatus (Oliveira, 1947)	m	16	47	217	0.68	27.78	2	3	14	0.40	24.64					
Clausocalanus arcuicornis (Dana, 1849)	m	<1	<1	<1	0.00	1.39										
Clausocalanus brevipes Frost & Fleminger, 1968	m	2	11	94	0.08	8.33	<1	<1	3	0.02	2.90	26	69	352	2.14	36.76
Clausocalanus furcatus (Brady, 1863)	m	48	69	319	2.00	72.22	2	5	22	0.55	27.54	1	4	25	0.08	5.88
Clausocalanus ingens Frost & Fleminger, 1968	m	<1	<1	<1	0.00	1.39										
Clausocalanus parapergens Frost & Fleminger, 1968	m	<1	1	5	0.01	6.94	<1	<1	2	0.01	2.90	4	12	63	0.32	36.76
Clausocalanus pergens Farran, 1929	m	1	4	21	0.06	25.00	1	2	9	0.17	18.84	3	7	35	0.22	27.94
Clausocalanus sp.	m	<1	2	14	0.01	1.39						<1	<1	<1	0.00	1.47
Ctenocalanus citer Heron & Bowman, 1971	m	10	33	226	0.42	25.00	7	26	196	1.72	20.29	17	36	166	1.38	50.00
Ctenocalanus vanus Giesbrecht, 1888	m	22	69	413	0.93	34.72	2	6	38	0.52	17.39	3	8	45	0.25	29.41
Ctenocalanus spp.	m	2	11	82	0.08	8.33	15	39	208	3.89	39.13	3	11	86	0.22	27.94
Delibus sewelli (Sewell, 1929)	m	4	13	94	0.18	30.56	2	4	30	0.46	33.33	<1	2	15	0.02	1.47

Table 1: Continuation

		Summer					Autumn					Winter				
Species		**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**	**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**	**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**
Drepanopus forcipatus Giesbrecht, 1888	m											<1	1	8	0.03	7.35
Euaetideus giesbrechti (Cleve, 194)	M						<1	1	5	0.02	1.45	<1	<1	<1	0.00	1.47
Euchaeta sp.	M						<1	<1	3	0.01	1.45					
Gaetanus kruppii Giesbrecht, 1893	m						<1	<1	1	0.00	1.45					
Heterorhabdus austrinus Giesbrecht, 1892	M						<1	<1	1	0.01	2.90					
Heterorhabdus spinifrons (Claus, 1863)	M	<1	<1	1	0.00	1.39	<1	1	4	0.04	5.80					
Labidocera fluviatilis F. Dahl, 1849	M											1	4	32	0.05	2.94
Lucicutia clausi (Giesbrecht, 1889)	m						<1	<1	1	0.00	1.45					
Lucicutia flavicornis (Claus, 1963)	m	<1	1	4	0.00	2.78	<1	1	11	0.05	4.35	<1	1	4	0.01	8.82
Lucicutia gaussae Grice, 1963	m	<1	<1	1	0.00	1.39										
Lucicutia sp.	m											<1	<1	<1	0	1.4706
Mecynocera clausi Thompson, 1888	m	5	11	71	0.22	48.61	5	10	49	1.26	44.93	4	14	83	0.32	30.88
Metridia gerlachei Giesbrecht, 192	M											<1	<1	<1	0.00	2.94
Nannocalanus minor (Claus, 1863)	m	1	2	15	0.03	15.28	1	2	16	0.19	18.84	<1	1	8	0.01	5.88
Neocalanus gracilis Dana, 1849	m	<1	1	4	0.01	5.56	<1	1	10	0.07	5.80	<1	<1	<1	0.00	1.47
Paracalanus aculeatus Giesbrecht, 1888	m	2	5	32	0.08	24.95										
Paracalanus indicus Wolfenden, 1905	m	<1	4	31	0.02	1.39										
Paracalanus nanus Sars G.O., 1925	m	<1	1	7	0.01	16.67	1	1	5	0.16	18.84	1	8	68	0.09	2.94
Paracalanus parvus (Claus, 1863)	m	39	130	828	1.66	26.39	10	23	104	2.56	28.99	33	157	1091	2.72	27.94
Paracalanus quasimodo Bowman, 1971	m	46	119	565	1.92	34.72	<1	1	6	0.04	2.90	59	220	1540	4.86	50.00
Paracalanus spp.	m	10	79	667	0.41	4.17	17	41	249	4.32	39.13	5	34	274	0.39	2.94
Paracandacia simplex (Giesbrecht, 1889)	M	<1	<1	1	0.00	1.39										
Paraeucalanus sewelli (Fleminger, 1973)	M						<1	<1	1	0.00	1.45					
Paraeuchaeta spinosa (Giesbrecht, 1893)	M						<1	1	5	0.04	4.35					
Parvocalanus crassirostris (Dahl, 1894)	m	8	45	320	0.33	6.94	2	11	83	0.54	8.70	4	25	202	0.31	5.88
Phaenna spinifera Claus, 1863	M	<1	<1	2	0.00	1.39										
Pleurommama abdominalis (Lubbock, 1856)	m						1	4	33	0.15	5.80					
Pleurommama gracilis Claus, 1863	m	<1	<1	3	0.00	2.78	<1	<1	2	0.01	1.45	<1	1	4	0.01	10.29
Pleurommama piseki Farran, 1929	m	<1	1	6	0.01	8.33	<1	<1	1	0.00	1.45	<1	<1	3	0.01	2.94
Pleurommama robusta (Dahl F., 1893)	m											<1	<1	1	0.00	1.47
Pleurommama xiphias (Giesbrecht, 1889)	m	<1	1	8	0.01	12.50	<1	1	10	0.04	2.90	<1	1	4	0.01	8.82

Table 1: Continuation

		Summer					Autumn					Winter				
Species		**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**	**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**	**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**
Racovitzanus antarcticus Giesbrecht, 192	M											<1	<1	1	0.00	2.94
Scolecithricella bradyi Giesbrecht, 1888	m	<1	<1	<1	0.00	1.39	<1	<1	1	0.01	2.90					
Scolecithricella dentata (Giesbrecht, 1892)	m	<1	<1	<1	0.00	1.39										
Scolecithrix danae (Lubbock, 1856)	m	<1	<1	2	0.00	1.39						<1	<1	4	0.00	1.47
Scolecithrix sp.	m	<1	<1	<1	0.00	1.39										
Scottocalanus securifrons (Scott T., 1894)	m						<1	<1	2	0.01	1.45					
Subeucalanus crassus (Giesbrecht, 1888)	m	1	9	77	0.05	4.17	<1	<1	2	0.01	1.45					
Subeucalanus pileatus (Giesbrecht, 1888)	m	1	3	25	0.02	2.78	1	4	20	0.26	10.14					
Subeucalanus subtenuis (Giesbrecht, 1888)	m	8	34	249	0.35	22.22	2	14	118	0.63	11.59					
Subeucalanus sp.	m											<1	<1	3	0.00	2.94
Temora stylifera (Dana, 1849)	m	48	86	579	2.02	68.06	<1	2	21	0.08	2.90					
Temoropia mayumbaensis T. Scott, 1894	m	<1	<1	3	0.00	2.78										
Undinula vulgaris (Dana, 1849)	m	2	10	67	0.09	13.89	<1	<1	3	0.01	1.45					
Cyclopoida																
Copilia mirabilis Dana, 1852	M	<1	1	5	0.00	2.78										
Corycaeus amazonicus Dahl F., 1894	M	2	9	73	0.09	11.11	7	22	125	1.75	18.84	<1	<1	4	0.00	1.47
Corycaeus dubius Farran, 1911	M	<1	2	19	0.01	4.17										
Corycaeus flacus Giesbrecht, 1891	M	<1	1	4	0.01	6.94										
Corycaeus giesbrechti Dahl F., 1894	M	38	125	969	1.61	48.61	<1	1	8	0.03	1.45	<1	1	9	0.017	2.941
Corycaeus latus Dana, 1849	M	1	7	50	0.06	6.94										
Corycaeus limbatus Brady, 1883	M	<1	1	6	0.01	2.78										
Corycaeus minimus Dahl F., 1894	M	<1	1	6	0.00	1.39										
Corycaeus speciosus Dana, 1849	M	<1	1	5	0.01	11.11										
Corycaeus typicus (Kroyer, 1849)	M	<1	<1	2	0.00	1.39										
Corycaeus spp.	M	35	86	365	1.47	45.83	13	34	194	3.46	50.72					
Farranula gracilis (Dana, 1849)	M	10	20	82	0.41	45.83	1	3	24	0.24	17.39					
Farranula rostrata (Claus, 1863)	M	1	3	11	0.04	23.61										
Farranula sp.	M	1	4	25	0.03	5.56	<1	1	7	0.04	2.90	<1	49	194	4.62	16.00
Halicyclops sp.	M	1	7	56	0.03	1.39	3	22	180	0.77	8.70					
Lubbockia aculeata Giesbrecht, 1891	M	<1	<1	2	0.00	4.17										
Lubbockia squillimana Claus, 1863	M	<1	1	7	0.01	4.17										

Table 1: Continuation

		Summer					Autumn					Winter				
Species		**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**	**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**	**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**
Monothula subtilis (Giesbrecht, 1893 ["1892"])	M	<1	4	31	0.02	1.39										
Oithona atlantica Farran, 1908	m	8	20	141	0.32	45.83	1	6	42	0.38	20.29	<1	<1	2	0.00	1.47
Oithona hebes Giesbrecht, 1891	m	7	30	245	0.29	19.44	<1	1	8	0.03	2.90	2	13	107	0.13	1.47
Oithona nana Giesbrecht, 1893	m	96	209	1277	4.05	63.89	2	11	90	0.62	20.29	39	138	802	3.23	50.00
Oithona ovalis Herbst, 1955	m											1	7	42	0.10	2.94
Oithona plumifera Baird, 1843	m	8	10	54	0.32	65.28	2	5	28	0.59	34.78	4	5	19	0.31	52.94
Oithona setigera Dana, 1852	m	1	3	14	0.04	22.22	<1	1	5	0.03	5.80					
Oithona similis Claus, 1866	m	41	59	306	1.74	79.17	35	47	230	9.13	82.61	120	189	1174	9.90	88.24
Oithona simplex Farran, 1913	m	46	339	2861	1.93	8.33										
Oithona tenuis Rosendorn, 1917	m	<1	1	3	0.00	2.78	<1	<1	4	0.01	1.45	36	146	1003	3.01	13.24
Oithona spp.	m	14	52	376	0.57	33.33	2	3	16	0.50	37.68	<1	2	18	0.02	1.47
Oncaea media Giesbrecht, 1891	M											<1	<1	4	0.00	1.47
Oncaea mediterranea (Claus, 1863)	M	1	2	17	0.02	12.50										
Oncaea venusta Philippi, 1843	M	21	51	323	0.89	47.22						<1	<1	3	0.00	1.47
Oncaea waldemari Bersano & Boxshall, 1996 ["1994"]	M	74	364	2971	3.11	23.61										
Oncaea spp.	M	482	1583	10824	20.28	73.61	66	370	3080	17.1	72.5	<1	2	9	0.03	7.35
Sapphirina angusta Dana, 1849	M	<1	1	4	0.00	1.39										
Sapphirina auronitens sinuicauda Lehnhofer ,1929	M	<1	<1	3	0.00	1.39										
Sapphirina nigromaculata Claus, 1863	M	<1	1	5	0.00	4.17										
Sapphirina spp.	M	<1	1	5	0.01	4.17										
Triconia conifera (Giesbrecht, 1891)	M	7	22	149	0.29	31.94										
Triconia minuta (Giesbrecht, 1893 ["1892"])	M	2	7	48	0.07	11.11										
Triconia similis (Sars G.O., 1918)	M	1	4	27	0.04	8.33										
Harpacticoida																
Clytemnestra scutellata Dana,1847	m	1	4	26	0.06	15.28	<1	2	13	0.09	2.90					
Clytemnestra sp.	m	<1	1	4	0.00	2.78	<1	<1	3	0.09	1.45					
Euterpina acutifrons (Dana, 1847)	m	2	8	56	0.08	12.50	8	16	78	2.00	30.43	50	185	1228	4.11	41.18
Goniopsyllus rostratus Brady, 1883	m	1	3	19	0.03	12.50	2	5	29	0.39	17.39	<1	1	5	0.01	1.47
Macrosetella gracilis (Dana, 1847)	m	4	9	60	0.16	43.06	<1	1	5	0.08	15.94					
Macrosetella sp.	m	<1	1	7	0.00	1.39										
Microsetella norvegica (Boeck, 1865)	m	4	9	52	0.16	41.67	<1	1	10	0.05	4.35	<1	<1	4	0.01	4.41

Table 1: Continuation

Species		Summer					Autumn					Winter				
Species		**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**	**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**	**A.D.**	**S.D.**	**MAX**	**R.A.**	**O.F.**
Microsetella rosea (Dana, 1847)	m	5	10	49	0.21	48.61	<1	1	7	0.07	5.80	<1	1	5	0.03	25.00
Miracia efferata Dana, 1849	m	<1	<1	2	0.00	1.39	<1	<1	3	0.01	1.45					
Copepodits		1049	2043	15096	44.10	100.00	162	228	941	42.01	95.65	727	1613	10877	60.13	100.00
Nauplii		108	311	2014	4.56	81.94	1	2	10	0.13	7.25	2	13	107	0.13	1.47

Table 2: Average and standard deviation (S.D.) density of copepoda (ind. m-^{3}) in each stratum of water column, in each one of the regions of continental shelf and in each one of the water mass.(PPW: Plume Plata Water; SASW: South Atlantic Shelf Water; STSW: Sub Tropical Shelf Water; SACW: South Atlantic Central Water; TW: Tropical Water)

	Summer				**Autumn**				**Winter**			
	Average	S.D.	Max	Min	Average	S.D.	Max	Min	Average	S.D.	Max	Min
Stratum 1(0-25m)	5001	6562	34428	2	631	988	5190	76	2407	3482	16845	174
Stratum 2 (25-50m)	1555	1389	5350	8	365	324	1138	16	558	563	1984	35
Stratum 3 (50-100m)	560	432	1569	91	266	369	1339	3	506	564	1762	11
Stratum 4 (100-200m)	148	99	273	10	27	7	38	19	89	75	182	3
Stratum 5 (200-500m)	66	57	154	2	9	13	33	1	31	19	54	11
PPW	NA	NA	NA	NA	745	1007	5190	76	2436	3998	16845	105
SACW	123	104	348	2	15	12	34	1	73	60	182	13
SASW	1493	418	1788	1197	439	458	763	115	927	794	2397	35
STSW	4408	5870	34428	2	266	199	669	16	860	721	2021	178
TW	720	579	2185	8	122	110	337	3	104	101	267	3
Coastal (< 50 m)	4961	7187	34428	75	699	1155	5190	76	2390	3912	16845	105
Intermediate (< 50 m)	2124	1830	7436	8	614	425	1299	16	1100	767	2394	127
Intermediate (50-100 m)	718	527	1569	91	497	453	1339	104	746	639	1762	115
External (< 50 m)	1862	1589	5397	2	215	151	653	57	761	804	2397	35
External (50-100 m)	376	200	708	175	67	51	131	3	171	147	409	11
External (>100 m)	107	88	273	2	20	13	38	1	60	60	182	3
Calanoida	436	2192	2202	59	120	136	630	14	408	806	4011	22
Cyclopoida	1568	8258	15059	109	243	668	3550	9	252	257	1091	9
Harpacticoida	21	103	82	0	18	23	69	0	118	283	1233	0
Copepodids + Nauplii	1928	10001	17111	163	243	262	941	0	1314	2399	10877	66

Table 3: Total occurrence of copepoda taxa in the strata of water column,in the regions of continental shelf and each one of the water mass.

	Summer	Autumn	Winter
Stratum 1	74	55	42
Stratum 2	49	43	38
Stratum 3	66	46	34
Stratum 4	40	25	25
Stratum 5	33	20	23
Coastal Shelf	62	39	30
Intermediate Shelf	51	41	35
External Shelf	80	50	46
PPW	NA	38	29
SACW	59	26	29
SASW	23	15	29
STSW	75	40	33
TW	70	40	27

Table 4: Biodivesity indexes in each water mass studied and season of the year. Note that for Simpson index is measured in each sample, thus average and standard deviation are shown. In other hand, for Shannon-Weaver (H Index) there is no standard deviaton since it is a ponctual value that considers all samples. (PPW: Plume Plata Water; SASW: South Atlantic Shelf Water; STSW: Sub Tropical Shelf Water; SACW: South Atlantic Central Water; TW: Tropical Water)

	Summer			**Autumn**			**Winter**		
	Simpson	Simpson S.D.	Shannon	Simpson	Simpson S.D.	Shannon	Simpson	Simpson S.D.	Shannon
PPW	NA	NA	NA	0.760	0.069	3.540	0.650	0.149	2.893
SACW	0.835	0.043	4.092	0.704	0.123	3.624	0.597	0.143	2.383
SASW	0.761	0.008	3.126	0.765	0.004	2.877	0.667	0.083	2.898
STSW	0.727	0.140	3.707	0.783	0.082	3.609	0.567	0.146	2.036
TW	0.767	0.060	3.702	0.803	0.105	4.104	0.525	0.135	2.020
First (0m-25m)	0.708	0.136	3.533	0.760	0.078	3.646	0.608	0.154	2.892
Second (25m-50m)	0.763	0.096	3.905	0.811	0.054	3.893	0.667	0.095	3.285
Third (50m-100m)	0.800	0.058	4.075	0.764	0.112	3.673	0.662	0.095	2.482
Fourth (100m-200m)	0.810	0.050	3.766	0.765	0.132	3.934	0.571	0.188	2.288
Fifth (>200m)	0.858	0.030	4.180	0.677	0.092	3.056	0.508	0.102	2.020
Coastal (<50 m)	0.718	0.143	3.488	0.755	0.073	3.465	0.680	0.113	2.937
Intermediate (<50 m)	0.767	0.098	2.298	0.785	0.044	3.332	0.597	0.139	2.673
Intermediate (50-100 m)	0.793	0.053	2.630	0.794	0.058	3.209	0.699	0.085	2.432
External (<50 m)	0.715	0.097	1.531	0.811	0.084	3.412	0.575	0.147	2.157
External (50-100 m)	0.808	0.067	2.286	0.739	0.144	3.475	0.609	0.091	2.351
External (>100 m)	0.834	0.047	2.137	0.728	0.121	3.330	0.539	0.147	2.319
TOTAL	0.762	0.110	3.738	0.769	0.091	3.822	0.624	0.134	3.045

Table 5. Main species present in each water masses, in every season of the year, considering the higher frequencies of occurrence, average density and Correspondence Analysis. (PPW: Plume Plata Water; SASW: South Atlantic Shelf Water; STSW: Sub Tropical Shelf Water; SACW: South Atlantic Central Water; TW: Tropical Water).

	Summer	**Autumn**	**Winter**
PPW		*Acartia tonsa*	*Acartia tonsa*
		Centropages velificatus	*Calanoides carinatus*
		Corycaeus amazonicus	*Calanus australis*
		Corycaeus spp.	*Clausocalanus brevipes*
		Euterpina acutifrons	*Ctenocalanus citer*
		Oithona similis	*Euterpina acutifrons*
		Oncaea spp.	*Oithona nana*
		Paracalanus parvus	*Oithona similis*
			Paracalanus quasimodo
SASW	*Centropages velificatus*	*Ctenocalanus citer*	*Calanoides carinatus*
	Clausocalanus furcatus	*Ctenocalanus vanus*	*Clausocalanus brevipes*
	Ctenocalanus vanus	*Euterpina acutifrons*	*Oithona similis*
	Oithona nana	*Oithona similis*	*Oithona tenuis*
	Oithona similis	*Paracalanus parvus*	*Paracalanus quasimodo*
	Paracalanus parvus		
	Paracalanus spp.		
STSW	*Corycaeus giesbrechti*	*Oithona similis*	*Clausocalanus parapergens*
	Oithona nana	*Ctenocalanus* spp.	*Clausocalanus pergens*
	Oithona simplex	*Oncaea* spp.	*Ctenocalanus citer*
	Oncaea spp.	*Mecynocera clausi*	*Mecynocera clausi*
	Oncaea waldemari	*Acartia negligens*	*Oithona plumifera*
	Temora stylifera		*Oithona similis*
			Paracalanus quasimodo
SACW	*Clausocalanus furcatus*	*Clausocalanus pergens*	*Calanoides carinatus*
	Clausocalanus pavoninus	*Delibus sewelli*	*Clausocalanus parapergens*
	Clausocalanus pergens	*Macrosetella gracilis*	*Clausocalanus pergens*
	Mecynocera clausi	*Oithona similis*	*Microsetella rosea*
	Oithona atlantica	*Oncaea* spp.	*Oithona plumifera*
	Oithona plumifera	*Paracalanus quasimodo*	*Oithona similis*
	Oithona similis		*Oncaea* spp.
	Oncaea spp.		
TW	*Clausocalanus furcatus*	*Clausocalanus furcatus*	*Clausocalanus pergens*
	Farranula gracilis	*Delibus sewelli*	*Mecynocera clausi*
	Microsetella rosea	*Mecynocera clausi*	*Microsetella rosea*
	Oithona plumifera	*Oithona atlantica*	*Oithona plimifera*
	Oithona similis	*Oithona similis*	*Oithona similis*
	Oncaea venusta	*Oncaea* spp.	
	Oncaea spp.		
	Oncaea waldemari		

Table 6: SIMPER (Similarity percentages analisys) results to compare summer, autumn and winter groups, whit the species contributions defined in the multivariate analysis. [A.D.: Average Density; Shelf Regions: C - Coastal, I - Intermediate and E - External Shelf; Strata: 1 (0 - 25 m), 2 (25-50m), 3 (50-100 m) and 4 (>100 m)].

Species	A.D.	Contrib %	Cum %	Shelf Regions			Strata			
Summer - Average Similarity: 15.73										
Oncaea spp.	525	20.29	20.29	C	I	E	1	2	3	4
Oithona similis	44	14.8	35.09	C	I	E	1	2	3	4
Clausocalanus furcatus	52	12.48	47.57		I	E	1	2	3	
Oithona nana	105	7.26	54.82	C	I		1	2		
Temora stylifera	52	7.25	62.07	C	I		1	2		
Coricaeus giesbrechti	42	4.08	66.15	C			1			
Oncaea venusta	23	4.03	70.18			E			3	
Calocalanus pavoninus	19	3.89	74.08			E		2		
Oithona plumifera	8	3.17	77.25			E			3	4
Corycaeus spp.	38	2.93	80.17	C	I		1			
Farranula gracilis	11	2.31	82.48			E	1	2	3	4
Oncaea waldemari	81	1.93	84.41	C	I		1	2		
Mecynocera clausi	5	1.56	85.97			E			3	
Oithona atlantica	8	1.51	87.47			E			3	4
Paracalanus quasimodo	50	1.33	88.81	C	I		1	2		
Microsetella rosea	5	1.25	90.05			E				4
Autumn - Average Similarity: 18.39										
Oithona similis	37	41.98	41.98	C	I	E	1	2	3	4
Oncaea spp.	71	18.79	60.78	C	I	E	1	2	3	4
Paracalanus spp.	18	5.19	65.97	C	I		1	2		
Ctenocalanus vanus	16	4.85	70.82	C	I		1	2	3	4
Corycaeus spp.	14	4.54	75.38	C	I		1	2	3	
Mecynocera clausi	5	4.3	79.65			E		2	3	4
Paracalanus parvus	11	3.38	83.03	C	I		1	2	3	
Euterpina acutifrons	8	2.3	85.33	C	I		1	2		
Oithona spp.	2	1.75	87.08	C	I		1	2	3	
Oithona plumifera	2	1.58	88.66		I	E				4
Acartia negligens	3	1.39	90.04		I	E	1	2	3	
Winter - Average Similarity: 22.88										
Oithona similis	128	73.53	73.53	C	I	E	1	2	3	4
Paracalanus quasimodo	63	4.05	77.58	C	I		1	2		
Oithona plumifera	4	3.07	80.65			E			3	4
Oithona nana	42	2.96	83.61	C	I			2		
Clausocalanus brevipes	28	2.39	86		I	E		2	3	
Calanoides carinatus	45	2.32	88.32	C	I		1	2	3	
Euterpina acutifrons	54	2.25	90.57	C	I		1			

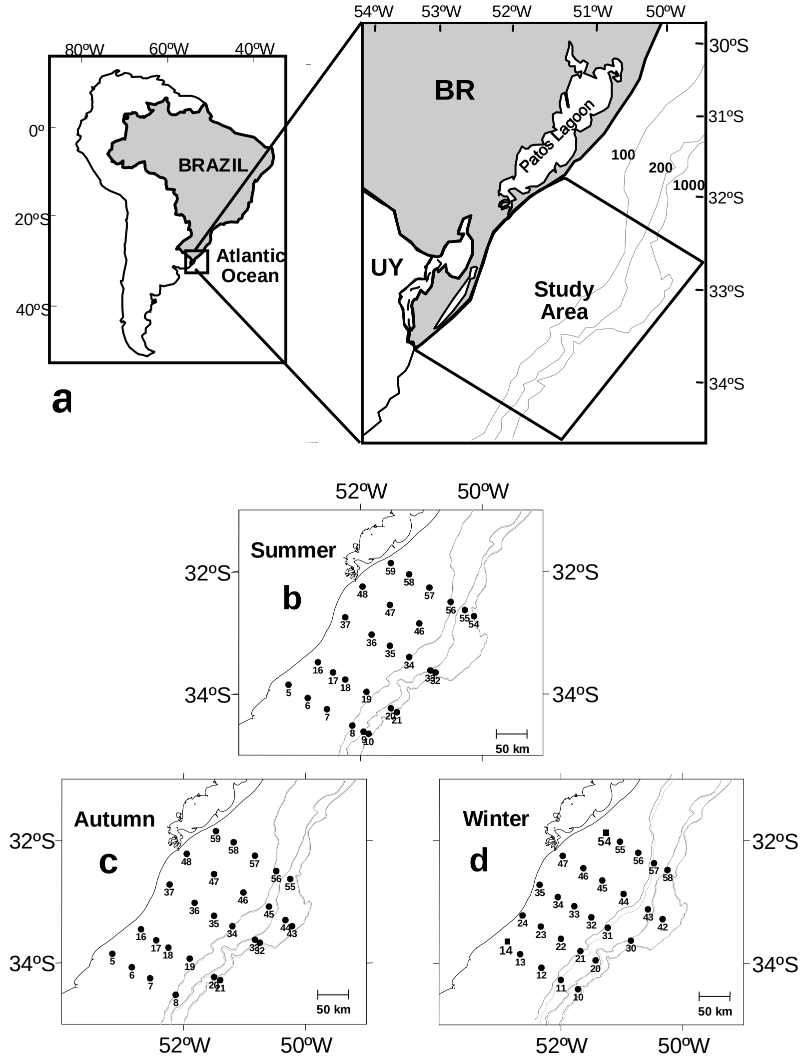


Fig. 1. Studied region (a) and the stations sampled each season: summer (b), autumn (c) and winter (d).

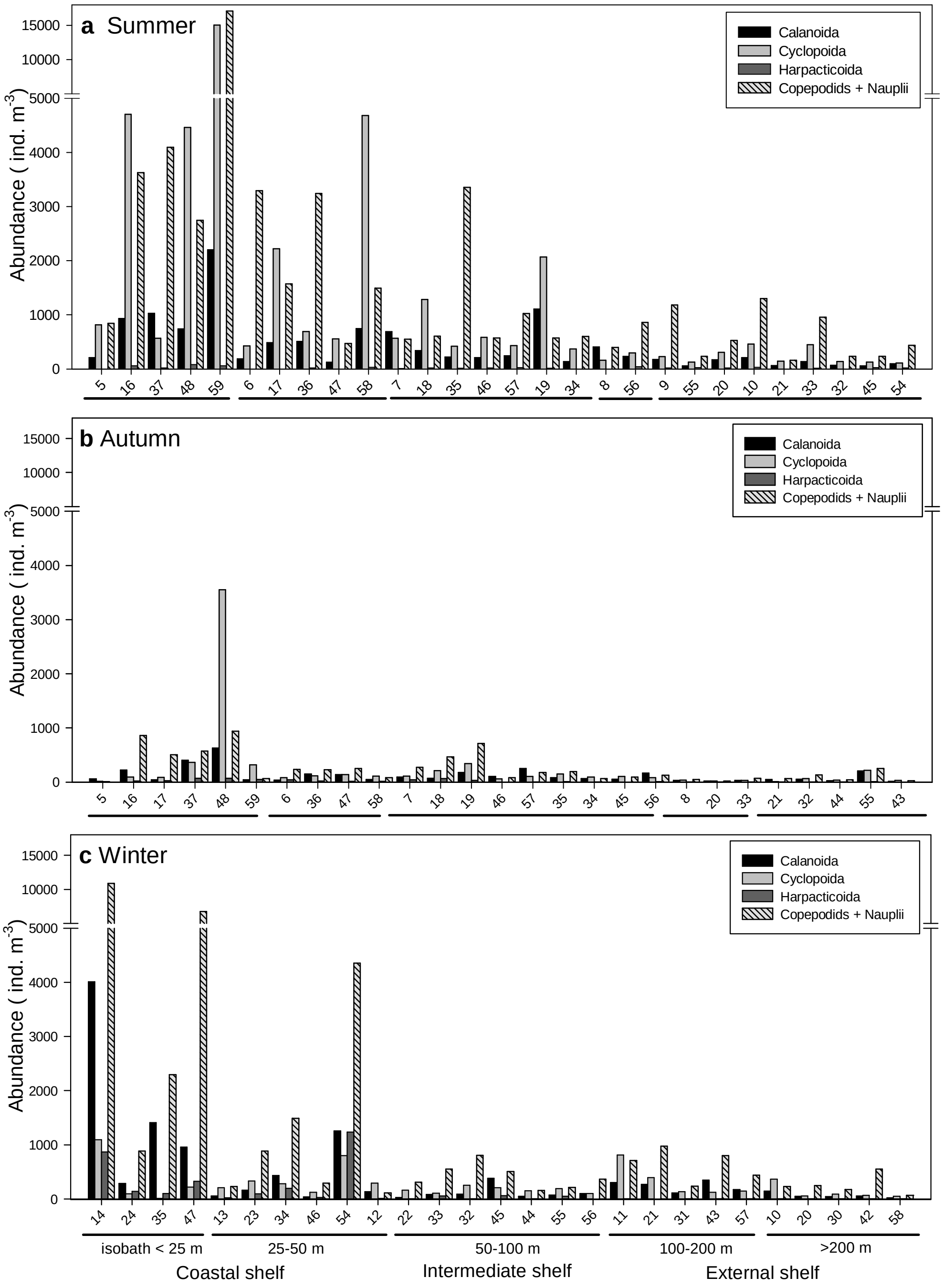


Fig. 2. Abundance of Calanoida, Cyclopoida, Harpacticoida, copepodits and nauplii of copepods in the stations sampling organized in regions of the continental shelf, in summer (a), autumn (b) and winter (c).

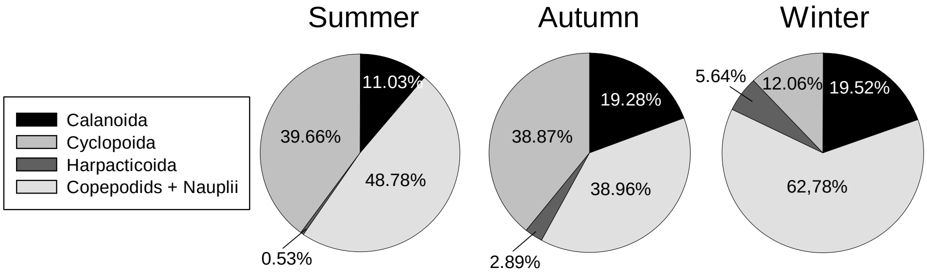


Fig. 3. Percentages of copepods orders (Calanoida, Cyclopoida and Harpacticoida) and copepodids and nauplii.

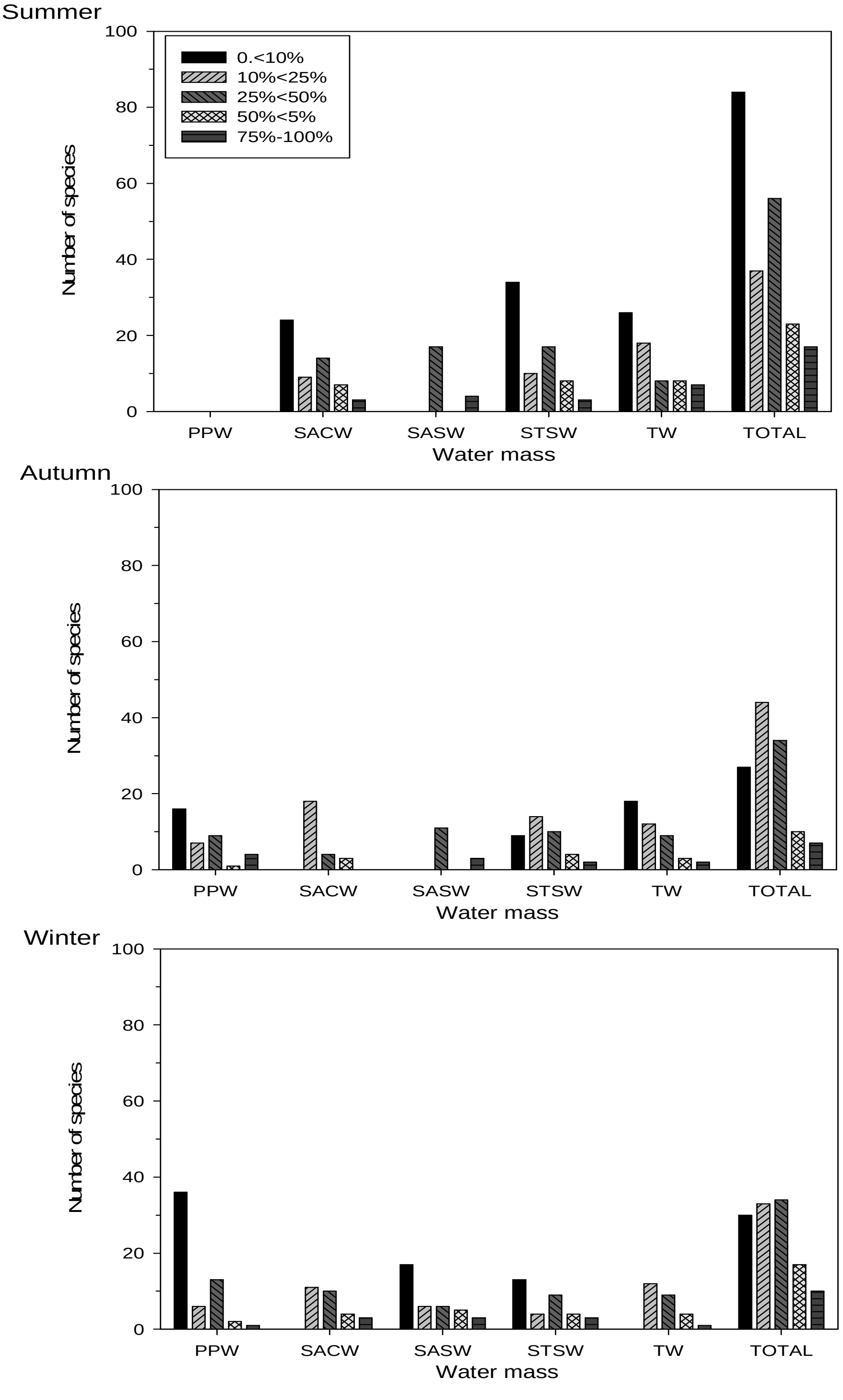


Fig. 4. Richness and equability in terms of number of species for studied water mass in summer, autumn and winter. Bars mean total observed species with occurrence up to 10% (black filled bars), from 10.1% up to 25% (diagonally hatched bars), from 25.1% up to 50 %(diagonally inverted hatched bars), from 50.1% up to 75% (diagonally hatched and diagonally inverted hatched bars) or from 75.1 up to 100% (horizontally hatched bars).

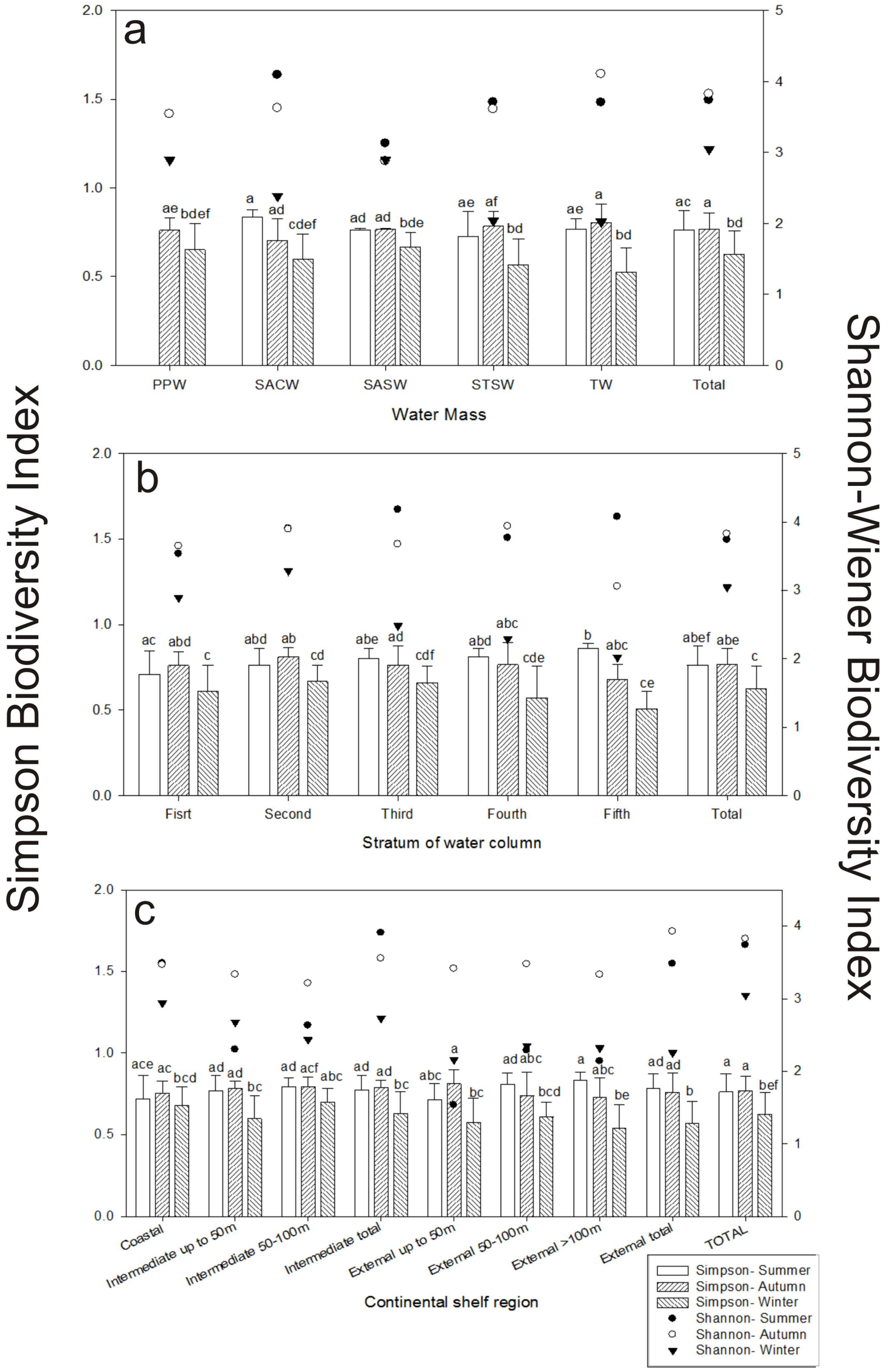


Fig. 5. Diversity indexes in each water mass (a), in the strata of water column (b) and at different continental shelf regions in the seasons of the year. Open bars, diagonally hatched bars and diagonally inverted hatched bars mean Simpson Biodiversity Index (average and standard deviation) for summer, autumn and winter, respectively. Bars sharing same letters point that there are no significant differences (Kruskal-Wallis test with posteriori of Dun, a= 0.05). Black filled and white filled circles and triangles mean Shannon-Wiener diversity index for summer, autumn and winter, respectively.

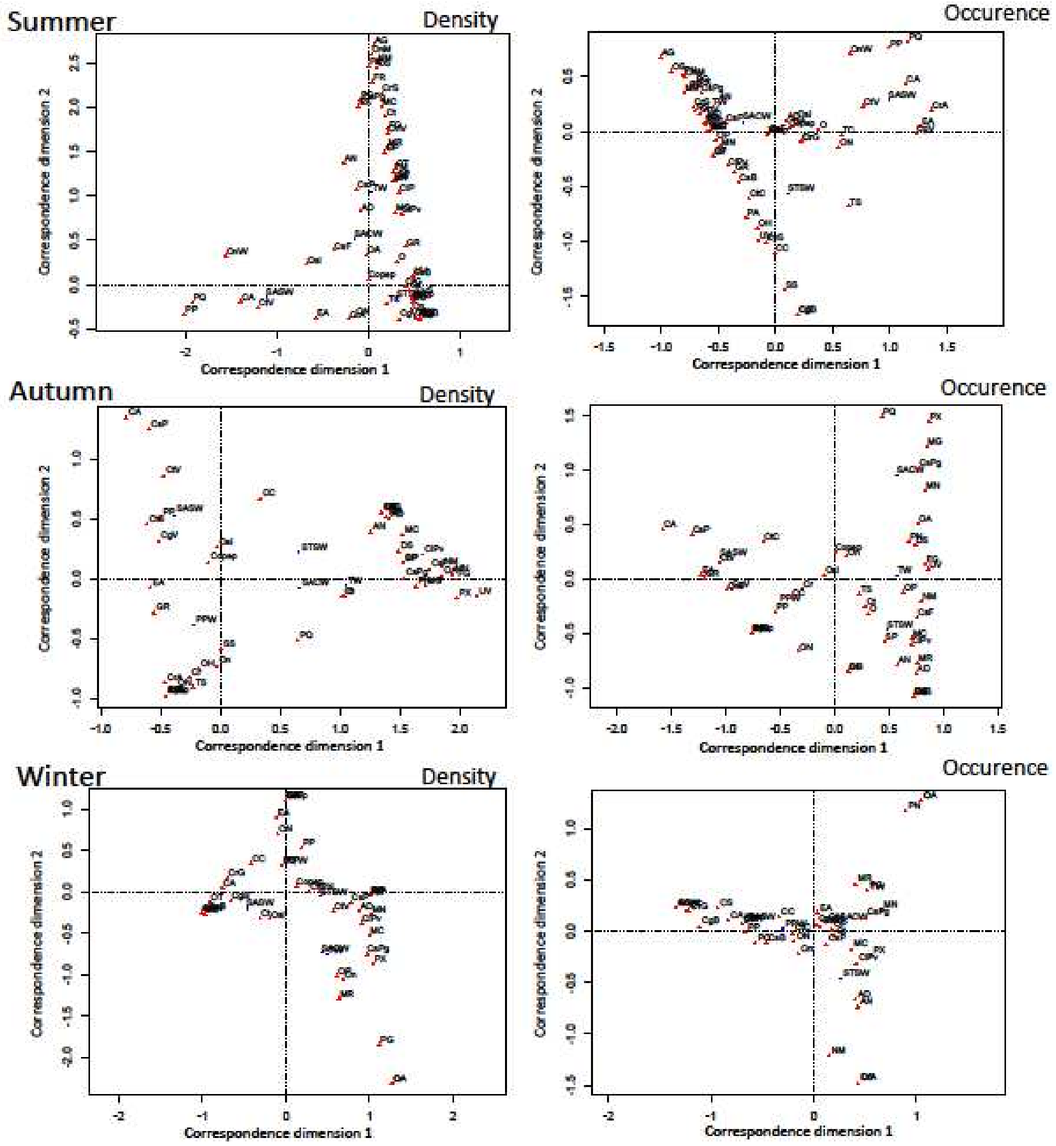


Fig. 6: Correspondence analysis for species association with studied water masses in summer, autumn and winter considering species density and species frequency. For these analyses were considered only species that presented five highest average density or frequency of occurrence for each water mass and season.

PPW: Plume Plate Water; SASW: Subantartic South Water; STSW: Subtropical South Water; SACW: South Atlantic Central Water; TW: Tropical Water; AD: *Acartia danae;* AN: *Acartia negligens;* AG: *Acrocalanus gracilis;* CC: *Calanoides carinatus;* CA: *Calanus australis;* CS: *Calanus similimus;* ClP: *Calocalanus pavo;* ClPv: *Calocalanus pavoninus;* CgB: *Centropages brachyatus;* CgV: *Centropages velificatus;* CsB: *Clausocalanus brevipes;* CsF: *Clausocalanus furcatus;* CsP*: Clausocalanus parapergens;* CsPg: *Clausocalanus pergens;* CyS: *Clytemnestra scutellata;* CrA: *Corycaeus amazonicus;* CrG: *Corycaeus giesbrechti;* CrS: *Corycaeus speciosus;* Cr: *Corycaeus spp;* CtC: *Ctenocalanus citer;* Ct: *Ctenocalanus spp;* CtV*: Ctenocalanus vanus;* DS: *Delibus sewelli;* EA: *Euterpina acutifrons;* FG: *Farranula gracilis;* FR: *Farranula rostrata;* GR: *Goniopsyllus rostratus;* MG: *Macrosetella gracilis;* MC: *Mecynocera clausi;* MN: *Microsetella norvegica;* MR: *Microsetella rósea;* NM: *Nannocalanus minor;* OA: *Oithona atlântica;* OH: *Oithona hebes;* ON: *Oithona nana;* OP: *Oithona plumifera;* OS *Oithona setigera;* OSi: *Oithona similis;* O: *Oithona spp;* OT: *Oithona tenuis;* OnM: *Oncaea mediterrânea;* On: *Oncaea spp;* OnV: *Oncaea venusta;* OnW: *Oncaea waldemari;* PA: *Paracalanus aculeatus;* PN: *Paracalanus nanus;* PP: *Paracalanus parvus;* PQ: *Paracalanus quasimodo;*

PG: *Pleurommama gracilis;* PX: *Pleurommama xiphias;* SP: *Subeucalanus pileatus;* SS: *Subeucalanus subtenuis;* TS: *Temora stylifera;* TC: *Triconia conífera;* TM: *Triconia minuta;* UV: *Undinula vulgaris;* Copep: Copepodites; Naup: Copepod nauplii.

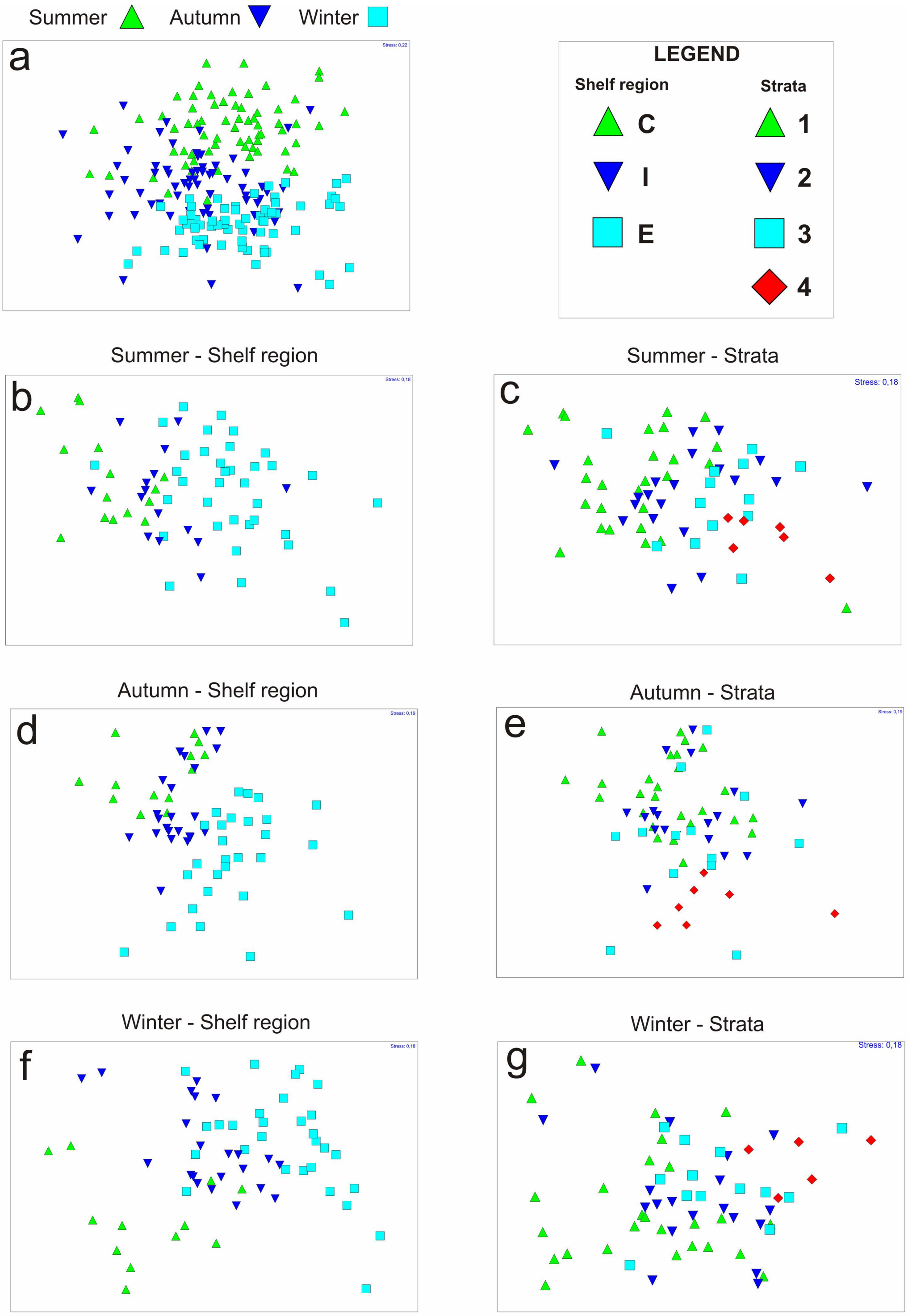
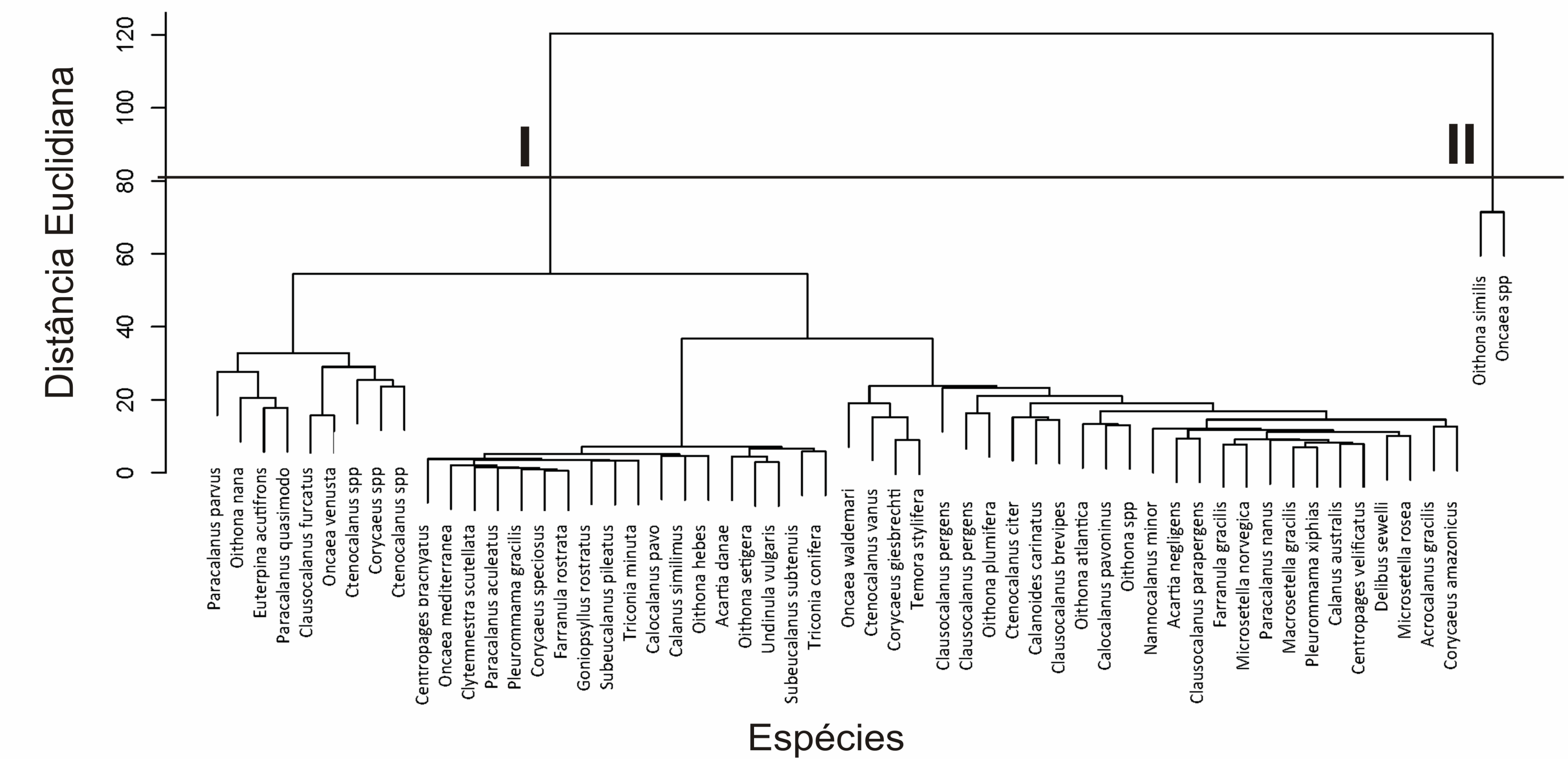


Fig. 7. Results of nMDS ordination analysis of sampling sites considering de density (square root transformed) of copepods species reflecting similar groupings for summer, autumn and winter (a), shelf region and strata, respect. in summer (b and c), autumn (d and e) and winter (f and g). (Abbreviations: S,summer; A, autumn; W, winter; C, coastal shelf; I, intermediate shelf; E, external shelf; strata 1: 0-25m; 2: 25-50m; 3: 50-100m; 4: >100m). (The legend refers to ‘b’ until ‘g’ figures).

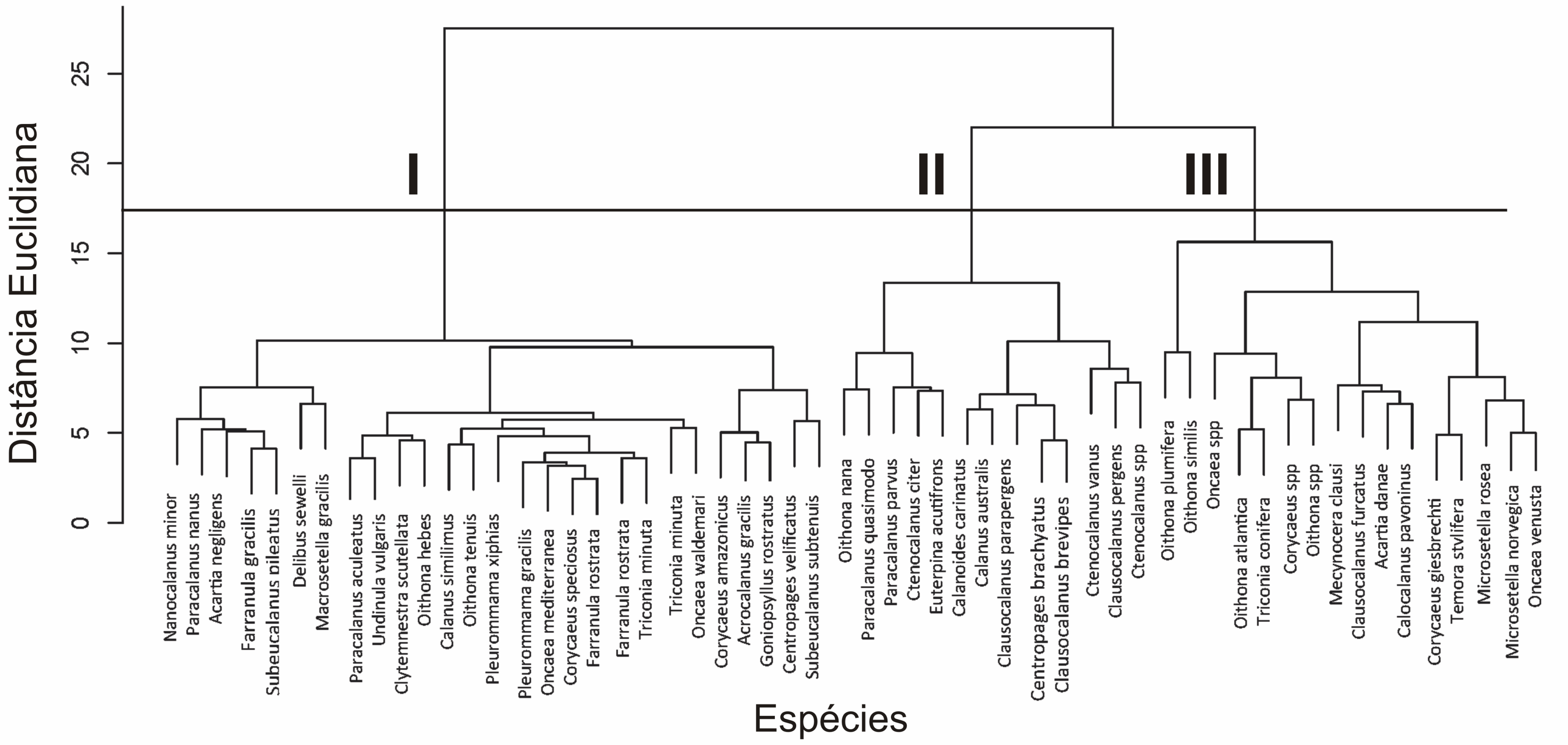
APÊNDICES

APÊNDICE I


Distância Euclidiana
0
20
40
60
80
100
120
I
II
Paracalanus parvus
Oithona nana
Euterpina acutifrons
Paracalanus quasimodo
Clausocalanus furcatus
Oncaea venusta
Ctenocalanus spp
Corycaeus spp
Ctenocalanus spp
Centropages brachyatus
Oncaea mediterranea
Clytemnestra scutellata
Paracalanus aculeatus
Pleuromamma gracilis
Corycaeus speciosus
Farranula rostrata
Goniopsyllus rostratus
Subeucalanus pileatus
Triconia minuta
Calocalanus pavo
Calanus similimus
Oithona hebes
Acartia danae
Oithona setigera
Undinula vulgaris
Subeucalanus subtenuis
Triconia conifera
Oncaea waldemari
Ctenocalanus vanus
Corycaeus giesbrechti
Temora stylifera
Clausocalanus pergens
Clausocalanus pergens
Oithona plumifera
Ctenocalanus citer
Calanoides carinatus
Clausocalanus brevipes
Oithona atlantica
Calocalanus pavoninus
Oithona spp
Nannocalanus minor
Acartia negligens
Clausocalanus parapergens
Farranula gracilis
Microsetella norvegica
Paracalanus nanus
Macrosetella gracilis
Pleuromamma xiphias
Calanus australis
Centropages velificatus
Delibus sewelli
Microsetella rosea
Acrocalanus gracilis
Corycaeus amazonicus
Oithona similis
Oncaea spp
Espécies

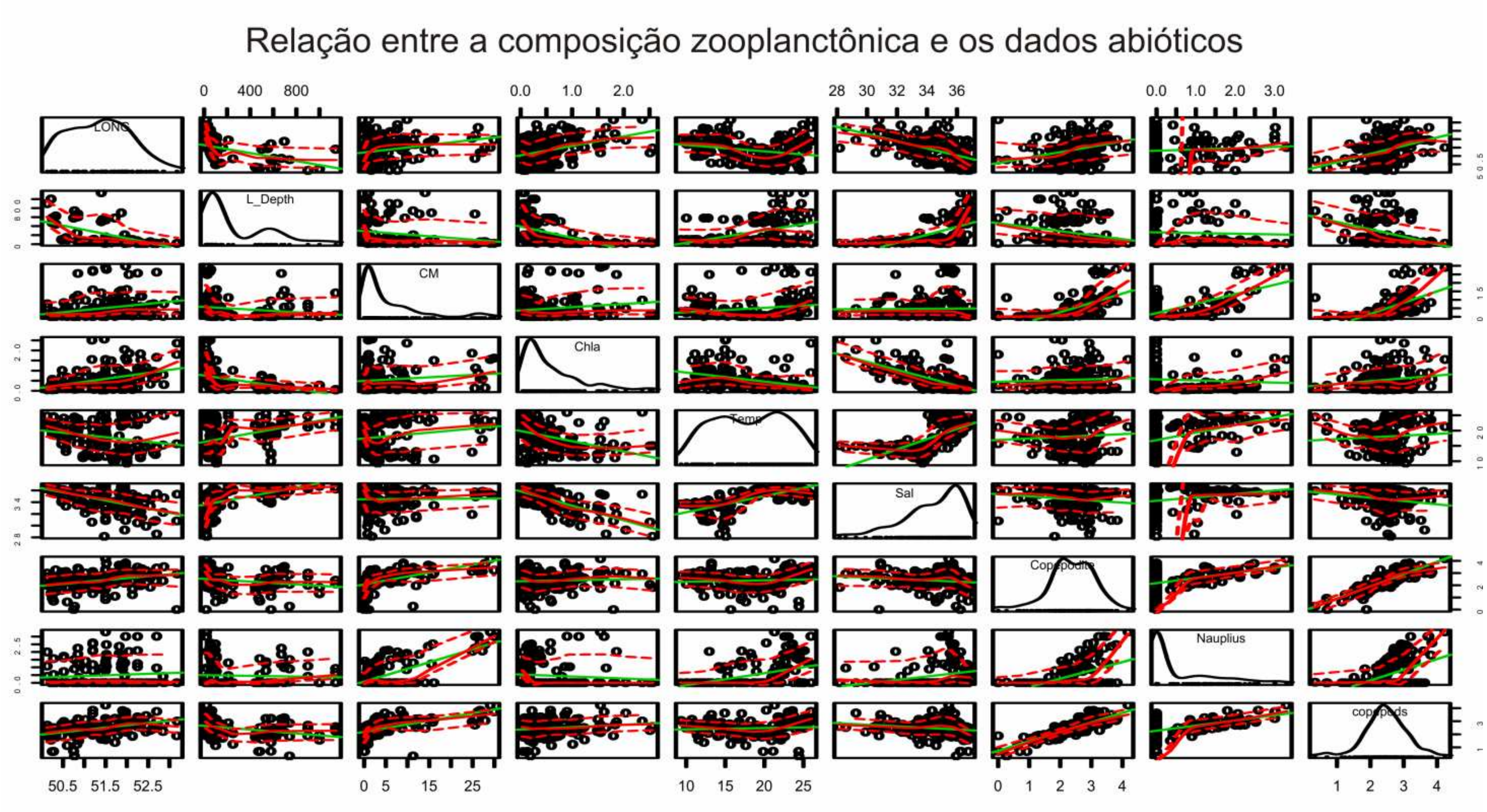
Análise de agrupamento hierárquicco (*Ward-Method*) com distância Euclidiana, considerando a densidade de organismos sem padronização das densidades (Kaufman & Rousseeuw, 1990) para organismos com FO maior que 10% em pelo menos uma estação do ano estudada. Nesta análise estão considerafas todas as estações do ano (verão, outono e inverno). O grupo I apresenta a maioria das espécies, com densidade individual máxima de 828 ind m $^{-3}$ para Calanoida e 2971 ind m $^{-3}$ para Cyclopoida (*O. waldemari*). O grupo II formado por *Oitona similis*,1174 ind m $^{-3}$, e *Oncaea spp* 10 824 ind m $^{-3}$.

APÊNDICE II


Distância Euclidiana
0
5
10
15
20
25
I
II
III
Nanocalanus minor
Paracalanus nanus
Acartia negligens
Farranula gracilis
Subeucalanus pileatus
Delibus sewelli
Macrosetella gracilis
Paracalanus aculeatus
Undinula vulgaris
Clytemnestra scutellata
Oithona hebes
Calanus similimus
Oithona tenuis
Pleuromamma xiphias
Pleuromamma gracilis
Oncaea mediterranea
Corycaeus speciosus
Farranula rostrata
Farranula rostrata
Triconia minuta
Triconia minuta
Oncaea waldemari
Corycaeus amazonicus
Acrocalanus gracilis
Goniopsyllus rostratus
Centropages velificatus
Subeucalanus subtenuis
Oithona nana
Paracalanus quasimodo
Paracalanus parvus
Ctenocalanus citer
Euterpina acutifrons
Calanoides carinatus
Calanus australis
Clausocalanus parapergens
Centropages brachyatus
Clausocalanus brevipes
Ctenocalanus vanus
Clausocalanus pergens
Ctenocalanus spp
Oithona plumifera
Oithona similis
Oncaea spp
Oithona atlantica
Triconia conifera
Corycaeus spp
Oithona spp
Mecynocera clausi
Clausocalanus furcatus
Acartia danae
Calocalanus pavoninus
Corycaeus giesbrechti
Temora stylifera
Microsetella rosea
Microsetella norvegica
Oncaea venusta
Espécies

Análise de agrupamento hierárquicco (*Ward-Method*) com distância Euclidiana, considerando a frequência de ocorrência (FO) dos organismos sem padronização das frequências (Kaufman & Rousseeuw, 1990) para organismos com FO maior que 10% em pelo menos uma estação do ano estudada. Nesta análise estão considerafas todas as estações do ano (verão, outono e inverno). O grupo I é formado por espécies com FO até 20-30%, várias ocorreram no outono, algumas no verão e poucas no inverno. Os grupos II e III são de espécies que ocorreram em maior FO (≈40-88%), sendo o grupo II mais associado ao inverno e com as águas frias (Pluma do Rio da Prata, PRP; e Água Subantática de Plataforma, ASAP), e o grupo III mais relacionado ao verão e águas quentes (Água Subtropical de Plataforma, ASTP; Água Tropical, AT; e Água Central do Atlântico Sul, ACAS).

APÊNDICE III



Relação entre a composição zooplanctônica e os dados abióticos

Matriz de relações entre alguns parâmetros biológicos e abióticos (longitude [LONG], profundidade local [L_Deep], biomassa de carbono do zooplâncton [CM], clorofila *a* [Chl-*a*], temperatura da água [Temp], salinidade [Sal], a densidade copepoditos [Copepoditos], densidade de náuplios [Nauplius] e densidade de copépodes adultos [copépodes]. Cada matriz tem o mesmo parâmetro «"eixo y", que tem a designação de uma das caixas. Cada coluna da matriz tem o mesmo parâmetro como "eixo x", que tem a designação de uma das caixas. Linhas pretas: a distribuição de parâmetro ao longo de todas as medidas, linhas verdes apontam tendências lineares, as linhas vermelhas contínuas tendências polinomiais, enquanto linhas tracejadas vermelha estabelece limites de confiança de 95 %.