RAFAEL GONÇALVES ARAUJO

INFLUÊNCIA DOS PARÂMETROS AMBIENTAIS NA VARIABILIDADE ESPACIAL E INTERANUAL DO FITOPLÂNCTON NO ESTREITO DE BRANSFIELD, ANTÁRTICA

RIO GRANDE Abril – 2012

UNIVERSIDADE FEDERAL DO RIO GRANDE PÓS-GRADUAÇÃO EM OCEANOGRAFIA BIOLÓGICA

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Dissertação apresentada ao Programa de Pós-graduação em Oceanografia Biológica da Universidade Federal do Rio Grande, como requisito parcial à obtenção do titulo de MESTRE.

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RESUMO

O presente trabalho descreve a variabilidade espacial e temporal da biomassa (Clorofila-a - Cla) e composição do fitoplâncton (grupos taxonônimos) em relação às condições ambientais no estreito de Bransfield. O estudo foi realizado com base em dados in situ (2003-05 e 2008-10) e imagens de satélite, durante os verões de 2002-2010. Uma frente termohalina foi geralmente observada entre as frias e relativamente salgadas águas sob influência do Mar de Weddell (ATW), posicionadas ao sul, e maior temperatura e menor salinidade foi encontrada nas águas sob influência do Mar de Bellingshausen (ATB), ocupando a porção norte. Análises de correspondência canônica mostraram que a dominância de diatomáceas microplanctônicas esteve associada com elevados níveis de Cla em águas ATB com camada de mistura rasa e com forte picnoclina, principalmente nas proximidades das Ilhas Shetland do Sul (SSI). As estações sob influência da ATW foram principalmente caracterizadas por baixa Cla relacionada com uma coluna d'água bem misturada e dominância de flagelados nanoplanctônicos (incluindo haptófitas e criptófitas). O gelo marinho mostrou-se importante no estabelecimento de uma camada de mistura com forte picnoclina (próximo das SSI) pelo aporte de água doce, através do seu derretimento. Com base em dados in situ e satelitais, a variabilidade espacial observada sugere que a comunidade fitoplanctônica no estreito de Bransfield é governada por uma combinação de processos atuando sinergéticamente: a retração do gelo marinho leva à formação de uma camada de mistura rasa associada a uma forte picnoclina que retém os organismos próximos à superfície, sob condições ideais de luz. Ainda, a variabilidade interanual na composição específica indica uma alternância na dominância de diatomáceas e flagelados, de acordo com as variações das propriedades físicas da coluna d'água, a priori. Desse modo, o derretimento do gelo pode ser considerado como o mais importante processo na modulação da variabilidade temporal do fitoplâncton.

Palavras chave: fitoplâncton, estreito de Bransfield, estrutura vertical da coluna d'água, nutrientes, sensoriamento remoto.

ABSTRACT

This article describes the spatial and interannual variability of phytoplankton biomass [chlorophyll a (Chl-a)] and taxonomic groups in relation to environmental conditions in the Bransfield Strait (BS). The study is based on both in situ (2003-2005 and 2008–2010) and satellite (2002–2010) data, during austral summer. A thermo-haline front was generally observed between cold and saltier waters under influence of the transitional water with Weddell Sea influence (TWW) in the southern BS and fresher and warmer waters associated with the presence of the transitional water with Bellingshausen Sea influence (TWB) in the northern BS. Canonical correspondence analysis showed that microplanktonic diatoms' dominance was associated with high Chl-a levels in shallow upper mixed layers with relatively strong pycnocline waters of TWB, mainly closer to the South Shetland Islands (SSI). TWW was mainly characterized by low Chl-a related to well mixed water column and dominated by nanoplanktonic flagellates (including haptophytes and cryptophytes). Sea ice seemed to be important in producing an upper mixed layer with strong pycnocline (mainly near to the SSI) by fresh water input through ice melting. Considering both in situ and satellite data, spatial variability suggests that phytoplankton community in the Bransfield Strait is governed by a combination of processes acting synergistically: sea ice retreat triggers the formation of a shallow upper mixed layer associated to a strong pycnocline that retains organisms near the surface, under ideal light conditions. Also, the observed interannual variability in species composition indicates an alternation between diatom-dominated and flagellate-dominated assemblages according to, a priori, varying physical features of the water column. Therefore, ice melting can be considered as the most important process modulating phytoplankton temporal variability.

Keywords: phytoplankton, Bransfield Strait, water column vertical structure, nutrients, remote sensing

1. INTRODUÇÃO

1.1. O fitoplâncton no Oceano Austral

O fitoplâncton, principal produtor primário no Oceano Austral (ou Oceano Antártico; OA), exerce influência sobre a teia trófica e transferência de energia, possuindo ainda papel de destaque na ciclagem de nutrientes ao redor do continente antártico e adjacências. Esse grupo é composto por organismos que afetam a estrutura e dinâmica dos ciclos biogeoquímicos e também auxiliam no processo de seqüestro do CO₂ pelo processo conhecido como bomba biológica (e.g. Garibotti et al., 2005). Entretanto, apesar da elevada biomassa fitoplanctônica descrita em muitos estudos conduzidos no Oceano Austral, as concentrações de Cla e produtividade primária, de um modo geral, são típicas de águas oligotróficas a mesotróficas (e.g. Garibotti et al., 2005).

Estudos realizados no Oceano Austral durante o verão apontaram que o fitoplâncton não parecia ser limitado por luz e tampouco por nutrientes inorgânicos dissolvidos (nitrogênio e fósforo) (e.g. Holm-Hansen & Mitchell, 1991; Arrigo *et al.*, 1999; Holm-Hansen *et al.*, 2004a). Assim, outros parâmetros que não macronutrientes e radiação solar seriam os responsáveis pela limitação do fitoplâncton nas águas antárticas. Além disso, foi observado que a biomassa do fitoplâncton foi proporcionalmente inversa à profundidade da camada de mistura e que esta seria a principal responsável por estimular o desenvolvimento das florações de verão observadas naquela circunstância (Mitchell & Holm-Hansen, 1991). Outros fatores tais como cobertura de gelo, ventos, disponibilidade do micronutriente ferro (Fe) e herbivoria pelo

zooplâncton exercem influência sobre o fitoplâncton na região (Mitchell et al., 1991; Marrari et al., 2008).

A produtividade primária em grande parte do Oceano Austral está envolvida em um paradoxo no qual se tem observado que, embora existam elevadas concentrações de macronutrientes inorgânicos (em geral, nitrogenados, fosfato e silicato), a biomassa fitoplanctônica é relativamente baixa. Tal paradoxo fez com que essa região fosse enquadrada no grupo das regiões de elevada concentração de nutrientes e baixa concentração de Cla (HNLC - High Nutrient Low Chlorophyll). Investigações com análises de micronutrientes revelaram que a disponibilidade do ferro é um elemento chave na limitação do crescimento do fitoplâncton, em elevada e praticamente constante concentração de macronutrientes apresentada na região (Martin et al., 1991; Boyd et al., 2002). Ainda assim, elevadas concentrações de Fe foram encontradas no OA em regiões costeiras (e.g. Hoppema et al., 2003), ao redor de ilhas (e.g. Blain et al., 2001) e também em frentes oceânicas, quando da ocorrência de eventos de ressurgência (e.g. Bracher et al., 1999). Estes eventos podem estimular a produção primária e o desenvolvimento do fitoplâncton o qual pode apresentar concentrações de Cla superiores a 10 mg m⁻³ (e.g. Garibotti *et al.*, 2005).

A formação de florações de mesoescala com elevada concentração de Cla em águas de plataforma e próximo à borda do gelo, é geralmente associada à estabilização da coluna d'água (favorecendo altos níveis de luz) e, principalmente, ao aporte de Fe na camada superficial. Esse micronutriente é introduzido no ambiente marinho antártico principalmente devido ao aporte de águas de menor densidade e ricas em Fe, provenientes do degelo (e.g. Arrigo *et al.*, 1999; Garibotti *et al.*, 2005). Entretanto, o estabelecimento de tais florações pode ser revertido quando da atuação de fortes ventos sobre a superfície do mar, mesmo na primavera, estabelecendo a presença de camadas de mistura profundas que, por sua vez, limitam o desenvolvimento fitoplanctônico pela menor disponibilidade de luz (Holm-Hansen *et al.*, 1997). Assim, uma estreita relação entre o fitoplâncton e a distribuição de algumas variáveis ambientais é observada, exercendo influência sobre a biomassa e a produtividade primária. Com base nestas relações, foi possível definir províncias biogeográficas nas quais os processos físicos e a disponibilidade de Fe influenciam o desenvolvimento fitoplanctônico: a Zona da Frente Polar, a Zona permanentemente aberta, as Zonas Marginais de Gelo e as Zonas Costeiras e de Plataforma Continental (e.g. Tréguer & Jacques, 1992; Arrigo *et al.*, 1998).

1.2. Área de estudo: O estreito de Bransfield

A região da Península Antártica, onde se insere o estreito de Bransfield, vem recebendo atenção da comunidade científica internacional devido ao fato de ser uma das regiões de maior susceptibilidade à influência dos fenômenos decorrentes das mudanças globais (Turner *et al.*, 2005; Steig *et al.*, 2009). Mudanças ambientais em nível regional na Península Antártica têm alterado a biomassa e também a composição das comunidades fitoplanctônicas nas suas adjacências (Garibotti et al., 2005; Ducklow et al., 2007; Montes-Hugo et al., 2009).

Situado a noroeste da Península Antártica, o estreito de Bransfield é um mar semifechado de aproximadamente 50000 km² cuja bacia é limitada ao

norte pelas Ilhas Shetland do Sul (ISS) e ao sul pela própria Península Antártica (Figura 1). A bacia na qual o estreito está localizado é conectada a oeste ao Mar de Bellingshausen e a leste ao Mar de Weddell. Um complexo sistema de circulação superficial dirigida pelo vento é observado na região, no qual duas principais massas d'água ocupam as camadas superficiais: Água Transicional com influência de Bellingshausen (ATB) e Água Transicional com influência de Bellingshausen (ATB) e Água Transicional com influência de Bellingshausen (ATB) e Água Transicional com influência de Ueddell (ATW), oriundas das bacias de Bellingshausen e Weddell, respectivamente (López *et a*l., 1999; Amos, 2001; Zhou *et al.*, 2006; Sangrà *et al.*, 2011). A dinâmica de tais massas d'água é a maior responsável pela variabilidade interanual na circulação do estreito de Bransfield e, consequentemente, no estabelecimento e desenvolvimento das comunidades fitoplanctônicas na região (e.g. Hewes *et al.*, 2009).

Estudos realizados no estreito de Bransfield mostraram que alguns setores da região apresentam elevada biomassa de fitoplâncton (Hewes *et al.*, 2009) que reflete nas taxas de produtividade primária da região (Lorenzo *et al.*, 2002). Desse modo, a região apresenta notável importância trófica devido à produtividade primária local, que sustenta alta biomassa de organismos zooplanctônicos, principalmente o krill (Loeb *et al.*, 2010). O krill e outros organismos zooplanctônicos atraem populações de organismos de níveis tróficos superiores, tais como pinguins, focas e baleias (Loeb *et al.*, 1997; Secchi *et al.*, 2001; Dalla Rosa *et al.*, 2008). A presença desses organismos predadores de topo na região estimulou a realização de muitos estudos com o intuito de aprimorar o conhecimento sobre a base da cadeia trófica local, o fitoplâncton, assim como as suas relações com o ambiente marinho e outros

organismos (e.g. Mitchell & Holm-Hansen, 1991; Figueiras *et al.*, 1998; Bode *et al.*, 2002; Castro *et al.*, 2002; Holm-Hansen *et al.*, 2004a; Hewes *et al.*, 2009).

Em um programa multidisciplinar conduzido no estreito de Bransfield entre Dezembro/1986 e Março/1987 (*RACER – Research on Antarctic Coastal Ecosystem Rates*) foi observada forte variação sazonal no desenvolvimento do fitoplâncton na região (Holm-Hansen & Mitchell, 1991). As maiores concentrações de Cla (Holm-Hansen & Mitchell, 1991; Mitchell & Holm-Hansen, 1991) bem como as maiores taxas de produtividade primária (Holm-Hansen & Mitchell, 1991) estavam associadas a regiões costeiras e sobre a plataforma continental. Ainda, neste estudo as maiores biomassas foram encontradas sobre as regiões de plataforma, onde a camada de mistura era mais rasa (Mitchell & Holm-Hansen, 1991). Os autores concluíram que a menor biomassa fitoplanctônica observada nas regiões de plataforma não era em função da limitação por luz, e nem pela concentração de nutrientes dissolvidos, que foram particularmente elevados. O pasteio, a sedimentação e a advecção foram importantes mecanismos para o massivo declínio observado na floração (Holm-Hansen & Mitchell, 1991).

Em um estudo baseado em séries temporais, as maiores concentrações de Cla foram encontradas ao redor das Ilhas Shetland do Sul, cuja temperatura variou entre 1,2 a 1,8°C, sob influência de camada de mistura rasa (Hewes *et al.*, 2009). Esse estudo encontrou correlações negativas entre a Cla e a profundidade da camada de mistura (22-60 m)e uma alta variabilidade interanual na concentração de Cla, com valores médios em superfície variando entre 0,3 a 2,3 mg m⁻³ (Hewes *et al.*, 2009). Tal variabilidade foi similar à prevista pela Teoria da Profundidade Crítica (Sverdrup, 1953) e também

conforme indicam alguns estudos conduzidos na região (e.g. Mitchell & Holm-Hansen, 1991; Nelson & Smith, 1991).

Além de estudos com relação à distribuição espacial do fitoplâncton, a distribuição vertical da biomassa fitoplanctônica também foi relatada para a região do estreito de Bransfield (e.g. Holm-Hansen *et al.*, 1997; Holm-Hansen & Hewes, 2004; Holm-Hansen *et al.*, 2005). Entretanto, tais estudos observaram que poucas áreas amostradas ao longo da região apresentavam um máximo de Cla em profundidade, mas queas maiores concentrações de Cla estavam geralmente concentradas na superfície ou distribuídas em uma camada superficial rasa. Ainda, Holm-Hansen *et al.* (1997) notaram que áreas sob influência da ATW apresentavam baixas concentrações de Cla associadas a uma camada de mistura com fraca estratificação, quando comparadas com o restante das áreas amostradas ao longo do estreito.

O fitoplâncton nos arredores da Península Antártica, incluindo o estreito de Bransfield, é dominado por três principais grupos taxonômicos: diatomáceas, haptófitas (principalmente *Phaeocystis antarctica*) e criptófitas (Rodriguez *et al.*, 2002; Garibotti *et al.*, 2005; Kozlowski *et al.*, 2011). Uma comunidade dominada pela criptófita *Cryptomonas* sp. foi relatada no estreito de Bransfield, durante o verão de 1995 (Rodriguez *et al.*, 2002). Por outro lado, durante o verão de 1996, os mesmos autores encontraram uma comunidade representada pela haptófita *Phaeocystis* cf. *antarctica* e pequenos flagelados, com contribuição de algumas diatomáceas em ambos os anos.

Sabe-se que as florações fitoplanctônicas ao redor da Península Antártica, tipicamente associadas com camada de mistura rasa e disponibilidade de Fe (e.g. Prézelin *et al.*, 2000), são normalmente dominados por diatomáceas e/ou *P. antarctica*. Contudo, alguns estudos têm destacado a crescente importância das criptófitas na região, as quais podem prevalecer sobre as diatomáceas, principalmente em regiões de derretimento recente de gelo (Moline & Prézelin, 1996; Moline *et al.*, 2004; Mendes et al., 2012).

Alterações na estrutura da comunidade fitoplanctônica refletem diretamente nas comunidades que ocupam os demais níveis tróficos. Por exemplo, o krill pode ser suprimido por um processo competitivo com salpas, quando em condições de baixa concentração de Cla no estreito de Bransfield (Loeb *et al.*, 2010). Tendo em vista que o krill antártico preda mais eficientemente sobre diatomáceas do que sobre criptófitas, uma mudança entre o domínio destes dois grupos afetaria diretamente as interações ao longo da cadeia trófica de tal ambiente (Haberman *et al.*, 2003).

2. OBJETIVOS DO TRABALHO

2.1. Objetivo geral

O presente trabalho tem por objetivo investigar a variação espacial e interanual do fitoplâncton em relação a alguns parâmetros ambientais na região do estreito de Bransfield, com base em dados adquiridos *in situ* e por satélites.

2.2. Objetivos específicos

- Avaliar a estrutura vertical da coluna d'água por meio de sua estabilidade e profundidade da camada de mistura;

- Analisar a variabilidade espacial e interanual dos grupos do fitoplâncton na região;

- Relacionar os parâmetros ambientais e a biomassa e composição dos grupos do fitoplâncton.

3. MATERIAL E MÉTODOS

3.1. Coleta dos dados e amostras

Os cruzeiros oceanográficos GOAL e SOS-CLIMATE foram conduzidos sob a responsabilidade do Grupo de Oceanografia de Altas Latitudes (GOAL) a bordo do N. Ap.Oc. *Ary Rongel* ao longo do estreito de Bransfield (Figura 1), nos verões de 2003-2005 e 2008-2010, durante os cruzeiros GOAL e SOS-CLIMATE, respectivamente. Os cruzeiros fazem parte do Programa Antártico Brasileiro (PROANTAR) e o projeto SOS-CLIMATE (*Southern Ocean Studies for Understanding Global Climate Issues*) está inserido no âmbito do Ano Polar Internacional (API 2007-2008).



Figura 1. Esquerda: Continente Antártico e Oceano Austral. Direita: Península Antártica e estreito de Bransfield (retângulo vermelho).

Perfis verticais de temperatura e salinidade foram adquiridos com auxílio de um sensor CTD (*Conductivity, Temperature, Depth*) modelo SeaBird® 911+ acoplado a um sistema de roseta. Ao mesmo sistema estavam acopladas garrafas de Niskin com capacidade para 5L de amostras de água, que foram coletadas em diversas profundidades para análises de fitoplâncton e concentração de macronutrientes dissolvidos. Amostras de água de superfície foram coletadas com garrafas Van Dorn, lançadas manualmente na lateral do navio.

3.2. Parâmetros físicos

A densidade potencial da água do mar (ρ) foi obtida com base nos perfis de temperatura e salinidade adquiridos com o CTD. A partir de perfis verticais de densidade potencial ($\partial \rho / \partial z$), a profundidade da camada de mistura (UMLD – *Upper mixed layer depth*) foi determinada, sendo aquela na qual a variação vertical para cada 5 m de profundidade era igual ou superior a 0,02 (adaptado de Mitchell & Holm-Hansen, 1991). A estabilidade da coluna d'água (*E*) foi calculada com base na variação vertical da densidade, expressa através da Frequência de Brunt-Väisälä (N^2), que é definida do seguinte modo: $N^2 = -\frac{g}{\rho} \frac{\partial \rho}{\partial z}$ (rad² s⁻²); levando a $E = \frac{N^2}{g}$ (10⁻⁸ rad² m⁻¹), onde *g* é a aceleração da gravidade (m s⁻²) e ρ é a densidade potencial da água do mar (kg m⁻³). Foi considerado que a estabilidade máxima imediatamente abaixo da UMLD representa a força da picnoclina e assim esse valor foi adotado como sendo *E* (Castro *et al.*, 2002).

3.3. Análise dos nutrientes

O processamento e análise das amostras de nutrientes inorgânicos dissolvidos (para análises de amônio, nitrito, nitrato, fosfato e silicato) foram realizados pelo Prof. Dr. Ricardo Pollery da Universidade Federal do Rio de Janeiro (UFRJ) segundo as recomendações descritas em Strickland & Parsons (1972). Maiores detalhes com relação aos métodos são encontrados na subseção "2.4. *Nutrient Analysis*" do Anexo I.

3.4. Análises do fitoplâncton

Amostras para análise de Cla total (mg m⁻³) e fracionada em classes de tamanho (< 20 μ m e > 20 μ m), coletadas em superfície e profundidades préestabelecidas (apenas para Cla total) foram filtradas em filtros de fibra de vidro Whatman GF/F. Os filtros foram mantidos congelados em nitrogênio líquido até análises em laboratório em terra. O pigmento foi extraído em acetona (90%) e analisado segundo duas técnicas distintas: a concentração do pigmento foi determinada por espectrofluormetria segundo a metodologia de Neveux & Lantoine (1993) (cruzeiros GOAL 2003 e 2004) e; por fluorimetria sem acidificação (Welschmeyer, 1994) (cruzeiros GOAL 2005 e SOS-CLIMATE 2008-2010). As amostras para análise da Cla por classes de tamanho foram filtradas em filtros de membrana de policarbonato (GE), para estimativa do microplâncton (> 20 µm). A água resultante desta filtração foi novamente filtrada (Whatman em fibra de vidro GF/F) para estimativa do nano+picoplâncton (< 20 µm). Para efeito de facilitar a fluência do texto, esta última classe será referida neste trabalho como "nanoplâncton". Foram obtidos perfis verticais discretos de concentração de Cla em todos os cruzeiros, cujas profundidades máximas de coleta variaram devido a questões logísticas. Com o objetivo de homogeneizar os dados, a concentração de Cla integrada na coluna d'água (mg m⁻²) foi calculada para a camada superficial de 50 m, que engloba amostragens discretas de Cla em todos as estações oceanográficas consideradas no presente estudo.

Amostras destinadas a contagem e identificação de organismos fitoplanctônicos em microscopia ótica foram coletadas apenas nos cruzeiros GOAL 2003-2004 e SOS 2008-2009. Essas consistiram em amostras de água de 200 mL coletadas na superfície e fixadas com formaldeído (concentração final de 4%) para amostras dos cruzeiros GOAL e em solução alcalina de Lugol (2%) para amostras relativas aos cruzeiros SOS. Estas amostras foram analisadas por Fernanda Oliveira (UFRJ) para os cruzeiros GOAL e Márcio Silva de Souza para os cruzeiros SOS-CLIMATE seguindo os procedimentos em Dodge (1982) e Hasle & Syvertsen (1996). Para as análises deste trabalho, as espécies foram agrupadas de acordo com os seguintes grupos: diatomáceas, dinoflagelados, criptófitas, flagelados (incluindo *Phaeocystis antarctica* e outros flagelados não identificados) e cocolitoforídeos.

3.5. Análises de dados de satélites

As imagens de satélites referentes à concentração superficial de Cla (CSM) e temperatura da superfície do mar (TSM) utilizadas no presente trabalho foram adquiridas pelo sensor MODIS (*Moderate Resolution Imaging Spectroradiometer*) acoplado ao satélite Aqua da NASA (*National Aeronautics and Space Agency*). Os dados utilizados no presente estudo referem-se a composições mensais L3 (*Level* 3) SMI (*Standard Mapped Image*), com

resolução espacial de 4 km. Entretanto, devido à extensa cobertura de gelo e nuvens, assim como falta de radiação solar durante o inverno, foram consideradas apenas as imagens MODIS-Aqua entre Setembro e Março, no período compreendido entre Setembro de 2002 e Março de 2010..

Através de dados adquiridos pelo sensor AMSR-E-Aqua (Advanced Microwave Scanning Radiometer for the Earth Observing System) foram geradas composições mensais da concentração de gelo marinho, com base em imagens diárias, para o mesmo período considerado para as imagens MODIS. Tais composições apresentam resolução espacial de aproximadamente 6x4 km em uma grade de 6,5 km. Os dados adquiridos pelo sensor consistem em informações sobre a temperatura de brilho, que é convertida em concentração de gelo marinho através da aplicação do algoritmo ASI (Artist Sea Ice) (Spreen et al., 2008), desenvolvido na Universidade de Bremen (Alemanha). O algoritmo baseia-se em um modelo empírico que tem como produto a concentração de gelo, expressa em porcentagem, variando entre 0 e 100% (Spreen et al., 2008). A área de gelo marinho foi determinada com base em pixels que apresentavam concentração de gelo marinho superior a 15% (Marrari et al., 2008; Spreen et al., 2008). A partir das imagens geradas, séries temporais foram elaboradas, as quais consistiram em médias mensais da área de estudo, em nível sinótico, para cada uma das variáveis analisadas (TSM, CSM e gelo marinho), considerando a área limitada pelas coordenadas 61,5° e 64,5°S e 54° e 62°W.

3.6. Análises estatísticas

Buscando identificar os padrões de variabilidade da comunidade, com relação à variação ambiental, foram realizadas análises de correspondência canônica (ACC) para os cruzeiros nos quais havia dados referentes à comunidade fitoplanctônica disponíveis (GOAL 2003–04 e SOS 2008–09). O padrão principal na média ponderada de cada um dos grupos foi avaliada com relação às variáveis ambientais (ter Braak & Prentice, 1988). As variáveis bióticas consistiram na abundância dos principais grupos taxonômicos do fitoplâncton. As variáveis abióticas foram expressas pela temperatura, salinidade, nitrogênio inorgânico dissolvido (NID: Amônio+Nitrito+Nitrato), fosfato, silicato, UMLD, *E*, Cla total, Cla-nanoplâncton (< 20 µm) e Cla-microplâncton (> 20µm). Maiores informações sobre a análise e interpretação dos resultados podem ser encontradas na subseção "2.6. *Statistical analysis*" no Anexo I.

Com o objetivo de detectar a relação temporal entre os sinais da temperatura da superfície do mar, Cla na superfície do mar e área de gelo marinho foi aplicada uma análise de correlação cruzada. Tal técnica permite a detecção de periodicidades comuns entre dois sinais de interesse. Informações complementares com relação ao método estão apresentadas na subseção "2.6. *Statistical analysis*" no Anexo I.

4. SÍNTESE DOS RESULTADOS E DISCUSSÃO

Esta seção trata de uma síntese dos principais resultados e discussões do presente trabalho, que constam no manuscrito "*Interannual variability of phytoplankton and oceanographic features in the Bransfield Strait, Antarctica*" (Anexo I).

4.1. Variabilidade espacial do fitoplâncton e variáveis ambientais

As duas principais massas d'água superficiais encontradas no estreito de Bransfield foram a ATB (temperatura superficial superior a 0,9°C) e ATW (temperatura superficial inferior a 0,9°C), conforme anteriormente descrito para a região (López et al., 1999; Amos, 2001; García et al., 2002, Sangrà et al., 2011). Tais massas d'água estavam separadas por uma feição denominada Frente da Península (e.g. Sangrà et al., 2011), exceto para o ano de 2010, quando não foi observada a distinção entre tais massas, devido às baixas temperaturas em toda a região. Esse gradiente físico também foi refletido na distribuição do fitoplâncton, principalmente em relação à biomassa. corroborando o que foi reportado na região nos trabalhos de Castro et al. (2002) e Hewes et al. (2009). As estações sob influência da ATB apresentaram camada de mistura rasa (< 30 m) e com estratificação relativamente forte (> 2000 10⁻⁸ rad² m⁻¹), cujo estabelecimento pode ter-se dado devido à entrada de água proveniente de degelo, da mesma forma como por Holm-Hansen & Hewes (2004) e Holm-Hansen et al. (2004a). Por outro lado, as estações localizadas sob o regime da ATW exibiram camada de mistura profunda (> 40 m), ou estavam totalmente misturadas, conforme observado por Sangrà et al., (2011). A concentração de macronutrientes em superfície se mostrou em concentrações semelhantes às reportadas por Castro *et al.* (2002) e García *et al.* (2002), e aparentemente não eram limitantes ao estabelecimento e crescimento de organismos fitoplanctônicos.

A partir dos dados in situ e informações de imagens de satélite tornou-se evidente a relação entre a concentração de Cla e as principais massas d'água encontradas na região: biomassa (Cla) relativamente elevada associada à ATB e adjacências das ISS enquanto que nas águas sob a influência da fria ATW, a biomassa foi significativamente menor (p<0,05) devido a uma provável limitação por luz. Estes resultados corroboram estudos conduzidos na região durante o verão de 2004 (Hewes et al., 2008). A biomassa relativamente elevada ao redor das ISS pode ser atribuída a um provável aporte do micronutriente Fe naquelas águas. Tal aporte pode ter sido associado ao degelo que, por sua vez, promove também a formação de uma camada de mistura rasa (Arrigo et al., 1999; Garibotti et al., 2003). Entretanto, estudos recentes em ilhas e regiões costeiras do Oceano Austral têm mostrado que outros fatores tais como a mistura vertical e ressurgência (muitas vezes associadas ao entorno de ilhas) são de importante papel na fertilização das águas superficiais limitadas principalmente por Fe (Bucciarelli et al., 2001; Bakker et al., 2007), papel este talvez maior que o representado pelo degelo (Klunder et al., 2011).

As análises de Cla fracionada e microscopia revelaram que a elevada biomassa encontrada nas proximidades das ISS foi dominada por diatomáceas microplanctônicas, assim como observado na região (e.g. Rodriguez *et al.*, 2002; Montes-Hugo *et al.*, 2008). Dentre essas diatomáceas, a grande *Corethron pennatum* ocorreu em todos os anos e foi dominante em 2003, sendo reportada como um importante representante da comunidade microfitoplanctônica em outras áreas do Oceano Austral (e.g. Froneman *et al.*, 1995; Kang & Lee, 1995). No entanto, em geral, conforme descrito em estudos realizados no Oceano Austral (e.g. Varela *et al.*, 2002; Jacques and Panouse, 1991; Garibotti *et al.*, 2005), os nanoflagelados foram os organismos dominantes: criptófitas foram dominantes nos cruzeiros GOAL, enquanto outros flagelados (incluindo a abundante *Phaeocystis antarctica*) dominaram nos cruzeiros SOS.

A análise de correspondência canônica mostrou que a variabilidade da biomassa fitoplanctônica foi correspondente com as massas d'água na área de estudo, com base nas elevadas raízes canônicas observadas para temperatura, salinidade e Cla. Elevados valores também foram encontrados para a profundidade da camada de mistura e estabilidade da coluna d'água, o que corrobora a premissa de que a estrutura vertical das massas d'água exerce influência na variabilidade do fitoplâncton (Mitchell & Holm-Hansen, 1991; Townsend *et al.*, 1991; Castro *et al.*, 2002; Ryabov *et al.*, 2010).

As águas frias e relativamente salgadas provenientes do Mar de Weddell, que entram no estreito de Bransfield, formam uma massa d'água verticalmente homogênea e relativamente instável. Associada a essa massa d'água, foi detectada uma comunidade com baixa biomassa, dominada por pequenas criptófitas e flagelados não identificados, nos cruzeiros GOAL e SOS, respectivamente. As estações sob a influência da ATB, por outro lado, foram caracterizadas por elevados níveis de Cla e domínio de diatomáceas microplanctônicas, associados à presença de uma camada de mistura rasa e estabilidade elevada, provavelmente associadas a um recente degelo. Estes organismos foram observados principalmente em estações com altos níveis de Cla, nas proximidades das ISS, conforme anteriormente apontado por Holm-Hansen & Hewes (2004) e Holm-Hansen *et al.* (2004a). Além do estreito de Bransfield, diatomáceas foram relacionadas com degelo e camada de mistura rasa em estudos conduzidos no Mar de Ross (Arrigo *et al.*, 1999) e ao norte da península Antártica (Moline & Prézelin, 1996; Moline *et al.*, 2004). No presente trabalho, processos como mistura vertical e ressurgência, ocorridos anteriormente ao período de estudo, podem ter sido responsáveis por fertilizar as águas superficiais nas adjacências das ISS. Entretanto, o aquecimento da camada superficial e o degelo promoveram uma camada de mistura rasa com estratificação relativamente forte, provavelmente com níveis relativamente elevados de Fe, um ambiente no qual as diatomáceas são fortes competidoras (Gerringa *et al.*, 2000; Hoppema *et al.*, 2003).

4.2. Variabilidade interanual no estreito de Bransfield

As séries temporais desenvolvidas a partir de imagens de satélite de TSM, CSM e gelo marinho mostraram uma notável tendência de variabilidade sazonal (ver figuras no Anexo I). Tal variabilidade na CSM foi anteriormente reportada por Holm-Hansen *et al.*, (2004b) quando analisando imagens SeaWiFS da região do Mar de Scotia e adjacências (incluindo o estreito de Bransfield). Além da variabilidade sazonal, uma forte variabilidade interanual foi observada na área de estudo, cujo máximo de CSM para a série temporal foi atingido no verão austral de 2005-06.

Sabe-se que florações de diatomáceas são geralmente encontradas durante o início do verão, quando da retração do gelo marinho. Mais tarde, quando a coluna d'água continua estratificada, a floração de diatomáceas é substituída por pequenos flagelados, tais como as criptófitas (Ducklow et al., 2007). Num estágio final de sucessão, é comum observar uma comunidade dominada por diatomáceas e flagelados (Moline & Prézelin, 1996; Garibotti et al., 2005). Embora as amostragens tenham sido realizadas durante o verão tardio, a comunidade fitoplanctônica variou significativamente entre os cruzeiros: criptófitas foram dominantes em 2003 e 2004, e outros flagelados em 2008 e 2009. Ainda em 2003, em algumas estações nas quais não foi exibido o domínio de criptófitas, houve dominância de diatomáceas, conforme observado por Garibotti et al. (2005), numa distribuição em mosaico. Tal variabilidade na composição dos grupos dominantes na região indica que a extensão e magnitude do gelo marinho refletem preponderância em uma de criptófitas/flagelados sobre as diatomáceas nos anos com menor cobertura de gelo marinho (2003, 2004 e 2008). Em situações de maiores áreas livres de gelo marinho (2009), caracterizadas por um possível aporte de ferro, as criptófitas foram substituídas pelas diatomáceas. Esta hipótese foi sugerida por C.R.B. Mendes (Comunicação pessoal), para explicar o domínio de criptófitas sobre diatomáceas no verão de 2010, no gual havia menor área livre de gelo. Ao mesmo tempo, alguns estudos relacionaram a dominância espacial e/ou temporal de criptófitas com condições de início de degelo marinho, nas quais foram observadas uma forte picnoclina e menor disponibilidade de ferro [Garibotti et al., 2005; Moline et al., 2004; C.R.B. Mendes (Comunicação pessoal)].

Embora a dominância de criptófitas seja relacionada à presença de água de degelo, com forte estratificação e disponibilidade de Fe (Garibotti *et al.*, 2005), estas dominaram inclusive em águas com a camada de mistura profunda ou colunas totalmente misturadas. Tais fatos levam à ideia de que UMLD e estabilidade não exercem influência direta no estabelecimento e desenvolvimento de criptófitas onde o desenvolvimento de diatomáceas fica comprometido por uma provável limitação por Fe, após uma floração. Entretanto, a conexão entre criptófitas, estrutura da coluna d'água e a disponibilidade de ferro continua vaga, principalmente devido à dificuldade na aquisição de dados referentes a esse composto na água do mar (Lancelot *et al.*, 2009).

4.3. Implicações tróficas

Além dos fatores físicos e químicos que controlam o desenvolvimento e distribuição das comunidades fitoplanctônicas, o papel do pasteio pelo mesozooplâncton, principalmente krill e salpas, deve ser considerado. Tais organismos são frequentemente detectados em níveis de concentração elevados ao longo do Oceano Austral (Loeb *et al.*, 1997, 2010). A região do estreito de Bransfield tem destaque na manutenção das populações de organismos mesozooplanctônicos, uma vez que é um importante berçário e local de desenvolvimento do krill antártico (*Euphausia superba*) (Loeb *et al.*, 1997, 2010). Isso faz da região uma importante fonte desses organismos para o Oceano Austral (Loeb *et al.*, 1997, 2010). Entretanto, a comunidade do krill antártico pode ser ocasionalmente suprimida pelo desenvolvimento de salpas, geralmente associado a condições de baixa Cla (Loeb *et al.*, 2010). Tal

variabilidade na composição específica do zooplâncton é decorrente da variabilidade apresentada pela comunidade fitoplanctônica estabelecida: diatomáceas são pastadas mais eficientemente pelo krill antártico, enquanto as criptófitas são preferencialmente pastadas por salpas. Desse modo, uma mudança de uma comunidade fitoplanctônica dominada por diatomáceas para uma comunidade dominada por criptófitas pode alterar as interações na cadeia trófica local (Haberman *et al.*, 2003). O presente trabalho identificou uma predominância de criptófitas e flagelados em 2003, 2004 e 2008, contrastando com 2009, quando diatomáceas foram mais abundantes. É possível que, além da influência física exercida pelo ambiente, a pressão pelo pasteio sobre os flagelados deve ter sido fraca, em geral, e o desenvolvimento do krill pode ter sido favorecido durante o verão de 2009.

Sabendo da influência que a composição da comunidade fitoplanctônica exerce na composição da comunidade zooplanctônica (Moline *et al.*, 2004; Montes-Hugo *et al.*, 2009), e ainda que organismos de elevados níveis tróficos, tais como pinguins, pinípedes e cetáceos, consomem preferivelmente o krill a salpas (Loeb *et al.*, 1997), fica evidente que mudanças na composição fitoplanctônica na região podem acarretar em *feedbacks* negativos sobre a ecologia desses consumidores.

5. CONCLUSÕES

A comunidade fitoplanctônica e as propriedades oceanográficas ao longo do estreito de Bransfield mostraram distintos padrões em sua distribuição espacial, em acordo com as duas principais massas d'água presentes na região: ATB e ATW. Áreas sob o domínio da ATW, caracterizadas por camada de mistura profunda e de estabilidade relativamente baixa, foram geralmente dominadas por nanoflagelados, associadas a baixa biomassa (Cla) Por outro lado, as estações sob influência da ATB apresentaram elevada biomassa fitoplanctônica, dominada principalmente por diatomáceas microplanctônicas. Essas áreas exibiram camada de mistura rasa atrelada a uma estratificação relativamente forte. Isso sugere que a variabilidade espacial do fitoplâncton é limitada primariamente pela estrutra da coluna d'água. Uma vez que ATB e ATW apresentam colunas d'água com estrutura muito diferentes, a dinâmica dessas massas d'água no estreito de Bransfield se mostra crítica na modulação da variabilidade espacial da biomassa e comunidade fitoplanctônica. Foram observadas variações interanuais na composição dos grupos taxonômicos dominantes ao longo da área, principalmente com relação às diatomáceas e pequenos flagelados/criptófitas, influenciado pela magnitude e extensão da cobertura de gelo marinho. Essa variabilidade temporal foi dirigida principalmente por variações na temperatura, a qual influencia a cobertura de gelo marinho e processos de degelo e, consequentemente, a estrutura da coluna d'água. Desse modo, a estrutura da coluna d'água e o degelo marinho são vistos como as principais forçantes na modulação da variabilidade espacial e temporal, respectivamente, da distribuição do fitoplâncton no estreito de Bransfield.

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7. ANEXO i: Manuscrito formatado para submissão para o periódico Journal of Marine Systems

RUNNING HEAD: Phytoplankton and environmental variability in the Bransfield Strait

Influence of oceanographic features on spatial and interannual variability of phytoplankton in the Bransfield Strait, Antarctica

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ABSTRACT

This article describes the spatial and interannual variability of phytoplankton biomass [chlorophyll a (Chl-a)] and taxonomic groups in relation to environmental conditions in the Bransfield Strait (BS). This study is based on both in situ (2003-2005 and 2008–2010) and satellite (2002–2010) data, during austral summer. A thermohaline front was generally observed between cold and saltier waters under influence of the transitional water with Weddell Sea influence (TWW) in the southern BS and fresher and warmer waters associated with the presence of the transitional water with Bellingshausen Sea influence (TWB) in the northern BS. Canonical correspondence analysis showed that microplanktonic diatoms' dominance was associated with high Chl-a levels in shallow upper mixed layers with relatively strong pycnocline waters of TWB, mainly closer to the South Shetland Islands (SSI). TWW was mainly characterized by low Chl-a related to well mixed water column and dominated by nanoplanktonic flagellates (including haptophytes and cryptophytes). Sea ice seemed to be important in producing an upper mixed layer with strong pycnocline (mainly near to the SSI) by fresh water input through ice melting. Considering both in situ and satellite data, spatial variability suggests that phytoplankton community in the Bransfield Strait is governed by a combination of processes acting synergistically: sea ice retreat triggers the formation of a shallow upper mixed layer associated to a strong pycnocline that retains organisms near the surface, under ideal light conditions. Also, the observed interannual variability in species composition indicates an alternation between diatomdominated and flagellate-dominated assemblages according to, a priori, varying physical features of the water column. Therefore, ice melting can be considered as the most important process modulating phytoplankton temporal variability.

1. Introduction

The Southern Ocean is recognized as a very important component in the global climate maintenance and seawater ventilation through the thermohaline circulation (Sarmiento et al., 2004). Also, the primary production in the region is an important fraction of the global productivity (Arrigo et al., 1998; Bracher et al., 1999). In the Southern Ocean, phytoplankton crop and production can be related to distinct biogeochemical provinces, where physical features exert a significant influence: the Polar Front zone (PFZ), the permanently open ocean zone (POOZ), the marginal ice zones (MIZ) and the coastal and continental shelf zones (CCS) (Arrigo et al. 1998; Tréguer and Jacques 1992). In general, the continental shelves and marginal ice zones around Antarctica show a much higher phytoplankton biomass and productivity as compared to deep pelagic areas (Arrigo et al. 1998). The development of mesoscale blooms in shelf waters and ice edges are normally associated with water column stabilization from melting ice and their magnitudes have an important effect on the annual Southern Ocean productivity (Garibotti et al., 2005; Nelson et al. 1987; Sullivan et al. 1988). However, this process can be prevented by strong wind stress, even in spring and summer, producing deep mixed layers, limiting phytoplankton production by light availability (Holm-Hansen et al. 1997a). In addition, iron availability has also been recognized as a key limiting factor for phytoplankton development in the Southern Ocean (de Baar et al. 1995; de Baar et al. 1999; Loscher et al. 1997; Martin et al. 1990a, 1991).

The tip of the Antarctic Peninsula (AP) has been of great scientific concern, since it is one of the world regions most susceptible to global climate change (Steig et al., 2009; Turner et al., 2005). Environmental changes in the AP region have been implicated in changes of biomass and composition of primary producers, particularly phytoplankton (Ducklow et al., 2007; Garibotti et al., 2005; Montes-Hugo et al., 2009; Schloss et al., 2012).

1.1. Study region

The Bransfield Strait (BS) (Figure 1) is a semi-closed sea, located in the northwest of the AP and limited to the north by the South Shetland Islands (SSI) and to the south by the AP. The BS is connected to Weddell (east) and Bellingshausen (west) Seas, whose surface waters in the BS produce a complex circulation system. As a result, in the Strait, the following water masses can be detected: transitional water with Weddell influence (TWW) and transitional water with Bellingshausen influence (TWB) (Amos, 2001; López et al., 1999; Sangrà et al., 2011; Zhou et al., 2006).

Concerning phytoplankton studies, an eighteen years research program conducted along the BS showed that the highest chlorophyll a (Chl-*a*) concentrations were found around the South Shetland Island (SSI), where upper mixed layer depth (UMLD) was shown to have a negative relationship with Chl-*a* concentration (Hewes et al., 2009). Those authors found high interannual variability in Chl-*a* concentration with mean surface values varying from 0.3–2.3 mg m⁻³, associated with UMLD values of 60–22 m, respectively, similar to what was predicted by the critical depth theory (Sverdrup, 1953) and also generally found for Antarctic ecosystems (Mitchell and Holm-Hansen, 1991; Nelson and Smith, 1991).

In the eastern BS, Chl-*a* vertical distributions showed highest Chl-*a* at or close to the surface, decreasing rapidly with increasing depth at sites with no well defined upper mixed layer (totally stratified profile) and euphotic layer varying from 40–50 m (Holm-Hansen et al., 1997b). Those authors also found that sites under Weddell Sea influence

were weakly stratified and associated to low Chl-*a* concentration and deeper euphotic zone, as compared to stations at the western BS.

During the austral summer, the phytoplankton community in the BS was mainly dominated by the cryptophyte Cryptomonas sp. (summer 1995) and by the colonial haptophyte Phaeocystis cf. antarctica and small flagellates (summer 1996), with contributions of some diatoms in both years, based on light microscopy and CHEMTAX analysis of HPLC pigment data (Rodriguez et al., 2002). Similar phytoplankton communities mainly dominated by diatoms, haptophytes (primarily Phaeocystis antarctica) and cryptophytes were found in coastal regions of the AP and also in coastal waters of the Weddell Sea (Arrigo et al., 1999; Garibotti et al., 2003, 2005; Kozlowski et al., 2011). In general, phytoplankton blooms around the AP are typically associated with the development of a shallow mixed layer (retaining phytoplankton within adequate light levels) and iron availability (e.g., Prézelin et al., 2000) and are normally dominated by diatoms and/or haptophytes (generally P. antarctica). Nevertheless, some studies have highlighted the increasing importance of cryptophytes in the AP region, which prevail over diatoms, particularly in ice melting areas (Moline and Prézelin, 1996; Moline et al., 2004). Several studies have related the seasonal succession of phytoplankton in the AP and BS regions to the timing of sea ice retreat (e.g., Moline and Prézelin, 1996; Garibotti et al., 2005; C.R.B. Mendes, Personal *communication*). Firstly, diatom blooms dominate the biomass, when the sea ice retreat is under way. Later, when the water column is still stratified, those diatoms are replaced by flagellates such as cryptophytes (Ducklow et al., 2007). Finally, the phytoplankton community at low Chl-a concentration, is dominated mainly by diatoms and unidentified flagellates (Moline and Prézelin, 1996; Garibotti et al., 2005).

This study aims at investigating the variability in the phytoplankton biomass and taxonomic groups in relation to some physical and chemical parameters (water column structure, dissolved macronutrients) along the BS, based on *in situ* data. Furthermore, interannual variability in remote sensing Chl-*a*, temperature and sea ice is assessed.

2. Material and methods

2.1. Sampling

Sampling and data collection were carried out during the GOAL (High Latitude Oceanography Group) and SOS-CLIMATE (Southern Ocean Studies for Understanding Global Climate Issues) cruises, during late summers 2003–2005 and 2008–2010, respectively (Table 1 and Figure 1), on board the Brazilian Navy R/V "Ary Rongel", as part of the Brazilian Antarctic Program and the International Polar Year (IPY 2007-2008). Vertical profiles of temperature and salinity were taken with a SeaBird® 911+ CTD attached to a Carrousel system bearing 5-L Niskin bottles for water sampling. Water was collected from surface and several depths for further laboratory analysis of phytoplankton and dissolved macronutrients.

2.2. Physical parameters

Potential density was calculated from temperature and salinity from CTD casts. Upper mixed layer depth (UMLD) was determined from vertical density profiles $(\partial \rho / \partial z)$. The depth where variations in density were equal or greater than 0.02 over 5 m depth interval was considered the UMLD (m) (adapted from Mitchell and Holm-Hansen, 1991). Water column stability parameter (*E*) was calculated based on vertical density variations, as a function of the buoyancy or Brunt-Väisälä frequency (*N*²), which is defined by: $N^2 = -\frac{g}{\rho} \frac{\partial \rho}{\partial z}$ (rad² s⁻²) leading to $E = \frac{N^2}{g}$ (10⁻⁸ rad² m⁻¹), where *g* is gravity and ρ is the potential water density. In this study, it was considered that maximum stability immediately below the UMLD represents the strength of the pycnocline (Castro et al., 2002).

2.3. Phytoplankton analysis

Discrete samples for total and size-fractionated (grater and smaller than 20 μ m) Chl-a determination were collected from the surface and selected depths and filtered onto Whatman GF/F filters. These were kept frozen in liquid nitrogen until further analysis. In the laboratory, the pigment was extracted in 90% acetone and analyzed by two techniques: in cruises GOAL-2003 and GOAL-2004 the pigment content was determined by a Perkin Elmer LS-60B spectrofluorometer (Neveux and Lantoine, 1993). The emission fluorescence spectra were recorded between 620 and 710 nm, at 0.5 nm intervals. In the GOAL-2005 and all SOS cruises, Chl-a was determined using a Turner Designs TD-700 fluorometer, following the non-acidification method of Welschmeyer (1994). Size-fractionated Chl-a concentration was determined from surface samples filtered through membrane filters into the following size classes: microplankton (> 20 μ m) and nanoplankton + picoplankton (< 20 μ m, hereafter referred to as "nanoplankton"). The latter was determined by filtering water (filtrate from 20 µm membrane) through Whatman GF/F filters. Vertical profiles of discrete Chl-a measurements were performed in the six cruises. However, the maximum sampling depth varied between the cruises, depending on logistical issues. In order to homogenize the data, 50 m-integrated Chl-a (mg m⁻²) was used in all cruises.

Phytoplankton counting and identification data is available for cruises GOAL-2003, GOAL-2004, SOS-2008 and SOS-2009. Discrete samples (200 ml) were collected from sea surface and fixed with formaldehyde (4% final concentration) in the

GOAL cruises and 2% alkaline Lugol's iodine solution in the SOS cruises, for later microscope examination. In the laboratory, 50 to 100 mL sub-samples were analyzed using an inverted microscope, at 200× and 400× magnifications (Utermöhl, 1958). Phytoplankton composition was determined according to specific literature (mainly Balech, 1988; Dodge, 1982; Hasle and Syvertsen, 1996). Due to either low concentration of some phytoplankton species or difficulties in distinguishing between species in the light microscope, individual species were grouped as follows: diatoms, dinoflagellates, cryptophytes, flagellates and coccolithophores.

2.4. Nutrient analysis

Samples for nutrient determination were collected from surface and selected depths and kept frozen until analysis. In the laboratory, samples were properly thawed and filtered through cellulose acetate membrane filters. All the samples were processed according to recommendations in Strickland and Parsons (1972). Ammonium was measured by the method of Koroleff (1969) following modifications in Grasshoff et al. (1983) and, the absorbance at 630 nm. Nitrite and nitrate were determined through cadmium column reduction of NO_3^{-1} to NO_2^{-1} , with standard curves and calculations made according to Strickland and Parsons (1972). Orthophosphate was measured by reaction with ammonium molibdate with absorption at 885 nm. Silicate in the form of reactive Si was measured according to Strickland and Parsons (1972) and correction for sea salts interference made following Aminot and Chaussepied (1983). Absorbance values for all nutrients were measured in a FEMTO® spectrophotometer.

2.5. Satellite data

Satellite images of both surface Chl-*a* concentration and temperature were acquired by the Moderate Resolution Imaging Spectroradiometer on NASA's Aqua satellite (MODIS-Aqua) and presented as Level 3 (L3) SMI (Standard Mapped Image) monthly composite images, at 4 km resolution. Only images from September to March (low cloud cover) were analyzed in this study.

Monthly composites from daily images of sea ice concentration (spatial resolution of approximately 6×4 km, in a 6.25 km grid) were obtained from the Advanced Microwave Scanning Radiometer (AMSR-E-Aqua). The Artist Sea Ice (ASI) algorithm was applied, which uses an empirical model to retrieve ice concentration between 0% and 100% (Spreen et al., 2008). For each month, open ice edge pixels were first identified by the ASI algorithm (sea ice concentration $\leq 15\%$), (Marrari et al., 2008; Spreen et al., 2008). The sea ice area was then determined based on pixels with sea ice concentration >15%.

Ice cover images (AMSR-E) were analyzed for every month during the study period, since microwaves scatterometers' signal does not suffer interference from atmospheric attenuation. Time-series analyses consisted of synoptic mean of each variable in the area between 61.5–64.5°S and 54–62°W.

2.6. Statistical analyses

Canonical correspondence analysis (CCA) was performed for the GOAL-2003 and 2004 and SOS-2008 and 2009 cruises. This analysis allows for the evaluation of the main patterns of community variability, as influenced by environmental variation, and the main pattern in the weighted means of each species with respect to the environmental variables (ter Braak and Prentice, 1988). For this analysis, only stations where both biotic and environmental data were available have been considered, totalizing a set of sixty-two cases. Biotic variables were represented by abundances of main phytoplankton taxonomic groups determined from microscopic analysis. Environmental variables included surface temperature, salinity, dissolved inorganic nitrogen (DIN: nitrate, nitrite and ammonium), phosphate, silicate, UMLD, stability, and also total and fractionated Chl-a ["nanoplankton" (<20 µm) and microplankton $(>20 \ \mu m)$]. All variables were log-transformed previously to the analysis for reducing the influence of the different scales in the sets of variables. In order to test for the significance of the CCA, Monte-Carlo tests were run based on 499 permutations under reduced model (p<0.05). The two first significant canonical roots were used to produce the canonical diagram. The canonical roots are the weighted sums of the phytoplankton variables, which are used to calculate the position of the stations in the diagram, according to their phytoplankton groups composition and abundance. Thus, the distances between stations in the ordination diagram reflect the similarity of their phytoplankton assemblages (ter Braak, 1994). Canonical factor loadings are the simple correlations between the environmental variables and the canonical roots, and are considered as a measure of the importance of the different environmental variables determining phytoplankton variability within the area.

In order to detect temporal correlations between the signals of sea surface temperature (SST), sea surface Chl-*a* (SSC) and sea ice area, a crosscorrelation analysis was applied. This technique allows for the detection of common periodicities between two signals of interest. The crosscorrelation coefficient (r_{xy}) of two time series *x* and *y*, each with *n* data points is determined by $r_{xy}(k) = \frac{c_{xy}(k)}{\sigma_x \sigma_y}$ [modified from Chatfield (1984)], where *x* and *y* are the two time series, *k* is the lag time, c_{xy} is the covariance coefficient and σ is the standard deviation of time series. The covariance coefficient (c_{xy}) , in turn, is defined by: $c_{xy}(k) = \frac{1}{p} \sum_{t_n}^{t_0} [(x_t - \bar{x})(y_{t+m} - \bar{y})]$ for $t_0=1$ to $t_n=P-1$ and *m*=0, considering positive values of *k* and $c_{xy}(k) = \frac{1}{P} \sum_{t_n}^{t_0} [(y_t - \bar{y})(x_{t+m} - x)]$ for $t_0 = 1$ to $t_n = P + 1$ and *m*=-1, considering negative values of *k*, where *P* is the total number of observations in the series and *t* is the time unit.

3. Results

3.1. Physical and chemical properties

Two surface water masses were found within the study area (Figure 2), as also found and named by López et al. (1999): a colder and more saline TWW, occupying mainly the southeastern portion of the Strait, and a warmer and fresher TWB in the northwestern domain, which were significantly different in temperature and salinity (Kruskal-Wallis test H, p<0.05). The lowest temperature (generally lower than 1 °C) and salinity (33.3) levels were observed in 2010, when no clear distribution pattern of TWW and TWB was detected (p>0.05). In this work, those water masses were separated by the 0.9 °C isothermal, depicting the shallow (from surface to ca. 100 m) Peninsula Front (PF) (Sangrà et al., 2011) (Figures 2 and 3), which is located close to the AP. It is noticeable that the warm shallow waters are associated with relatively high concentrations of Chl-*a* (Figure 3).

Vertical density profiles, UMLD and water column stability data for all occupied stations during GOAL and SOS-CLIMATE cruises showed four distinct water column structure types: stations with shallow UMLD (<40 m), stations with deep UMLD (generally >40 m), stations with homogeneous/well mixed profiles and stratified profiles where no upper mixed layer was identified. In general, stations under TWB influence (Figure 4) were represented by shallow UMLD (<40 m) and strong pycnocline (generally >2000 × 10^{-8} rad² m⁻¹). Stations under TWW regime were represented by deep homogeneous water column (Figure 4), associated to the lowest

stability values, significantly different from the TWB stations (Kruskal-Wallis test H, p<0.05). Few stations (4 stations in all cruises) located close to the SSI presented a very shallow upper mixed layer (<20 m) with high stability. Finally, a few stratified water column stations (3 stations, not shown in Figure 4) with no marked upper mixed layer were found during the study periods, and those were located to the eastern of the BS central basin.

The surface distribution of nutrients in the BS (Table 2) showed that, in general, average DIN and silicate levels were high in all cruises (26.3 μ M and 55.5 μ M, respectively, on average) in the studied years, but showed no marked pattern in horizontal distribution (not shown). Silicate concentration was particularly high in 2004 and 2010, reaching up to 85 μ M. Phosphate was mostly >1 μ M in surface waters, but it may have been limiting phytoplankton growth in a few cases. No significant difference was found between nutrients concentration at TWB and TWW for all cruises (Kruskal-Wallis test H, p>0.05).

3.2. Spatial patterns in phytoplankton distribution

In 2003, 2005, 2008 and 2009, a similar marked pattern of low Chl-*a* at stations near the AP under TWW influence was found, while stations under TWB influence presented high Chl-*a* (Kruskal-Wallis test H, p<0.05) (Figure 2). In the GOAL 2004 cruise, however, Chl-*a* did not show a distribution pattern in association with the surface water masses in the study area, and low Chl-*a* (generally <1 mg m⁻³) was observed at all sampling stations. Also, in this year, no significant difference was found between Chl-*a* concentrations from TWW and TBW stations (Kruskal-Wallis test H, p>0.05), although the physical front was clearly identified (see Figure 2). In 2010, as observed in 2004, no marked differences in Chl-*a* was found between stations under

TWB and TWW influence, although concentrations were higher. At the same time, the highest Chl-*a* level was found at a station near the SSI, under the lowest salinity level (see Figure 2). MODIS Chl-*a* images (Figure 5) showed the same distribution pattern described in our *in situ* data and the high Chl-*a* belt surrounding waters of SSI was clear in all years. However, Chl-*a* was particularly high around the Islands (including Bransfield) in February 2005, coinciding with a relatively low ice cover. On the other hand, ice cover was particularly high in the first two studied summers (2002–2003 and 2003–2004) and again in 2009–2010, associated with relatively low Chl-*a* concentrations.

Except for a few stations, deep Chl-*a* maximum (DCM) layers were not detected in vertical Chl-*a* profiles in the BS (see Figure 4). Therefore, a relationship between surface Chl-*a* and 50 m-integrated Chl-*a* was investigated for all sampling stations. A strong relationship was observed between 50 m-integrated Chl-*a* and surface Chl-*a* concentration ($r^2=0.61$; p<0.05, Figure 6), thus, the surface Chl-*a* concentration was considered to represent phytoplankton biomass over the 50-m water column.

Surface distribution of size-fractionated Chl-*a* showed that the "nanoplankton" fraction (< 20 μ m) was dominant in almost all sampling stations (Figure 7). This fraction represented, on average, 79%, 84%, 93% and 40% of total Chl-*a* in 2003, 2004, 2008 and 2009, respectively. Microplankton cells (>20 μ m), however, were more important to the north of the Strait, particularly near the SSI (especially King George) and the Elephant Island, mainly in 2003 and 2009 cruises (Figure 7).

The phytoplankton community showed a patchy distribution, with dominance of nanoplanktonic flagellates or microplanktonic diatoms (Figure 8, Table 3). For the GOAL cruises (2003-04), the phytoplankton community was dominated mainly by cryptophytes, reaching abundances higher than 2.5×10^5 cells L⁻¹ in 2003 and 8×10^5 cells

 L^{-1} in 2004, in almost the whole sampling area, being replaced by diatoms near the SSI (Figure 8a and b). During the SOS-CLIMATE cruises cryptophytes were detected only at few stations. At those periods, phytoplankton communities were dominated by other unidentified nanoplanktonic flagellates $(3.5 \times 10^5 \text{ cells } \text{L}^{-1})$, on average; Figure 9) and haptophytes, mainly *Phaeocystis antarctica*, (reaching 6×10^5 cells L⁻¹ in 2008, but almost absent in 2009). Dinoflagellates were also detected at low concentrations, up to 0.9×10^5 cells L⁻¹ in 2008 and 0.2×10^5 cells L⁻¹ in 2009 (not shown). This group was mainly represented by *Gymnodinium* spp., *Gyrodinium* spp. and *Prorocentrum* spp. The diatom *Corethron pennatum* was detected throughout the area and was especially abundant in 2003 (reaching 0.7×10^5 cells L⁻¹), while *Thalassiosira* spp. dominated in 2004, and Pseudo-nitzschia spp. and Chaetoceros spp. were dominant in the 2009s diatom assemblage. Other representative diatoms in all cruises were *Fragilariopsis* spp. and other unidentified pennate species. Coccolithophores presented a minor contribution to the phytoplankton community along the surveyed area (not shown), with relative cell numbers lower than 10% in all cruises, except at station 7 (GOAL-2003) where they contributed 34.5% to the phytoplankton community. Kruskal-Wallis' H-test, applied to assess differences in phytoplankton communities between TWB and TWW stations, showed that only diatoms were in significantly (p<0.05) higher concentrations at TWB.

3.3. Relationship between the phytoplankton communities and oceanographic features

The response of the phytoplankton community to environmental variability was investigated using a canonical correspondence analysis (CCA) (Table 4 and Figure 9). A Monte Carlo permutation test of F-ratio, applied to the CCA analysis, showed that the environmental variables (temperature, salinity, DIN, phosphate, silicate, UMLD, stability, total Chl-a, "nanoplankton" and microplankton fractions of Chl-a) reasonably explained (61%) the spatial distribution variability of phytoplankton groups (p<0.01). The first two significant canonical roots cumulatively explained 60.5% of the observed variance. The first canonical root (58.3% of variation explained) clearly distinguished species/groups of GOAL-2004 cruise most positively related to silicate concentration (Figure 9). However, during that cruise there was no clear distribution pattern in both total Chl-a and phytoplankton community (either groups or size classes) in relation to the main surface water masses (TWW and TWB), as compared to the other sampling years (see Figures 7 and 8). The second canonical root explained only 2.2% of the variation and separated the stations positively related with temperature, total Chl-a concentration and microplanktonic fraction of Chl-a from the opposite stations associated with salinity, UMLD and "nanoplanktonic" fraction of Chl-a (see Figure 9 and factor loadings in Table 4). High factor loadings were found for temperature, salinity and Chl-a variables (Table 4; Figure 9), which reflected a strong association between phytoplankton biomass variability and water masses distribution. Other important variables that contributed to explain phytoplankton variability were UMLD and stability, with factor loadings fairly similar to those for temperature and salinity. The second canonical root could also be interpreted as indicating a gradual change in phytoplankton structure from stations near to the AP (under TWW influence) to stations near the SSI (under TWB influence). Stations under TWB influence were related to a diatom-dominated community, positively associated with total Chl-a, microplanktonic Chl-a (>20 μ m) and temperature (Figure 9). Contrarily, stations under TWW influence seemed to be related to salinity, UMLD and "nanoplankton" (Chl- $a < 20 \mu m$), represented by cryptophytes, haptophytes and other unidentified flagellates (Figure 9).

3.4. Seasonal/interannual analysis

Time series of satellite data (Figure 10) showed a noticeable seasonal trend for all the three variables [sea surface Chl-*a* (SSC), sea surface temperature (SST) and sea ice], with interannual variability. Peaks in SSC (gray bars) were detected in February for 2003, 2004 and 2007, while the highest temperatures were observed between January and February. Sea ice, as expected, presented an inverse behavior to the other variables, with maximum values in July/August and smallest in January to March, depending on the year. The austral spring/summer 2005–06 showed the highest SSC and SST in the time series (2002–2010) associated with an earlier start in sea ice retreat than in other years. Two SSC peaks were observed in that year (December and February). The 2007 winter season was apparently the coldest, reaching more than 2500×10^2 km² of sea ice during a period of over three months.

Crosscorrelation analysis between variables from satellite data (Table 5) showed maximum correlations for the zero lag time (p<0.01). This indicates that the response of SSC (either directly or indirectly) to the other analyzed variables (SST and sea ice) is probably within a time-scale lower than the time series resolution of a month. Considering the monthly time resolution, the three variables, therefore, varied in phase. Sea ice was inversely related with both SSC and SST (r_{xy} =-0.51 and r_{xy} =-0.76, respectively; lag=0; p>0.01) and SSC was directly related to SST (Table 5).

4. Discussion

4.1. Spatial variability of phytoplankton and environmental factors

The TWB and the TWW were the major surface water masses within the BS in the present work (see Figures 2 and 3), as previously described by García et al. (2002), López et al. (1999), and Sangrà et al. (2011). Those contrasting water masses generated a noticeable physical gradient across the BS, through the Peninsula Front (Basterretxea and Arístegui, 1999; Sangrà et al., 2011; Zhou et al., 2002). That gradient was reflected in phytoplankton biomass and community distribution, with high Chl-*a* associated to the warmer and fresher TWB, and low Chl-*a* coupled with the colder and saltier TWW, as observed in Castro et al. (2002) and Hewes et al. (2009).

Four different types of vertical density profiles were observed in this study, which have already been identified by Holm-Hansen et al. (2004a) during the CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) program, in the BS and Scotia Sea. These authors found that stations with deep UMLD were typical from TWW while stratified water columns were found in the easternmost part of BS. The shallow upper mixed layers with strong pycnocline found in the present study, under TWB influence, near SSI, can be attributed to sea ice melting (Holm-Hansen and Hewes, 2004; Holm-Hansen et al., 2004a). Stations under TWW regime were, however, represented by deep homogeneous water columns, as previously described by Sangrà et al. (2011), and associated with the lowest stability values.

Nutrients availability is fundamental for phytoplankton development and for primary production at sea (e.g. Hecky and Kilham 1988; Smith, 1984). High variability in nutrient concentration in the oceans can reflect in species/taxonomic groups' variability, since each taxon presents particular nutrient requirements (Arrigo, 2005; Klausmeier et al., 2004). In our study, high dissolved macronutrient concentrations were observed in surface waters during all cruises (Table 2), as reported in other studies at the same area (Castro et al., 2002; García et al., 2002). However, surface Chl-*a* was irregularly distributed over the study area (see Figure 2). The Southern Ocean is recognized as a high nutrient and low Chl-*a* zone (HNLC) (e.g. Hoppema et al., 2003) in which phytoplankton development is iron-limited (Boyd et al., 2000; Feng et al., 2010; Martin et al., 1990a, 1990b). As it had been demonstrated in previous studies, variations in Chl-*a* biomass and primary production in the Southern Ocean can be associated with parameters other than light availability, namely fronts and upwelling (Bathmann et al. 1997; Jacques and Panouse, 1991; Lovenduski and Gruber, 2005), or proximity to coast, or islands (Blain et al. 2001; Comiso et al. 1993; Hoppema et al., 2003), where iron availability is enhanced. Nevertheless, it has been established that irradiance availability, as a consequence of shallow mixed layer depth (Mitchell and Holm-Hansen, 1991; Nelson and Smith, 1991), combined with iron supply, are two of the major factors affecting phytoplankton dynamics in the Southern Ocean (Arrigo et al., 1999). In our study, Chl-*a* varied from year to year and it seemed to be more associated with the water column properties than nutrient distribution, evidencing that the region is not under dissolved macronutrients limitation (Ducklow et al., 2007).

Based on both *in situ* and satellite data (Figures 2 and 6, respectively), high Chl-*a* concentration was found under TWB regime and surrounding the SSI, while regions under TWW influence were marked by low Chl-*a* levels. The same clear Chl-*a* gradient between the northern and southern BS was detected during the AMLR (Antarctic Marine Living Resources) sampling program in late February and March 2004 (Hewes et al., 2008). This distribution pattern was attributed to the input of poor- Chl-*a* waters from the Weddell Sea into the southern BS through a surface current (Holm-Hansen and Hewes, 2004; Zhou et al., 2002). Also, the high Chl-*a* belt observed around the SSI (see Figure 5) is likely related to iron availability in those waters. Ice melting could explain the shallow UMLD found near SSI, associated to the presence of strong pycnocline. However, recent studies have demonstrated that other factors, such as vertical mixing and upwelling, play an important role in fertilizing surface HNLC waters with Fe

(Bakker et al., 2007), even more important than ice melting processes (Klunder et al., 2011). In the present work, an early input of iron probably took place in the upper mixed layer by vertical mixing and/or upwelling associated with the Islands topography, fertilizing the surface waters around the SSI, as found in other islands in the Southern Ocean (Bakker et al., 2001; Bucciarelli et al., 2001).

The size structure of phytoplankton communities is a relevant feature of the pelagic ecosystem, because it determines its trophic organization. Moreover, the cells' size directly influences their sedimentation rates and, therefore, the potential enhancement of carbon flux to deeper layers. Previous studies on Southern Ocean phytoplankton (e.g. Holm-Hansen and Mitchell 1991; Mitchell and Holm-Hansen 1991; Montes-Hugo et al., 2008) suggested a clear contrast between "oceanic" areas, with low biomass and dominance of small cells [pico ($<2 \mu m$) and nanoplankton (2–10 μm)], and "shelf" waters, where the development of phytoplankton blooms is common in spring and summer, with dominance of microplankton (>10 µm). Other studies have demonstrated that elevated biomass found near the SSI was characterized by microplanktonic diatoms, which dominated the total biomass in areas with high Chl-a (Heywood and Priddle, 1987; Montes-Hugo et al., 2008). Nonetheless, a great variability in terms of diatoms contribution to total biomass has been observed, since smaller size fractions can be more regular and become relatively more important in lower biomass regimes (Bröckel, 1981). This pattern was also observed in the present work, where microplanktonic diatoms were dominant at shelf stations near the SSI in contrast to the dominance of small flagellates in offshore waters of BS (see Figure 7). The large diatom *Corethron pennatum* was frequent in all sampled years and especially dominant in 2003, being a very important component of the large microphytoplanktonic cells, as seen in other sites of the Southern Ocean (e.g. Froneman et al., 1995; Kang &

Lee, 1995). This is a relevant species in terms of food web dynamics, because it is preferentially grazed by krill and copepods (Graneli et al. 1993). The centric diatoms *Thalassiosira* spp. were especially abundant in 2004 and also seemed to be dominant in open waters of the Weddell Sea (Fryxell, 1989). This could probably explain the abundance of this species associated with a significant presence of TWW in the BS in 2004 (see Figure 2). The high density of small ($<20 \mu$ m) *Thalassiosira* spp. and their constant occurrence in almost all sampling stations in 2004 may be related to their growth as gelatinous colonies, which is a competitive advantage in avoiding heavy zooplankton grazing (Fryxell and Kendrick, 1988).

Similarly to that found by other studies in the Southern Ocean (e.g. Garibotti et al., 2005; Jacques and Panouse, 1991; Varela et al., 2002), the nanoplankton fraction (nano+picoplankton) was more abundant and dominated mainly by flagellates: cryptophytes in GOAL cruises and other flagellates (including *Phaeocystis antarctica*) in SOS-CLIMATE cruises. Probably, the picoplankton contribution was less important than the nanoplankton fraction, since the former is generally not a relevant component in the Southern Ocean (Scott and Marchant, 2005). In our work, a pronounced relative contribution of cryptophytes was generally associated to low Chl-*a* concentrations (<1 mg m⁻³), when compared to those studies that reported a cryptophyte dominance in association with high Chl-*a* concentrations (>1 mg m⁻³) over the BS or in adjacent regions (Jacques and Panouse, 1991; Mura and Agustí, 1998; Moline and Prézelin, 1996; Moline et al., 2004; Rodriguez et al., 2002). This difference can be related to the different spatial coverage of occupied stations between the surveys. In this work, shelf and oceanic sites were sampled while the other studies concentrated mainly in coastal sites. Cryptophytes/flagellates could thus attain that high biomass level under ice

melting processes near the coast, while the same organisms would be constrained by unfavorable conditions (lower stability and deeper UMLD) in oceanic waters.

The CCA ordination diagram (Figure 9) evidenced a strong association between phytoplankton biomass variability and water masses distribution, as seen through the high factor loadings displayed by temperature, salinity and Chl-a. High factor loadings were also observed for the UMLD and water column stability, which agree with the hypothesis of strong influence of the water column physical structure on phytoplankton variability (Mitchell and Holm-Hansen, 1991; Ryabov et al., 2010; Townsend et al., 1991). The presence of cold and relatively salty TWW in the BS was associated with homogeneous and unstable water column conditions, which resulted in a low Chl-a community composed by small cryptophytes and unidentified flagellates, during the GOAL and SOS-CLIMATE cruises, respectively. On the other hand, stations located under TWB (near the SSI) domain were characterized by high Chl-a levels in association to shallow UMLD (<40 m) and high stability levels. Those conditions favored large diatoms (>20 µm) associated with high Chl-a concentration mainly in stations closer to the SSI. Kopczynska (1992) also associated similar distribution patterns of specific phytoplankton assemblages with water column structure in the BS. In the present work, the diatoms' dominance near SSI could be related to local recent ice melting, that would induce the establishment of a shallow UMLD and, probably, iron input from ice melting and/or upwelling influenced by island topography.

4.2. Interannual variability in phytoplankton, temperature and sea ice

In the Southern Ocean, phytoplankton production is influenced by the extent of open water area, which can vary slightly from year to year, exhibiting distinct seasonal cycles (e.g. Arrigo et al., 2008). The extent of open water area, in turn, is related to the

annual cycle of sea ice retreating. Thus, the timing of both sea ice retreat and ice formation at the end of the growth season are considered important factors in the time variability of phytoplankton seasonal cycles (Arrigo et al., 1999; Garibotti et al., 2003, 2005; Moline and Prézelin, 1996). This variability has been recently studied based on both in situ data and satellite images in large areas of the Southern Ocean, and also in the BS region (Hewes et al., 2009; Holm-Hansen et al., 2004a, 2004b; Lovenduski and Gruber, 2005). The lowest Chl-a values in the Scotia Sea and adjacent waters (including sectors of the BS) were observed in December, reaching maxima in January and started to decline in February (Holm-Hansen et al., 2004b). In the present study, SSC, SST and sea ice were best correlated on a zero lag time (see Table 5). Thus, we can suggest that the studied variables are interrelated in phase considering a monthly time resolution, except for sea ice, which inversely varied in relation to the other variables. The timeseries analysis (Figure 10) showed an increase in Chl-a generally from September to January or February, when a decline was observed. However, the 2004–05 summer season presented an unexpected Chl-a maximum in December, followed by a decrease in January and again an increase in February. The high Chl-a observed in December 2004 was due to a massive bloom in the vicinity of the James Ross Island, a region included in the considered image area (see Figure 5). On the other hand, very high Chl*a* biomass in the 2005-06 season was related to an early sea ice retreat process (beginning in September) that provided a longer time of available sea ice free areas.

Analysis of *in situ* data waters displayed deep UMLD from eighteen summers around the SSI region has shown that the control of phytoplankton biomass can be resolved across a salinity gradient that separates the co-limiting conditions of either deep UMLD or low-iron concentration, (Hewes et al., 2009). In our study, a salinity gradient was also detected across the BS, where southern probably light limited, and a similar pattern of enhanced Chl-*a* surrounding the SSI was detected. Salinity varied interannually (not shown), but phytoplankton biomass variability was apparently not associated with that variation (data not shown). Indeed, water column structure, expressed by UMLD and stability, might have been more important to phytoplankton biomass variability.

It is known that diatom blooms develop in the early summer, when sea ice retreat is under way and later the community is dominated by flagellates such as cryptophytes (Ducklow et al., 2007). In a final stage diatoms and unidentified phytoflagellates are often observed (Moline and Prézelin, 1996; Garibotti et al., 2005). Although all sampling efforts were carried out during the late summer (February-March), the phytoplankton community varied between years. Cryptophytes were dominant in 2003 and 2004, except in a few diatom-dominated stations in 2003. Flagellates, occasionally encompassing some inconspicuous cryptophytes, were observed in 2008 and 2009 and, as in 2003, diatoms were also more important at stations where flagellates were less abundant. An alternate pattern was found in phytoplankton composition (although on a spatial scale) between diatom- and flagellate-dominated sites, including cryptophytes. This indicates that the magnitude and extension of sea ice coverage may have reflected in a predominance of cryptophytes/flagellates over diatoms in those years (2003, 2004) and 2008) with smaller sea ice-free areas. Conversely, cryptophytes were overcome by diatoms under greater sea ice-free areas (2009). This process was also demonstrated for 2010's summer, when cryptophytes dominated over diatoms under a relatively greater sea ice covered area (C.R.B. Mendes, Personal communication). At the same time, cryptophyte dominance has been related to early ice melting conditions, with strong pycnocline and little iron availability (Garibotti et al., 2005; Moline et al., 2004). In the present work, a dominance (in cell numbers) of cryptophytes/flagellates (<20 µm) was

also observed in many sites with deep UMLD with relatively low stability and wellmixed waters, although in terms of biomass, other groups (e.g. diatoms, dinoflagellates) tend to be more important (C.R.B. Mendes, *Personal communication*). These findings suggest that water column stability and a shallow UMLD would not be the only conditions leading to a predominance of cryptophytes in the BS. The cryptophytes/flagellates seem to be good competitors in poor iron waters, after extensive diatom blooms, as found in nearshore coastal sites of the AP (Moline et al., 2004). Overall, based on the present data and on reports from the literature, the relationship between cryptophytes/flagellates and iron availability needs to be better understood.

Concerning long-term Chl-*a* fluctuations in the region, modes of climate variability have to be considered as possible influencing factors. For instance, the Southern Annular Mode (SAM) is a dominant climate variability mode over the Southern Hemisphere, varying from intra-seasonal to interannual scales, due to alternations in the atmospheric masses between medium and high latitudes (Gong and Wang, 1999). It is known that positive phases of SAM influence the Antarctica climate, intensifying cooling in the region (Gillet et al., 2006). Lovenduski and Gruber (2005) observed Chl-*a* concentration anomalies (SeaWiFS – 1997-2004) positively correlated with the SAM in the south of the Antarctic Polar Front. These authors also suggested that positive phases of the SAM are associated with enhanced westerly winds over the Antarctic Zone, resulting in upwelling movement, increasing iron supply. In the present study, a low (r_{xy} =0.14) but significant (p<0.05) relationship was estimated between SAM and satellite Chl-*a* time-series (data not shown). This is probably due to both a relatively small area and a short time scale, less than two complete SAM cycles. . In addition, the amount of sea ice and, consequently, phytoplankton variability, could be

impacted by the El Niño-Southern Oscillation (ENSO) (e.g., Stammerjohn et al., 2008; Yuan, 2004). A recent study showed that during El Niño, a decrease in northwest winds results in northward displacement of the Antarctic Circumpolar Current Front and intensification of the Weddell Gyre, allowing Weddell Sea water to flow into eastern BS (Loeb et al., 2010). During those periods, mixing between oceanic and coastal waters is reduced, and Chl-*a* concentrations are low in the BS. However, in the present study, no influence of ENSO was observed along the relatively short study period. Despite the important influence of large scale phenomena (such as SAM and ENSO) on phytoplankton variability in the Southern Ocean, regional scale factors such as amount of sea ice free areas (providing light availability), UMLD and water column stability can largely explain the variations in phytoplankton biomass and community composition in the BS, according to the results found within the present work.

4.3. Trophic implications

Apart from the physical and chemical factors controlling the development and distribution of phytoplankton communities, the role of mesozooplankton grazing, mainly krill and salps, has to be considered. Those organisms are frequently detected in high concentrations throughout the Southern Ocean (e.g., Loeb et al., 1997, 2010). The BS region is an important spawning and nursery ground of Antarctic krill (*Euphausia superba*) and a relevant source of these organisms to other regions of the Southern Ocean (Loeb et al., 1997, 2010). However, the krill can be occasionally suppressed by salp development in the area, particularly under low Chl-*a* conditions, caused by intensification of Weddell Sea water flow into the eastern BS (Loeb et al., 2010). Concerning grazer-prey associations, the Antarctic krill feeds more efficiently on diatoms than on cryptophytes, while salps are less selective, praying over a wide

spectrum of phytoplankton groups and size classes (Haberman et al., 2003). Therefore, a shift from a diatom to a cryptophyte-dominated community can significantly affect food-web trophic interactions (Haberman et al., 2003). In the present study, a predominance of cryptophytes/flagellates was observed in 2003, 2004 and 2008 in contrast to 2009, when diatoms were more abundant. It is possible that in those years of relatively low biomass (2003, 2004 and 2008), apart from the influence of the physical environment, the phytoplankton assemblages would be suitable for salp development at the expense of survival and maintenance of krill populations. In the summer of 2010, an enormous concentration of salp swarms (visual detection) was observed in the BS, in association with a massive dominance of cryptophytes (identified through their pigments) (C.R.B. Mendes, *Personal communication*). This highlights the association between the type of primary consumers and the phytoplankton assemblage in the Southern Ocean. Changes in the phytoplankton community around the AP waters have been associated with recent increases in temperature and dominance of salps over krill, as main phytoplankton consumers (e.g., Moline et al., 2004; Montes-Hugo et al., 2009). Since organisms from higher trophic levels, such as penguins and seals, preferably consume krill rather than salps (Loeb et al., 1997) changes in the phytoplankton community composition can have serious consequences to main Antarctic consumers.

5. Conclusions

Phytoplankton community and associated oceanographic features showed distinct spatial patterns along the BS, in straight association with the two main surface water masses within the area: TWB and TWW. Stations under TWB influence, mainly near the SSI, showed high Chl-a concentration and a dominance of diatoms, in shallow UMLD and relatively strong pycnocline. Stations under TWW influence were dominated by nanoplankton (cryptophytes or unidentified flagellates), associated with low Chl-a concentration and generally coupled with low stratification levels seen through low magnitudes of the stability parameter. This suggests that the phytoplankton spatial variability was primarily limited by the water column structure. As TWB and TWW presented very different water column conditions, the dynamics of both water masses within the BS is critical in modulating the spatial variability of phytoplankton biomass and community. Interannual fluctuations were observed in composition of dominant phytoplankton groups over the area, mainly between diatoms and small flagellates/cryptophytes, influenced by the magnitude and extension of sea ice coverage. This temporal variability was mainly driven by varying temperature, which influences sea ice coverage and melting process and, consequently, the water column structure. Therefore, water column structure and ice melting are seen as the major driving forces that modulate the spatial and temporal variability, respectively, of phytoplankton distribution in the Bransfield Strait.

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TABLES

Table 1. Information about the cruises (period and number of sampling stations) andsurface ranges of temperature (°C), salinity and Chl-a (mg m⁻³).

CRUISE	PERIOD	STATIONS	Temperature	Salinity	Chl-a
GOAL	23–31 Jan 2003	40	-0.51 - 2.51	34.09 - 34.41	0.24 - 1.2
	21–29 Jan 2004	76	-1.22 - 1.83	33.61 - 34.32	0.02 - 1.38
	24 Jan–07 Feb 2005	38	-0.58 - 1.74	33.93 - 34.46	0.3 - 1.74
SOS- CLIMATE	21 Feb–04 Mar 2008	27	-0.81 - 1.76	34.02 - 34.39	0.38 - 1.97
	25 Feb–01 Mar 2009	22	-0.46 - 1.83	34.08 - 34.36	0.37 - 2.47
	16–21 Feb 2010	22	-1.29 - 1.34	33.3 - 34.2	0.38 - 4.16

Table 2. Mean, minimum and maximum surface nutrient values (μM) for all cruises. DIN=nitrate+ nitrite+ammonium.

CRUISE	n	DIN (µM)	Phosphate (µM)	Silicate (µM)
GOAL-2003	20	24.02 4.75 – 31.99	2.05 0.62 - 3.67	51.07 32.66 - 69.05
GOAL-2004	72	26.63 13.61 – 39.97	$2 \\ 0.8 - 5.03$	62.98 40.33 - 85.26
GOAL-2005	33	19.72 5.77 – 29.42	1.51 0.43 - 2.75	41.05 21.32 - 62.45
SOS-2008	25	23.72 16.61 – 32.68	0.82 0.31 - 1.61	44.36 6.89 – 58.7
SOS-2009	15	32.69 26.1 – 36.39	2.67 2.18 - 3.4	46.51 42.04 – 50.69
SOS-2010	21	39.98 32.93 – 47.81	1.92 1.56 - 2.19	71.6 52.9 – 92

SPECIES	2003	2004	2008	2009
Corethron pennatum	0 - 70000	0 - 10000	0 - 560	0 - 4220
Pseudo-nitzschia spp.	0 - 14000	0 - 35000	0 - 130000	0 - 410000
Chaetoceros spp.	ND	ND	ND	1800 - 360000
Thalassiosira spp.	0 - 5000	0 - 300000	0 - 1400	170 - 57000
Gymnodiniaceae	0 - 3000	0 - 1000	4100 - 75000	3500 - 27000
Gyrodinium spp.	0 - 1000	0 - 7000	670 - 7200	2000 - 11500
Prorocentrum minimum	0 - 2000	ND	0 - 10000	450 - 22500
Unidentified flagellates	0 - 30000	0 - 200000	27000 - 345000	116000 - 1169191
Phaeocystis antarctica	ND	ND	14000 - 665000	0 - 365000
Coccolithophores	0 - 6000	0 - 60000	0 - 50000	0 - 69000
Crytophytes	1000 - 300000	600 - 2000000	ND	0 - 79000
Pyramimonas sp.	0 - 30000	0 - 200000	ND	ND

Table 3. Main phytoplankton taxa and abundance ranges (cells L^{-1}) in four cruises (2003–04 and 2008–09) to the Bransfield Strait. ND: not detected.

Table 4. Factor loadings (correlation coefficients) of environmental variables for the

 two canonical roots, estimated by canonical correspondence analysis.

Parameter	1 st canonical root	2 nd canonical root
Temperature	-0.0921	0.3928
Salinity	-0.3739	-0.2639
DIN	-0.1	0.1562
Phosphate	0.1755	0.2289
Silicate	0.4556	0.123
Chl-a	-0.4493	0.3031
"Nanoplankton"	-0.3618	-0.104
Microplankton	-0.196	0.4703
UMLD	-0.3947	-0.1313
Stability	-0.3095	-0.0742

Table 5. Crosscorrelation coefficient (r_{xy}) , lag time e *p* value for the satellite data (Sea Surface Temperature "SST", Sea Ice Area and Sea Surface Chl-a "SSC"), from crosscorrelation analysis.

PARAMETER	r _{xy}	Lag	р
SST × Sea Ice	-0.76	0	< 0.01
SST × SSC	0.65	0	< 0.01
Sea Ice × SSC	-0.51	0	< 0.01

FIGURES

Figure 1. The Bransfield Strait region.



Figure 2. Surface Chl-*a* (mg m⁻³) distribution during the six summer cruises conducted along the Bransfield Strait. Black dots indicate the position of sampling stations the black line indicates the 0.9° C isothermal, which separates TWW (south) and TBW (north).





Figure 3. Vertical distribution of temperature (°C) and Chl-*a* (mg m⁻³) of a transect east



Figure 4. Typical vertical profiles of potential density (kg m⁻³) (a) and Chl-*a* (mg m⁻³) (b) for stations under influence of TWB (blue), TWW (red) and close to the South Shetland Islands (SSI, green).



Figure 5. Combined images of monthly MODIS Chl-*a* (color bar) and AMSR-E sea ice (black pixel areas) of the Antarctic Peninsula tip in 2003-2005 and 2008-2010 austral summer seasons, corresponding to the years when GOAL and SOS-CLIMATE cruises were conducted. White patches in the ocean indicate lack of data due to clouds.



Figure 6. Relationship between surface Chl-*a* (mg m⁻³) and 0-50 m integrated Chl-*a* (mg m⁻²) in the Bransfield Strait for all sampling years ($r^2=0.61$; n=92; p<0.05). Triangle represents Station B315 in SOS-2010 cruise, which showed high surface Chl-*a* associated to low integrated Chl-*a* due to an extremely shallow UMLD (<10m) and was not included in the regression data.



Figure 7. Surface distribution of "nanoplankton" (<20 μ m; left) and microplankton (>20 μ m; right) fractions of Chl-*a* (in percentage of total Chl-*a*) for 2003, 2004, 2008 and 2009. No data on fractionated Chl-*a* are available for 2005 and 2010.



Figure 8. Spatial distribution of the three main taxonomic groups found within the study area [diatoms, flagellates (including *Phaeocystis antarctica*) and cryptophytes] in relation to Chl-*a*, in 2003 (a), 2004 (b), 2008 (c) and 2009 (d). No data is available for 2005 and 2010.



Figure 9. Canonical correspondence analysis ordination diagram relative to data on surface abundance of phytoplankton. The first two significant canonical roots represent 60.5% of phytoplankton groups-environment relationships. Arrows refer to environmental variables (note that Micro and Nano correspond to the Microplankton and "Nanoplankton" fractions of Chl-*a*, respectively). Triangles refer to surface absolute abundance of major species/groups. Sampling stations (where all data were available) are represented by colored circles, as follows: stations under TWW (blue) and TWB (red) influence. Circled dots represent stations from GOAL-2004 cruise.



Figure 10. Time series from 2002 to 2010 of MODIS Chl-a (SSC, in mg m⁻³; bars) and temperature (SST, in °C; dash-dotted line) and AMSR-E sea ice area $(10^2 \text{ km}^2; \text{ dotted line})$, calculated as areal mean in the box shown in Figure 8 (61.5°–64.5°S and 54°–62°W). Chl-a and temperature data refer to September to March each year.

