



**UNIVERSIDADE FEDERAL DE SANTA CATARINA
CENTRO DE CIÊNCIAS BIOLÓGICAS
DEPARTAMENTO DE ECOLOGIA E ZOOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA**

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**COMUNIDADE PLANCTÔNICA, ESPECIALMENTE
COPÉPODES, DA PLATAFORMA CONTINENTAL DE SANTA
CATARINA (26-29°S): ASSOCIAÇÃO COM PROCESSOS
OCEANOGRÁFICOS E ESTRUTURA DE TAMANHO DE
FITOPLÂNCTON**

**Florianópolis/SC
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FITOPLÂNCTON**

Dissertação de Mestrado apresentada ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina, como parte dos requisitos necessários à obtenção do título de Mestre em Ecologia.

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**Florianópolis/SC
2014**

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Becker, Érica Caroline

Comunidade planctônica, especialmente copépodes, da
plataforma continental de Santa Catarina (26-29°S):
Associação com processos oceanográficos e estrutura de
tamanho de fitoplâncton / Érica Caroline Becker ;
orientadora, Andrea Santarosa Freire ; coorientador,
Leonardo Rubi Rôrig. - Florianópolis, SC, 2014.

122 p.

Dissertação (mestrado) - Universidade Federal de Santa
Catarina, Centro de Ciências Biológicas. Programa de Pós-
Graduação em Ecologia.

Inclui referências

1. Ecologia. 2. Ecologia de zooplâncton - copépodes -
cladóceros - quetognatos. 3. Estrutura de tamanho de
fitoplâncton e microzooplâncton. 4. Massas d'água -
processos oceanográficos - ressurgência - pluma estuarina.
5. Plataforma Continental de Santa Catarina - Plataforma
Brasileira Sudeste. I. Santarosa Freire, Andrea. II. Rubi
Rôrig, Leonardo. III. Universidade Federal de Santa
Catarina. Programa de Pós-Graduação em Ecologia. IV. Título.

“Comunidade Planctônica, Especialmente Copépodes, Da Plataforma Continental De Santa Catarina (26-29°S): Associação com Processos Oceanográficos e Estrutura De Tamanho De Fitoplâncton”.

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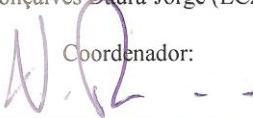


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Florianópolis, 02 de outubro de 2014.

AGRADECIMENTOS

Eu terminei a dissertação com o apoio e cooperação de muitas pessoas da Universidade Federal de Santa Catarina e gostaria de agradecer à Profa. Dra. Andrea Santarosa Freire, minha orientadora, proporcionou-me apoio acadêmico e incentivo à minha proposta inicial um pouco audaciosa, porém sempre me orientou a buscar recursos em outros laboratórios e contato com outros pesquisadores para realização das atividades propostas. Sua ajuda com o planejamento e concepção desse projeto e como incorporá-las em minha dissertação foi inestimável, teria sido muito mais fácil para ela desencorajar esses esforços, mas ela fez justamente o contrário e isso fez toda a diferença. Obrigada, Andrea! Por explorar universos novos e acreditar no meu trabalho, por momentos de discussão do trabalho (brainstorms) e por dividir a sua experiência da melhor maneira possível para meu crescimento pessoal e profissional.

Ao meu co-orientador, Prof. Dr. Leonardo Rubi Rörig, por ceder o espaço para as identificações de fitoplâncton, assim como boas conversas sobre o andamento das análises e hipóteses para a construção do capítulo 2. Falando em fito, não poderia faltar o agradecimento especial à Profa. Dra. Denise Rivera Tenenbaum, que trouxe grandes esclarecimentos sobre aspectos metodológicos e por demonstrar grande interesse em continuar contribuindo para os resultados e conclusão do segundo capítulo. Ainda espero que a nossa parceria possa ir muito além desse mestrado, porque realmente adorei tê-la conhecido e trabalhado (mesmo que à distância) com essa excelente profissional na área do fitoplâncton no Brasil. Você é uma grande referência para mim!

À Dra. Graziela Persich, grande companheira nas identificações e quantificações de fitoplâncton, inclusive no período em que estive ausente durante a licença maternidade. Obrigada por toda a sua contribuição com os resultados, boas conversas e boa amizade.

À Dra. Cristina Dias (UFRJ), que me apresentou ao mundo dos copépodes e me ensinou a identificar esses microcrustáceos mais adoráveis da vida! Tens minha total gratidão e admiração.

Ao MCT II o apoio financeiro para o desenvolvimento dos projetos realizados na plataforma e talude Sul-sudeste do Brasil, sob coordenação do Dr. Carlos Alberto Eiras Garcia (FURG), Dra. Andrea Santarosa Freire (UFSC) e Dra. Áurea Maria Ciotti (USP) que forneceram as amostras do estudo. E a CAPES pela concessão da bolsa de mestrado que me deu subsídio para morar em Florianópolis e realizar minha pesquisa, inclusive durante o período de licença maternidade.

Aos professores e funcionários da Pós-graduação em Ecologia, especialmente aqueles envolvidos no andamento do projeto (em termos burocrático e prático) até sua total finalização.

Colegas de pós-graduação, técnicos e estagiários de graduação do Laboratório de Plâncton e Crustáceos e Laboratório de Ficologia (UFSC) que me ajudaram muito durante o trabalho de laboratório. Aos amigos e colegas de mestrado – Marê, Tamila, Clau, Leandro, Moacyr, Renan, Bianca, Luiza e Vivi – que vivenciaram (vivenciam) a experiência do mestrado e dividiram bons momentos de alegria e desespero, seja no caminho do RU, do bar ou no corredor, sempre com muita descontração e bom humor. Em particular, ao Luis Carlos Pinto de Macedo-Soares e à Manoela Costa Brandão, por me ajudar no início com o projeto, adaptação à rotina do laboratório e atenciosamente me ensinaram todos os procedimentos de identificação e quantificação de zooplâncton que até então só conhecia de aulas práticas da graduação. Muito obrigada, vocês são grandes pesquisadores e amigos.

Minha família pelo apoio de sempre. Ao amor, confiança e segurança pra seguir com tudo. Acima de tudo, quero agradecer aos meus cacheados Marcelo e Miguelzinho, com vocês eu entendi o que formar uma família linda. E ver o Miguelzinho crescer junto com a dissertação tá sendo uma experiência maravilhosa, sempre surpreendendo, ainda mais agora gritando ‘manheeeeeee e papaiêeeeeee’ por toda a casa. Obrigada Marcelo por estar sempre ao meu lado (sempre com paciência) tolerando as minhas ausências (idas e vindas à Florianópolis) e cuidando muito bem do nosso filho. Você sempre me inspira pessoal e profissionalmente! Amo vocês!

Ao meu playlist, Kings of Leon, Death Cab For Cutie, The Head and the Heart, Arcade Fire, Baden Baden, Arctic Monkeys, Bom Iver, Of monsters and Men, Band of Horses, Cage the Elephant, Caetano Veloso, Chico Buarque, Maria Rita, Marcelo Camelo e outros. Melhor companhia durante as identificações, leituras e escrita.

E finalmente, ao plâncton, meu objeto de estudo que me permite ter um conhecimento inestimável em diversas áreas do conhecimento – biologia, oceanografia, ecologia - e me inspira a se especializar cada vez mais na profissão que escolhi para minha vida.

RESUMO

A comunidade mesozooplânctônica foi analisada em relação à estrutura de tamanho do fitoplâncton, às massas d' água e aos processos oceanográficos da plataforma continental de Santa Catarina. Arrastos verticais de zooplâncton (200 μm), amostras de água para nutrientes, clorofila e quantificação do fitoplâncton, registros de temperatura, salinidade e fluorescência (Rosette/CTD) foram obtidos no início do verão (dezembro/2010). Transectos perpendiculares à Baía da Babitonga (BB-26°S), Rio Itajaí (IR-27°S), Santa Catarina island (SCI-28°S) e Cabo de Santa Marta (CSM-28.5°S) foram conduzidos pelo NHo Cruzeiro do Sul. No CSM, a intrusão da Água Central do Atlântico Sul (ACAS) próximo à superfície coincidiu com altas concentrações de clorofila-*a* (2 mg . m⁻³) e biomassa zooplânctônica (1.40 mg.m⁻³) caracterizando o início da ressurgência de verão. O plâncton foi dominado por nanoflagelados, diatomáceas penadas, tintínídeos e o copépode detritívoro *Oncaea venusta*. A pluma da BB foi observada até 120km da costa(salinidade<35), associada à alta concentração de fosfato e a comunidade dominada por dinoflagelados tecados e diatomáceas penadas associados ao pico da abundância do copépode herbívoro *Temora turbinata*. Na plataforma externa e talude, a Água Tropical (AT) teve grande influência na composição de assembleias de espécies de águas quentes, com altas abundâncias de nanoplâncton e dinoflagelados associados ao copépode indicador da Corrente do Brasil (CB), *Clausocalanus furcatus*. Estas três estruturas de comunidades encontradas são semelhantes a assembleias de espécies de copépodes, cladóceros e quetognatos do S-SE do Brasil. As concentrações de formas nitrogenadas foram muito baixas e estiveram associadas a dominância de nanoflagelados e baixa abundância de microplâncton em ambos os processos costeiros. Em geral, a plataforma apresenta uma estrutura planctônica muito complexa e diversificada, formada principalmente por organismos pequenos (5-20 μm : >70%), mesmo para copépodes (0.5-1mm: ~60%). Estes resultados refletem que a presença de processos de enriquecimento na plataforma interna e as águas quentes da CB controlam a variação da composição da comunidade planctônica no gradiente costa-oceano e determinam a estrutura de tamanho do plâncton.

Palavras-chave: Zooplâncton, copépodes, massas d' água, nanoplâncton, microplâncton, ressurgência, pluma estuarina, Plataforma Brasileira Sudeste

ABSTRACT

The mesozooplankton community was analyzed in relation to phytoplankton size structure, the water masses and oceanographic processes of the Santa Catarina continental shelf. Vertical hauls of zooplankton (200 μm), water samples for nutrients and chlorophyll-*a*, records of temperature, salinity and fluorescence (Rosette/CTD) were obtained in early summer (December 2010). Cross-shelf transects were carried out off Babitonga Bay (BB-26°S), Itajai river (IR- 27°S), Santa Catarina island (SCI-28°S) and Cape Santa Marta (CSM-29°S) with the NHO Cruzeiro do Sul. In CSM, the intrusion of the SACW near the surface coincided with high chlorophyll-*a* (2 $\text{mg}\cdot\text{m}^{-3}$) and zooplankton biomass (1.40 $\text{g}\cdot\text{m}^{-3}$) at the beginning of the upwelling. Plankton was dominated by nanoflagellates, pennate diatoms, tintinnid ciliates and the detritivore copepod *Oncaea venusta*. A narrow coastal plume in BB waters of relative less saline water (< 35 psu) extending ~120 km offshore was associated with high values of phosphate and thecate dinoflagellates and pennate diatoms associated with the peak of the herbivore copepod *Temora turbinata*. In the outer shelf and slope, the Tropical Water (TW) had greater influence on the establishment of species assemblies of warm waters with high abundances of nanoplankton and dinoflagellates associated with the indicator species of the Brazil Current (BC), *Clausocalanus furcatus*. These three community structures are found share similarities with species of copepods, cladocerans and chaetognaths of the S-SE Brazil shelf. The different forms of dissolved inorganic nitrogen were very low and were associated with the nanoflagellates dominance and low abundances of microplankton in both coastal processes. In general, the continental shelf has a very complex and diversified plankton structure, primarily composed by small organisms (5-20 μm : >70%), even for copepods (0.5-1mm: ~60%). These results reflect that the presence of enrichment processes in the inner shelf and the warm waters of the BC control the variability of plankton community composition in coastal-offshore gradient and determine the plankton size structure.

Keywords: Zooplankton, copepods, water masses, nanoplankton, microplankton, upwelling, estuarine plume, southeastern Brazil shelf

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1 INTRODUÇÃO

Os processos relacionados à produção primária e secundária, como a transferência e reciclagem da matéria orgânica e energia na cadeia alimentar pelágica envolvem interações tróficas complexas entre protistas (auto- e heterotróficos) e metazoários (Dennett *et al.*, 1999). Deste modo, a complexidade natural das comunidades plantônicas pode ser reduzida a unidades que representam os principais processos biológicos, como guildas alimentares que representam funções ecológicas similares (Dennett *et al.*, 1999; Tenenbaum *et al.*, 2001). O mais utilizado atualmente é baseado no tamanho de acordo com o esquema proposto por Sieburth *et al.* (1978), o que pressupõe ordem de grandeza, dependente do tamanho, interações tróficas (e.g. picoplâncton, 0.2-2.0 μm ; nanoplâncton, 2.0-20 μm ; micropoplâncton, 20-200 μm e; mesoplâncton, 0.2-20 mm). Neste sentido, a compreensão da estrutura de tamanho da comunidade planctônica tem um importante papel na determinação dos fluxos de carbono e as interações tróficas na cadeia alimentar pelágica (Calbet & Landry, 2004; Finkel, 2007; Vargas *et al.*, 2007; Guenther & Valentin, 2008; Guenther *et al.*, 2008, 2012).

No gradiente costa-oceano, é possível se observar as diferentes estruturas tróficas planctônicas relacionadas principalmente à concentração de nutrientes na zona eufótica e hidrodinâmica local (Arin *et al.*, 2002; Guenther *et al.*, 2008). Em regiões costeiras, cadeias curtas e menos complexas formadas por células grandes estão associadas à maior hidrodinamismo e maiores concentrações de nutrientes, resultando em maior produção de biomassa de produtores secundários e terciários, sendo conhecida como a cadeia alimentar clássica ou herbívora. Além disso, diatomáceas grandes relacionadas com a ocorrência de pulsos de nutrientes episódicos em águas oligotróficas, embora reduzida em números, podem ser os produtores primários mais importantes em áreas onde a injeção de nutrientes sustenta um aumento de produção nova (Goldman, 1993) e está concentrada na profundidade da clorofila-*a* máxima (Odebrecht & Djurfeldt, 1996; Brandini *et al.*, 2013). Em ambientes oceânicos oligotróficos, cadeias longas dominadas por organismos pequenos caracterizam a alça microbiana (Pomeroy, 1974; Azam *et al.*, 1983), onde pico- e nanoplâncton autotróficos e heterotróficos predominam e podem ser considerados como a principal fonte de alimento do microzooplâncton e mesozoplâncton (Sherr & Sherr, 1988; Calbet, 2008).

Os copépodes representam um elo trófico chave em ecossistemas marinhos dominando os níveis tróficos intermediários. Na

maioria das plataformas tropicais e subtropicais os copépodes dominam o mesozooplâncton e atingem abundâncias e biomassas superiores a 70% (Björnberg, 1981; Bradford-Grieve *et al.*, 1999), como no caso da plataforma sudeste do Brasil (Lopes *et al.*, 2006) e em macroescala, podem responder por 90-97% da biomassa do Oceano Atlântico Sul Ocidental (Boltovskoy *et al.*, 1999). Copépodes de tamanho pequeno (<1 mm) constituem uma fração dominante e diversa (Turner, 2004) e são determinantes no tamanho potencial dos estoques pesqueiros (Bradford-Grieve *et al.*, 1999). Além de disso, possuem um papel fundamental como elo entre a cadeia trófica microbiana e os níveis tróficos superiores alimentando-se principalmente de microzooplâncton, especialmente ciliados e dinoflagelados (Calbet & Landry, 2004; Calbet, 2008). Cladóceros e quetognatos são também importantes grupos holoplantônicos marinhos sendo taxa dominantes nas massas d'água da Corrente do Brasil (Resgalla Jr., 2011) e usados como indicadores de massas d'água na plataforma sul do Brasil (Resgalla Jr., 2008). Neste sentido, o estudo sobre associações entre grupos dominantes do mesozooplâncton é essencial para a compreensão das interações tróficas na cadeia alimentar planctônica.

Durante o verão, ressurgências (Odebrecht & Djurfeldt, 1996; Brandini *et al.*, 2013; Campos *et al.*, 2013) e plumas estuarinas (Schettini *et al.*, 1998, 2005) ricas em nutrientes promovem a fertilização natural da coluna d'água. Em Santa Catarina, a região norte é caracterizada principalmente pela drenagem das águas continentais e ao sul, pela advecção e ressurgência na plataforma interna (Carvalho *et al.*, 1998; Hille *et al.*, 2008). Além disso, dentro de seus domínios encontram-se a Reserva Biológica Marinha do Arvoredo que abriga uma grande diversidade biológica (Braga & Niencheski, 2006) e o rio Itajaí-açu que é considerado como o maior contribuinte de descarga fluvial para o litoral (Schettini *et al.*, 1998). A estrutura oceanográfica varia de acordo com a distribuição de quatro massas de água: Água de Plataforma Subtropical (APST), Água Tropical (AT), Atlântico Central do Atlântico Sul (ACAS) e Água da Pluma do Prata (APP) (Piola *et al.*, 2000, 2008; Möller *et al.*, 2008). Assim, a plataforma interna é submetida a uma grande variabilidade anual, com uma forte termoclina no verão e quase nenhuma estratificação no inverno quando ocorre influencia da APP.

A distribuição da comunidade planctônica é afetada principalmente por influências sazonais, onde as maiores abundâncias de diatomáceas e copépodes estão associadas às camadas de clorofila-*a* máxima, decorrente as intrusões de ACAS próximo à superfície

(Brandini *et al.*, 2013). No gradiente latitudinal sudeste-sul, a plataforma de Santa Catarina representa o limite norte da extensão da APP em relação ao limite de distribuição de assembleias de espécies de larvas de decápodes e estomatópodes (Brandão & Freire, submetido) e larvas de peixes (Macedo-Soares *et al.*, 2014), indicando o papel fundamental desta massa d' água na produção planctônica regional. O zooplâncton da desembocadura do rio Itajaí-açu tem sido estudado por Schettini *et al.* (1998, 2005), Resgalla Jr. *et al.* (2008), Resgalla Jr. (2009) e destacam maior concentração de espécies tipicamente costeiras próximas à desembocadura do rio, além disto, a pluma influencia diretamente a distribuição de comunidades planctônicas das praias adjacentes a sua foz (Rörig *et al.*, 2003).

A estrutura de tamanho dos diferentes compartimentos do plâncton pode ser descrita em termos de biomassa total auto e heterotrófica (Susini-Ribeiro, 1999; Cupelo, 2000; Tenenbaum *et al.*, 2001, 2007; Guenther *et al.*, 2008, 2012), onde a contribuição de células pequenas para a biomassa total em carbono é maior, 64% composto por picoplâncton e 33% por nanoplâncton, sustentando o desenvolvimento de uma cadeia alimentar microbiana (Susini-Ribeiro, 1999). Aliás, as células grandes de fitoplâncton são ineficientes no consumo de nutrientes em concentrações baixas e dependem da turbulência para permanecer na zona eufótica, o que torna microfítoplâncton um bom indicador de processos de turbulência e de intrusão de nutrientes através da picoclina nos oceanos oligotróficos (Susini-Ribeiro *et al.*, 2013). De acordo com essas observações, é esperado que o zooplâncton seja um bom indicador de processos no oceano e que certos grupos taxonômicos serão capazes de qualificar determinadas massas d'água através da distribuição e hábito das espécies mais abundantes. Além disso, eventos intermitentes de ressurgência e formação de plumas na região trazem nutrientes para camadas superiores provocando variações na estrutura de tamanho do fitoplâncton, neste contexto, células maiores e bem estruturadas, em termos de formação de cadeias, são esperadas e isso terá um reflexo na estrutura de tamanho de copépodes. Em locais da plataforma onde processos de enriquecimento não ocorrem frequentemente, como em direção ao oceano, uma estrutura planctônica baseada em células pequenas pode estar associada às condições mais oligotróficas.

A presente dissertação consiste em dois estudos:

O primeiro estudo inclui uma amostragem da comunidade zooplanctônica na plataforma continental e talude de Santa Catarina, onde influências costeiras e oceânicas são apresentadas através de

processos oceanográficos e massas d'águas dominantes na região. Copépodos, cladóceros e quetognatos são grupos holoplanctônicos dominantes e receberam maior destaque na descrição da comunidade e resolução taxonômica.

O segundo estudo integra a comunidade de nano, micro e mesoplâncton (5 μ m à 2mm), estudando a interação entre o fito, proto e zooplâncton, em cenários oceanográficos distintos, que privilegiam a princípio a cadeia alimentar microbiana – *microbial loop* – e a herbívora – *classical food chain*. Os constituintes do nanoplâncton, microfítoplâncton, microzooplâncton e copépodos (mesozooplâncton) são estudados a partir da estrutura de tamanho para descrever a cadeia alimentar plágica nesses cenários oceanográficos.

1.1 OBJETIVOS

Geral

Analisar a variação espacial do mesozooplâncton, especialmente copépodos, em relação a estruturadores físicos e biológicos do ecossistema pelágico da plataforma e talude de Santa Catarina: às massas de água, os aportes costeiros, à ressurgência de águas frias, à abundância do nanoplâncton, microplâncton.

Específicos

- Analisar a estrutura da comunidade de zooplâncton, com ênfase nas espécies de copépodos e de outros grupos secundariamente dominantes (cladóceros e quetognatos), em diferentes cenários oceanográficos (costa, pluma estuarina, ressurgência, plataforma e oceano);

- Analisar a relação da estrutura de tamanho das espécies de copépodos com a composição do nanoplâncton (5-20 μ m), microfítoplâncton e microzooplâncton (20-200 μ m) no gradiente costa-oceano, sob influência da pluma estuarina da Baía da Babitonga e ressurgência de água frias no Cabo de Santa Marta.

2 CAPÍTULO 1 – Zooplankton community and Copepoda, Cladocera and Chaetognatha species meso scale distribution in Santa Catarina continental shelf, south western Atlantic Ocean (26°S-29°S)

Zooplankton community, specially copepods, cladocerans and chaetognaths species meso scale distribution in Santa Catarina continental shelf, southwestern Atlantic Ocean (26°S-29°S)

Abstract: This study analyzes the zooplankton community structure through different oceanographic scenarios: estuarine plume, upwelling, coast and shelf. Vertical hauls of zooplankton (200 μm), water samples for nutrients and chlorophyll-*a*, records of temperature, salinity and fluorescence (Rosette/CTD) were obtained in early summer (December 2010). Cross-shelf transects were carried out off Babitonga Bay (BB-26°S), Itajaí River (IR- 27°S), Santa Catarina Island (SCI-28°S) and Cape Santa Marta (CSM-29°S) with the NHO Cruzeiro do Sul. In CSM, the intrusion of the South Atlantic Central Water (SACW) near the surface overlapped with high chlorophyll concentrations (2.3 $\text{mg}\cdot\text{m}^{-3}$), biovolume (1.18 $\text{mL}\cdot\text{m}^{-3}$), biomass (1.40 gm^{-3}) and zooplankton abundance (7.441 $\text{ind}\cdot\text{m}^{-3}$), featuring the beginning of the summer upwelling. The influence of BB waters (salinity <35) was observed up to 120 km offshore and was associated with a second increase of zooplankton abundance (2.303 $\text{ind}\cdot\text{m}^{-3}$). The Tropical Water (TW) had greater influence in the oceanic region where the Brazil Current flows. It were registered 62 copepod species, 4 cladoceran species and 8 chaetognath species. Copepods constituted 90%, cladocerans 2.5% and chaetognaths (2%) of the zooplankton off the Santa Catarina shelf and were the dominant taxonomic groups. *Oncaea venusta* (21.1%) and *Clausocalanus furcatus* (18.8%) were dominant on the shelf and ocean, respectively, *Temora turbinata* (7.6%) and *T. stylifera* (6.8%) on the coast. The composition of the zooplankton groups (10% - except Copepoda) were similar in BB and SCI with *Penilia avirostris* (32%) and invertebrate larvae (22%) abundant in the coastal region and chaetognaths (47%), appendicularians (25%), siphonophores (20%) and thaliaceans (13%) often found in the oceanic region. In CSM, Brachyura larvae (28%) and *Flaccisagitta enflata* (18%) were associated with coastal upwelling and *Evadne spinifera* (34%), appendicularians (21%) and siphonophores (14%) to the shelf and slope waters. Cross-shelf gradients from the coast influenced by the continental runoff, coastal upwelling and water masses mixing in mesoscale defined the distribution of abundant/dominant species of the zooplankton of the Santa Catarina shelf ecosystem and provided important insights about the pelagic food webs.

Keywords: pelagic zooplankton, Copepoda, Cladocera, Chaetognatha, coastal processes, water masses, south Brazil shelf

INTRODUCTION

Efforts to characterize structural complexity of the marine environment through the relationships between the taxonomic composition of the communities and oceanographic processes are one of the greatest challenges to aggregate properties about the functioning of the pelagic ecosystem and food webs (Goericke, 2011). Coastal environments and water masses interactions may create important subregions of intense biological responses at several trophic levels, from plankton to nekton (Schettini *et al.*, 1998; Acha *et al.*, 2004). In the Santa Catarina continental shelf, intermittent upwelling events bring the salty and nutrient-rich South Atlantic Central Water (SACW) into the surface (Castro *et al.*, 2006; Campos *et al.*, 2013). The presence of strong horizontal and vertical density gradients resulting from the Plata Plume Water (PPW) (Acha *et al.*, 2004) and the meandering of the Brazil Current (Silveira *et al.*, 2000) makes the shelf one of the most heterogeneous and productive areas of the Southern Brazilian coast (Brandini, 2006). However, due to the strong influence of the Brazilian Current and the warm Tropical Water (TW) throughout the year, there is a general high-diversity and low-density pattern in the zooplankton community (Boltovskoy, 1999).

The copepods represent one of the keystone trophic links in aquatic ecosystems dominating the mid trophic-level position and might exert top-down control on its food and bottom-up control on its predators. Hence, the small size spectrum (< 1 mm) are the most abundant metazoans on Earth (Turner, 2004) and are an important determinant of the potencial size of the fishery (Bradford-Grieve *et al.*, 1999) generating about 70% of the herbivorous mesozooplankton biomass in the South Brazilian Bight (Lopes *et al.*, 2006) and at wider scale, might account for 90-97% of the biomass of the southwestern Atlantic Ocean (Boltovskoy *et al.*, 1999). As well as the Copepoda group, Cladocera and Chaetognatha are important marine holoplankton being dominant key taxa (by number and frequency) in the water masses in the Brazil Current (Campaner, 1985; Resgalla Jr, 2011; Domingos-Nunes & Resgalla Jr., 2012).

Previous research on south-southeastern Brazilian shelf had shown that seasonal and annual changes in the planktonic communities are mainly related to the Subtropical Convergence, the brackish water outflow of La Plata River and Patos Lagoon and seasonal processes as the principal oceanographic processes associated with the water masses

distribution. The studies mainly addressing ecological aspects, as the influence of inorganic nutrient and phytoplankton, photosynthesis and primary production (Soares, 1983, Brandini, 1988, 1990; Ciotti *et al.*, 1995; Fernandes & Brandini, 1999), as well as the decapod and stomatopod larvae (Brandão & Freire, *in press*) and ichthyoplankton latitudinal distribution and cross-shelf gradients associated to specific water masses and seasonal processes such as the Plata Plume Water (Macedo-Soares *et al.*, 2014), the mesozooplankton biomass variability due to offshore displacement of water masses by Ekman transport (Resgalla Jr *et al.*, 2001), the copepod and ichthyoplankton related to the extreme south oceanic fronts (Muelbert *et al.*, 2008), chaetognath and cladoceran considering as hydrological indicators (Resgalla Jr. & Montú, 1993; Resgalla Jr., 2008; Domingos-Nunes & Resgalla Jr., 2012) and, the diversity of epipelagic chaetognaths and copepods from the Brazil-Malvinas Confluence area, where tropical and cold-water faunas converge (Crelier & Daponte, 2004; Berasategui *et al.*, 2005; Avila *et al.*, 2009).

The zooplankton community over the 26°S-29°S Brazilian continental shelf, including the dominant crustaceans (Copepoda and Cladocera) and chaetognaths species, deserves further research compared to the north and southern coast. The available studies focus mainly on the shallow coastal region (Resgalla Jr. & Veado, 2006; Resgalla Jr., 2009; Veado *et al.*, 2010) which has been for decades highlighted in baseline reviews (Valentin *et al.*, 1994, Brandini *et al.*, 1997, Lopes, 2007, Resgalla Jr., 2011). Despite the regularity of the SACW intrusions and of the fresh water plumes formation, there is a limited knowledge on the role of these enrichment processes on the zooplankton community around CSM on the south and around Itajaí-açu river and Babitonga bay on the north of Santa Catarina shelf and slope. Recently studies highlighted the copepods and cladocerans species distribution indicate the major water masses (Domingos-Nunes & Resgalla Jr., 2012) and the diatom-copepod dominance related to the onset of the SACW intrusions in the euphotic zone and the onset of the rich deep chlorophyll maximum layers (Brandini *et al.*, 2013). In accordance with these observations we would expect that the zooplankton multi taxa assemblies are the result of the oceanographic features and the species interactions. The research aims to analyze the distribution and composition of the zooplankton community, highlighting the dominant Copepoda, Cladocera and Chaetognatha species connected to the main oceanographic processes and water masses off Santa Catarina shelf and slope.

MATERIAL AND METHODS

Study area

The Santa Catarina shelf and slope (Fig. 1B) is considered a transitional environment under tropical and subtropical conditions of the S-SE Brazilian shelf. To the south, the Cape Santa Marta (CSM) signs the border of the Southern Brazilian Bight (SBB: 23–28°S) and the Southern Subtropical Shelf (SSS: 28–35°S – Fig. 1A).

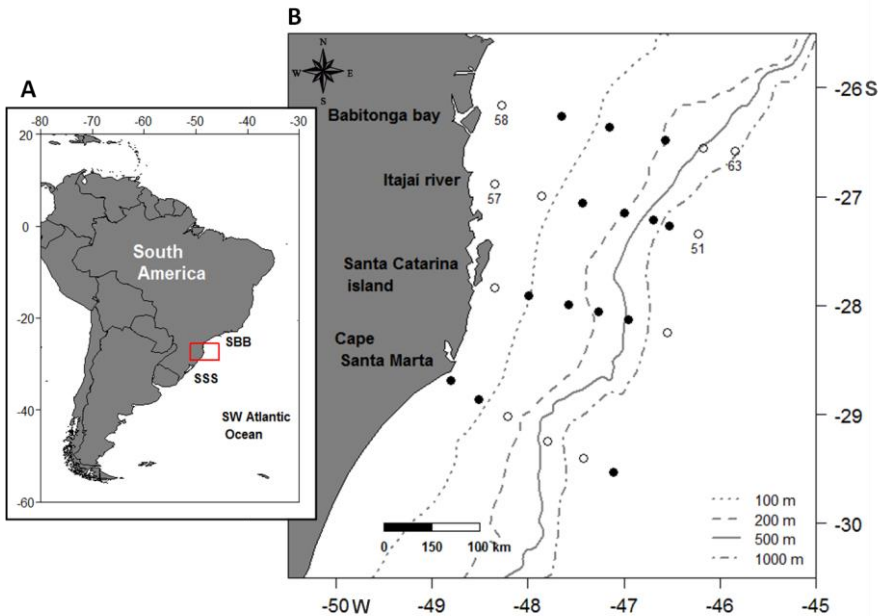


Figure 1. A. Location of the Santa Catarina shelf in the southwest Atlantic Ocean, the South Brazilian Bight (SBB) and the Southern Subtropical Shelf (SSS). B. Distribution of oceanographic stations in the 4 transects off the Santa Catarina continental shelf, during early austral summer (December 2010). Stations were sampled at daytime (white circles) and at night (black circles).

The CSM area comprises a relatively steep and narrow continental shelf under the influence of the Brazil Current and intense seasonal variations of the wind field that affects the composition of water masses and their circulation resulting in upwelling episodes (Castello & Möller, 1977; Matsuura, 1986; Campos *et al.*, 2013).

Associated with the upwelling event, the presence of South Atlantic Central Water (SACW) at the surface is clearly depicted in the coastal region south of the cape and drives the subsurface chlorophyll *a* maximum (Odebrecht & Djurfeldt, 1996) and high zooplankton biomass (Resgalla Jr. *et al.*, 2001) turning one of the most important areas of the Brazilian fishing grounds (Acha *et al.*, 2004; Castello *et al.*, 2009). Besides, the La Plata Plume Water and the Sub-antarctic waters (Subtropical Shelf Front) reach the southern coast in winter and promote the major seasonal dynamics during an annual cycle (Möller *et al.*, 2008; Piola *et al.*, 2008). The northern extreme is strongly influenced by the Babitonga bay estuary characterized by an extensive formation of mangroves with continental inputs and several river systems of Itapocu, Itajaí-açu and Tijucas rivers (Carvalho *et al.*, 1998).

The main water masses occurring on the continental shelf are the warm Tropical Water (TW – $T \geq 18.5^{\circ}\text{C}$, $S \geq 36$), which flows in the upper portion of the Brazil Current southward near the shelf break with high-temperature and high-salinity, low nutrient concentration and oxygen high concentration. The cool SACW ($T \leq 18.5^{\circ}\text{C}$, $S \geq 35.3$), which also flows southwards into the lower portion of the Brazil Current (200-500 m) has low-temperature, high-salinity and high nutrient concentrations, especially nitrate. There are onshore bottom intrusions of the SACW, which may be enhanced by cyclonic eddies and meandering of the Brazil Current along the continental slope (Gaeta & Brandini, 2006). The Subtropical Shelf Water (STSW – $T > 18.5^{\circ}\text{C}$, $35.3 < S < 36$) results from mixing of the continental and oceanic waters (TW) and has low salinity due to the influence of continental waters discharges and spreads throughout the neritic region. These water masses features have been described in the area by Carvalho *et al.* (1998), Piola *et al.* (2000; 2008), Silveira *et al.* (2000), Schettini *et al.* (2005), Hille *et al.* (2008) and Möller Jr. *et al.* (2008).

Field and laboratory work

Sampling was conducted during early austral summer from 12th to 20th December 2010 at 25 oceanographic stations distributed at 4 cross- shelf transects in Santa Catarina continental shelf aboard the NHO NHO Cruzeiro do Sul of the Brazilian Navy (Fig. 1). Vertical profiles of salinity, temperature, oxygen and fluorescence were registered with a conductivity-temperature-depth (CTD) profiler Sea Bird Electronics model 911. Water samples were collected by 5 L Niskin bottles in the rosette system to determine the concentration of chlorophyll-*a* and

inorganic nutrients (ammonium, nitrite, nitrate, phosphate, silicate) at selected depths (at 3 m or 5 m, at the chlorophyll maximum depth and at the base of the mixture layer). Nutrients were estimated following the methods described by Grasshoff *et al.* (1983) and Strickland & Parsons (1968) and chlorophyll-*a* according to Welschmeyer (1994).

Zooplankton samples were collected through vertical hauls from the maximum fluorescence depth up to the surface in deeper than 20 m, from 10 m above the sea floor when the water column was homogenous and from about 10 m depth at shallow stations (up to 20 m). A conical-cylindrical plankton net with a 0.5-m diameter mouth and 200 μ m mesh size, equipped with a General Oceanics® was used. The samples were immediately fixed in 4% buffered seawater-formaldehyde solution. The maximum fluorescence depth ranged from 10 to 95 m and the plankton sampling depth ranged from 14 to 107 m. The distance from the coast ranged from 11 to 280 km. The mean volume of water filtered by the net was $31.1 \pm 14.1 \text{ m}^3$.

Zooplankton was quantified through wet biomass and displacement biovolume (Boltovskoy, 1981). Samples were subsampled with a Folsom splitter (McEwan *et al.*, 1954) in fractions of $\frac{1}{2}$ or $\frac{1}{4}$, before counting. Aliquots of 10 mL were taken from known volume of the fractions (500 to 800 mL) for counting copepods and sometimes chaetognaths and cladocerans (Frontier, 1981). The other taxa were counted in the fraction. For all the zooplankton taxa, including copepods at least 100 individuals in each sample were counted or sorted for further identification. Zooplankton samples were identified and quantified under a stereo-microscope and microscope (10x and 40x magnification). The identification employed Onbé (1999) for Cladocera; Björnberg (1981), Bradford-Grieve *et al.* (1999), Campos-Hernández & Suárez (1999) and Dias & Araújo (2006) for Copepoda; Alvariño (1967) and Casanova (1999) for Chaetognatha and Boltovskoy (1981) for general zooplankton.

Data processing and statistical analyses

Zooplankton major taxa and species abundance was standardized to number of individuals per m^3 of filtered water. The copepod taxa were selected according to the frequency of occurrence (FO > 60%), relative abundance (RA > 1%) or absolute abundance (AA > 300 ind/ m^3) for further statistical analyses. The cross-shelf stations were categorized according to the isobaths: until the 100 m isobath was nominated as inner shelf, the outer shelf between the 100 m and 500 m

isobaths and the slope was the stations deeper than 500 m. The shallowest station in the inner shelf is also referred as “coastal station” in each transect. The water masses were characterized according to the termohaline index following Piola *et al.* (2000; 2008) and Möller Jr. *et al.* (2008). They were graphically illustrated in the T-S diagram and vertical profiles performed in the Ocean Data View.

The association of Copepoda, Cladocera and Chaetognatha species and the major zooplankton taxa as Appendicularia (Oikopleuridae and Fritillariidae), invertebrate larvae, Siphonophorae, Euphausiacea and Thaliacea was verified by non-metric multidimensional scaling (nMDS) and an accompanying cluster analysis based on the Bray-Curtis similarity and UPGMA linkage classification (Field *et al.*, 1982). Prior to the analysis, abundance data were square-root transformed. The Similarity Profile Routine (SIMPROF) was used to test for the presence of sample groups (or more continuous sample patterns) in *a priori* unstructured sets of samples (Clarke *et al.*, 2008). Groups of samples are separated (at $p < 0.05$) by a permutation procedure with a frequency of 999 permutations.

In order to examine the associations among the most abundant and frequent zooplankton taxa and the environmental variables, a multivariate canonical correspondence analysis (CCA) was applied (Legendre and Gallagher, 2001). The average temperature, salinity, average chlorophyll, distance from the coast, the nutrients (ammonium, nitrate, nitrite, phosphate, and silicate) and the oxygen stratification index were included as possible explanatory variables. The oxygen stratification was calculated using the surface oxygen value and the value for the bottom of the oxycline, and respective depths. Prior to the analysis, explanatory variables were standardized to remove the effect of differing units between parameters. The statistical significance of the analysis was tested using the Monte Carlo permutation procedure, performing 999 permutations. The colinearity between the explanatory variables was verified through the Variance inflation factor (VIF) where the variables with VIF value > 20 were considered strongly colinear and consequently removed from the analysis. All multivariate analyses were carried out in the R program using the *Vegan* package (Oksanen *et al.*, 2013) and *HH* (Heiberger, 2013; R Development Core Team, 2011).

RESULTS

Oceanographic conditions

Three water masses were identified in the study until the maximum zooplankton sampling depth (107 m): Subtropical Shelf Water (STSW), Tropical Water (TW) and South Atlantic Central Water (SACW) (Fig. 2). The STSW was distributed in the upper layer of the continental shelf in all transects sampled. Only in the shallow station (St.35) of Cape Santa Marta the intrusion of SACW was detected close to the surface. At the slope, oceanic waters were mainly influenced by TW in the surface layer of the water column.

The STSW (33.5 to 36, $> 20^{\circ}\text{C}$) was the dominant water mass over the shelf in the surface layer and the salty and warm TW (> 36 , $> 20^{\circ}\text{C}$) in the slope area (Fig. 3). The mixture of the Babitonga estuarine waters with the shelf waters extended the < 34.5 isohaline up to 120 km far from the coast (Fig. 3). A weaker mixture with Itajaí-açu River plume (34.5 S) was also registered in shallow coastal stations of IR. The low-salinity water (< 34) of the BB plume waters is also shown in the TS diagram in the upper 25 m depth (St.58 - fig. 2). In the slope areas, TW was shallow in BB, IR and CSM, being replaced by SACW around 75 m, and deeper than 150 m in SCI. The cool waters of SACW reached 15 m depth in Cape Santa Marta, disclosing the upwelling occurrence in subsurface waters (Fig. 3).

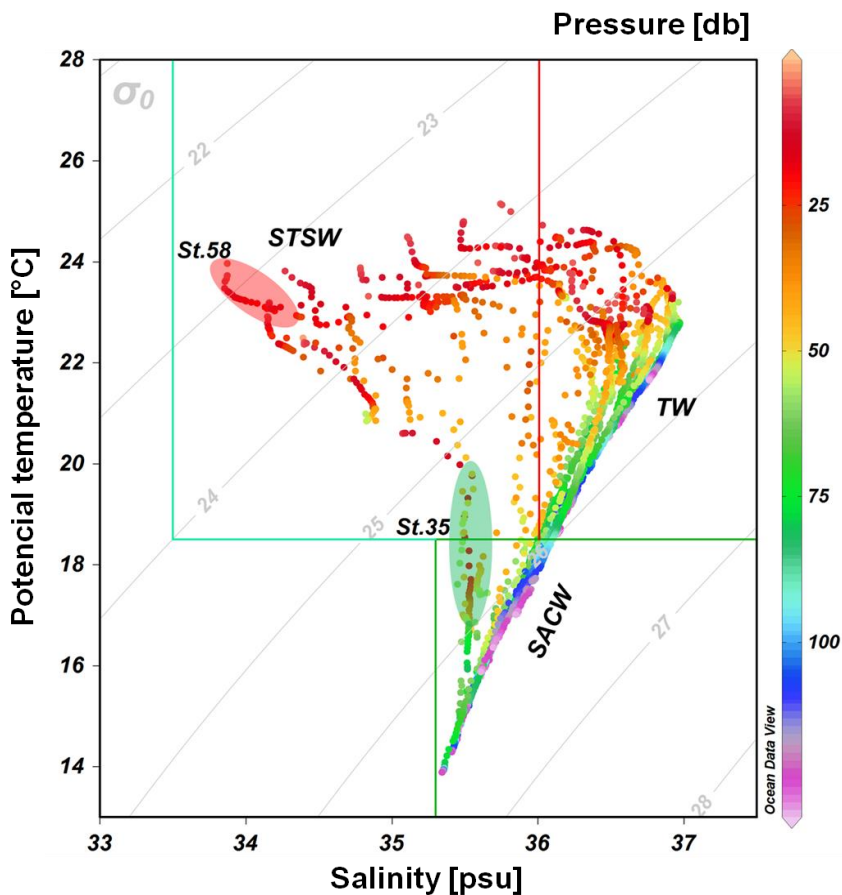


Figure 2. Temperature-salinity diagram in the 4 transects off Santa Catarina shelf and slope during early austral summer (December 2010). The lines represent the limits of the thermohaline indexes of each water mass. TW: Tropical Water; STSW: Subtropical Shelf Water; SACW: South Atlantic Central Water. St.35: shallow station of Cape Santa Marta; St.58: shallow station of Babitonga bay. Only stations up to 107 m depth (maximum zooplankton sampling depth) are displayed.

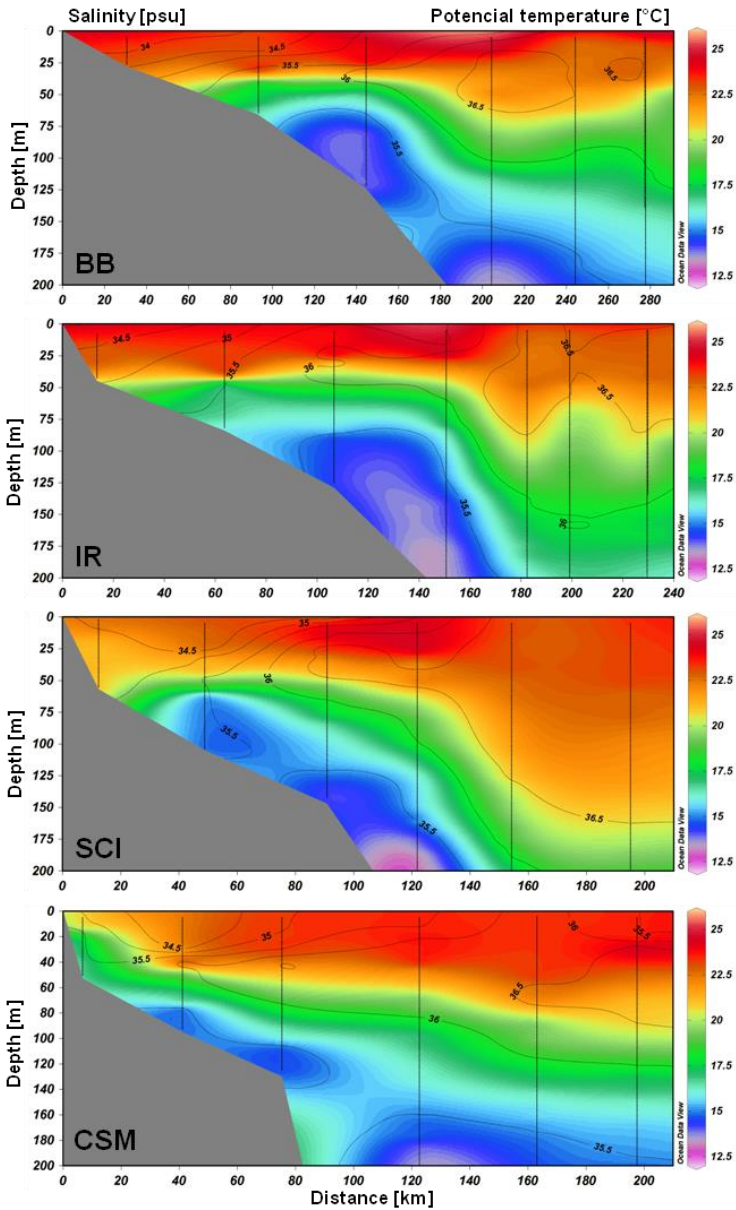


Figure 3. Vertical distribution of temperature and salinity in Babbitonga Bay (BB), Itajaí River (IR), Santa Catarina Island (SCI), Cape Santa Marta (CSM) in the 4 transects off Santa Catarina shelf and slope during early austral summer (December 2010).

Spatial variations in abundance, biomass and biovolume of zooplankton community

The zooplankton abundance was higher in all coastal stations at the inner shelf. Along the shelf waters, the abundance were constantly high over the entire transect in BB and CSM. The lowest abundances were registered in the IR transect. In the outer stations, the abundances decreased abruptly especially in SCI, where TW was deeper (Fig. 4A). There was no evidence of night/ day effect in the overall quantitative pattern observed.

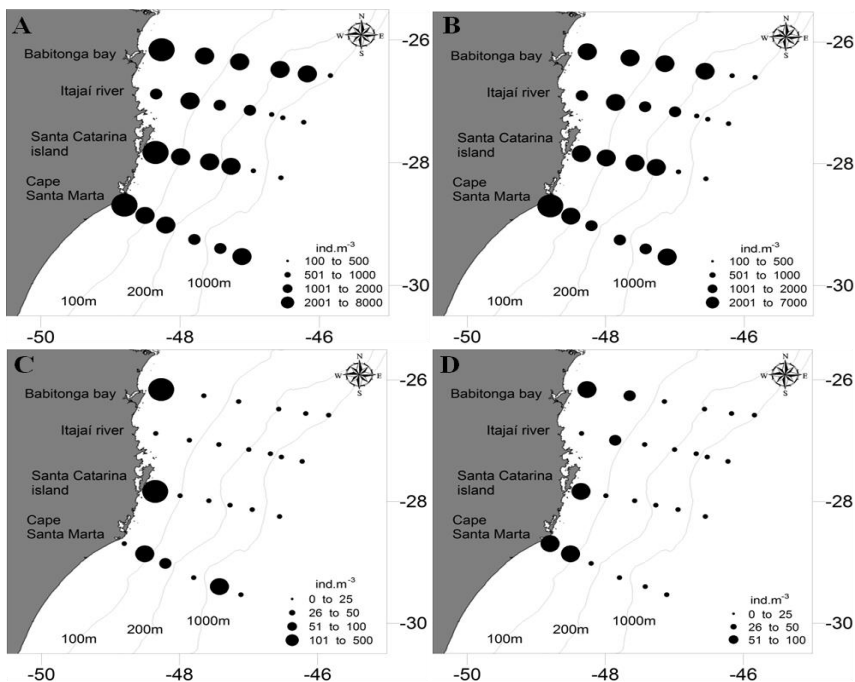


Figure 4. Spatial variations in abundance of the total zooplankton community (A) and abundance of Copepoda (B), Cladocera (C), Chaetognatha (D) along 4 transects off Santa Catarina shelf and slope during early austral summer (December 2010). Note the difference in abundance scales.

The zooplankton and Copepoda abundance distribution was very similar, excepting an outer BB station (St. 62), a shelf station (St. 37) in CSM and the coastal station (St. 45) of SCI (Fig. 4A and B), where copepods values decreased in relation to zooplankton. Copepods

had low abundance only in the outer shelf northern than CSM. Copepoda had the highest abundance reaching up to 6.417 ind . m⁻³ in the upwelling station of CSM (St. 35). Cladocera and Chaetognatha concentrated mostly in the inner shelf (Fig. 4C and D), showing a strong coast-ocean gradient. It is noteworthy that in CSM, *Penilia avirostris* abundance peak were in the shallow stations (St. 36, 45 and 58) while *Evadne spinifera* in the outer region (St. 39) (Fig. 5).

Spatial patterns of the zooplanktonic community

The zooplankton groups, except copepods, represented only 10% of the total abundance (Fig. 5; Table S1). The Cladocera (Table S3) and Chaetognatha (Table S4) were also numerically dominant, often numbering after only to copepods.

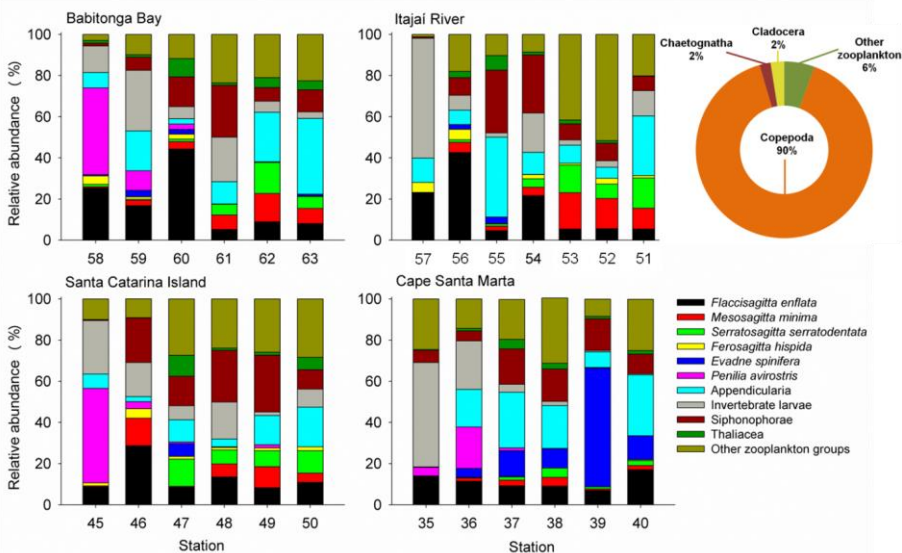


Figure 5. General zooplankton groups contribution (top right) and relative abundance of the principal taxonomic components (except Copepoda) of zooplanktonic community along 4 transects off Santa Catarina shelf and slope during early austral summer (December 2010).

In BB and SCI, the composition of the zooplankton groups was very similar in the coastal station, where *P. avirostris* (more than 40%) and invertebrate larvae (13 to 26%) were dominant. In the BB, IR and SCI outer stations, where low values of copepods had previously been

described (Fig. 4B), zooplankton composition was also very similar. Chaetognaths species *Mesosagitta minima* and *Serratogitta serratodentata*, Oikopleuridae and siphonophores shared their dominance in these deep stations. There was a high variability of zooplankton composition in the intermediate stations.

The species *Flaccisagitta enflata* and *Ferosagitta hispida* were typically found nearshore, whereas the species *M. minima* and *S. serratodentata* were abundant in the outer shelf and slope. The zooplankton coastal–ocean gradient in CSM was unique. Invertebrate larvae (40%, being 28% *Brachyura* zoea) and crustacean nauplii (10%) and chaetognaths (*F. enflata* - 13%) were associated to the coastal upwelling (St. 35) and *E. spinifera* (St. 39 - 58%), Appendicularia (St. 40 - 30%) and siphonophores (St. 37 - 17%) to the outer shelf and slope (Fig. 5). Besides, this transect had the lowest proportion of *F. enflata* in the inner shelf and the highest in the outermost station (St. 40 – 16%) compared to the other transects. The coastal station of IR was also particularly different, invertebrate larvae and *F. enflata* comprised about 80% of the total abundance, which the invertebrate larvae were approximately 60% of the total.

Spatial patterns of the copepod species

A total of 78 taxa and 62 species were identified in the samples (Table S2). Copepods constituted 90% of the total zooplankton (Table S1); average abundance of zooplankton was 1.800 ind.m⁻³ and of copepods was 1.650 ind.m⁻³.

Among the copepod assemblage, the 18 taxa selected by the high abundance and frequency of occurrence accounted for almost 90% of the total abundance. These species are listed according to their RA values as follows: *Oncaea venusta* (21%), *Clausocalanus furcatus* (19%), *Temora turbinata* (8%), *Temora stylifera* (7%), Clausocalanidae (7%), *Oithona plumifera* (6%), *Calocalanus pavoninus* (6%), *Farranula gracilis* (4%), *Ctenocalanus vanus* (2%), *Corycaeus giesbrechti* (2%), *Subeucalanus pileatus* (1%), *Oncaea media* (1%), *Paracalanus aculeatus* (1%), *Clytmemnestra scutellata* (1%), *Corycaeus copepodites* (1%), *Corycaeus speciosus* (0.6%) and *Mecynocera clausi* (0.5%). The last two were elected due to FO higher than 60%.

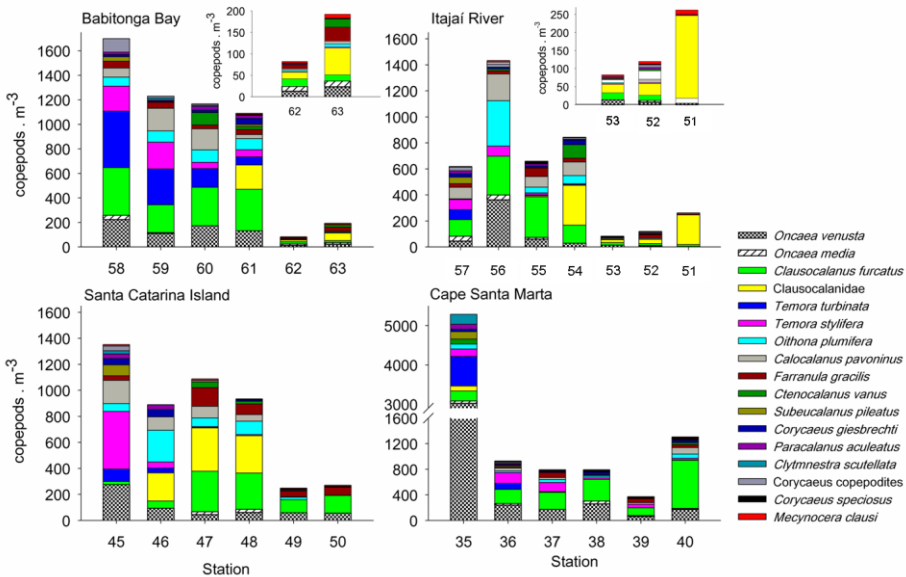


Figure 6. Spatial distribution of the Copepoda dominant species of zooplanktonic community along 4 transects off Santa Catarina shelf and slope during early austral summer (December 2010). Highlighted in the upper right the Babitonga Bay and Itajaí River slope stations. Note the difference of abundance scales.

The copepods species *O. venusta*, *C. furcatus* and *C. pavoninus* were the most abundant and frequent species in all transects sampled (Fig. 6). *O. venusta* spread from the inner to the outer shelf, but was dominant in the inner shelf with highest abundance under the upwelling of CSM (3.020 ind. m^{-3}), which reached almost the double of the average abundance in the samples (1.650 copepods. m^{-3}). *C. furcatus* was often very abundant in the inner to outer shelf (mean abundance > 200 ind. m^{-3}), but was less abundant in the inner shelf of SCI where *P. avirostris* was dominant (St. 45 and 46 - Fig. 5). *C. pavoninus* also spread widely decreasing in CSM and the slope in the whole sampling. *T. turbinata* and *T. stylifera* were dominant mainly in the inner shelf of BB and SCI, where similar zooplankton composition had been already described (Fig. 5), although *T. turbinata* reached the highest abundance in CSM upwelling. *O. plumifera* occurred in the inner to outer shelf and Clausocalanidae (most copepodites of *Clausocalanus* spp.) from outer

shelf to the slope, except in CSM where these two taxa were less recorded.

Accordingly, the other species were rarely abundant and presented a more restricted distribution to the inner, outer shelf or slope in this coast-ocean scenario. *C. giesbrechti*, *P. aculeatus*, *C. scutellata* and *S. pileatus* occurred mainly in the inner and in some cases in the outer shelf, while *O. media*, *C. speciosus* and *M. clausi* in the outer shelf and slope. *C. vanus* recurrent in the outer shelf in all transects, particularly in the southern region.

Matching spatial patterns in zooplankton community structure with environmental forcing factors

The spatial distribution of different zooplankton taxa, especially the cladocerans, chaetognaths and copepods species, showed strong inshore-offshore and north-south patterns that were statistically consistent with the results from the SIMPROF test (999 permutations). The nMDS plot showed a stations division according to the shelf position (inner, outer, slope) highlighted by the 5 clustering groups (Fig. 7; Table 1).

The shallow station in CSM (St. 35) under the influence of the SACW intrusion was unique in group 1. Most of the stations in the inner shelf molded group 2. Offshore stations under TW influence were separated in a central (4) and northern (5) groups. All the remaining stations under STSW influence were grouped together (3).

The first group is the station 35 of CSM under the influence of SACW cold waters and formed by the particularly coastal copepod species of *T. turbinata*, *S. pileatus* and *C. scutellata*. The group 2 indicates the inner shelf group under the influence of coastal conditions. It was mainly represented by the copepod species *T. stylifera* and *Corycaeus* copepodites, the chaetognath *F. enflata*, invertebrate larvae, crustacean nauplii and the cladoceran *P. avirostris*. The large group 3 comprised the dominant copepod species *O. plumifera*, *C. pavoninus*, *O. venusta* and *C. furcatus*, among others such *P. aculeatus* and *O. media*, also were formed by the chaetognaths *F. hispida* and *M. minima* and the zooplankton groups Oikopleuridae, Siphonophorae and Thaliacea. The slope groups 4 and 5 were grouped by warm water species under the influence of TW, which were constituted by the copepods *F. gracilis* and *C. speciosus* and the appendicularian Fritillariidae at southward slope stations (49 and 50) and the copepod *M. clausi*, the chaetognath *S. serratodentata* and Euphausiacea and were particularly represented in the northern slope stations (IR and BB).

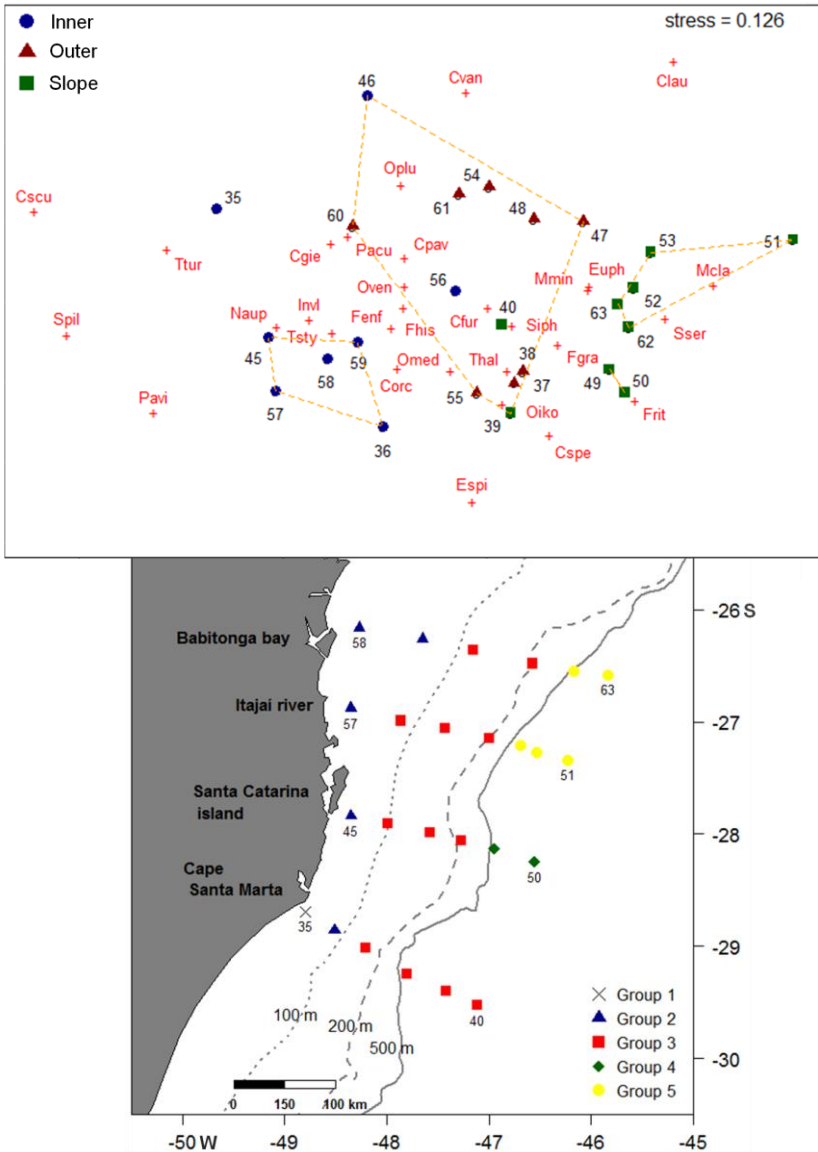


Figure 7. The nMDS plot of species ordination by shelf position and the station clustering performed on the Bray-Curtis similarity using square-root transformed abundance data from most abundant Copepoda, Cladocera, Chaetognatha and the principal taxonomic components of zooplanktonic community along 4 transects off Santa Catarina shelf and slope during early austral summer (December 2010). Note table 1 for zooplankton taxa codes.

There were some special cases, where the taxon represented more than one group and was close to the inner and also outer shelf distribution (e.g., *C. giesbrechti*). Some taxa could be found in the outer and slope stations associated to the influence of both STSW and TW water masses characteristics (e.g. Oikopleuridae and Euphausiacea).

Table 1. Zooplankton taxa codes used in the multivariate analyses (nMDS and CCA)

| Zooplankton groups | Taxa codes |
|--|-------------------|
| Invertebrate larvae | Invl |
| Oikopleuridae | Oiko |
| Fritillaridae | Frit |
| Siphonophorae | Siph |
| Nauplii | Naup |
| Euphauseacea | Euph |
| Thaliacea | Thal |
| Copepoda | |
| <i>Subeucalanus pileatus</i> (Giesbrecht, 1888) | Spil |
| <i>Calocalanus pavoninus</i> Farran, 1936 | Cpav |
| <i>Paracalanus aculeatus</i> Giesbrecht, 1888 | Pacu |
| <i>Clausocalanus furcatus</i> (Brady, 1883) | Cfur |
| <i>Ctenocalanus vanus</i> Giesbrecht, 1888 | Cvan |
| Clausocalanidae | Clau |
| <i>Temora stylifera</i> (Dana, 1849) | Tsty |
| <i>Temora turbinata</i> (Dana, 1849) | Ttur |
| <i>Oithona plumifera</i> Baird, 1843 | Oplu |
| <i>Oncaea media</i> Giesbrecht, 1891 | Omed |
| <i>Oncaea venusta</i> Philippi, 1843 | Oven |
| <i>Corycaeus giesbrechti</i> (F. Dahl, 1894) | Cgie |
| <i>Corycaeus</i> sp. (copepodites) | Corc |
| <i>Farranula gracilis</i> (Dana, 1849) | Fgra |
| Cladocera | |
| <i>Penilia avirostris</i> Dana, 1849 | Pavi |
| <i>Evadne spinifera</i> P.E. Müller, 1867 | Espi |
| Chaetognatha | |
| <i>Ferosagitta hispida</i> (Conant, 1895) | Fhis |
| <i>Flaccisagitta enflata</i> (Grassi, 1881) | Fenf |
| <i>Mesosagitta minima</i> (Grassi, 1881) | Mmin |
| <i>Serratosagitta serratodentata</i> (Krohn, 1853) | Sser |

In the CCA (Fig. 8), the first ordination axis (39%) is mainly created by the distance from the coast in opposition to silicate and chlorophyll-a. Ammonium, nitrite and nitrate contribute mainly to the second axis (24%). Temperature in opposition to salinity, oxygen and phosphate contributes equally to the first and second axes.

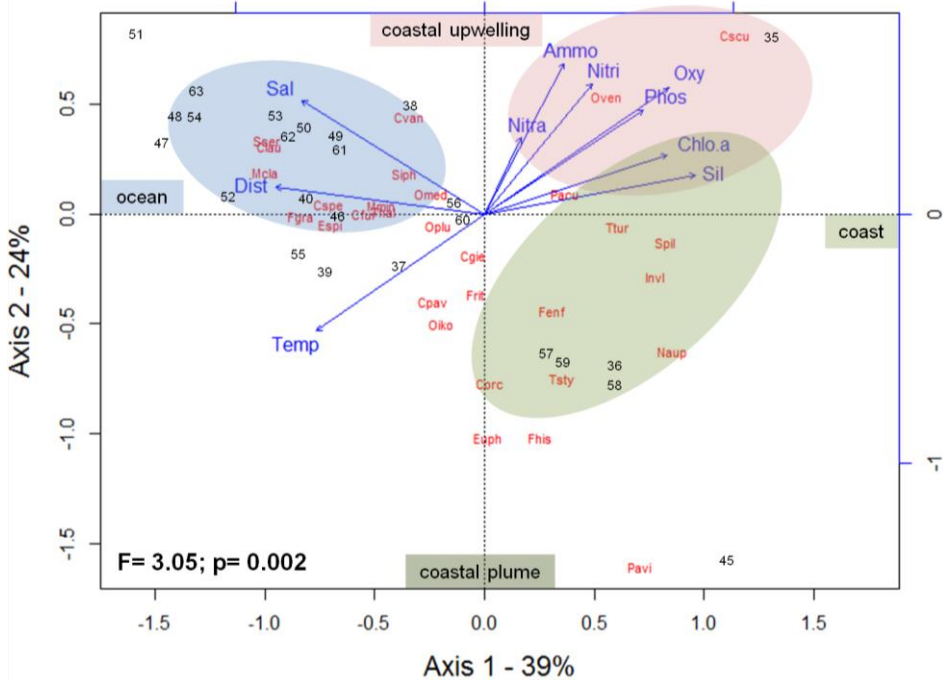


Figure 9. Canonical correspondence analysis on Bray-Curtis similarities from raw data of the most abundant species of Copepoda, Cladocera, Chaetognatha and the principal taxonomic components of zooplanktonic community and standardized environmental variables along 4 transects off Santa Catarina shelf and slope during early austral summer (December 2010). Note table 1 for zooplankton taxa codes.

The species with oceanic affinities such as the copepods *C. furcatus*, *C. vanus*, *F. gracilis*, *C. speciosus*, Clausocalanidae and *M. clausi*, the chaetognaths *M. minima* and *S. serratodentata*, the cladoceran *E. spinifera* and the Thaliacea and Siphonophorae were positively correlated with distance and salinity, as most of outer shelf and slope cluster groups 4 and 5 (Fig. 7).

Maximum silicate and chlorophyll-a were related to station 45 and 35. At station 45, the cladoceran *P. avirostris* was the most abundant species (Figs.4 and 5). At station 35, the copepods *O. venusta* and *C. scutellata* were associated to upwelling environmental features as higher phosphate, oxygen, nitrate, nitrite and ammonium, besides *C. scutellata* reached its highest abundance (Fig. 5) and was especially related to higher oxygen stratification and phosphate.

In the second axis we also had the coastal stations defined by the cluster 2. It was negatively correlated with salinity and distance to the coast, where the cladoceran *P. avirostris*, the chaetognaths *F. inflata* and *F. hispida*, the copepods *T. stylifera*, Corycaeus copepodites and *C. pavoninus*, the appendicullarians Oikopleuridae and Fritillariidae and crustaceans nauplii were remarkable. In addition, coastal associations were also related to the first axis variables as silicate and integrated chlorophyll-a and the taxa invertebrate larvae, the copepods *S. pileatus* and *T. turbinata* occurring in abundance and alternated their dominance mainly in the coastal stations (Figs. 5 and 6).

Finally, the analysis describes the coast-ocean gradient, where temperature, salinity and distance from the coast are the most explanatory variables. Besides, we have the contrast of cold, salty and nutrients rich waters, of the CSM upwelling (35) with the warm, less saline and average nutrient waters under the influence of Babitonga Bay and Itajaí River.

DISCUSSION

The zooplankton community showed the typical inshore-offshore pattern, where the decrease of the abundance and the species replacement followed the transition from the mesotrophic shallow waters to the oligotrophic waters of the Brazil Current. The same trend was described in the extreme south and southeastern Brazilian shelf (Vega-Pérez, 1993; Muxagata, 1999; Sant'Anna & Björnberg, 2006; Lopes *et al.*, 2006; Domingos-Nunes & Resgalla Jr., 2012). However, a very distinct species assembly was detected associated to the northern Babitonga Bay plume and to the southern cold water intrusion as well as the distincted zooplankton patches in only 300 km apart in the outer shelf.

Zooplankton warm water patches in the outer shelf were a product of oceanographic process and species interactions. The present distribution of chaetognaths distinguished warm inner (*Flaccisagitta inflata* and *Ferosagitta hispida*) and warm outer shelf and slope

(*Serratosagitta serratodentata* and *Mesosagitta minima*) species assemblies indicating the influence of the Brazil Current (Resgalla Jr. & Montú, 1995; Resgalla Jr. & Veado, 2006). During spring and summer, the TW has a major influence on mid depth layers and the cyclonic eddies and meanders of the Brazil Current (Campos *et al.*, 2000) may allow the establishment of species assemblies of warm waters. The zooplankton biomass and biovolume peaks in the inner shelf agreed to the *F. enflata* inshore-offshore decrease, suggesting the strong predation nearshore (Ayón *et al.*, 2008). Large zooplankton cores recorded on the outer shelf and slope were also linked to the presence of gelatinous animals, as thaliaceans, siphonophorans and chaetognaths, such as *M. minima*, *S. serratodentata* and *S. bipunctata*.

The importance of salp patches to the zooplankton biomass have been highlighted in the southeast (São Paulo - 24°S) and nearby in the Arvoredo Island (27°S) (Resgalla Jr. *et al.*, 2004). Patches of *Thalia democratica* are expected to increase sharply in the late summer and early autumn (Meneghetti, 1973; Resgalla Jr. *et al.*, 2004). However, singular peaks of *Salpa fusiformis* were found particularly at SCI outer shelf and slope (St. 47 and 50). *S. fusiformis* might have a pronounced impact in the zooplankton biomass acting as biological pumps in the removal of CO₂ fixed by phytoplankton production, being a direct competitor to other herbivores (Esnal, 1981; Esnal & Daponte, 1999).

The remarkable highest abundance of the copepod *O. venusta* (3.020 ind.m⁻³) in CSM upwelling was associated to the high abundance and biovolume values of Hydromedusae, Siphonophorae and the chaetognath species *F. enflata*. High number of predators is expected after the first days of upwelling, when there is a high abundance of herbivorous organisms (Parsons *et al.*, 1984). Our results suggest the trophic interaction of the gelatinous zooplankton huge abundances and the *O. venusta* peak. This poecilostomatoid copepod species is associated with gelatinous zooplankton (especially *Sagitta*, *Oikopleura* and *Salpa*), which singularly attach themselves to a host with the maxilliped and feed on particulate matter on the host, or on its body wall, and piercing the body wall and feeding on body fluids (Wickstead, 1962). A similar behavior was also observed in the upwelling around Cheju Island (Go *et al.*, 1998). While this pronounced abundance indicates the intrinsic favorable environmental conditions created around the upwelling area it also shows that the peculiar feeding behavior known for the family Oncaeidae may lead their populations to a dominance status in upwelled waters.

The dominance of the copepods in the holoplankton has been widely reported in the pelagic ecosystems (Björnberg, 1963, 1981; Campaner, 1985; Bradford-Grieve *et al.*, 1999; Resgalla Jr, 2011) and is due to their unique features related to feeding, survive and reproduce strategies (Kjørboe, 2011). In our study, the copepods displayed a great impact in the total zooplankton biomass (86-95%) following the same trend (Fig. 4A and B). The copepod species assemblages reflect the magnitude of the resulting water masses since Santa Catarina shelf receives tropical and subtropical oceanographic influences. In general, the copepod assemblages were dominated by epipelagic and tropical species and there were numerous herbivorous and predators species that were previously recorded in the southeastern Brazil shelf (Dias *et al.*, 2010) and Southwestern Atlantic Ocean (Björnberg, 1963, 1981). In turn, *Acartia tonsa*, *Subeucalanus pileatus* and *Ctenocalanus vanus* are important cold water species of the SSS assemblages (Avila *et al.*, 2009) and were also found in our study, mainly *C. vanus* in the CSM upwelling zone.

Chaetognaths and cladocerans also reflect the same water masses affinities. In the southern Brazil shelf, *S. serratodentata* is classified as indicator species of subtropical water masses as well as *Pterosagitta draco*, *F. hexaptera*, *M. minima* and *F. enflata* being important warm water contributors (Crelie & Daponte, 2004). Cladocerans can on some occasions have representativeness comparable to that of copepods despite their lower total abundance. The lowest copepod dominance in the inner shelf of SCI (St. 45–67%) occurred under the increase of the cladoceran *Penilia avirostris*. The large abundance of *P. avirostris* indicates the domain of TW in the area (Resgalla Jr. & Montú, 1993; Resgalla Jr. *et al.*, 2008; Domingos-Nunes & Resgalla Jr., 2012).

In this concern, Santa Catarina shelf represents a transitional area between different zoogeographic provinces. During summer, when a shallow thermocline occurs, oligotrophic conditions prevail off the SBB due to TW predominance in upper layers (Matsuura, 1986; Lopes *et al.*, 2006) and characterize the dominance of the warm water species assemblages found in the area added to, the interaction of the Malvinas and Brazil Current in the southern shelf that able the distribution of some cold water chaetognath, cladoceran and copepod species northward (Crelie & Daponte, 2004; Berasategui *et al.*, 2005).

Copepod species that often appear on the shelf during the early upwelling phase (Lopes *et al.*, 2006) were also registered. *Haloptilus longicornis* and *Lucicutia gaussae* (unique at station 35) are cold water

species that usually occurs below the permanent thermocline in oceanic waters. *Ctenocalanus vanus* and *Temora stylifera* are two recurrent species in the upwelling of Cape Frio (23°S) (Valentin, 1984; 1989; Campaner, 1985) and in other areas of the world, such the Benguela upwelling system (Gibbons and Hutchings, 1996; Peterson, 1998). The peak abundance of *C. vanus* was found in the upwelling station, as well as other 18 copepod species. In this naturally eutrophic scenario with abundant food throughout the water column, the dominant herbivores were the copepods *T. stylifera* and *T. turbinata* and associated species, such as *Subeucalanus pileatus*, *Paracalanus aculeatus*, *Parvocalanus crassirostris*, *C. giesbretchi*, *Oithona nana*, *Clytemnestra scutellata* and *Euterpina acutifrons*. They might be the major consumers of phytoplankton and microzooplankton around CSM upwelling.

Recently, *C. vanus* was reported dominating the mid-shelf chlorophyll-rich intrusion usually accumulated on the deep chlorophyll maximum off Itajaí River (Brandini *et al.*, 2013). High densities of zooplankton associated with Itajaí-açu river are related to plankton patches as result of a natural response to enrichment in the water column (Schettini *et al.*, 1998; Rörig *et al.*, 2003) and in response to surface waters convergence (Coutinho de Souza, 2005). Indeed, invertebrate larvae and crustacean nauplii, the cladoceran *P. avirostris* and the chaetognaths *F. enflata* and *F. hispida*, the copepods *T. stylifera* and *T. turbinata*, reached high abundances at the northern shallow stations, and these holoplanktonic species are considered indicator species of TW in warm months (Björnberg, 1981; Resgalla & Montú, 1993; Resgalla Jr. & Montú, 1995; Resgalla Jr. *et al.*, 2008; Resgalla Jr., 2011). However, typical coastal species traditionally reported in the studies related to the presence of the IR plume on the shelf was not recorded, such as *Acartia lilljeborgi* and *Oithona oswaldocruzii* (Björnberg, 1981; Resgalla Jr., 2009; Brandini *et al.*, 2013).

Large copepod species as *T. stylifera*, *Oithona plumifera*, *Oncaea venusta*, *T. turbinata*, *Centropages velificatus* and *A. lilljeborgi* are considered dominant in very shallow areas off Santa Catarina, sampled with a large mesh size (330 µm – Domingos-Nunes & Resgalla Jr., 2012). The use of a large mesh size net underestimated the abundance of copepodites and small size species (<1 mm). The small size spectrum copepod represents the most abundant metazoans on Earth (Turner, 2004) and comprises many numerically diverse genera (e.g. *Paracalanus*, *Oithona*, *Oncaea*) in our study. The mesh size also explains the higher abundance obtained in our study (average abundance 1.650 ind. m⁻³) compared to those authors (153 ind.m⁻³). Additionally,

the species richness and abundance underestimation is a usual problem in copepod ecology and it is often reported as a mesh size issue (Campaner, 1985; Nakamura & Tuner, 1997; Gallienne & Robin, 2001; Dias *et al.*, 2010). Despite the importance of small copepods in oligotrophic waters, they have historically been undersampled due to the use of nets with meshes $> 200\text{-}333\mu\text{m}$. Failure to adequately account for small copepods may cause serious underestimations of zooplankton abundance and biomass, of the copepod grazing impact on phytoplankton primary production, zooplankton-mediated fluxes of chemicals and materials and trophic interactions in the sea (Turner, 2004).

The CCA analysis (Fig. 9) disclosed the general picture of the whole oceanographic structure. It described the cross-shelf distribution of the zooplankton clearly disguising neritic from oceanic assemblages in response to contrasting oceanographic features across the shelf, defining the coast-ocean gradient and the two coastal processes. The first case showed the importance of higher temperature, salinity and distance from the coast clearly discriminating the gradient across the coast, where TW prevailed in the mid and outer-shelf. The opposite (axis 2) presented the physical processes mentioned above, the CSM upwelling station was associated to high inorganic nitrogen, oxygen stratification and lower temperature values in opposition to the BB plume with low salinity, short distance from the coast and high temperatures. These processes indicated the inner shelf as a transition between the tropical and subtropical environment and therefore the zooplankton composition also a shift between the south and southeast shelves assemblages (Valentin, 1984; Lopes *et al.*, 1999; Resgalla *et al.*, 2008; Resgalla Jr., 2011). In the warm months, the northeast winds transport the surface waters offshore and allows the entrance of deep cold waters from SACW (Resgalla Jr. *et al.*, 2001) and the plume fronts from the Itajaí-açu river and the Babitonga Bay estuary northward sporadically peaks and may form the local coastal water (Schettini *et al.*, 1998; Schettini *et al.*, 2005). These circumstances could be seen in the uniqueness of the station 35 and the coastal assemblage, where the plume stations presented great similarity with the southern inner shelf, as revealed by the cluster and nMDS analyses (Fig. 7 and 8).

In conclusion, our study supports the hypothesis that in the Santa Catarina shelf and slope, the advection of water masses and the nearshore oceanographic structure played an important role in the changes of the meso-scale distribution of the major holoplanktonic groups studied. In addition, typical species of Tropical Water from the

Brazil Current, shifts their dominance due to estuarine plume water extension in the north, cold water intrusions southward and the meandering of the BC offshore. Species are more abundant at these distinctic areas under the influence of specific physico-chemical characteristics in the water column, which provide the similarities shared with the chaetognath, cladoceran and copepod species of the S-SE Brazilian Shelf. This results may be relevant for further studies performed to assess the role of the size structure of the different plankton compartments in relation to the mesozooplankton abundance and trophic interactions.

ACKNOWLEDGEMENTS

We would like to thank the Brazilian Navy and all crew from Cruzeiro do Sul vessel for their logistical support during fieldwork. We are also grateful to the researches that helped conducting the intensive field work and analysis in the laboratory. Dr^a. C.O. Dias (UFRJ) who helped to improve copepods identification. Dr. C.A.E. Garcia, Dr^a. A.M. Ciotti (USP), and Dr. R. Pollery (UFRJ), who provided physical, chlorophyll-*a* and nutrient data, respectively. M.Sc. L.C.P. Macedo-Soares (UFSC) who assisted with statistics and graphs. CAPES for the first author grant.

3 CAPÍTULO 2 – Plankton size structure under distinct oceanographic systems in a continental shelf, southeastern Brazil (26-29°S)

Manuscrito formatado para submissão segundo as normas da revista Marine Ecology Progress Series.

Plankton size structure under distinct oceanographic systems in a continental shelf, southeastern Brazil (26-29°S)

ABSTRACT: Spatial size structure of the planktonic food web considering nanoplankton, microphytoplankton, microzooplankton and copepods was studied in the Santa Catarina shelf, S-SE Brazilian Shelf. Different oceanographic scenarios were sampled in the shelf, comprising an estuarine plume, a coastal upwelling, the shallow coast and the shelf. Temperature, salinity and chlorophyll-*a* profiles disclosed the upwelling at Cape Santa Marta (CSM; $T < 20^{\circ}\text{C}$) and the extension of the Babitonga Bay (BB) plume in the shelf up to 120 km. These features were related to low nitrogen values (nitrate $< 10 \mu\text{M}$) in the upper 50 m, nanoflagellates dominance ($> 79\%$, $\sim 23.000 \text{ cel.L}^{-1}$), the relatively low microphytoplankton (often $< 2.000 \text{ cel.L}^{-1}$) and high copepod abundances ($> 6.000 \text{ ind.m}^{-3}$) at the inner-shelf. Besides, the microphytoplankton species assemblies were of typical coastal/estuarine waters (*Prorocentrum* spp.) at the BB plume and of pennate diatom species (*Thalassionema* spp., *Thalassiothrix* sp.) at the CSM upwelling. Both processes were associated also to opportunistic copepod species, as the herbivorous *Temora turbinata* and the detritivorous *Oncaea venusta*, in each area. In the whole mid and outer shelf the plankton was mainly composed of warm water species, usually registered in Tropical Water. Nanoflagellates ($\sim 50\%$), dinoflagellates and non-loricate ciliates and the copepods *Clausocalanus furcatus* and *Oncaea venusta* were widespread but occurred with low values. Variations in abundance and species distribution, both phyto and zooplankton, were strongly associated with the size structure of the planktonic assemblages and can be summarized in the context of a continuum between the extremes state of the herbivorous and the microbial food webs characterizing a multivorous food web.

KEY WORDS: Nanoplankton, microplankton, copepods, upwelling, estuarine plume, pelagic food webs, South Brazilian Bight

INTRODUCTION

The plankton size structure is an important factor controlling the carbon cycle in aquatic ecosystems (Legendre & Le Frèvre 1991, Calbet & Landry 2004) as well as trophic interactions in the pelagic food web (Pomeroy 1974, Landry 1977, Finkel 2007). Dominance of any size category in the photic layer will be facilitated by its ability to

solve the problems caused by flotability, uptake of nutrients, growth and grazing impact (Margalef 1978, Malone 1980; Litchman & Klausmeier 2008). Zooplankton community structure also has a large number of properties that are influenced by the specimens size, such as prey size, feeding and growth rates, metabolism, mortality and vital rates, which can be used as a proxy for many size traits within the taxonomic groups (Litchman et al. 2013). The resulting size structure will strongly affect the food web by determining the material and energy flows between primary producers and consumers and therefore the overall efficiency of marine ecosystems (Takahashi & Bienfang 1983, Peña et al. 1990).

The phytoplankton size structure reflects the local hydrography (Arin et al. 2002). The importance of very small pico- (<2 μm) and nanoplanktonic cells (2-20 μm) as primary producers prevails in nutrient depleted areas where long and complex food webs prevails (Platt & Li 1986). Large-cell based phytoplankton communities (>20 μm), are dominated by large diatoms associated with shorter and less complex trophic interactions and is frequently related to higher hydrodynamism and higher nutrient concentrations (Arin et al. 2002), known as the “classical food chain” (Cushing 1989). However, both situations are simplifications of a more complex scenario, which large diatoms related to the occurrence of episodic nutrient pulses in oligotrophic waters, although reduced in numbers, may be the most important primary producers in areas where the injection of nutrients provides the subsurface chlorophyll maxima (Odebrecht & Djurfeldt 1996, Brandini et al. 2013) and sustains opportunistic herbivorees, such as large calanoid copepod species (Guenther et al. 2008; Brandini et al. 2013). When small phytoplankton and bacteria dominate, the carbon produced is channeled through flagellates and ciliates before reaching the omnivores-dominant mesozooplankton species (Guenther et al. 2008).

The autotrophic and heterotrophic plankton were combined in the same research providing new insights about the plankton community structure and trophodynamics in the S-SE Brazilian shelf. A preliminary view of the microbial plankton structure (Tenenbaum et al. 2001), a full array of planktonic compartments related to carbon fluxes to higher trophic levels (Guenther et al. 2008, 2012, Guenther & Valentin 2008), copepods and ichthyoplankton dynamics at the Subtropical Shelf Front (Muelbert et al. 2008) and phytoplankton and zooplankton structure highlighting the role of diatoms and copepods species in the planktonic food web (Brandini et al. 2013) comprised the major findings of the spatio-temporal variability in the pelagic food web structure. Mesozooplankton studies, especially copepods, were mainly associated

to water masses (reviewed in Lopes et al. 2007), rather than linked to trophic interactions in the planktonic food web.

The grazed phytoplankton are channeled up through the food web to higher trophic levels such as flagellates, ciliates, as well as small metazoans e.g. copepod nauplii, consisting the microzooplankton (Calbet & Saiz 2005, Calbet 2008). These organisms occupy a key and midway position in flow of organic matter as top predators within the microbial loop (Sherr & Sherr 2002), feeding mainly on bacteria and nanoflagellates (0.2 to 20 μm) (Verity 1986, Fenchel 1988, Capriulo 1990), size classes generally not captured efficiently by mesozooplankters, such as copepods and other crustaceans (Lynn & Montagnes 1991, Pierce & Turner 1992, Calbet 2008). Despite the great importance, the microzoo-mesozooplankton link is traditionally overlooked in plankton studies (Calbet 2008, Montagnes et al. 2010).

Copepods are the keystone trophic links in aquatic ecosystems dominating the mid trophic-level position and consume large amounts of microplankton, in turn, they are eaten by fish and other predators thereby transferring energy and carbon to higher trophic levels (Calbet 2008). Hence, the small size spectrum ($< 1\text{mm}$) are the most abundant metazoans on Earth (Turner 2004) and are an important determinant of the potential size of the fishery (Bradford-Grieve et al. 1999) generating about 70% of the herbivorous mesozooplankton biomass in the South Brazilian Bight (SBB) (Lopes et al. 2006) and at wider scale, might account for 90-97% of the biomass of the southwestern Atlantic Ocean (Boltovskoy et al. 1999).

Due to the strong stratification in summer, the subtropical waters of southeastern Brazilian shelf are regarded as an oligotrophic ocean of relative low phytoplankton abundance, low biomass, and regenerative production instead of new production (Metzler et al. 1997, Brandini 2006). In contrast, this region is characterized by several physical and biological processes, as the frontal zone around the Cape Santa Marta, where intermittent upwelling brings nutrients into the upper layers of the water column. The Babitonga Bay plume is also an important seasonal fertilization source for Santa Catarina inner shelf (Schettini et al 2002, Resgalla Jr. 2011), and both features eventually keep the system in a persistent mesotrophic state. In this context, we seek to understand the contribution of nano and microplankton and the further relationship with the copepods dominant species under the nearshore upwelling and the estuarine plume contrasted to the oceanic waters conditions along cross-shelf transects off southeastern Brazilian shelf. The main hypothesis was that, the two main processes of nutrient

enrichment on the Santa Catarina inner shelf result in distinct planktonic size structure, in terms of species distribution and trophic interactions. Besides, the general plankton trophic structure will be related to physical features of the shelf, where larger phytoplankton cells should prevail in the inner shelf in contrast to the small producers dominating in the outer shelf (Fig. 1).

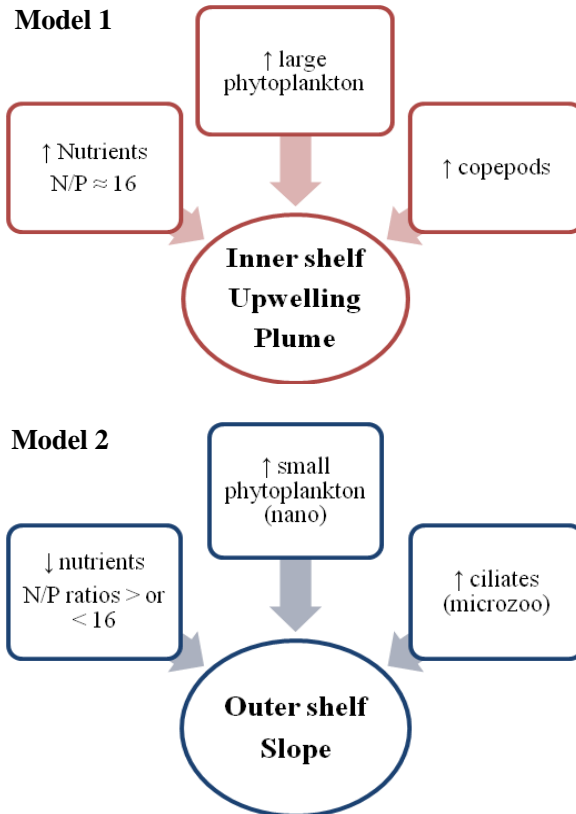


Fig. 1. Hypothetical models of the variability of plankton size structure in the planktonic food webs in relation to the shelf location and oceanographic processes. Models based in specific literature (Pomeroy 1974, Cushing 1989, Goldman 1993, Susini-Ribeiro, 1999, Tenenbaum et al. 2001, Arin et al. 2002).

MATERIAL AND METHODS

Study area

The Santa Catarina continental shelf is located in the Southwestern Atlantic water in the limit of the South Brazilian Bight (23-28.5°S) (Fig. 2A). The surveyed area is located near the entrance of the Babitonga Bay (26°S) and at the Cape Santa Marta (29°S). The oceanographic cruise was conducted during austral early summer (December 2010) at 12 stations in 2 cross-shelf transects (Fig. 2B).

The main water masses occurring on the shelf are the Tropical Water (TW), an oligotrophic water mass, occupies the first 200 m of the water column, being carried by the Brazil Current off the 200 m isobath with temperatures higher than 20°C and salinities higher than 36. The South Atlantic Central Water (SACW) predominates in 200 to 500m depth below the TW, with temperatures lower than 18.5°C and salinities higher than 35.3, representing a permanent thermocline about the 20 to 50 m depth (Matsaura 1986). On the inner and mid-shelf, until the shelf-break, there is the Subtropical Shelf Water (STSW – $T > 18.5^{\circ}\text{C}$, $35.3 < S < 36$), less saline and highly influenced by the continental water discharges, resulting from the mix of the coastal water and TW (Piola et al. 2000, 2008, Möller et al. 2008). Chlorophyll *a* concentrations are low in the BC ($< 0.5 \mu\text{g}\cdot\text{L}^{-1}$), while upwelling of the nutrient rich SACW and freshwater outflow induce Chlorophyll *a* increases up to $> 5 \mu\text{g}\cdot\text{L}^{-1}$ (Gaeta & Brandini 2006).

During the winter, the freshwater discharge from Rio de La Plata and the hydrological basin of the Patos Lagoon influence biological productivity along their northward path forced by southeastern winds. During the summer, northeastern winds lead to the retreat of the freshwater plume, and induce coastal upwelling of the South Atlantic Central Water (SACW) (Acha et al. 2004, Piola et al. 2008), mainly in Cape Santa Marta, due to the steep and narrow shelf (120 km wide), compared to the shelf width northwards (up to 200 km) (Matsaura 1986, Campos et al. 2013). Meteorological fronts cause sudden changes of wind direction to southeastern and the whole established pattern of upwelling and alongshore currents may reverse to a downwelling condition. The northern extreme is strongly influenced by continental inputs and several river systems such as the Babitonga Bay estuary, Itapocu, Itajaí-açu and Tijucas rivers (Carvalho et al. 1998).

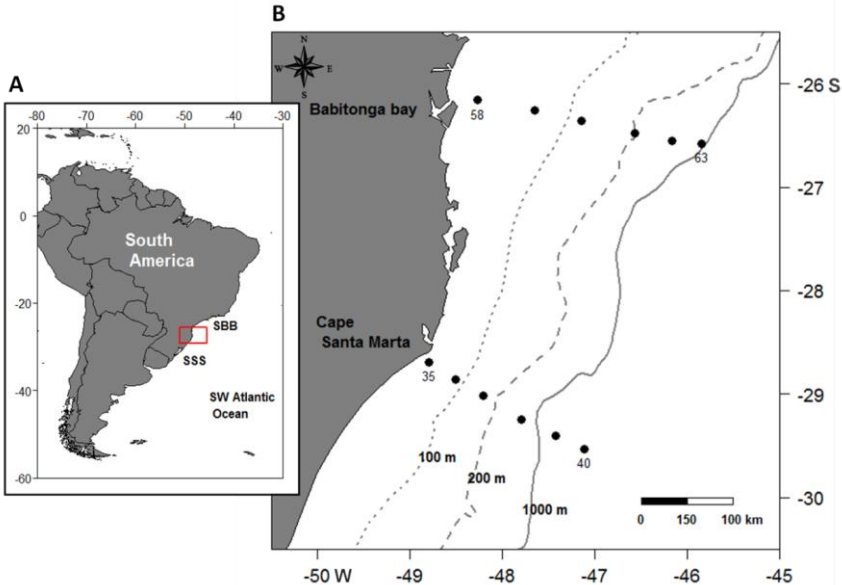


Fig. 2. A. Location of the Santa Catarina shelf between the South Brazilian Bight (SBB) and the Southern Subtropical Shelf (SSS). B. Sampling stations off Babitonga Bay and Cape Santa Marta, during early austral summer (December 2010).

Hydrographical measurements and plankton sampling

Water temperature, salinity, *in vivo* chlorophyll *a* fluorescence and dissolved oxygen were determined from CTD vertical profiles, using a Sea Bird Electronics profiler casts. Water samples were collected to determine the chlorophyll *a*, the nutrient concentrations (ammonium, nitrite, nitrate, phosphate and silicate), the nanoplankton and the microplankton quantification, using a 5-L Niskin bottles, at selected depths (3 or 5 m, maximum fluorescence depth and base of the mixing layer). Chlorophyll and nutrient concentrations were estimated following methods described in Welschmeyer (Welschmeyer 1994) and Grasshoff (Grasshoff et al. 1983), respectively.

Vertical plankton hauls were performed from the maximum fluorescence depth up to the surface in deep stations, from 10 m above the sea floor when the water column was homogenous and from about 10 m depth at shallow stations (max. 20 m depth). A conical-cylindrical net with a 0.5-m \varnothing mouth and 200- μ m mesh equipped with a flowmeter (General Oceanics) was used. The mean volume of water filtered by the

net was $30.2 \pm 15.7 \text{ m}^3$. All samples were immediately fixed and preserved in 4% buffered seawater-formaldehyde solution.

The maxima *in vivo* chlorophyll *a* fluorescence depths ranged from 10 to 95 m, and the plankton sampling depth ranged from 14 to 100 m. The distance from the coast ranged from 11 to 280 km. The mean volume of water filtered by the net was $30.2 \pm 15.7 \text{ m}^3$.

Nanoplankton and Microplankton analyses: counting and identification

Prior to phytoplankton cell counts, the sedimentation method was performed (Utermöhl 1958). First of all, the samples preserved in a 4% Formaldehyde solution were decanted in a becker for 4 days and were siphoned to 400 mL. Secondly, 100- mL of the concentrated sample was left to settle for 24 hours and then, was observed using an inverted microscope.

From the fixed water sample, plankton populations were analyzed by size fraction of the organisms (Sieburth *et al.*, 1978). For nanoplankton counting, cells with a diameter between 5-20 μm were counted at the central stripe at 400x magnification. In stations, the less abundant in organisms more stripes were done until at least 400 individuals were counted. For microphyto- and microzooplankton ($> 20 \mu\text{m}$), half of the sedimentation chamber was counted at 200x magnification. Microphytoplankton was identified to the lowest taxonomic level possible and divided into diatoms (centric and pennates), cyanobacteria, coccolithophorids and flagellates following the taxonomic descriptions of Tomas (1997) while atecate and thecate dinoflagellates (Balech, 1988; Steidinger & Tangen, 1997; Tenenbaum, 2006). The microzooplankton comprised ciliates aloricate and tintinnids (loricate) (Souto 1981, Fernandes 2004a, 2004b, Tenenbaum 2006) and foraminiferans (not identified at the species level). The majority of the nanoplankton cells were identified solely as morphotype.

Mesozooplankton analyses: counting and Copepoda identification

Zooplankton was quantified through wet biomass (Boltovskoy 1981) for all 12 samples. Samples were subsampled with a Folsom splitter (McEwan *et al.* 1954) in fractions of 1/2 or 1/4, before counting. After that, 10-mL aliquots were taken for copepod counting (Boltovskoy, 1981), and at least 100 individuals in each sample were sorted.

Copepods were identified and counted under stereoscopic and optical microscopes to the lowest possible taxonomic level following descriptions by Björnberg (1981), Bradford-Grieve *et al.* (1999), Campos-Hernández & Suárez (1999) and Dias & Araújo (2006). The developmental stages were also determined and considered as a proxy for the community size structure, thus they were separated in nauplii, copepodites and adults. In addition, adults were classified in adult 1 (size class: 0.5-1 mm), adult 2 (size class: 1.1-2 mm) and adult 3 (size class: 2.1-3 mm) in agreement with the size range presented in the Boltovskoy (1981) to female and male adults.

Statistical treatment

The nonparametric Spearman correlation coefficients (Zar 2010) was used to test the relationship between all plankton abundance and size categories to the total phytoplankton (chlorophyll-a) and zooplankton biomass.

The BIO-ENV routine was applied to find the best subset of environmental variables, so that the Euclidean distances of scaled environmental variables have the maximum (rank) correlation with community dissimilarities (Clarke & Ainsworth 1993). In this case, the similarity matrix of the community is fixed (nanoplankton: 10 taxa, microplankton: 47 taxa, copepods: 20 species), while subsets of the environmental variables are used in the calculation of the environmental similarity matrix (10 variables). A Spearman rank correlation coefficient were then calculated between the two matrices and the best subset of environmental variables were then identified and further subjected to a permutation test to determine significance (SIMPROF; 999 permutations).

The similarity percentages analysis (SIMPER, Clarke 1993) was performed to identify which species that most contributed to similarities within groups. For this, the sample groups were defined *a priori* taking into account the main oceanographic features of the area (Table 1).

For all multivariate analyses, microphyto- and microzooplankton were considered as microplankton (> 20 µm). The fraction which has been traditionally studied as microphytoplankton, however, includes a large number of species known to be mixotrophs and absolute heterotrophs, that is, “microphytoplankton” corresponds to organisms with a wide spectrum of nutritional strategies (Tenenbaum *et al.* 2001). Thus, our position is in better agreement with the size

structure approach proposed in the study for plankton community, as the former dichotomy have been questioned in the current research (Flynn et al. 2013). All the multivariate analyses were performed using the PRIMER version 6 with PERMANOVA + add on software package (Clark & Gorley 2006, Anderson et al. 2008).

Table 1. Oceanographic features of the sampling stations for the groupings of the SIMPER analysis

| Station | Distance from the coast (km) | Local depth (m) | Sample depth (m) | General oceanographic features | SIMPER groups |
|----------------|-------------------------------------|------------------------|-------------------------|---------------------------------------|----------------------|
| 35 | 11 | 53 | 14 | coastal and shallow | upwelling |
| 36 | 45 | 95 | 58 | coastal and shallow | upwelling |
| 37 | 79 | 130 | 68 | mid-shelf | outer shelf |
| 38 | 127 | 589 | 70 | mid-shelf | outer shelf |
| 39 | 166 | 1375 | 85 | offshore and deep | slope |
| 40 | 200 | 1999 | 100 | offshore and deep | slope |
| 58 | 33 | 28 | 25 | coastal and shallow | plume |
| 59 | 96 | 66 | 37 | coastal and shallow | plume |
| 60 | 147 | 124 | 49 | mid-shelf | outer shelf |
| 61 | 207 | 242 | 66 | mid-shelf | outer shelf |
| 62 | 247 | 525 | 85 | offshore and deep | slope |
| 63 | 280 | 995 | 85 | offshore and deep | slope |

BIO-ENV models

The explanatory matrix for the BIO-ENV analysis (Clarke & Warwick 1993) were formed by biotic and abiotic variables following an *a priori* categorisation which characterise nutrient supply (environmental variables) and selective grazing (Copepoda abundance size structure) as suggested controls for the subsurface distribution of nanoplankton, microphyto- and microzooplankton similarity matrices (Bray-Curtis). However, in the Copepoda species similarity matrix model, the explanatory matrix included environmental variables as well as resource driven variables (phytoplankton abundance size structure). The heuristic approach adopted here is to display the selecting of possible quantitative biological interactions between the plankton

compartments which delineate strategies structuring plankton communities.

Prior to the analysis, Spearman correlations were performed to verify collinearity between the variables, generally the ones which exceeded a upper limit value of 0.75 were excluded from the model. Since explanatory variables strongly inter-correlated amongst themselves can generate other combinations and also can inflate the correlation subsets, it is important to remove such variables to provide a reliable result (Clarke & Warwick 1993).

Explanatory variables included in the phytoplankton model were temperature ($^{\circ}\text{C}$, average), dissolved oxygen (ml.L , average), nitrate (NO_3 , μM , average), orthophosphate (PO_4 , μM , average), silicate (Si , μM , average), chlorophyll *a* (mg.m^{-3} , average), zooplankton wet biomass (mg.m^{-3}), nauplii (ind.m^{-3}), copepodites (ind.m^{-3}), adult copepods (ind.m^{-3}). The set of explanatory variables for Copepoda model were temperature ($^{\circ}\text{C}$, average), dissolved oxygen (ml.L , average), nitrate (NO_3 , μM , average), orthophosphate (PO_4 , μM , average), silicate (Si , μM , average), chlorophyll *a* (mg.m^{-3} , average), zooplankton wet biomass (mg.m^{-3}), nanoplankton (cel.L^{-1}), microphytoplankton (cel.L^{-1}), microzooplankton (cel.L^{-1}).

RESULTS

Environmental conditions

Detailed descriptions of the physical oceanography and water masses during the cruise can be found in Macedo-Soares et al. (2014), Brandão & Freire (*in press*) and Becker & Freire (chapter 1). However, the relevant features are presented in the vertical distribution of temperature, salinity, oxygen and fluorescence as shown in Fig. 3 and nutrients concentrations in Fig. 4.

In Cape Santa Marta (CSM - Fig.3A), St. 35 had unique features, with the sharp decrease of temperature, *in vivo* chlorophyll *a* fluorescence and oxygen with depth and a strong isocline was found at 20 m, together with the salinity increase. On the other hand, Babitonga Bay coastal station (BB – St. 58) had no clear isoclines. Salinity reached values less than 34, temperature was constant and higher than 22°C . Fluorescence increased with depth and dissolved oxygen was constant and close to 5 mL.L^{-1} (Fig. 3B).

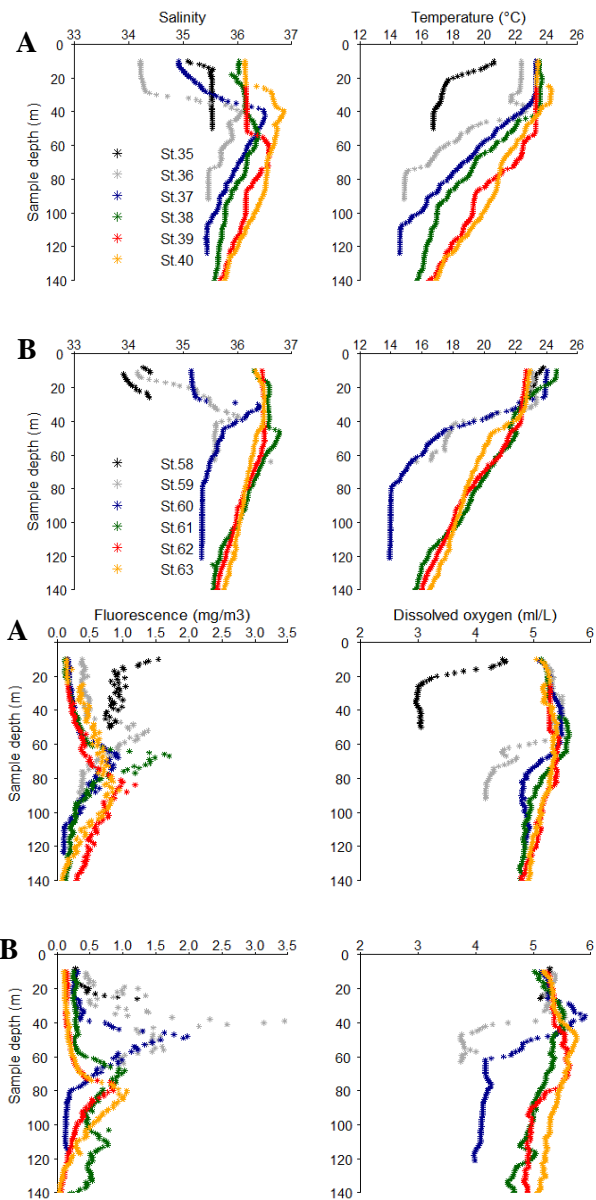


Fig. 3. Vertical distribution of the hydrographic variables off Cape Santa Marta (A) and Babitonga Bay (B) until the maximum zooplankton sampling depth, during early austral summer (December 2010).

The outer shelf and slope stations (38 to 40 and 61 to 62) had a similar pattern in both transects. Salinity and temperature were typical of TW in the upper layers and the influence of SACW was registered under 100 m depth. Fluorescence peaked in the top ~70 m and dissolved oxygen was almost constant with depth.

Nitrate concentrations were very low in the upper layers and an increase in nitrate concentrations were recorded in the outer shelf only in CSM deeper stations (>50 m; Fig. 4A). As it is possible to see, the N:P ratios in the euphotic zone is nitrogen deficient while the N:P ratios becomes normal concerning the Redfield ratio (16:1) only in the deeper outer shelf stations (> 20 m). However, the phosphate concentrations were higher in the inner and outer shelf of CSM (>0.5 μM and ~1 μM , respectively). In the BB stations low phosphate concentrations were recorded in the surface (<0.5 μM) and a pronounced increase occurred just below 20 m depth in the outer shelf (>1 μM). The silicate were highest in the subsurface waters of CSM (>5 μM) inner shelf (St. 35). In BB stations, the silicate concentrations were constant with depth and often lower than 5 μM (Fig. 4B).

In general, the parameters temperature, salinity, dissolved oxygen, fluorescence and nutrients displayed great differences as sources of variability. In these terms, three distinct features were defined for the sampling areas included in this study: upwelling at the inner shelf of CSM (St. 35 – $T < 20^\circ\text{C}$ in the 14 m depth, $S > 34$ and higher nutrients concentrations), BB estuarine plume (St. 58 - $T < 22^\circ\text{C}$, $S < 34$) and the oceanic conditions ($S > 36$).

Relationships between plankton size structure to the chlorophyll *a* and zooplankton biomass

Most of the plankton abundance presented a positive and significant correlations with Chlorophyll-*a*, except the nanoplankton abundance. Microphytoplankton and Chlorophyll-*a* presented the stronger positive and significant correlation ($r = 0.772$), as well as copepodites ($r = 0.718$) and adults copepods ($r = 0.725$). Microzooplankton and nauplii presented a moderate correlation with chlorophyll-*a*, 0.616 and 0.567, respectively. As zooplankton biomass, adults copepods were the only size category that presented higher positive and significant correlation ($r = 0.715$). Thus, no significant correlations were found between nano- and microplankton size structures and zooplankton biomass.

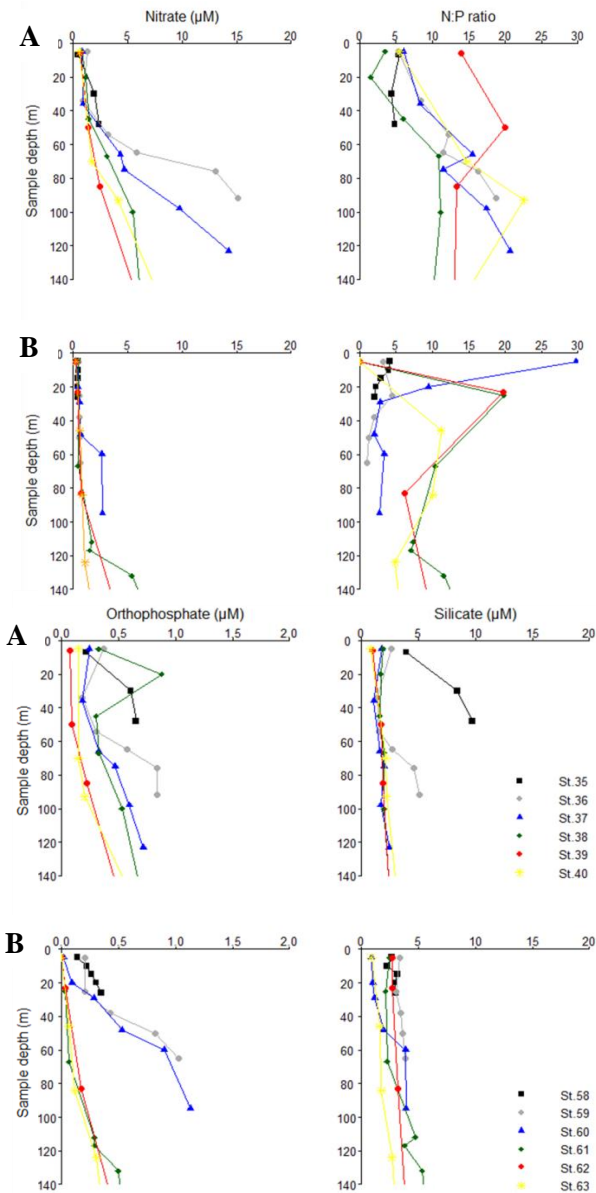


Fig. 4. Vertical distribution of the nutrient concentrations off Cape Santa Marta (A) and Babitonga Bay (B) until the maximum zooplankton sampling depth (107 m), during early austral summer (December 2010).

Phyto and microzooplankton composition and the relative contribution of the size fractions

The relative contributions of the different planktonic taxa and size categories to the total abundance of the nano and microplankton assemblages are depicted in Fig. 5. The small flagellates (5-20 μm) dominated the different taxonomic groups, mostly in the CSM transect and BB outer shelf stations ($> 60\%$; Fig. 5A). Coccolithophorids (37%), dinoflagellates (36%) and diatoms (21%) reached higher abundances in the inner and mid-shelf at BB plume waters, whereas flagellates decreased abruptly (19-49%; Fig. 5A) and microphytoplankton made up a bigger contribution to the phytoplankton communities ($\sim 20\%$; Fig. 5B). Ciliates were present in all samples but in very low numbers.

Nanoplankton was the most abundant size category in all samples (Fig. 5B – 79-96%), mainly because flagellates dominated this size category (22-82%), except for a single sample when flagellates decline and coccolithophorids had a pronounced increase (40%; St. 60). Coccolithophorids, centric diatoms and athecate dinoflagellates contributed rather similar ($> 20\%$) in the BB inner station (St. 58) where nanoflagellates decreased (Fig. 5C). Microphytoplankton made marked contributions during the influence of the estuarine plume ($\sim 20\%$ – Fig. 5B) and was composed mainly by thecate dinoflagellates (St. 58 – 72%), centric and pennate diatoms (St. 59; 28% and 54%, respectively; Fig. 5D). In BB outer-shelf, the thecate dinoflagellates were higher in the mid and outer (32-42%) and athecate taxa were located mainly in the outer-shelf (38-54%). In CSM stations, pinnate diatoms were the principal component in the coastal upwelling station (78%; St. 35). Thecate dinoflagellates and coccolithophorids contributed mostly to the middle and outer-shelf waters. Cyanobacteriae and flagellates composed the less representative groups in the microphytoplankton and had major contributions in the middle and outer stations, respectively (Fig. 5D). The contribution of non-loricate and tintinnid ciliates were had great variability, except at the coastal upwelling station (St. 35) dominated by tintinnids. Even though non-loricate ciliates reached higher abundances at mid-shelf in the two transects, while foraminiferans and tintinnids had greater importance at outer-shelf (Fig. 5E).

In general, nanoflagellates dominated the entire sampling areas mostly in CSM transect. The microphytoplankton structure had high numbers of pennate diatoms at CSM upwelling and both thecate dinoflagellates and diatoms represented mostly the BB plume waters.

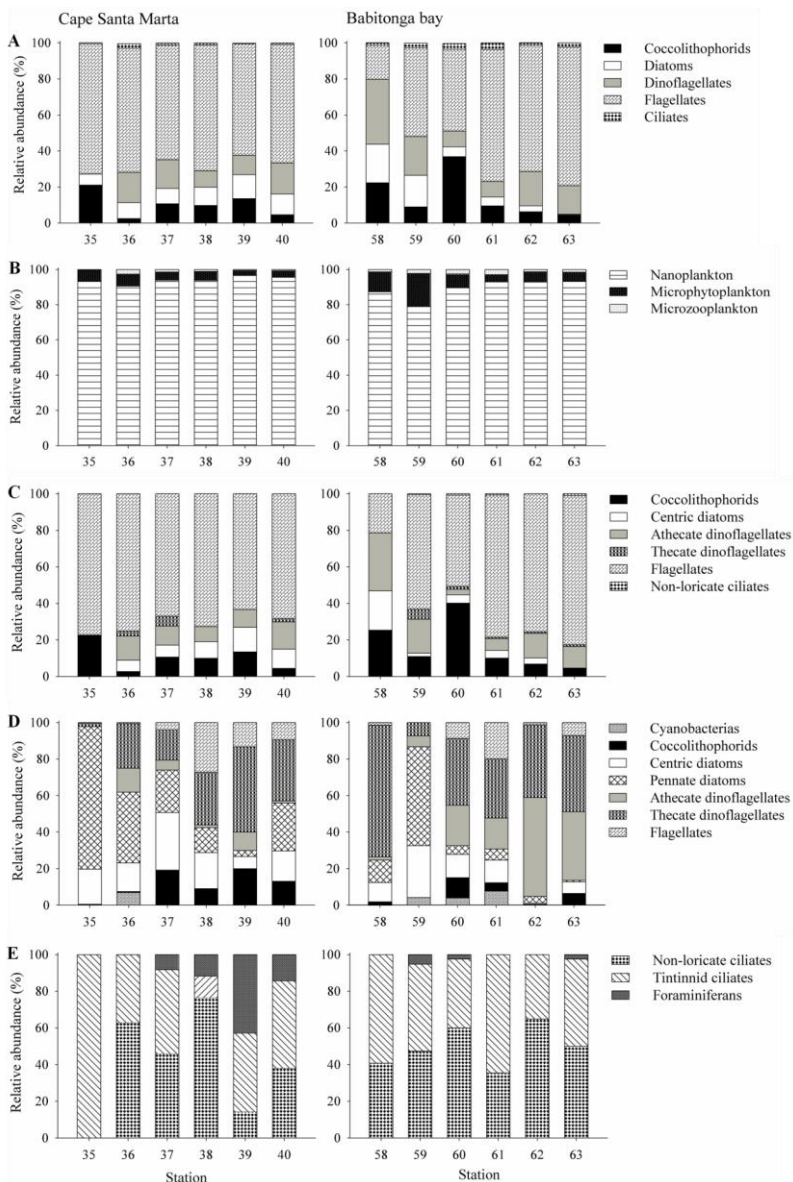


Fig. 5. Relative contributions of the main taxa and size fractions to the abundance (cel.L^{-1}) of the nanoplankton, microphyto- and microzooplankton off Cape Santa Marta and Babitonga Bay, during early austral summer (December 2010). A: total by taxonomic group. B: total by size fractions. C: taxonomic groups in the fractions of nanoplankton, of microphytoplankton (D) and of microzooplankton (E).

Finally, the microzooplankton was dominated by ciliates that presented high variability in all stations. Although, the non-loricate ciliates abundance were higher at mid-shelf, whereas both foraminiferans and tintinnid ciliates were most abundant in the outer-shelf.

The relative contribution of the different copepods size fractions and feeding patterns

The copepods was a dominant fraction in the mesozooplankton sampled (Fig. 6A).

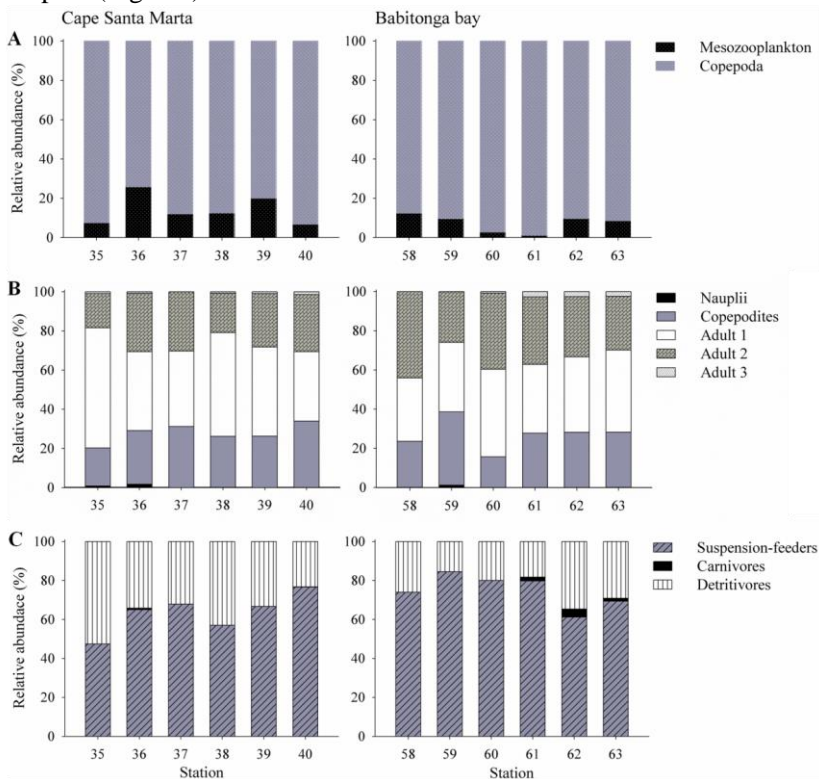


Fig. 6. Copepods relative abundance (ind.m^{-3}) and size fractions off Cape Santa Marta and Babitonga Bay, during early austral summer (December 2010). A: Copepoda abundance in relation to the total mesozooplankton. B: Copepoda by size structure (Adult 1: 0.5-1 mm; Adult 2: 1.1-2 mm; Adult 3: 2.1-3 mm). C: Copepoda abundance in relation to the feeding patterns.

Some higher mesozooplankton values were found in the CSM shelf, accounting for >20% of the total abundance. Small adult copepods (Adult 1) constituted the dominant size fraction in the CSM transect (35-61%) while the medium-sized adult copepods (Adult 2) were most representative in BB waters (26-44%). Copepodites (16-37%) were also an important component and were distributed homogeneously throughout the sampling area with highest contribution at St. 59 (37%; Fig. 6B). Nauplius and large copepods (>2 mm) were always a small fraction of the total abundance, corresponding only 1-2% of the coastal stations and 1-3% of the outer stations, respectively. About the feeding patterns, most of copepods were classified as suspension-feeders (47-85%) being the highest values registered in the BB shelf waters and secondly, the copepods were best represented by the detritivores (15-53%). The lowest contribution of suspension-feeders and the highest contribution of the detritivores were found in the upwelling station (Fig. 6C).

Composition and abundance of the nanoplankton, microplankton and copepod assemblages

In general terms, the smaller size fractions (Fig. 7A) had higher abundance in the coastal processes ($17.10^3 - 30.10^3$ cel.L⁻¹) than in the entire offshore stations (mean abundance > 5.10^3 cel.L⁻¹). Nanoplankton was mainly represented by nanoflagellates ($\sim 23.10^3$ cel.L⁻¹) and the coccolithophorid *Umbilicosphaera* sp. ($\sim 7.10^3$ cel.L⁻¹) in the coastal upwelling station. Gymnodiniales (> 2.10^3 cel.L⁻¹ – St. 59) and small centric diatoms (> 1.10^3 cel.L⁻¹ – St. 40 and 58) in the stations under the influence of the coastal plume. The overall microphytoplankton abundance (Fig. 7B) were often less than 1.10^3 cel.L⁻¹, except in station 59 (> 4.10^3 cel.L⁻¹) and the upwelling station 35 (> 2.10^3 cel.L⁻¹).

The chlorophyll-*a* peak occurred in the BB transect station 59 and was related to the extension of a plume in front of the BB inner shelf (> 3 mg.m⁻³; Fig. 3). It is noteworthy that the northern area surface waters are 5°C warmer than the southern area (Fig. 7A and B). The highest SSC occurred in the south of the BB and there is a slight tongue of intermediate SSC values northward in the mid-shelf (Fig. 7C and D). The SSC values were around $0,5$ mg . m⁻³ until the outer shelf in the northern transect, but only outer shelf in the south.

The plume comprised a different assemblage composition, where *Guinardia* sp., (881 cel.L⁻¹), *Thalassionema* spp. (352 cel.L⁻¹), *Thalassiothrix* sp. (1.384 cel.L⁻¹) and other pennate diatoms (528 cel.L⁻¹)

1) reached higher abundances. Besides, dinoflagellates were important contributors with *Prorocentrum rostratum* in the coast (268 cel.L⁻¹ – St. 58) and athecate dinoflagellates higher abundances in the ocean (322 cel.L⁻¹ – St. 62). Thus, CSM upwelling station 35 were also formed mainly by pennate taxa rather than centric ones, as *Diploneis* sp. (550 cel.L⁻¹), the family Naviculaceae (445 cel.L⁻¹), *Thalassionema* spp. (245 cel.L⁻¹) and *Pleurosigma* spp. (190 cel.L⁻¹) composed more than 70% of the microphytoplankton assemblage (Fig. 7B).

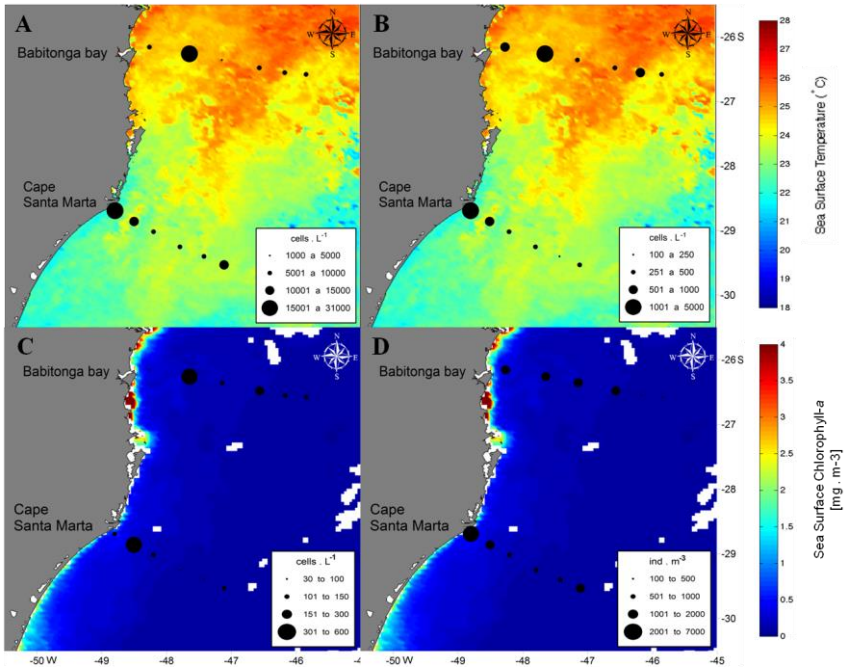


Fig. 7. Nanoplankton (A) and phytoplankton (B) total abundance (cel.L⁻¹ – black circles) overlaid onto the monthly surface sea temperature (SST) satellite image from December 2010. Microzooplankton (C) and Copepoda (D) abundance (cell.L⁻¹ and ind.m⁻³) overlaid onto the monthly surface sea chlorophyll *a* (SSC) satellite image from December 2010 off Cape Santa Marta and Babilonga Bay. Note the difference in abundance scales.

Microzooplankton abundances were higher close to the coast (355 ind.L⁻¹ – St. 36) in CSM and outer stations in BB waters, with highest abundances in the shelf stations 59 and 61, 503 and 272 ind.L⁻¹, respectively (Fig. 7C). The most conspicuous microzooplankton group

was the non-loricate ciliates and the taxa *Strombidium* spp. and *Strobilidium* spp. comprising ~40% of the total abundance. Furthermore, tintinnids ciliates *Tintinnopsis* spp. (288 ind.L⁻¹), *Eutintinnus tubulosus* (190 ind.L⁻¹) and *Dadayella ganimedes* (116 ind.L⁻¹) were also important contributors.

Copepod assemblages were higher in the coast and shelf in BB waters decreasing abruptly after the shelf break. The highest abundance were found in the upwelling waters of CSM (>6.400 ind.m⁻³), decreased offshore (Fig. 7D). Sixty-five copepod taxa and sixty species were identified (Supplementary). Mean abundance was 1403 ind.m⁻³, ranging between 295-6.417 ind.m⁻³. The *Oncaea venusta* (13 ind.m⁻³ – St. 62 and 3.020 ind.m⁻³ – St. 35), *Clausocalanus furcatus* (14 ind.m⁻³ – St. 63 and 752 ind.m⁻³ – St. 40), *Temora turbinata* (0 ind.m⁻³ – offshore stations in both transects and 755 ind.m⁻³ – St. 35), *Temora stylifera* (1 ind.m⁻³ – St. 62 and 218 ind.m⁻³ – St. 59), *Calocalanus pavoninus* (0 ind.m⁻³ – St. 35 and 184 ind.m⁻³ – St. 59) and *Oithona plumifera* (0 ind.m⁻³ – St. 39 and 126 ind.m⁻³ – St. 35) were the most abundant copepods (minimum and maximum abundance and the stations).

The upwelling (average similarity 37%, SIMPER analysis), the plume (average similarity 60%), the mid shelf (average similarity 73%) and the oceanic (average similarity 75%) groups were characterized by four functional nanoplankton taxa each, except the upwelling group which the average similarity contributor was only the nanoflagellates. However, in the plume waters the contribution of the nanoflagellates was similar to the coccolithophorids and gymnodiniales (~25%), nanodiatoms was also an important group (>12%). Equally, mid-shelf and oceanic waters were comprised mainly by the nanoflagellates (~50%) and secondly, gymnodiniales and coccolithophorids (Table 2). The microphytoplankton were mainly composed by pennate diatoms, such as *Thalassiothrix* sp., *Thalassionema* spp. and *Nitzschia* spp., together with the ciliate *Tintinnopsis* spp. accounting for more than 50% of the contribution to the average similarity of the upwelling group (average similarity 30%), and the dinoflagellates *Prorocentrum rostratum* and *P. gracile* and centric diatoms to more than 50% of the plume group (average similarity 34%), matching with the greater contribution of the thecate dinoflagellates to the microphytoplankton size fraction (Fig. 5D). The mid shelf (average similarity 57%) and oceanic (average similarity 46%) groups were heterogeneous in their composition and made up of 12 to 14 taxa to reach 80% of the average similarity in the group. The ciliate *Strombidium* spp., large coccolithophorids, *Climacodium frauenfeldianum* and the centric





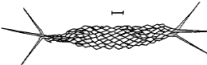
diatoms were the major contributor corresponding to 25% of the average similarity of the mid shelf group. The *Protoperidinium* spp., thecate dinoflagellates, large coccolithophorids, *Prorocentrum* spp. and athecate dinoflagellates corresponded to more than 50% of the oceanic group (Table 2). Finally, the mesozooplanktonic Copepoda groups were characterized by seven species each, where the upwelling (average similarity 51%) and the plume group (average similarity 80%), where *Oncaea venusta*, *Clausocalanus furcatus*, *Temora stylifera* and *T. turbinata* were the main copepods species corresponding for 62% and 58% of the group contribution, respectively.

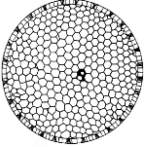


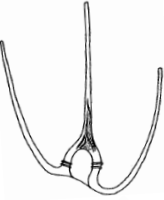
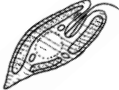
Matching the environmental conditions with the nanoplankton, microplankton and copepod community structure

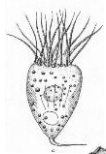
The environmental variables in best fit with the nanoplankton, microplankton and Copepoda size structure similarity matrices were determined through the application of the BIO-ENV analysis (Table 3, 4 and 5).

The strongest rank correlation of the nanoplankton model comprised the following variables, zooplankton biomass, nauplii and adult copepods ($\rho = 0.658$). All the subsequent results included temperature, integrated chlorophyll *a* and zooplankton biomass as explanatory variables. The copepods size categories, nauplii, copepodites and adult copepods were other consistent contributors (Table 3). The second model comprised the combined structure of microphyto- and microzooplankton (Table 4), the best five variables combination were oxygen, integrated chlorophyll, nauplii, copepodites and adult copepods ($\rho = 0.794$). Others subsets also considered silicate and temperature and were highly significant statistical correlations. The variables best describing the copepods species distribution were a simple two variable rank including temperature and silicate. Oxygen and zooplankton biomass were also important contributors (Table 5).

Table 2. SIMPER (similarity percentages analysis) results to compare the upwelling, plume, outer shelf and slope groups off Cape Santa Marta and Babitonga Bay, divided into 14 major taxonomic/functional plankton groupings. Typical nanoplankton and microplankton taxa contributing more than 80% to the average similarity for each group and Copepoda species contributing more than 90% to the average similarity for each group are listed. Note table 1 to see the groups features.

| Planktonic groups | Average similarity (%) | | | |
|---|---------------------------------------|--------------------|--------------------------|--------------------|
| | Upwelling group 37% | Plume group 60% | Outer shelf group 73% | Slope group 75% |
| | Nanoplankton | | | |
|  | Contribution to similarity (%) | | | |
| Coccolithophorids | | 26 | 22 | 15 |
|  | | 13 | 14 | 7 |
|  | | 28 | 11 | 19 |
|  | 100 | 24 | 46 | 50 |
| | Microplankton | | | |
|  | 30% | 34% | 57% | 46% |
| Large coccolithophorids | 5 | | 9 | 9 |

| | | | | | |
|---|------------------------------------|----|----|---|----|
|  | Centric diatoms | | 12 | 7 | |
| | <i>Climacodium frauenfeldianum</i> | | 5 | 7 | |
| | <i>Coscindiscus</i> spp. | | | 5 | |
|  | Pennate diatoms | | | 4 | |
| | <i>Thalassionema</i> spp. | 19 | | | |
| | <i>Thalassiothrix</i> sp. | 13 | 14 | | |
| | <i>Nitzschia</i> spp. | 10 | | | |
| | <i>Pseudo-nitzschia</i> spp. | | | | 3 |
|  | Athebate dinoflagellates | | 5 | 5 | 9 |
| | Thecate dinoflagellates | 7 | 5 | 6 | 12 |
|  | <i>Prorocentrum gracile</i> | 7 | 10 | | |
| | <i>Prorocentrum rostratum</i> | | 17 | 6 | |
| | <i>Prorocentrum</i> spp. | | | | 9 |
| | <i>Neoceratium</i> spp. | | | 5 | 8 |
| | <i>Protoperidinium</i> spp. | 7 | | 5 | 13 |
|  | Flagellates | | | 4 | 4 |
| | <i>Phaeocystis</i> sp. | | | 4 | |



Strombidium spp.

7

10

5

Strobilidium spp.

5

3



Tintinnopsis spp.

12

Tintinnid ciliates

4



Foraminifera

3

Copepoda

51%

79%

67%

51%

Clausocalanus furcatus

17

16

26

17

Oncaea venusta

18

11

19

16

Temora stylifera

15

15

9

6

Paracalanus aculeatus

5

Subeucalanus pileatus

5

Temora turbinata

11

18

Oithona plumifera

6

9

10

Calocalanus pavoninus

9

7

9

Farranula gracilis

7

6

15

Oncaea media

6

13

Corycaeus giesbrechti

7

Corycaeus speciosus

6

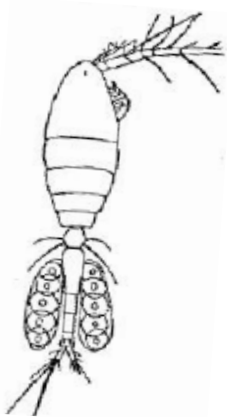


Table 3. Results of BIO-ENV analysis. The largest rank correlations between the most abundant nanoplankton and explanatory similarity matrices. The first six subsets listed, best overall fit in bold. $p = 0.026$.

| Number of variables (k) | Best variable combinations | | | | | Correlation (ρ_w) |
|-------------------------|----------------------------|----------------|-----------------------|----------------|----------------|--------------------------|
| 3 | Zooplankton biomass | Nauplii | Adult copepods | | | 0.658 |
| 5 | Temperature | Chlo-a | Zooplankton biomass | Nauplii | Adult copepods | 0.657 |
| 5 | Temperature | Chlo-a | Zooplankton biomass | Nauplii | Copepodites | 0.657 |
| 4 | Temperature | Chlo-a | Zooplankton biomass | Nauplii | | 0.655 |
| 4 | Temperature | Chlo-a | Zooplankton biomass | Adult copepods | | 0.655 |
| 3 | Temperature | Chlo-a | Zooplankton biomass | | | 0.653 |

Table 4. Results of BIO-ENV analysis. The largest rank correlations between the most abundant microplankton (microphytoplankton and microzooplankton) and explanatory similarity matrices. The first six subsets listed, best overall fit in bold. $p = 0.004$.

| Number of variables (k) | Best variable combinations | | | | | Correlation (ρ_w) |
|-------------------------|----------------------------|---------------|----------------|--------------------|-----------------------|--------------------------|
| 5 | Oxygen | Chlo-a | Nauplii | Copepodites | Adult copepods | 0.794 |
| 5 | Oxygen | Silicate | Nauplii | Copepodites | Adult copepods | 0.791 |
| 4 | Oxygen | Silicate | Nauplii | Copepodites | | 0.790 |
| 5 | Temperature | Silicate | Chlo-a | Nauplii | Copepodites | 0.790 |
| 5 | Oxygen | Silicate | Chlo-a | Nauplii | Copepodites | 0.788 |
| 4 | Oxygen | Chlo-a | Copepodites | Adult copepods | | 0.787 |

Table 5. Results of BIO-ENV analysis. The largest rank correlations between the most abundant Copepoda structure and explanatory similarity matrices. The first six subsets listed, best overall fit in bold. $p = 0.196$.

| number of variables (k) | Best variable combinations | | | | | Correlation (ρ_w) |
|-------------------------|----------------------------|-----------------|---------------------|---------------------|---------------------|--------------------------|
| 2 | Temperature | Silicate | | | | 0.465 |
| 3 | Temperature | Silicate | Zooplankton biomass | | | 0.458 |
| 4 | Temperature | Nitrate | Silicate | Zooplankton biomass | | 0.444 |
| 3 | Temperature | Oxygen | Silicate | | | 0.442 |
| 4 | Temperature | Oxygen | Silicate | Zooplankton biomass | | 0.440 |
| 5 | Temperature | Oxygen | Nitrate | Silicate | Zooplankton biomass | 0.429 |

DISCUSSION

Our findings reveal that in summer, there is a great variability in the planktonic size structure due to the seasonal changes in the oceanographic processes, nutrient availability and species associations of the southeastern Brazilian shelf. The two main oceanographic structures present in the inner shelf were the nearshore upwelling southward and the plume formation in the north compared to the more stratified, outer shelf and slope waters. Copepods were, in general, dominated by some selected copepod species distributed widespread, such as *Clausocalanus furcatus*, *Oncaea venusta*, *Temora stylifera* and *T. turbinata*. In contrast, nanoplankton and microplankton community structure were associated with specific coastal processes and the offshore region. The coastal upwelling was characterized by the silicate-rich nitrogen depleted waters at Cape Santa Marta (CSM) under cold sea surface temperature (SST) was reflected in the highest abundance of nanoflagellates co-occurring with higher abundances of pennate diatoms and the ciliate *Tintinnopsis* spp. In the north plume extension under warm SST, the microplankton was based on centric and pennate diatoms, the dinoflagellates *Prorocentrum rostratum* and *P. gracile*. The outer shelf and slope were characterized by high abundance of nanoflagellates, large coccolithophorids, the thecate dinoflagellate *Protoperidinium* spp. and the aloricate ciliate *Strombidium* spp.

The general dominance of nanoplankton (>70% of total) and small copepods in coastal processes of the inner shelf masked the pelagic food web structure expected in the study (suggested by Cushing 1989), where large species dominated the margins and small phytoplankton cells the offshore, although a high abundance of nanoflagellates were also found in the outer shelf and slope. Nutrient concentrations in the upper layers of the water column were often depleted and N/P ratios were low, under these conditions, small organisms would perform better than large ones.

Spatial pattern of plankton size structure and assemblage composition

The remarkable presence of small cells in the upper layers could be explained by several mechanisms. In Brazilian shelf waters, areas under the influence of coastal upwelling such as Cape Frio, the initial phase of the process recorded low microphytoplankton abundance and autotrophic biomass, and dominance of nanoplankton associated to the

gap between the dilution of upwelled waters and the physiological responses of algae (Souza 2006). Another factor that might increase nanoflagellates abundance in the inner shelf is the depth layers. Odebrecht & Djurfeldt (1996), working in CSM waters, found that nutrient injection into the euphotic zone fuels the subsurface growth of large diatoms in the deep chlorophyll-a maxima (DCM), contrasting with the small organisms (pico and nanoplankton) in the upper layer and offshore. In fact, we only quantified the nanoplankton and microplankton at upper layers (10-20 m), which favour an increase in the contribution of small cells (Arin et al. 2002). In the highly productive coastal area of Chile, high concentrations of nanoflagellates at the upper layers were unaffected by the season or water stratification, in such conditions, the contribution of diatoms and dinoflagellates were low (Anabalón et al. 2007, Böttjer & Morales 2007, González et al. 2007).

The dominance of small cells could also be related to the dissolved inorganic nitrogen concentrations. The phytoplankton biomass usually presents N limitation. This leads to a decrease in the growth rate of populations and nanoplankton organisms better suited to explore efficiently low levels of nutrients (due to their large surface/volume ratio) are taken largely dominant (Aidar et al. 1993, Gaeta & Brandini 2006), which might explain dinoflagellates (BB plume – 22-36%) and nanoflagellates (CSM upwelling – 69-72%) reaching highest abundances in the inner shelf processes (Fig. 5).

The temperature–size relationship also has an indirect effect on phytoplankton community size structure, large phytoplankton increase with the nutrient availability and decrease with increasing temperature (Marañón et al. 2012, Mousing et al. 2014). Small phytoplankton have an advantage in low nutrient waters due to a higher surface:volume ratio (Kiørboe 1993) and thus lower sinking rates, remaining longer in suspension at the euphotic zone (Guenther & Bozelli 2004), explaining the large values of nanoplankton in the coastal processes. In addition, the BIO-ENV analyses supported that temperature was one of the best predictor of the community size structure, particularly the nanoplankton and copepods (table 3 and 5, respectively), which is in agreement with the plankton trophic structure at Guanabara Bay that is directly affected by temperature oscillation (Guenther et al. 2012).

The BB waters was dominated by a mixture of coastal and estuarine species, mainly formed by the centric *Climacodium frauenfeldianum* and the pennate diatom *Thalassiothrix* spp., and the dinoflagellates *Prorocentrum rostratum* and *P. gracile*. The

Prorocentrum species were mentioned to prevail in tropical and subtropical waters, occurring mainly in the neritic region of the Arvoredo Island (Cardoso, 1998). Autotrophic production might enter several different routes, such as export to adjacent areas through filaments (Marín et al. 2003, Vargas et al. 2007) or through sedimentation out of the mixed layer (Lignell et al. 1993). Diatoms resuspended in the nearshore Itajaí-açu river are transported offshore by Ekman forces, where they sink faster due to poor nutrient conditions. Sinking cells find better nutrient conditions in the nutricline layers, become shade-adapted and increase their buoyancy, contributing to the formation of the DCM. The cells at the DCM might be carried out again nearshore by SACW intrusions, closing the loop (Brandini et al. 2013). Thus, the microplankton assemblages in BB inner shelf are probably the result of species associations from adjacent waters of the Itajaí plume.

In contrast, the CSM waters presented a very atypical phytoplankton community structure for an upwelling event, dominated by three pennate diatom, such as *Thalassionema* spp., *Thalassiothrix* sp. and *Nitzschia* spp. instead of the large centric diatoms *Coscinodiscus* spp. and *Thalassiosira* spp., previously reported to the region (Odebrecht & Djurfeldt 1996). Besides, other diatoms presented in the microplankton in the CSM were also typical of deep and cold waters such as *Diploneis* spp, *Navicula* spp, *Paralia sulcata* and *Pleurosigma* sp., as in the Cape Frio upwelling (Valentin et al. 1977, Souza 2006). There were also benthic diatom species that were probably resuspended from the nearshore due to the SACW intrusions on the inner shelf (Valentin 1984).

Oligotrich ciliates and tintinnids often dominated the microzooplankton assemblages proportionally (Fig. 5E), although their abundance was relatively low both inshore and offshore (< 3%). Microzooplankton abundance was similar to other offshore area at Abrolhos bank (Tenenbaum et al. 2001) and was lower than that found in other eutrophic systems in the S-SE Brazil, such as the Guanabara bay (Gomes et al. 2007) and the coastal lagoon (Odebrecht 1988). Here it is shown that the microzooplankton were mostly composed by small ciliates (21-50 μm), which was concentrated at the coastal processes, such as *Tintinnopsis* spp. at the upwelling zone (117 cells.L⁻¹) and *Strobilidium* spp. at the estuarine plume (151 cells.L⁻¹). These same size classes make up 79-96% of total abundances in southern East China Sea (Chen et al. 2012). The two aloricate taxa *Strobilidium* spp. and *Strobilidium* spp. as well as tintinnids *Eutintinnus* spp. and *Tintinnopsis* spp. were the most important taxa, which is in agreement with the ciliate

composition and biomass off the Chilean upwelling system (Vargas et al. 2007).

The spatial variability of the nanoplankton and microplankton reflect well-defined ecological requirements of the most abundant groups, which were due the nutrient availability along the cross-shelf gradient (Margalef 1978, Tenenbaum et al. 2001). However, the copepod assemblages composition was spatially generalist, since the most abundant species spread throughout the whole area, in accordance with the cross-shelf gradients and not to the different coastal processes. *Clasocalanus furcatus*, *Farranula gracilis* and *Oncaea media* were more abundant in the offshore warm oligotrophic waters; *Oncaea venusta*, *Oithona plumifera* and *Calocalanus pavoninus* were the main mid-shelf species and; *Temora stylifera* and *T. turbinata* peaked nearshore. These species alone comprised more than 90% of the contribution to similarity within groups (SIMPER) and are common and abundant in coastal and mid-shelf regions, affected by the SACW intrusions (Valentin 1984, Lopes et al. 1999, 2006, Brandini et al. 2013).

Trophic interactions in the different planktonic food webs

The observed differences in the plankton community size structure and composition were mainly influenced by the nutrient availability along the cross-shelf gradient in the continental shelf waters. This reflected in a strong plankton gradient (Fig. 7), from high abundances of the nanoplankton (5-20 μ m) and microplankton (20-200 μ m) at the coastalmost stations to low values in the stratified waters of the Brazil Current, both leading to the similar pattern found for copepods.

Nanoflagellates can be a food supply for microzooplankton, small copepods and nauplii, which ingest small particles with more effectiveness than the larger copepods (Nakamura & Turner 1997, Vargas & González 2004). Small copepod species and copepodites, contributed to more than 80% of the total copepods in the CSM transect (Fig. 6B). Strong grazing of mesozooplankton, especially microcrustaceans, on phagotrophic flagellates and ciliates were reported in various marine and freshwater systems (Sherr & Sherr 1988, Turner 2004). In the coastal upwelling region off Chile (36°S), large copepods were found only occasionally abundant, and therefore, most grazing was done by small grazers, such as copepodites, adult small copepods and appendicularians (Vargas & González 2004). Since the nanoplankton abundance variability was mainly explained by zooplankton biomass,

nauplii and adult copepods distribution (BIO-ENV analysis – Table 3), we suggest that the nanoplankton is a dominant food source for small zooplankton during summer.

Microzooplankton was mainly composed by ciliates (57-100%) and they are known to be grazers of nanoplankton and picoplankton in marine ecosystems (Bernad & Rassoulzadegan 1990), as they consume 32-80% of nanoflagellate production (Verity 1985, 1986, Nakano et al. 2001). In our study, the ciliates assemblage distribution was similar to the nanoplankton and mainly composed by small oligotrich ciliates *Strombidium* spp. and *Strobilidium* spp. (21-50 μm). In the southern East China Sea, small ciliates (< 45 μm) are the major consumer of the nanoflagellate community. The ciliates *Strombidium* spp., *Strobilidium* spp. and tintinnids composed the most abundant groups, consumed 100% of nanoflagellates production in inner-shelf and 43% in offshore oceanic waters (Chen et al. 2012). Small oligotrich ciliates are known to exert high grazing pressure on heterotrophic nanoflagellates, which are abundant in surface waters (Jürgens et al. 1996). The lack of significant correlation between chlorophyll-*a* and nanoplankton, suggest that they might be mostly heterotrophic flagellates and thus, a potential food source for the dominant small oligotrich ciliates *Strombidium* spp. and *Strobilidium* spp. Therefore, ciliates may compete with small copepods for nano-sized food resource.

A great number of filamentous fungi and large amounts of detrital particles were observed in the samples of CSM (E. C. Becker pers. obs.). Those kinds of detritus have already been reported in the area and were related to phytoplankton grazing and/or senescence due to nutrient exhaustion, leading to residual organic matter of empty diatom valves and clumped particles in the water column (Odebrecht & Djurfeldt 1996). In addition, it suggests a usual mechanism of organic matter recycle. Fontes et al. (submitted) highlights the importance of further studies focused on the interplay between the microbial and detritivorous food chain. The presence of key species of zooplankton affects the magnification of the detritivorous food chain such as the detritivorous/omnivorous copepod *Oncaea venusta*. The major suspension-feeders species *Temora turbinata*, *Clytemnestra scutellata*, *Clausocalanus furcatus*, *T. stylifera* and *Subeucalanus pileatus* were also in high concentration in the upwelling and their strong grazing pressure resulted in low microphyto and microzooplankton abundances. All these facts indicated that the system might be under top-down control.

The dominance of nanoplankton in both coastal processes indicates the energy is channeled through small cells rather than the diatom-copepod food chain. This implies a food web structure that can be classified as multivorous food web (Legendre & Rassoulzadegan 1995), which grazing by copepods may follow either of two alternative pathways: with classical herbivorous and microbial food webs playing an important role in the copepod community structure and trophodynamics of the world ocean.

Oceanographic structure controlling the planktonic assemblages

The SACW intrusion (Matsuura 1986, Campos et al. 2013) was observed in the upper layers at CSM coastal region, characterizing the summer upwelling ($T < 20^{\circ}\text{C}$; 14 m). However, the nutrient data and the planktonic size structure does not agree to the usual scenario observed in coastal upwelling: nitrogen-limited and high silicate waters up to 50 m, and a nanoflagellates based system. In summer, high nutrient concentration (e.g. nitrate) are trapped in deep layers and a strong thermocline takes place preventing the availability of nutrients for photosynthesis (new production) in the upper layers (Muelbert et al. 2008). Accordingly, low N:P ratios (Fig. 4) suggested nitrogen-limited waters for SACW intrusions during the early summer at CSM waters. This agrees with previous observations at Cape Frio upwelling (Souza 2006), which recorded nitrate concentrations quite low during the whole upwelling cycle, not exceeding $2 \mu\text{M}$ throughout the water column. Low nitrate values during upwelling probably indicate depletion of the nutrients associated to the phytoplankton use (Souza 2006).

CSM receives great influence of the southern shelf, especially the influence of the Plata Plume Water (PPW) in winter (Piola et al. 2008). Thus, the silicate-rich water merged to the coastal upwelling could be attributed to a persistent northward influence of the PPW. The intensification of southerly winds in winter pushes the PPW up to low latitudes (Möller et al. 2008, Piola et al. 2008) and therefore increases the abundance of the small bacterioplankton (Fontes et al. submitted). We suggest that some unusual condition related to late spring/early summer improved silicate values around CSM.

The satellite images presented a meandering feature of SST and SSC in the northern transect, which may be attributed to the Itajai-açu plume flowing northward and reaching the BB mid-shelf waters. Chlorophyll-*a* peak, high abundances of pennate diatoms, athecate dinoflagellates and coepodites seems to be related to this oceanographic

condition. The circulation in the Itajaí-açu River is predominantly of the highly stratified type (Schettini, 2002), which favors the liberation of water with low salinity to the adjacent shelf and a river plume is formed. This develops rapidly from the river mouth, and fans out in a northeastern direction, being more notable several kilometers away from the river mouth (Schettini et al. 1998).

Concluding remarks

Trophic gradients, alongshore coastal processes (north: extension of the estuarine plume waters – south: the beginning of the upwelling) and offshore nutrient-poor waters of the Brazil Current were the main features that accounted for the relative abundance variability and the taxonomic composition of the plankton assemblages.

The nano- and microplankton distribution probably plays an important role for the growth and success of copepods and thus, might present adaptive strategies to achieve the production generated by these intermittent mechanisms. The dominance of small organisms in the upper layers suggested a more complex and less efficient food web, with a pronounced magnification at the coastal processes. Although phytoplankton abundance is largely concentrated in the nanoplankton fraction, the tropical system has many large species, particularly dinoflagellates and diatoms, which are always present in small numbers. Yet, episodic injections of new nutrients at the base of the euphotic zone fuels the subsurface growth of large phytoplankton ($> 20 \mu\text{m}$, Goldman 1993, Brandini et al. 2013), which was dominated by pennate diatoms at CSM upwelling and dinoflagellates at BB plume extension promoting a disproportionately large contribution to the primary production and optimal food for most filter feeders. In this case a simple and short trophic system, with low losses, is predicted as a result of the growth of a highly diversified microphytoplankton.

These results indicate that the plankton size structure found in the study influence the kind of planktonic food web and trophic interactions and is assigned as multivorous food web due to the high complex of the planktonic food webs and diversified community structure. Further studies should take into account the carbon pathways within these plankton compartments and also the picoplankton size fraction to better understand the microbial processes of the S-SE Brazil Shelf.

Acknowledgments. This work is part of the project about the dynamics of carbon between the ocean/atmosphere interface of the S-SE Brazil Shelf, coordinated by Dr. C.A.E. Garcia (FURG), Dr^a. A.M. Ciotti (USP) and Dr^a. A.S. Freire (UFSC). The Brazilian Navy for logistic support, the crew of the *Cruzeiro do Sul* and the scientific team for assisting in the fieldwork. A.G. Koetker, M.C. Brandão and L.C.P. Macedo-Soares for conducting the plankton sampling on the cruises and to the undergraduate students who helped in samples processing. E.M. Lucio and G.R. Persich for supporting in the phytoplankton quantification and to C.O. Dias who helped to improve copepods identification. Dr^a. M. Carvalho (UFSC) who provided the satellite images. We also thank Dr. R. Pollery (UFRJ) who provided nutrients data.

4 CONCLUSÃO FINAL

O estudo da estrutura das comunidades planctônicas avaliadas por faixas de tamanho (5 à 200 μm) na plataforma e talude de Santa Catarina durante o início do verão (Dezembro de 2010) permitiu identificar que:

Gradientes ao longo e perpendiculares à costa resultante da interação de processos costeiros e massas d'águas promoveram a heterogeneidade espacial e a distribuição e abundância das principais espécies da comunidade planctônica. Desta maneira, a plataforma continental de Santa Catarina pode ser caracterizada por três regiões definidas pelos diferentes estados tróficos (Fig. 8): 1) ao norte do estado, a plataforma interna apresenta águas menos salinas (até 120 km da costa) sob influência da extensão da pluma estuarina da Baía da Babitonga, 2) no extremo sul, a ressurgência decorrente da intrusão da Água Central do Atlântico Sul no Cabo de Santa Marta (~14 m) e 3) sobre a plataforma média e talude, águas sujeitas principalmente à influência da mistura de massas d' água quentes, a Água Subtropical de Plataforma e Água Tropical, que caracterizam a Corrente do Brasil.

As maiores abundâncias do nanoplâncton e micropoplâncton e do mesozoplâncton (copépodes, cladóceros e quetognatos) foram encontradas próximo à costa associadas à extensão da pluma estuarina da Baía da Babitonga na plataforma e à intrusão da ACAS em subsuperfície no Cabo de Santa Marta, além de núcleos de alta concentração de biomassa e biovolume dispersos ao longo da plataforma e região oceânica. Os fenômenos descritos acima modificam o cenário oceanográfico, em termos de grau de trofia e dinâmica no aporte de nutrientes na zona eufótica. A ação intermitente da ACAS e plumas estuarinas, e a ocorrência episódica de vórtices são os principais processos de enriquecimento da área.

As variações da distribuição dos grupos zooplânctônicos em função das condições oceanográficas são principalmente determinadas pela influência das águas quentes e salinas da Água Tropical da Corrente do Brasil. Os copépodes tiveram menor representatividade ao sul (CSM: 74% e SCI: 67%), particularmente nas estações em que os cladóceros *Penilia avirostris* atingiram as maiores abundâncias. Além disso, os picos de abundâncias dos cladóceros ocorreram em situações pontuais, onde *P. avirostris* atingiu maior abundância na costa (15%) e *Evadne spinifera* na região oceânica (11%). As espécies de quetognatos oceânicos estiveram associadas à aumentos de biomassa (> 1 mg.m⁻³) e

biovolume ($> 1 \text{ mL.m}^{-3}$) na plataforma e região oceânica elevando a condição oligotrófica da região oceânica, além disso, a espécie *Flaccisagitta* enflata provocou as maiores abundâncias registradas na costa ($> 6.000 \text{ ind.m}^{-3}$).

Apesar das diferenças particulares de cada zona produtiva e estrutura de comunidade planctônica, em geral, algumas simplificações sobre as estrutura trófica podem ser apresentadas: 1) devido aos baixos valores de nitrogênio inorgânico dissolvido (nitrato, nitrito, amônio) percebe-se que este nutriente é um dos fatores limitantes da região, contribuindo para as abundâncias relativamente baixas de microfitoplâncton observado na superfície, 2) os diferentes sistemas estão baseados em organismos pequenos, de células do nanoplâncton (5-20 μm , geralmente $>79\%$) aos copépodes (copepoditos: 16-37%; adultos menores que 1 mm: 32-61%), 3) componentes da cadeia alimentar microbiana (nanoplâncton e microzooplâncton) parecem contribuir para formação de uma via alternativa na cadeia alimentar planctônica, caracterizando uma cadeia alimentar multívora devido à mudança no estado trófico da plataforma interna em resposta à intrusão de nutrientes e à variabilidade da salinidade e da temperatura.

Os resultados encontrados indicam que a estrutura de tamanho do plâncton influencia o tipo de cadeia alimentar planctônica e as interações tróficas da cadeia alimentar pelágica. Novos estudos devem levar em conta as vias de carbono dentro destes compartimentos planctônicos, auto e heterotrófica, assim como a fração de tamanho picoplanctônica para compreender melhor os processos microbianos do plataforma S-SE Brasileira.

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APÊNDICES
Capítulo 1

Table S1. Principal taxonomic groups of zooplankton off Santa Catarina shelf and the most abundant species code names used in the CCA analysis. FO: frequency of occurrence; RA: relative abundance

| Zooplankton groups | FO (%) | RA (%) | Total abundance (ind.m⁻³) |
|---------------------------|---------------|---------------|---|
| Copepoda | 100 | 89.93 | 26977.34 |
| Cladocera | 80 | 2.48 | 742.65 |
| Chaetognatha | 96 | 2.02 | 606.14 |
| Invertebrate larvae | 100 | 1.78 | 534.54 |
| Oikopleuridae | 100 | 1.05 | 313.80 |
| Fritillariidae | 68 | 0.15 | 44.62 |
| Siphonophorae | 100 | 0.74 | 222.89 |
| Nauplii | 80 | 0.52 | 157.40 |
| Euphausiacea | 96 | 0.24 | 70.73 |
| Thaliacea | 100 | 0.16 | 47.39 |
| Others groups | 100 | 0.93 | 280.46 |
| Total contribution | | | 29997.95 |

Table S2. Copepods species composition off Santa Catarina continental shelf and the most abundant species code names used in the CCA analysis (bold). FO: frequency of occurrence; RA: relative abundance.

| Copepoda | FO (%) | RA (%) | Abundance (ind.m⁻³) |
|--|-------------------|-------------------|---|
| Ordem Calanoida | | | |
| Family Calanidae | | | |
| <i>Nannocalanus minor</i> (Claus, 1863) | 44 | 0,39 | 104,48 |
| <i>Neocalanus gracilis</i> (Dana, 1849) | 16 | 0,19 | 50,42 |
| <i>Undinula vulgaris</i> (Dana, 1849) | 12 | 0,08 | 21,05 |
| Family Eucalanidae | | | |
| <i>Subeucalanus pileatus</i> (Giesbrecht, 1888) | 24 | 1,46 | 392,64 |
| <i>Subeucalanus subtenuis</i> (Giesbrecht, 1888) | 4 | 0,14 | 37,45 |
| Eucalanidae copepodids | 4 | 0,01 | 2,34 |
| Family Paracalanidae | | | |
| <i>Calocalanus contractus</i> Farran, 1926 | 8 | 0,02 | 5,79 |
| <i>Calocalanus equalicauda</i> (Bernard, 1958) | 32 | 0,20 | 53,91 |
| <i>Calocalanus pavo</i> (Dana, 1852) | 56 | 0,59 | 158,57 |
| <i>Calocalanus pavoninus</i> Farran, 1936 | 88 | 5,99 | 1616,50 |
| <i>Calocalanus</i> sp. | 16 | 0,23 | 62,10 |
| <i>Mecynocera clausi</i> I.C. Thompson, 1888 | 68 | 0,52 | 139,70 |
| <i>Paracalanus aculeatus</i> Giesbrecht, 1888 | 72 | 1,39 | 374,75 |
| <i>Paracalanus campaneri</i> Björnberg, 1980 | 36 | 0,55 | 147,27 |
| <i>Paracalanus indicus</i> Wolfenden, 1905 | 8 | 0,24 | 65,39 |
| <i>Paracalanus parvus</i> (Claus, 1893) | 16 | 0,21 | 56,97 |
| <i>Paracalanus quasimodo</i> Bowman, 1971 | 8 | 0,02 | 4,61 |
| <i>Paracalanus</i> sp. | 20 | 0,90 | 241,94 |

| Copepoda | FO (%) | RA (%) | Abundance (ind.m⁻³) |
|---|-------------------|-------------------|---|
| <i>Parvocalanus crassirostris</i> (F. Dahl, 1894) | 8 | 0,32 | 86,84 |
| <i>Acrocalanus longicornis</i> Giesbrecht, 1888 | 40 | 0,32 | 85,15 |
| Family Clausocalanidae | | | |
| <i>Clausocalanus arcuicornis</i> (Dana, 1849) | 20 | 0,19 | 52,29 |
| <i>Clausocalanus brevipes</i> Frost & Fleminger, 1968 | 12 | 0,03 | 7,90 |
| <i>Clausocalanus furcatus</i> (Brady, 1883) | 100 | 18,77 | 5064,98 |
| <i>Clausocalanus paululus</i> Farran, 1926 | 20 | 0,37 | 100,02 |
| <i>Clausocalanus cf. parapergens</i> Frost & Fleminger, 1968 | 4 | 0,15 | 40,45 |
| <i>Clausocalanus cf. pergens</i> Farran, 1926 | 4 | 0,06 | 16,09 |
| <i>Ctenocalanus vanus</i> Giesbrecht, 1888 | 44 | 1,82 | 491,68 |
| <i>Ctenocalanus</i> sp. | 16 | 0,54 | 146,17 |
| Clausocalanidae | 56 | 6,84 | 1846,14 |
| Family Aetideidae | | | |
| <i>Aetideus giesbrechti</i> Cleve, 1904 | 4 | 0,01 | 2,32 |
| <i>Euchaeta marina</i> (Prestandrea, 1833) | 20 | 0,15 | 41,77 |
| <i>Paraeuchaeta scotti</i> (Farran, 1908) | 4 | 0,01 | 3,31 |
| Family Scolecitrichidae | | | |
| <i>Scaphocalanus medius</i> (Sars G.O., 1907) | 4 | 0,01 | 2,30 |
| <i>Scolecithrix danae</i> (Lubbock, 1856) | 32 | 0,19 | 52,04 |
| Family Lucicutiidae | | | |
| <i>Lucicutia flavicornis</i> (Claus, 1863) | 12 | 0,04 | 10,91 |
| <i>Lucicutia gaussae</i> Grice, 1963 | 12 | 0,25 | 68,39 |
| Family Augaptilidae | | | |
| <i>Haloptilus longicornis</i> (Claus, 1863) | 8 | 0,02 | 5,79 |

| Copepoda | FO (%) | RA (%) | Abundance (ind.m⁻³) |
|--|-------------------|-------------------|---|
| <i>Pleuromamma gracilis</i> (Claus, 1863) | 12 | 0,10 | 25,95 |
| Family Heterorhabdidae | | | |
| <i>Heterorhabdus papilliger</i> (Claus, 1863) | 12 | 0,03 | 7,97 |
| Family Centropagidae | | | |
| <i>Centropages furcatus</i> (Dana, 1849) | 12 | 0,26 | 70,40 |
| Family Temoridae | | | |
| <i>Temora stylifera</i> (Dana, 1849) | 92 | 6,76 | 1824,50 |
| <i>Temora turbinata</i> (Dana, 1849) | 52 | 7,64 | 2060,49 |
| <i>Temoropia mayumbaensis</i> T. Scott, 1894 | 4 | 0,01 | 1,56 |
| Family Candaciidae | | | |
| <i>Paracandacia simplex</i> (Giesbrecht, 1889) | 24 | 0,10 | 26,34 |
| Family Acartiidae | | | |
| <i>Acartia danae</i> Giesbrecht, 1889 | 16 | 0,12 | 32,21 |
| <i>Acartia longiremis</i> (Lilljeborg, 1853) | 20 | 0,15 | 41,57 |
| <i>Acartia negligens</i> Dana, 1849 | 36 | 0,29 | 77,70 |
| <i>Acartia tonsa</i> Dana, 1849 | 16 | 0,07 | 19,83 |
| <i>Acartia</i> sp. | 12 | 0,11 | 29,02 |
| Order Cyclopoida | | | |
| Family Oithonidae | | | |
| <i>Oithona nana</i> Giesbrecht, 1892 | 16 | 0,29 | 78,62 |
| <i>Oithona plumifera</i> Baird, 1843 | 84 | 6,00 | 1617,65 |
| <i>Oithona robusta</i> Giesbrecht, 1891 | 8 | 0,02 | 4,78 |
| <i>Oithona setigera</i> (Dana, 1849) | 24 | 0,16 | 42,82 |
| <i>Oithona similis</i> Claus, 1866 | 28 | 0,70 | 188,19 |

| Copepoda | FO (%) | RA (%) | Abundance (ind.m⁻³) |
|---|-------------------|-------------------|---|
| <i>Oithona tenuis</i> Rosendorn, 1917 | 60 | 0,79 | 213,54 |
| <i>Oithona sp.</i> | 16 | 0,20 | 53,57 |
| Order Harpacticoida | | | |
| Family Clytemnestridae | | | |
| <i>Clytemnestra scutellata</i> Dana, 1848 | 20 | 1,15 | 310,96 |
| Family Euterpinidae | | | |
| <i>Euterpina acutifrons</i> (Dana, 1848) | 8 | 0,56 | 149,75 |
| Family Ectinosomatidae | | | |
| <i>Microsetella norvegica</i> (Boeck, 1865) | 4 | 0,01 | 3,31 |
| Family Miraciidae | | | |
| <i>Macrosetella gracilis</i> (Dana, 1847) | 32 | 0,60 | 162,94 |
| Order Poecilostomatoida | | | |
| Family Oncaeidae | | | |
| <i>Oncaea antarctica</i> Heron, 1977 | 8 | 0,02 | 5,79 |
| <i>Oncaea media</i> Giesbrecht, 1891 | 60 | 1,40 | 378,95 |
| <i>Oncaea venusta</i> Philippi, 1843 | 100 | 21,14 | 5702,33 |
| <i>Oncaea sp.</i> | 4 | 0,14 | 38,73 |
| <i>Triconia conifera</i> (Giesbrecht, 1891) | 4 | 0,02 | 4,63 |
| <i>Lubbockia squillimana</i> Claus, 1863 | 8 | 0,03 | 8,00 |
| Family Sapphirinidae | | | |
| <i>Copilia mirabilis</i> Dana, 1852 | 8 | 0,02 | 6,62 |
| <i>Sapphirina angusta</i> Dana, 1849 | 4 | 0,01 | 3,31 |
| <i>Sapphirina nigromaculata</i> Claus, 1863 | 4 | 0,02 | 5,17 |
| <i>Sapphirina iris</i> Dana, 1849 | 4 | 0,23 | 62,91 |

| Copepoda | FO (%) | RA (%) | Abundance (ind.m⁻³) |
|--|-------------------|-------------------|---|
| Family Corycaeidae | | | |
| <i>Corycaeus flaccus</i> Giesbrecht, 1891 | 12 | 0,11 | 29,63 |
| <i>Corycaeus giesbrechti</i> (F. Dahl, 1894) | 72 | 1,79 | 481,68 |
| <i>Corycaeus limbatus</i> Brady, 1883 | 20 | 0,22 | 58,93 |
| <i>Corycaeus speciosus</i> Dana, 1849 | 60 | 0,59 | 158,93 |
| <i>Corycaeus typicus</i> (Krøyer, 1849) | 8 | 0,04 | 9,51 |
| <i>Corycaeus</i> sp. copepodids | 60 | 1,10 | 295,81 |
| <i>Farranula gracilis</i> (Dana, 1849) | 92 | 3,61 | 973,00 |
| <i>Farranula rostrata</i> (Claus, 1863) | 24 | 0,18 | 49,36 |
| Total contribution | | | 26977,34 |

Table S3. Cladocera species composition off Santa Catarina continental shelf and the most abundant species code names used in the CCA analysis (bold). FO: frequency of occurrence; RA: relative abundance

| Cladocera | FO (%) | RA (%) | Abundance (ind/m³) |
|---|---------------|---------------|--|
| Ordem Ctenopoda | | | |
| Family Sididae | | | |
| <i>Penilia avirostris</i> Dana, 1849 | 67 | 74.54 | 559.69 |
| Order Onychopoda | | | |
| Family Podonidae | | | |
| <i>Pleopsis schmackeri</i> (Poppe, 1889) | 33 | 0.37 | 4.40 |
| <i>Evadne spinifera</i> P.E. Müller, 1867 | 72 | 20.25 | 142.89 |
| <i>Pseudevadne tergestina</i> (Claus, 1877) | 50 | 4.81 | 35.52 |
| Unidentified Cladocera | 6 | 0.02 | 0.15 |
| Total contribution | | | 742.65 |

Table S4. Chaetognatha species composition off Santa Catarina continental shelf and the most abundant species code names used in the CCA analysis (bold). FO: frequency of occurrence; RA: relative abundance

| Chaetognatha | FO (%) | RA (%) | Abundance (ind/m³) |
|--|---------------|---------------|--|
| Family Eukrohniidae | | | |
| <i>Krohnitta subtilis</i> (Grassi, 1881) | 39 | 0.9 | 5.55 |
| Family Pterosagittidae | | | |
| <i>Pterosagitta draco</i> (Krohn, 1853) | 50 | 1.2 | 9.31 |
| Family Sagittidae | | | |
| <i>Ferosagitta hispida</i> (Conant, 1895) | 89 | 5.7 | 36.47 |
| <i>Flaccisagitta enflata</i> (Grassi, 1881) | 100 | 66.4 | 390.35 |
| <i>Flaccisagitta hexaptera</i> (d'Orbigny, 1843) | 17 | 0.1 | 0.73 |
| <i>Mesosagitta mzinima</i> (Grassi, 1881) | 100 | 8.4 | 56.72 |
| <i>Sagitta bipunctata</i> Quoy & Gaimard, 1827 | 11 | 0.4 | 2.35 |
| <i>Serratogitta serratodentata</i> (Krohn, 1853) | 94 | 6.5 | 42.11 |
| Unidentified juvenile | 94 | 10.8 | 62.54 |
| Total contribution | | | 606.14 |