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

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**Abstract.** Zooplankton is a vital element in pelagic trophic links in marine ecosystems. Despite its importance in controlling phytoplankton production and in modeling pelagic ecosystems, several aspects of zooplankton ecology are still not fully understood, especially regarding its biomass and trophic interactions. The present study assessed the distribution of zooplankton biomass (as carbon mass, CM), its seasonal variations and relationship to water masses and chlorophyll-*a* in the extreme south of Brazil. The values of zooplankton biomass ranged between 0.01 and 32.89 mg C m$^{-3}$, and were higher in spring and summer. The high values in spring were related to Plata Plume Water (PPW) and in summer to Subtropical Shelf Water (STSW). The values of chlorophyll-*a* (Chl-*a*) showed a pattern opposite to that of the CM, with low values in summer and high in autumn. The average daily production inferred for zooplankton (2.36 mg C m$^{-3}$ d$^{-1}$), corresponded to an average annual production of 861 mg C m$^{-3}$ yr$^{-1}$. The zooplankton biomass, mainly related to the coastal and cold waters in southern Brazil, plays an important role in the flow of matter and energy, and contributes to the maintenance of large fish stocks in the region, one of the most productive of the Brazilian coast.

**Keywords:** zooplankton, carbon mass, continental shelf, water masses, seasonal variations

**Resumo**. **Distribuição da biomassa de zooplâncton no Oceano Atlântico Sudoccidental Subtropical: relação com fatores ambientais e clorofila a**. O zooplâncton é um elemento vital nas relações tróficas pelágicas nos ecossistemas marinhos. Apesar de sua importância no controle da produção fitoplanctônica e na modelagem dos ecossistemas pelágicos, vários aspectos da sua ecologia não são totalmente compreendidos, especialmente em relação à sua biomassa e interações tróficas. O presente estudo avaliou a distribuição da biomassa do zooplâncton (como massa de carbono, CM), suas variações sazonais e sua relação com as massas de água e clorofila-*a* no extremo sul do Brasil. Os valores de biomassa de zooplâncton variaram entre 0,01 e 32,89 mg C m$^{-3}$, e foram maiores em primavera e verão. Os altos valores na primavera foram relacionados com a Pluma do Rio da Prata (PRP) e no verão com a Água Subtropical de Plataforma (ASTP). Os valores de clorofila-a (Chl-*a*) apresentaram padrão oposto ao da biomassa de zooplâncton, com valores baixos no verão e altos no outono. A produção diária média inferida para o zooplâncton (2,36 mg C m$^{-3}$ d$^{-1}$), correspondeu a uma produção média anual de 861 mg C m$^{-3}$ ano$^{-1}$. A biomassa de zooplâncton, relacionada principalmente com as águas costeiras e frias do sul do Brasil, tem papel importante no fluxo da matéria e energia na região, contribuindo para a manutenção das populações de peixes nesta área, uma das mais produtivas da costa brasileira.

**Palavras-chave**: zooplâncton, massa de carbono, plataforma continental, massas de água, variações sazonais.

## Introduction

Zooplankton is an important component in pelagic trophic links in marine ecosystems. Their organisms can be predators, prey and competitors that contribute to the transfer of energy and carbon through the food chains, connecting phytoplankton primary production and organisms of higher trophic levels (Skjoldal *et al.* 2000; Escribano 2006). Zooplankton is recognized as the main food source of several species of planktonic and benthonic invertebrates as well as commercially important fish (larvae, juveniles and adults). The zooplankton grazing determines to a large extent the amount and vertical flow of particles, providing energy to benthic communities, exporting carbon from the surface to deeper layers, and contributing to the removal of excess $CO_2$ in the oceans through sedimentation and burial of organic and inorganic carbon compounds (Lenz 2000; Moriarty *et al.* 2012). The abundance and biomass of zooplankton are useful parameters in studies of climate impacts on marine ecosystems (Dvoretsky and Dvoretsky, 2013). Despite the importance of zooplankton in controlling phytoplankton production and in modeling pelagic ecosystems, some aspects of its ecology are still not fully understood, especially regarding its composition, biomass and trophic interactions (Mauchline 1998; Lenz, 2000; Skjoldal 2000). Zooplankton global distribution and the intensity of the temporal and spatial variability of its structural and functional characteristics are related to the different environmental hydrographic aspects (Escribano *et al.* 2007). Globally, the trend is towards a high biomass in the tropics, decreasing until the subtropical regions and slightly increasing toward the poles (Moriarty *et al.* 2012). Estimates show that most values are lower than 10 mg C m$^{-3}$, and the overall average value is 5.52 mg C m$^{-3}$ (Strömberg *et al.* 2009). At mesoscale, the physical structure of the water column is highly dynamic, making zooplankton communities more dependent on the mode of transfer of matter and energy throughout the pelagic trophic food chains, which in turn are related to the qualitative and quantitative characteristics of primary producers (Alcaraz *et al.* 2007). At this scale, the gradients of salinity and temperature may define the composition and structure of zooplankton assemblages (Hoffmeyer 2004; Berasategui *et al.* 2006), and together with primary producers influence their abundance and biomass (Coyle & Pinchuk 2003). Thus, interactions between hydrodynamics and zooplankton occur often at the community level and are related to the availability of nutrients for primary production (Alcaraz *et al.* 2007).

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

The continental shelf of the extreme south of Brazil is one of the regions with the highest biological production of the Brazilian coast (Castello *et al.* 1990; Lopes *et al.* 2006b; Muelbert *et al.* 2008), presenting high amount of chlorophyll *a* related to nutrients from subantarctic waters, continental waters and upwellings (Huboldt 1980a; Ciotti *et al.* 1995; Odebrecht & Garcia 1997; Ciotti *et al.* 2010). The high primary production stimulates the growth of zooplankton populations, and the various water masses increase the diversity of species, of which around 80 % belong to Copepoda, contributing to the increase in zooplankton biomass in the region.

This study aims to determine the horizontal and vertical distribution of zooplankton biomass (in carbon content), its seasonal variations and related factors, especially the water masses and chlorophyll-*a*, in the extreme south of Brazil. Considering the importance of zooplankton and the lack of information on the distribution of its biomass, this study is essential for understanding the ecological processes in the pelagic environments.

## Material and Methods
### Study area

The study area (31º 40´ S - 34º 45´ S;

approximate area 46 750 km$^2$) (Fig.1) in Southern Brazil extends from Santa Marta Grande Cape (28°40'S) to Chuí (34°40'S), as part of the Southwestern Atlantic Continental Shelf. This area has a slow slope with the shelf break between 160 and 190 m (Calliari 1998).

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

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

According to the previous studies (Ciotti *et al.* 1995; Piola *et al.* 2000; Soares & Möller Jr 2001; Möller *et al.* 2008; Piola *et al.* 2008), the PPW is a coastal water mass, rich in nutrients, that results from the mixture of the continental discharge of the La Plata River with the waters from the continental shelf, and flows to the north. It is frequent in spring, autumn and winter, reaching as far north as 28º S during winter and 32º S in summer. The SASW, rich in nutrients, is transported from the south by the Patagonian Current, and is stronger during winter and spring, particularly in the south. The TW, warm, saline and poor in nutrients, is transported to the south/southwest by the Brazil Current on the continental slope, in all seasons. It is more frequent in summer when it can be bound in shallow locations within the continental shelf. The SACW is formed by the mixture of TW e Subantarctic Water (SAW) in the Brazil Malvines Confluence (BMC). It moves south on deep layers along the slope, between 200 and 500 m, below the Brazil Current (Campos *et al.* 1996). Although rich in nutrients, solar radiation at these depths is insufficient to stimulate primary production. The STSW results from the dilution of the SACW with shelf waters. It is present in all seasons of the year, particularly to the north of the region. However, it dominates the continental shelf during summer.

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

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

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

The zooplankton, in this study, concerns the holoplanktonic invertebrates collected with a WP-2 net fitted with 150 μm mesh size, 60 cm diameter at the mouth, equipped with a flow meter and closing device. In the spring, the net was towed from the bottom to the surface in 14 stations: 08 located between the 20 and ~ 50 m isobaths, and 06 in the zone of the external shelf between 300 and 600m, totaling 14 samples. In the summer, autumn and winter cruises, 27, 27 and 26 sampling stations, were respectively performed, totaling 240 samples (73, 99
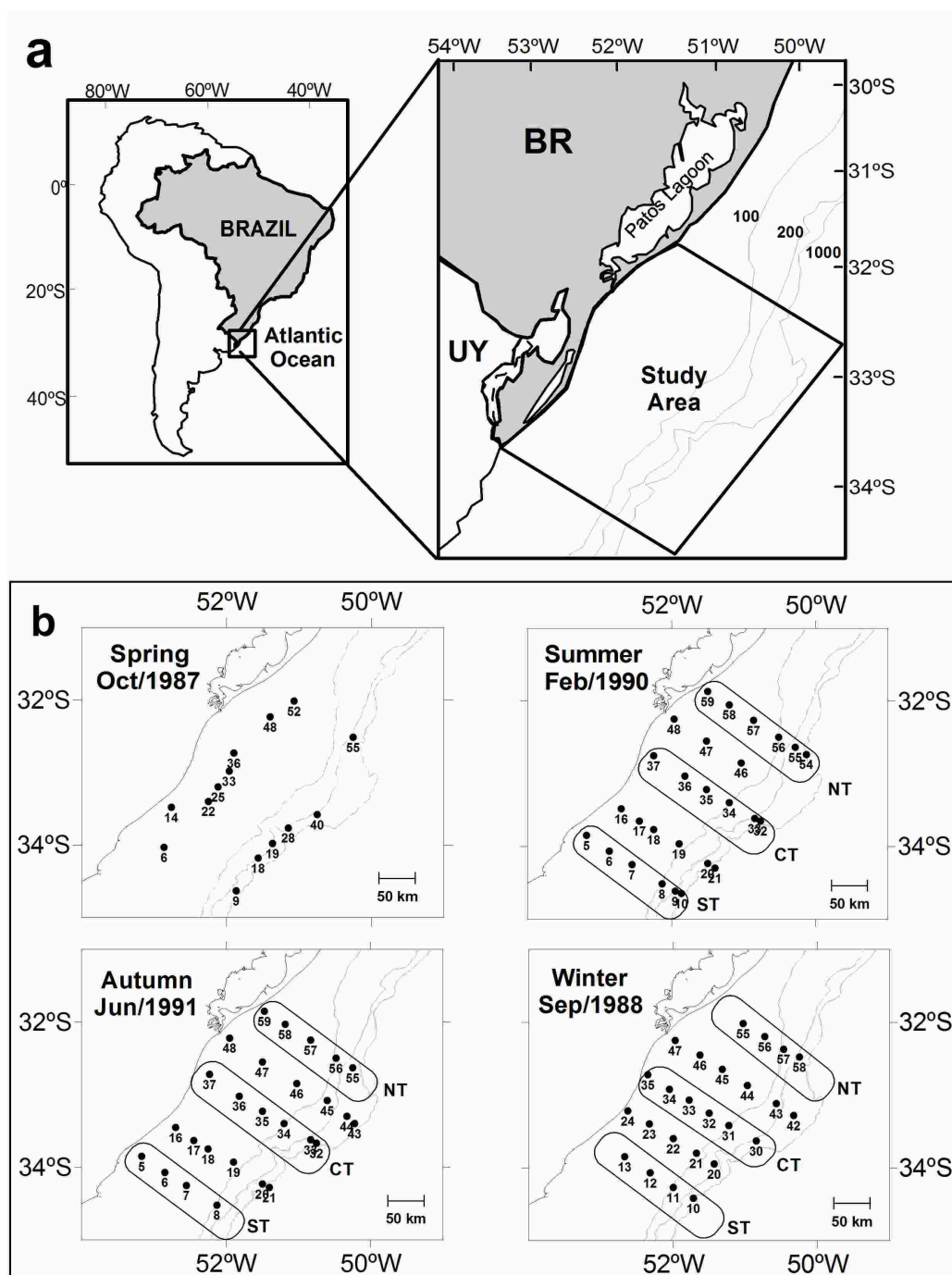
**Figure 1.** Study area (a) with detail showing the sampling stations in spring, summer, autumn and winter (b)*.* Selected transects in (b) indicate witch vertical profiles were chosen to represent the distribution of zooplankton biomass (CM) and chlorophyll (Chl-*a*) in Fig. 5. (NT: Northern Transect, CT: Central Transect and ST: Southern Transect; isobaths in meters).

and 68 samples, respectively). In these cruises, tows were vertical in five onshore-offshore transects, in the 0-25 m, 25-50 m, 50-100 m, 100-200 m and 200-500 m strata. In the last two strata, the average of the values was obtained, and both were considered as one single stratum ($>100$ m) in analyzes and results, because of the very low values

of biomass and reduced number of stations.

Summer, autumn and winter samples were subdivided soon after collection. 50% of the volume of the samples was preserved in 4% formaldehyde-seawater solution buffered with borax (Steedman 1976) for the study of the taxonomic composition. The remaining volume was preserved

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

Salinity and temperature data were obtained at predetermined depths (5, 10, 20, 30, 50, 75, 100, 150, 200, and 300, 400 and 500 m) *in situ* by a Sensordata CTD (model 200) in summer, autumn and winter. Reversing thermometers attached to Nansen sample bottles and KAHLSICO salinometer, ware used in spring. Water samples for analysis of chlorophyll-*a* were obtained at the same intervals up to 100 m, with plastic containers on surface and with Niskin bottles (3 L) at the other depths. The water masses were classified according to thermohaline indexes proposed by Piola *et al.* (2000), adapted by Assef *et al.* (2009). The calculation of the frequency of occurrence of the water masses, considered the presence of each water mass within each depth stratum of all stations collected every season. The chlorophyll-*a* (Chl-*a*) content was determined by fluorimetric analysis (see Ciotti *et al.* 1995). For comparison of Chl-*a* and CM values in the different strata, the mean values of Chl-*a* at the standard depths corresponding to each stratum of zooplankton collection were used. CM and Chl-*a* values were integrated to the water column (g m⁻²), through the sum of the average values (mg m⁻³) of each depth stratum, multiplied by the path (m) traveled by the net in each stratum, above 100 m for Chl-*a*, and for the entire sampled water column (maximum 600 m) for CM.

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

Two groups of GLM were proposed: i) response variable CM with Gamma distribution and logarithmic link function; and ii) response variable log (CM) with Normal distribution and identity link function. Within each model family, different covariate combinations were proposed and compared with Akaike Information Criteria (AIC); comparisons of models from group (i) and (ii) were done with "pseudo-$R^2$" (proportion of deviance explained, Naglekerke 1991).

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

$E(CM) = \mu$   and   $\eta = log\ \mu = a + \beta_1 \cdot sea + \beta_2 \cdot wm + \beta_3 \cdot depth + \beta_{dc} \cdot lat$

This model estimates a different intercept for each combination of season (*sea*), water mass (*wm*) and depth strata (*depth*) and includes a linear function of latitude (*lat*) with distance-from-coast specific (*dc*) coefficients. The intercept $\alpha$ estimates $\eta$ for *sea* = autumn, *wm* = PPW and *depth stratum* = 0-25 m. The effects of other seasons, water masses and depth strata are given by the correspondent $\beta$s. The models were adjusted with function *glm ()* of the statistical software R (R Development Core Team 2012).

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

## Results
### Water masses

The temperature (minimum of 4.85 ⁰C in winter, maximum of 26.27 ⁰C in summer) and salinity (minimum of 26.5 in spring, maximum of 37.05 in summer) values observed and its combinations, allowed to classify five water masses: Plata Plume Water (PPW), Subantarctic Shelf Water (SASW), Subtropical Shelf Water (STSW), South

Atlantic Central Water (SACW) and Tropical Water (TW), according to Piola (2000) and Aseff *et al.* (2009) termohalines indexes (Table I). These water masses were present in most of the seasons in the study area (Fig. 2), however with different frequencies of occurrence.

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

Regarding the seasons (Fig. 2), in spring, PPW was the most frequent water mass in the study area. The SASW occupied most of the water column, sometimes up to 100 m in the south, reducing its influence towards the north. During summer, the STSW dominated the continental shelf, while the TW occurred near the shelf break from the north, advancing on the shelf up to the south. In autumn PPW was present along the entire coastal zone, the SASW was present in the intermediate and external shelf in the south, and the STSW was present along the entire water column to the north. In winter the SASW occurred in most of the shelf to the south, moved away from the coast towards the north, while the PPW advanced over the shelf. The STSW and the TW were limited to the north. The SACW occurred in all seasons and the TW was present along the area, with greater influence to the north.

*Zooplankton main groups*

Several zooplankton groups, including cnidarians (Siphonophora and Hydromedusae) to vertebrates such as fish larvae, were found. The copepods comprised between 63 and 99.99 % of the zooplankton, generally more than 82%, with highest values (ca. 100 %) in winter. The copepodids were present in 99 % of the summer and winter samples, and 95 % of samples in autumn. Nauplii were frequently present in summer (82 % of samples), less in autumn (7 %) and negligible in winter (1.5 %). (There is no similar data of copepods larvae for spring).

Others representative groups in decreasing order of occurrence frequency were: Pteropoda, Larvacea, Chaetognatha and Cladocera in summer; Cladocera, Chaetognatha, Larvacea and Gastropoda and Bivalvia larvae in autumn; and Gastropoda and Bivalvia larvae, Pteropoda, Larvacea and Cladocera in winter, and Chaetognatha, Hydromedusae, Larvacea, Pteropoda and Cladocera in spring.

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

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

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

CM (g m$^{-2}$): Summer (0.52) > Spring (0.43) > Winter (0.28) > Autumn (0.05),

Chl-*a* (g m$^{-2}$): Spring (0.04) > Autumn (0.03) > Winter (0.02) > Summer (0.01).

*Zooplankton biomass and chlorophyll-a in depth strata*

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

CM ranged from minimum values (0.01 and

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

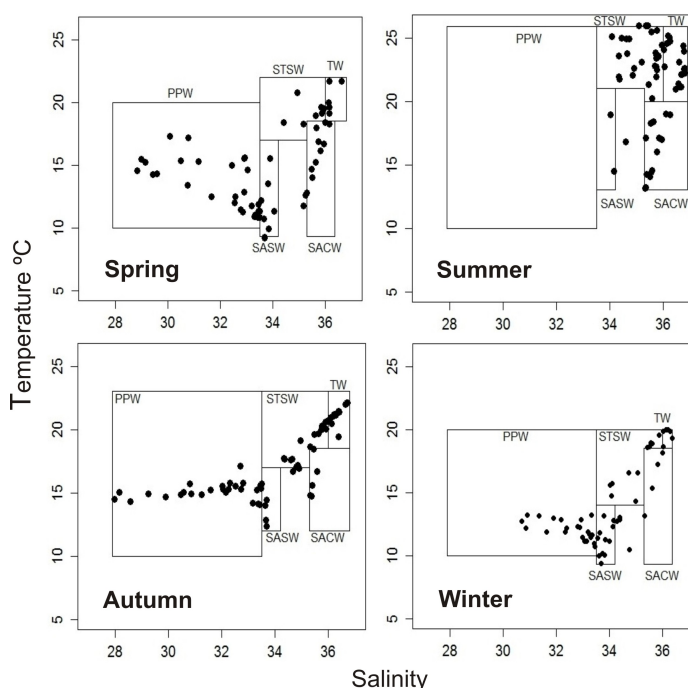| | PPW | SASW | SACW | STSW | TW |
|---|---|---|---|---|---|
| **Spring** | $S \leq 33.5$ | $33.5 < S < 34.2$ | $S \geq 35.3$ | $33.5 < S < 35.3; T > 17;$ | $S \geq 36$ |
| | $T \geq 10$ | $T \leq 17$ | $T < 18.5$ | $35.3 \leq S < 36; T \geq 18.5$ | $T \geq 18.5$ |
| **Summer** | $S \leq 33.5$ | $33.5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



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

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

Chl-*a* ranged between minimum values (0.04 - 0.05 mg m⁻³) in the summer in all strata, and maximum (2.56 mg m⁻³) in the autumn, between

0-25 m. Below (25-50 m) the values were high in the autumn (1.56 mg m⁻³) and winter (1.83 mg m⁻³).

During the summer, CM values >10 mg m⁻³ were observed up to the depth of approximately 70 m, mainly in the coastal zone, and towards the slope at latitudes >33ºS (Central and North Transects, CT and NT; Fig. 1b; Fig. 4a; Figs. 5a-5b). High Chl-*a* values occurred only in the coastal zone in the south and in the north (Figs. 4d and 5d, e, f). During the autumn (Fig. 4b), the lowest CM values (<5 mg m⁻³)

of the whole area were obtained, and the highest Chl-*a* values (>1.5 mg m$^{-3}$) particularly in the coastal area in the north of the mouth of the Patos Lagoon (Fig. 4e), under the influence of its outflow, where the maximum CM value (Fig. 4b) was also found (4.76 mg m$^{-3}$, not visible in the figure due to the scale). In winter, the distribution pattern of the CM and Chl-*a* showed some similarity (Figs. 4c-4f), the higher values occurred in the coastal zone to the south of the mouth of the Patos Lagoon, and in the intermediate zone of the shelf to the south (maxima: CM 24.87 mg m$^{-3}$; Chl-*a* 1.86 mg m$^{-3}$) (Figs. 4c-4f; Figs. 5m-5r).

Comparison of CM and Chl-*a* values of the coastal zone (stations up to the 50 m isobath), in the

seasons of the year (Kruskal-Wallis and Wilcoxon tests; Fig. 6; Table III), shows that there was a large range of CM values during summer, small range during spring and winter and minimum range in autumn. CM was higher in the summer and spring, and lower in winter and autumn, with significant differences (H =27.4; gl=3; p=0.47x10$^{-5}$) between the seasons, except between summer and spring (median values 13 and 15 mg  m$^{-3}$; Table III b). In summer, the distribution of biomass values was wide, while in spring the values were close to the median. The maximum CM values in spring (32.89 mg m$^{-3}$) and summer (29.95 mg m$^{-3}$) were similar. However, in spring the maximum value was out of the distribution.

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

|  | 0 - 25 m | 25 - 50 m | 50 - 100 m | > 100 m | depth integrated |
|---|---|---|---|---|---|
|  | ( mg m$^{-3}$ ) | | | | ( g m$^{-2}$ ) |
| **Spring** | | | | | |
| **CM** | | | | | |
| Max / Min | 32.89 / 0.93 | — | — | — | 0.82 / 0.13 |
| Mean/ S.D. | 9.23 / 9.14 | — | — | — | 0.43 / 0.20 |
| **Chl- *a*** | | | | | |
| Max / Min | 4.34 / 0.12 | — | — | — | 0.07 / 0.01 |
| Mean/ S.D. | 1.44 / 1.19 | — | — | — | 0.04 / 0.02 |
| **Summer** | | | | | |
| **CM** | | | | | |
| Max / Min | 29.95 / 2.55 | 27.23 / 0.11 | 3.58 / 0,80 | 1.66 / 0,09 | 1.36 / 0.15 |
| Mean/ S.D. | 14.00 / 8.68 | 5.46 / 6.12 | 1.94 / 0.94 | 0.71/ 0.60 | 0.52 / 0.35 |
| **Chl-*a*** | | | | | |
| Max / Min | 2.36 / 0.05 | 0.58 / 0.05 | 0.44 / 0.04 | — | 0.03 / 0.00 |
| Mean/ S.D. | 0.43 / 0.58 | 0.23 / 0.15 | 0.14 / 0.10 | — | 0.01 / 0.01 |
| **Autumn** | | | | | |
| **CM** | | | | | |
| Max / Min | 4.76 / 0.31 | 2.82 / 0.08 | 1.67 / 0.01 | 0.20 / 0.05 | 0.12 / 0.01 |
| Mean/ S.D. | 1.19 /1.04 | 0.73/0.63 | 0.38 / 0.47 | 0.10 / 0 06 | 0.05 / 0.03 |
| **Chl-*a*** | | | | | |
| Max / Min | 2.56 / 0.26 | 1.55 / 0.28 | 0.63 / 0.21 | — | 0.07 / 0.02 |
| Mean/ S.D. | 1.10 / 0.60 | 0.61 / 0.27 | 0.34 / 0.13 | — | 0.03 / 0.01 |
| **Winter** | | | | | |
| **CM** | | | | | |
| Max / Min | 24.87 / 0.07 | 10.99 / 0.24 | 11.82 / 0.02 | 1.27 / 0.05 | 1.4 / 0.06 |
| Mean/ S.D. | 6.44 / 5.66 | 2.92 / 3.08 | 2.93 / 4.00 | 0.51 / 0.46 | 0.28 / 0.24 |
| **Chl-*a*** | | | | | |
| Max / Min | 1.86 / 0.21 | 1.83 / 0.14 | 0,19 / 0.05 | — | 0.05 / 0.01 |
| Mean/ S.D. | 0.77 / 0.49 | 0.55 / 0.49 | 0.11 / 0.05 | — | 0.03 / 0.01 |
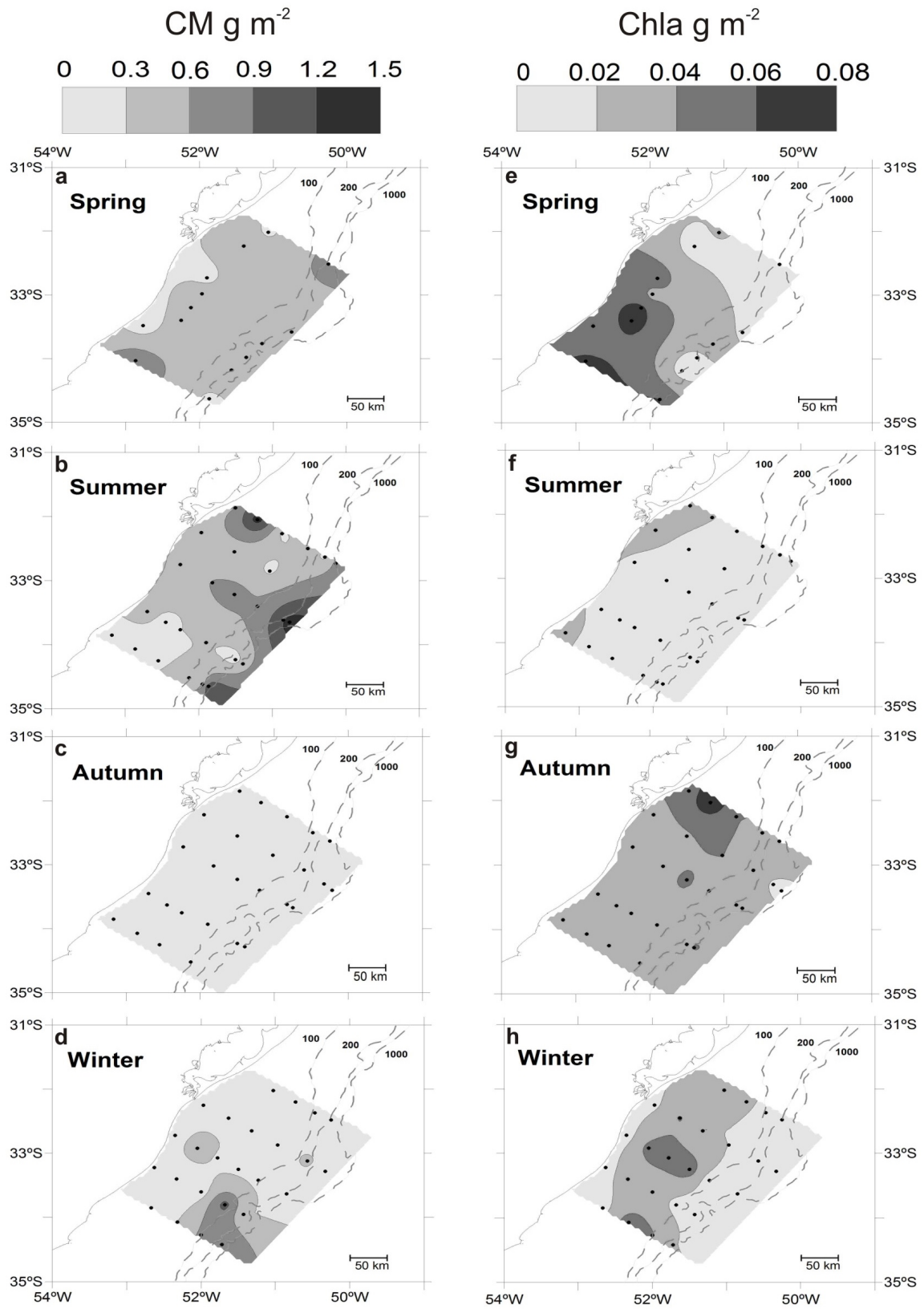
**Figure 3**. Zooplankton biomass (CM) (a, b, c, d) and chlorophyll (Cla-*a*) (e, f, g, h) distribution per unit of area (g m$^{-2}$) in spring, summer, autumn and winter. (Isobaths in meters).
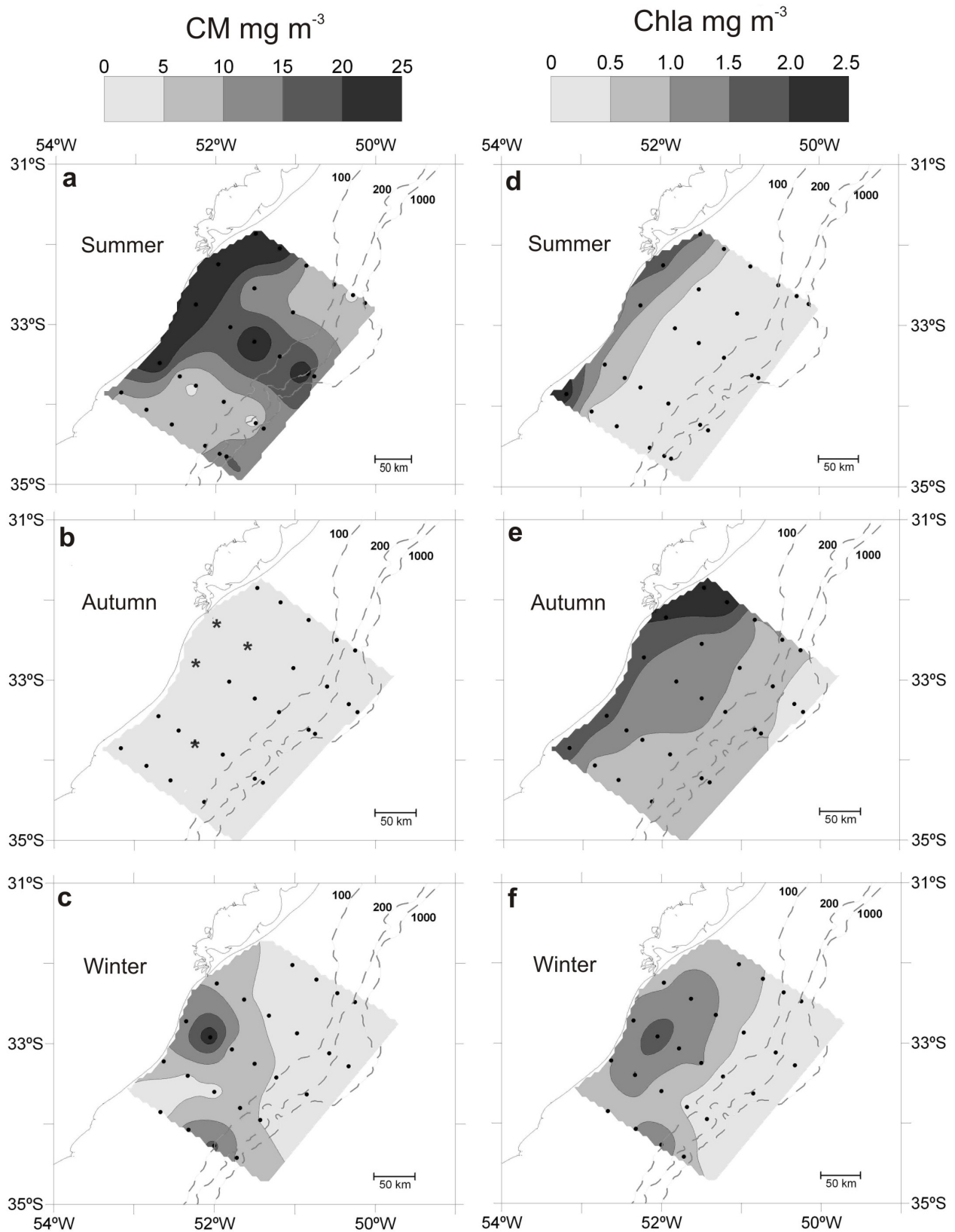
**Figure 4**. Horizontal distribution (0-25 m) of zooplankton biomass (CM) (a, b, c) and chlorophyll (Chl-*a*) (d, e, f) in summer, autumn and winter. Star sign (*) in the autumn (b) shows the sampling stations where the highest CM values (3 to 4.8 mg C m$^{-3}$) were found. (Isobaths in meters).

The same occurred with the maximum value (24.83 mg m⁻³) in winter (Fig. 6a). Analysis of Chl-*a* (Fig. 6b) showed a high range of values in spring and summer, and a low range in autumn and winter. The low values in summer and winter were significantly different from those in the autumn (H=10.5; gl=3; p=0.01), (Table III b). The lowest medians were observed in summer and winter (0.6 and 1.0 mg m⁻³, respectively); the highest in spring and autumn (2.2 and 1.6 mg m⁻³, respectively). However, there were no differences in the *a posteriori* test, and spring was similar to autumn, summer and winter, due to the high range of Chl-*a* values in spring. In summer, in turn, the values were significantly lower than in autumn (median 1.6 mg m⁻³), almost triple the values of summer. No differences were found between summer and winter, but winter was significantly different than autumn, with a higher median value.

*Relationship between zooplankton biomass and environmental factors*

The high values found in spring and winter, were related to the Plata Plume Water (PPW), and in summer with the Subtropical Shelf Water (STSW). Intermediate values in winter in the 0-25 m and 25-50 m strata were associated to the Subantarctic Shelf Water (SASW) (Fig. 7).The CM values were explained by the season of the year, stratum depth and water masses (Table IV). There were no difference between summer and winter values (high CM values) but they were significantly different (p<0.001) from those in autumn (low values).

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

Based on pseudo-R², the data in the model GLM, explained approximately 65% of the variation in CM. Deviance residuals between -2.66 and 2.56 indicate that there were no remaining outliers and that the model fits the data. The qualification of the fitted model (Fig. 8) can be visualized comparing observed log (CM) against estimate values *η*. A perfect fit would imply that all points are on the drawn line. The observed linear correlation is r = 0.814 indicating an acceptable model fit.
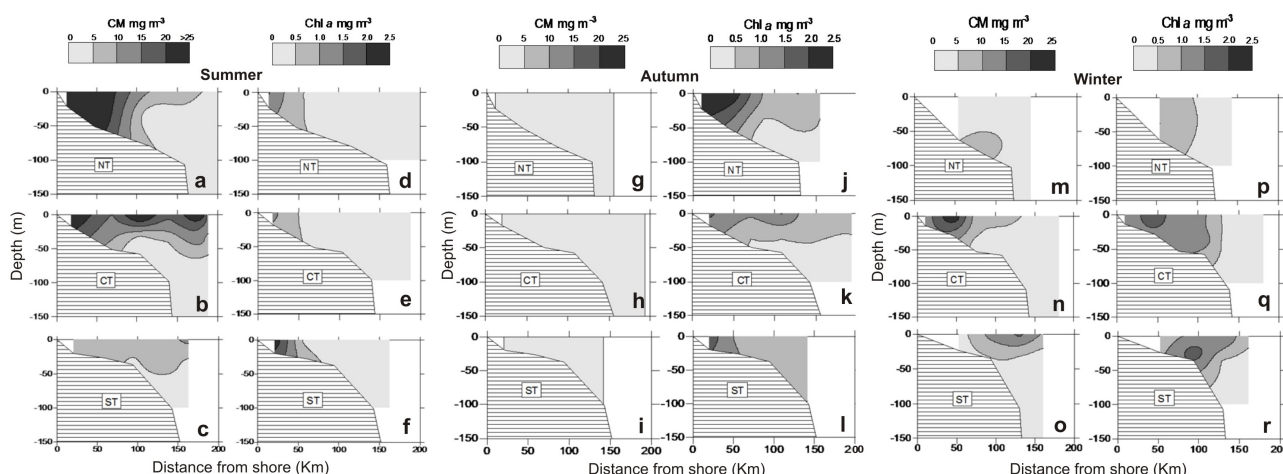


**Figure 5**. North (NT), Central (CT) and South (ST) onshore-offshore transects of zooplankton biomass (CM) and chlorophyll (Chl-*a*), respectively, in summer (a, b, c / d, e, f), autumn (g, h, i / j, k, l) and winter (m, n, o / p, q, r).
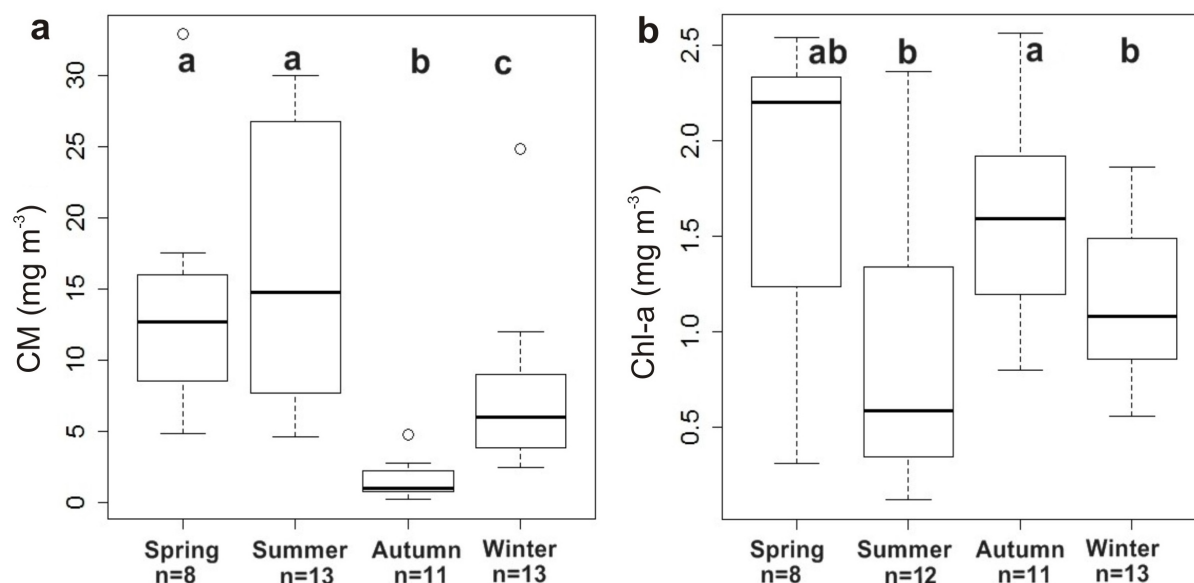
**Figure 6**. Box-plot of the Kruskal-Wallis test for values of CM (a) and Chl-a (b) in the coastal zone in the four seasons. The boundaries of the rectangles indicate the 25th and 75th percentiles, and the horizontal bars indicate the median. The dotted vertical bars indicate upper and lower distribution limits.

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

| **a** Zooplankton biomass (CM) | | | **b** Chlorophyll (Chl-*a*) | | |
|---|---|---|---|---|---|
| **Seasons** | **W** | **p** | **Seasons** | **W** | **p** |
| Winter X Summer | 32 | **0.000765** | Spring X Summer | 73.5 | 0.05 |
| Winter X Autumn | 134 | **0.0000077772** | Spring X Autumn | 54 | 0.44 |
| Winter X Spring | 22 | **0.03023** | Spring X Winter | 78 | 0.06 |
| Summer X Autumn | 129 | **0.00000818** | Summer X Autumn | 23.5 | **0.009** |
| Summer X Spring | 57 | 0.74 | Summer X Winter | 51 | 0.14 |
| Autumn X Spring | 0 | **0.000002646** | Autumn X Winter | 107 | **0.04** |

## Discussion

The zooplankton biomass (CM) in the extreme south of Brazil was associated with the seasons of the year, the water masses and the depth of the water column. The highest CM values occurred in spring and summer, which was probably related to the growth of zooplankton populations, stimulated by the presence of rich waters and high temperature that favor the reproduction and development of organisms. High densities of meroplanktonic larvae were observed in spring and summer (Montú *et al.* 1997), and of copepodids in summer, which may account for the higher CM values. Intermediate and high values were observed in winter, which although it is not a typical reproduction period for most species has a predominance of crustaceans (Montú *et al.* 1997), mainly copepods in the present study, which have a

high carbon content (Postel *et al.* 2000).

The water masses associated with the higher CM values were the Plata Plume Water (PPW) in spring, winter and autumn, and the Subtropical Shelf Water (STSW) in summer. The distribution pattern of zooplankton biomass and the relationships with the water masses observed in the present study are similar to the reported distribution of biovolume in this area (Meneghetti 1973; Navas-Pereira 1973; Huboldt 1980a, b; Bruno 2009). The high biovolume reported for autumn in the region (Resgalla *et al.* 2001) was due to the presence of tunicates, organisms with high water content, but low carbon content (Postel *et al.* 2000).

There are few reports in the literature on the zooplankton biomass estimated as carbon content by area (g C m⁻²), particularly in latitudes similar to those in the present study.
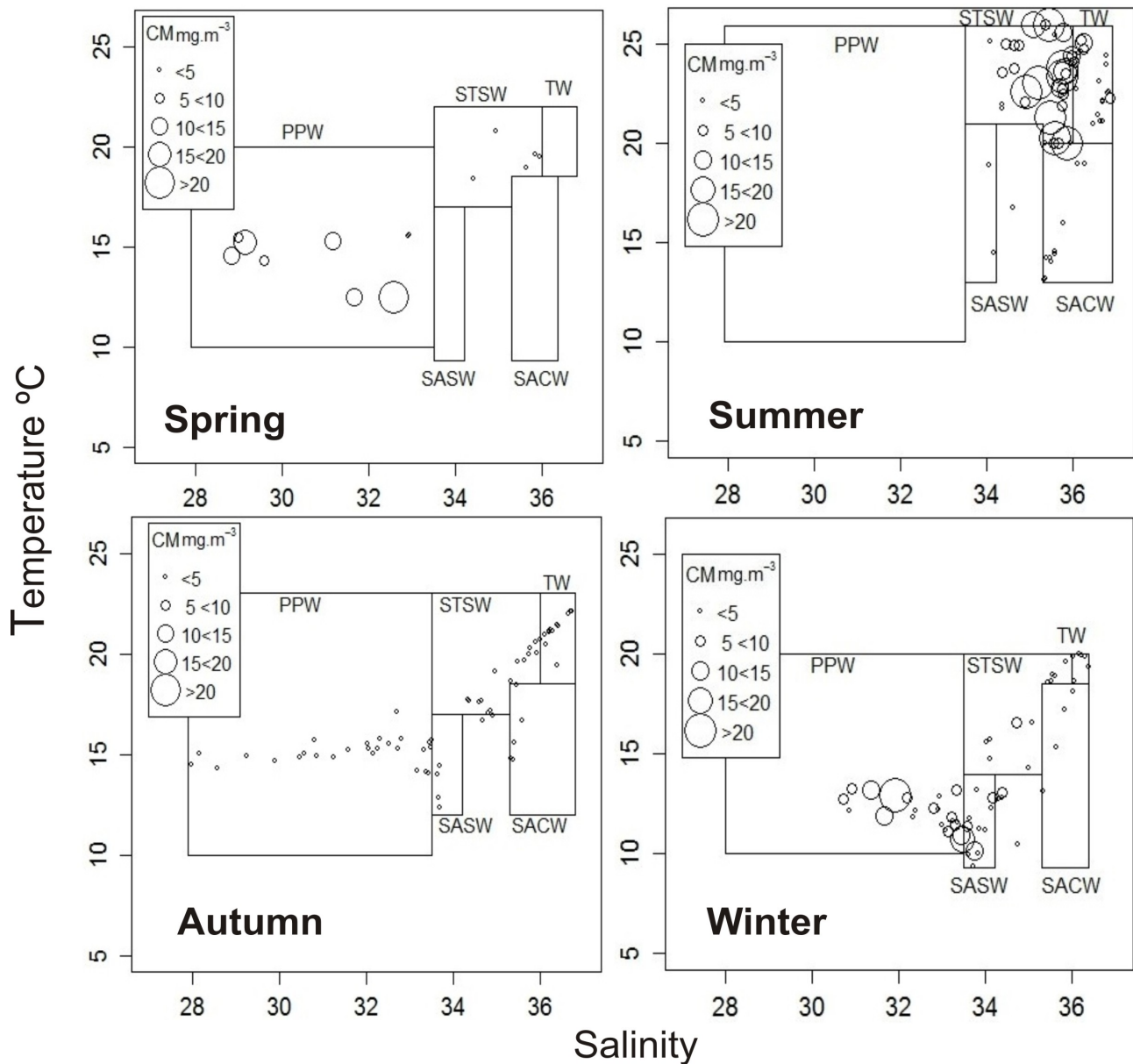
**Figure 7**. Temperature, salinity and zooplankton biomass diagrams (TSZ) for spring, summer, autumn and winter. Rectangles indicate each water mass according termohaline indexes on Table 1. PPW: Plata Plume Water, SASW: Subantartic Shelf Water, STSW: Subtropical Shelf Water, SACW: South Atlantic Central Water and TW: Tropical Water.

The comparison of the values for summer in this region to those of the Barrents Sea shelf, Arctic, one of the most productive regions of the world (0.74 - 3.72 g C $m^{-2}$; Dvoretsky & Dvoretsky 2013), and to those of Bransfield Strait, Antarctic (0.23 g C $m^{-2}$ for crustaceans and 14.71 g C $m^{-2}$ for salps; Alcaraz *et al.* 1998), shows that they are lower here (0.15 -1.36 g C $m^{-2}$), but indicate the importance of zooplankton in the local pelagic production.

Globally, estimates of zooplankton biomass were obtained based on the color of the ocean by SeaWiFS satellite and parametric models that related the transfer of energy from primary production to zooplankton biomass with *in situ* data (Strömberg *et al.* 2009). In the Atlantic Ocean, the estimated biomass of zooplankton is higher (7.35 mg C $m^{-3}$; S.D. 8.62) than the global average value (5.52 mg C $m^{-3}$; S.D. 8.94). The average value in the present study (6.54 mg C $m^{-3}$; S.D. 6.03) is intermediate to the values mentioned.
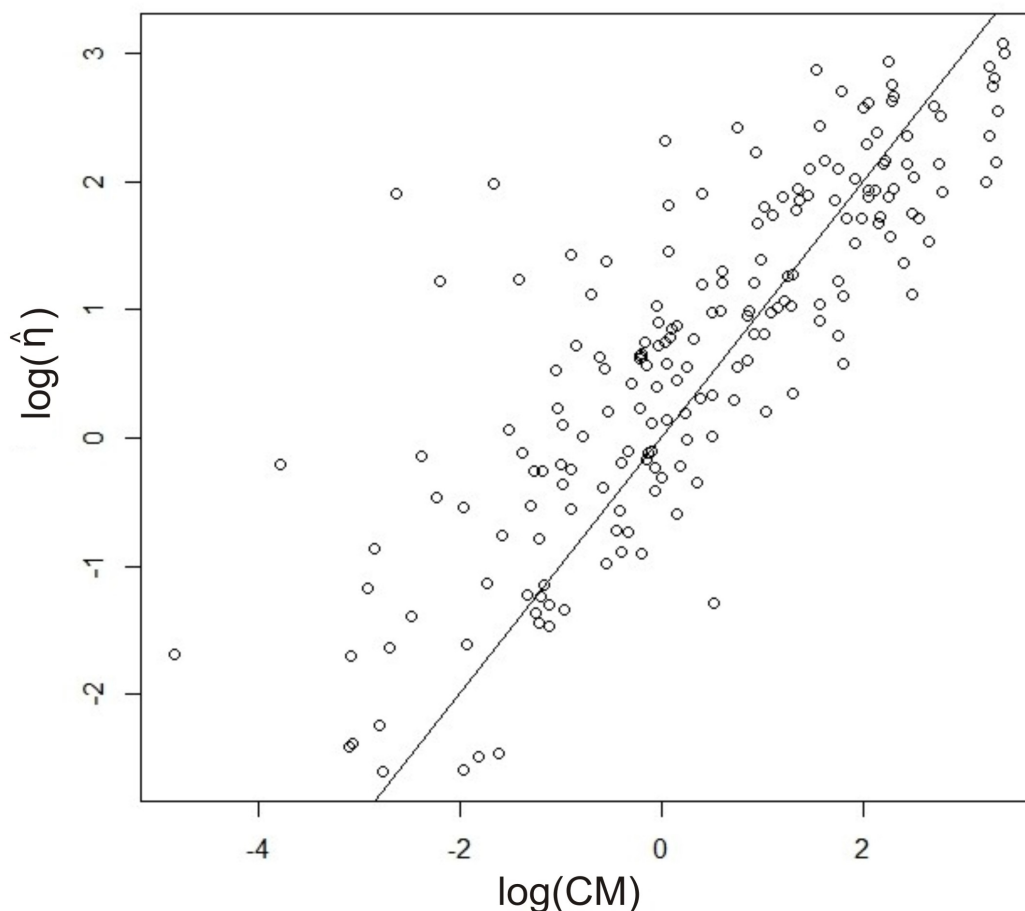
**Figure 8**. Fitted model that compares the log (CM) observed with the values estimated in the GLM analysis. The correlation is linear, r = 0.814.

On the map of global distribution of zooplankton biomass presented by the authors, the values for the extreme south of Brazil to the south of Argentina reach 20-30 mg C m$^{-3}$, consistent with the values found in this study, and are higher in the mouth of Rio de La Plata, indicating the positive influence of these waters for the entire region. In the Gulf of Trieste (NE Mediterranean) the average biomass (7.14 mg C m$^{-3}$ ; S.D. 4.3; Kamburska & Fonda-Umani 2009) was slightly higher than the value found in our study. Moriarty *et al.* (2012) found a global average biomass of 8.4 mg C m$^{-3}$ (S.D. 63.46), though for the macrozooplankton, a zooplankton fraction, which is larger than in the present study and in studies of the other cited authors. In Brazil, the biomass of zooplankton reaches higher values in the upwelling region of Cabo Frio (~23°S, around 88 mg C m$^{-3}$ based on its dry mass, 220 mg m$^{-3}$; Valentin 2001). Nevertheless, the average values in the coastal estuarine zone of São Paulo State (2.55 and 3.45 mg C m$^{-3}$; Miyashita *et al.* 1999), and between São Paulo and Rio de Janeiro States neritic region (2.4 and 5.6 mg C m$^{-3}$,

based on its dry mass, 6 and 14 mg m$^{-3}$, Muxagata 1999) were low compared to those in the region of this study and in the other referred regions.

A very high value (98 mg C m$^{-3}$) was reported in the summer, in a coastal area south of the study area by Montú *et al.* (1997), which was probably overestimated by the high level of suspended material (45 mg l$^{-1}$) and organic matter (18 mg l$^{-1}$) (Muelbert *et al.* 2008). On the other hand, the concentration of mysids in the surf zone of Cassino beach (32°S) yielded an extreme value, one of the highest in the literature (8,142 mg C m$^{-3}$; Bersano 1994).

A decreasing gradient, from the coast to the ocean, in the density of zooplankton has been observed in the Brazilian southern region previously (Lopes *et al.* 2006; Muelbert *et al.* 2008). However, no significant differences were reported in this study among the three zones regarding biomass, although the highest values occurred more frequently in the coastal zone. Also, the biomass did not show a latitudinal pattern, despite the presence of two groups during the summer: a group of high values

($>20$ mg C m$^{-3}$) to the north of the study area (31ºS a 33ºS), and another group with lower values ($< 15$ mg C m$^{-3}$) to the south of the area (latitude $> 33$ºS). This may be related to the position of the Subtropical Shelf Front (STSF) between 32ºS and 36ºS (Piola *et al.* 2008). The daily vertical migration did not significantly influence the results of this study, since, regardless of the time of collection, CM values were higher in the surface layer (0-25 m).

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

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

the amount of chlorophyll in the region, which should benefit the zooplankton.

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

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

4e).

Cycles of warm and cold events of the ENSO (*El Niño*-Southern Oscillation) phenomenon determine rainy and dry periods, respectively, in the south of South America (Brazil, Uruguay and Argentina), changing the hydrographic characteristics, particularly the flow of freshwater in the region (Ciotti *et al.* 1995; Möller *et al.* 2008). Strong and moderate *El Niño* phenomena occurred in the spring of 1987 and autumn of 1990, respectively (http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml) periods with high Chl-*a* values, probably influenced by the higher inflows of continental waters. The high CM value observed in coastal zone in spring (~33 mg m⁻³) was possibly related with the *El Niño*. However, there was no apparent influence of this event in autumn, when the lowest values (<5 mg m⁻³) were observed.

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

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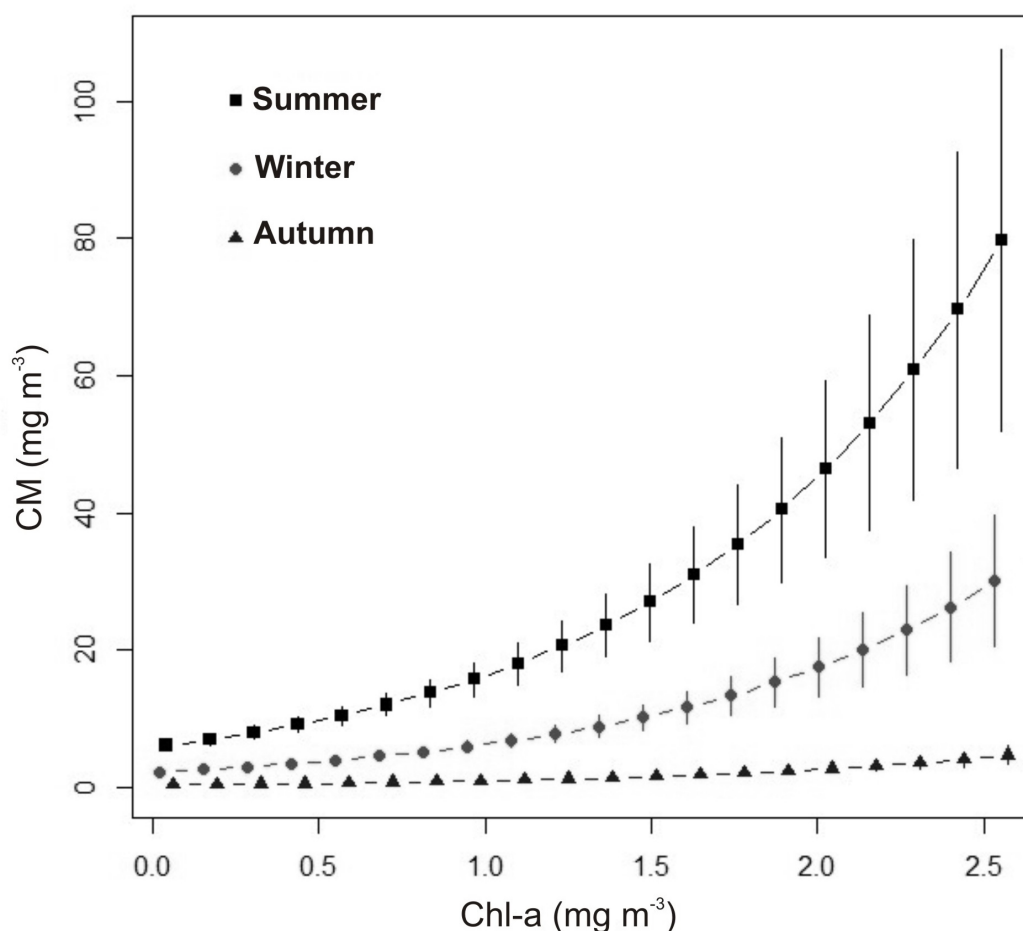


**Figure 9**. Predictive model indicating the possible effects of increased Chl-*a* over CM values in summer, winter and autumn, according to the GLM analysis. Vertical lines are the prediction intervals of 95% for the mean value of response (y) for each value specified on the axis (x).

The biomass of zooplankton also increased from spring to the early autumn further south, on the continental shelf of Argentina, with high values in coastal zone and close to the shelf break, while the main peak of Chl-*a* occurred in spring, followed by a second one in the autumn (Sabatini & Colombo 2001).

In the South Pacific coastal region off Chile, the increase in carbon content of zooplankton was related to the high concentration of diatoms (Escribano *et al.* 2007). Kamburska and Fonda-Umani, 2009 found that the changes were related with the taxonomic composition of phytoplankton, demonstrating the relationship between these two pelagic components.

However, Escribano *et al.* (2007) did not find a significant relationship between zooplankton biomass and chlorophyll, assigning that the heterotrophic components provides continuous food supply to the zooplankton. They suggested that perhaps Chl-*a* alone may not be a reliable index to assess the availability of food for zooplankton and the general lack of a relationship between CM and Chl-*a* in the present study confirm this idea.

In marine ecosystems, the efficient transfer from producers to herbivores is estimated in around 30% (Coyle & Pinchuk 2003). Given the average values of Chl-*a* (Table II), and equating them to their carbon content (C/Chl-a = 40; Parsons *et al.* 1984), we would obtain the average values of autotrophic biomass by area: spring 1.6 g C m$^{-2}$, autumn 1.2 g C m$^{-2}$, winter 0.8 g C m$^{-2}$, and summer 0.4 g C m$^{-2}$.

Based on these values and on zooplankton carbon content values by area (Table II) in the same periods, transfer efficiency can be inferred of 27% in spring, 35% in winter and 3% in autumn. However, in summer the zooplankton biomass was greater than the available autotrophic biomass, suggesting a high consume of microalgae and other components (protozooplankton and bacteria).

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

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

We can also infer zooplankton production per area (Table V), whose daily average value would be 0.12 g C m$^{-2}$ d$^{-1}$, resulting in a secondary annual production of 44 g C m$^{-2}$ yr$^{-1}$, which corresponds to 28% of the estimated average primary production in this region (160 g C m$^{-2}$ yr$^{-1}$; Odebrecht & Garcia 1997). This percentage is consistent with the transfer efficiency (~30%) estimated between these two trophic levels. Our data of secondary annual production (44 g C m$^{-2}$ yr$^{-1}$) is similar to that reported (54 g C m$^{-2}$ yr$^{-1}$; Coyle & Pinchuk 2003) to Alaskan Gulf region. Considering the total study area (~ 46 750 km$^2$), the zooplankton would produce about 2 x 10$^6$ t of carbon, and 7.5 x 10$^6$ t of carbon would be generated by the primary producers in the area per year. These values indicate the region as a highly productive zone of the ocean, considering the estimate of 45-50 Gt C yr$^{-1}$ of global primary net production, which corresponds to 125-139 g C m$^{-2}$ yr$^{-1}$ for the global ocean (Longhurst *et al.* 1995). Thus, it can be concluded that zooplankton and phytoplankton in the extreme south of Brazil play an important role in the carbon cycle and CO2 balance.

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

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

—    Not available

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

[2] Values obtained considering 5m local depth.

## Acknowledgements

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