



Influence of oceanographic features on the spatial and seasonal patterns of mesozooplankton in the southern Patagonian shelf (Argentina, SW Atlantic)



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ABSTRACT

Surveys conducted during spring, summer and late winter in 2005–2006 over the southern Patagonian shelf have allowed the seasonal distribution of mesozooplankton communities in relation to water masses and circulation to be investigated. In this system, most of the shelf is dominated by a distinct low salinity plume that is related to the runoff from the Magellan Strait (MSW), while the outer shelf is highly influenced by the cold and salty Subantarctic water (SAW) of the boundary Malvinas Current. Separating these two, the Subantarctic Shelf water mass (SASW) extends over the middle shelf. Correspondingly, the structure of the MSW and SAW mesozooplankton communities was found to be clearly different, while the former and the SASW assemblages were barely separable. This relatively fresh water mass is actually a variant of Subantarctic water that enters into the region from the south and the shelf-break, and hence its mesozooplankton community was not significantly different from that of the SAW water mass. Dissimilar species abundance, in turn associated with different life histories and population development, was more important than species composition in defining the assemblages. Total mesozooplankton abundance increased about 2.5-fold from the beginning of spring to late summer, and then decreased at least two orders of magnitude in winter. Across all seasons copepods represented >70–80% of total mesozooplankton over most of the shelf. Copepod species best represented through all seasons, in terms of both relative abundance and occurrence, were *Drepanopus forcipatus* and *Oithona helgolandica*. Although seasonal differences in abundance were striking, the spatial distribution of mesozooplankton was largely similar across seasons, with relatively higher concentrations occurring mainly in Grande Bay and surroundings. The well defined spatial patterns of mesozooplankton that appear from our results in conjunction with the southward wide extension of the shelf and the predicted current path and speed suggest that plankton production is locally enhanced in the Grande Bay area and has the potential to be exported downstream.

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1. Introduction

The recognition of planktonic biogeographic patterns in the ocean and the mechanisms responsible for their establishment and maintenance can provide significant insights about the configuration and variability of communities (e.g., Brinton, 1962; Frost, 1989; Ohman et al., 2012). Ocean water masses represent specific habitats for pelagic organisms, their characteristics mostly defining the niche of plankton communities either directly or indirectly, by conditioning preferred depths, food availability, feeding modes, etc. Boundaries between

water masses are characterized by dynamic oceanographic fronts, physical interfaces which play a role in regulating the spatial and temporal variations in the plankton diversity and productivity patterns (Le Fèvre, 1986). Determining where biogeographic boundaries exist is therefore a necessary step to understanding the processes that underlay the patterns. At the same time, large scale studies of changes occurring in the ocean, due to climate change or anthropogenic effects, are mostly performed running biogeochemical models (e.g., Aumont et al., 2015). These models are built based on the, so far, limited knowledge on the ecosystem components and processes. Hence, studies of community structure, trophic relations and niche adaptation to the environment are crucial to develop more realistic biogeochemical models.

Extending from Cape Blanco (~47°S) to Burdwood Bank (~55°S) in the Southwestern Atlantic, the wide southern Patagonian shelf (Fig. 1)

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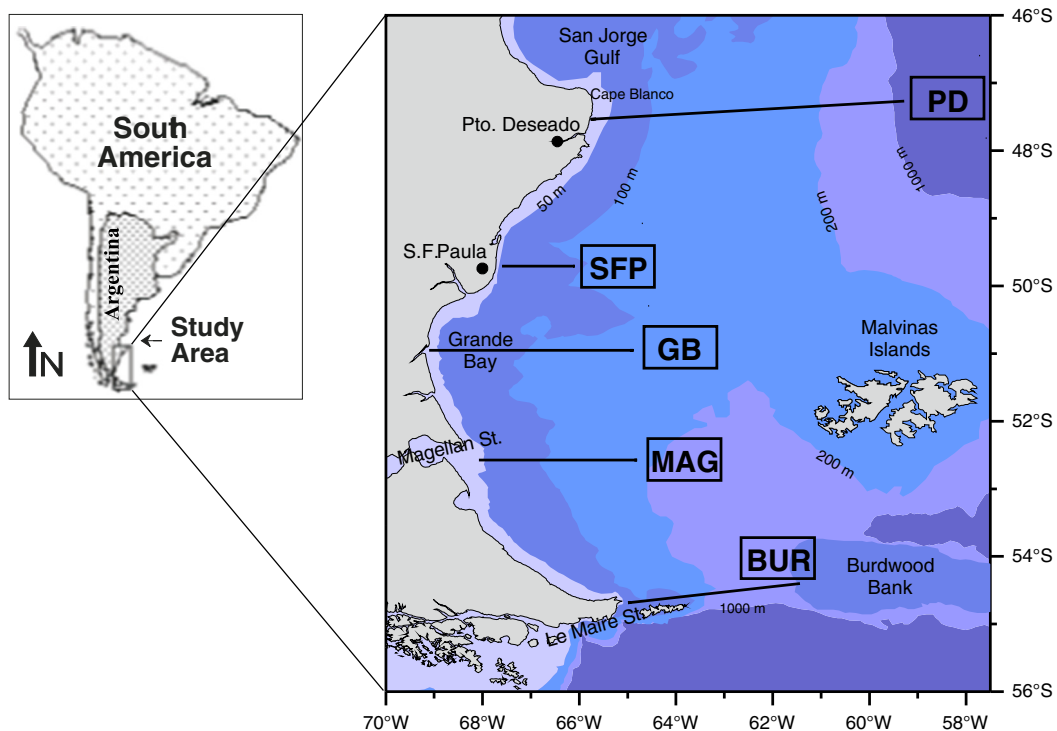


Fig. 1. Location of sampling transects across the southern Patagonian shelf during early spring (October 2005, GEF 01), late summer (March 2006, GEF 02) and late winter (September 2006, GEF 03). PD, Puerto Deseado; SFP, San Francisco de Paula; GB, Grande Bay; MAG, Magellan Strait; and BUR, Burdwood Bank.

sustains a highly productive ecosystem (Lutz et al., 2010; Segura et al., 2013; Dogliotti et al., 2014). Zooplanktivorous taxa are dominant at intermediate levels of the food web (Ciancio et al., 2008; Padovani et al., 2012) and mesozooplankton, in turn preying on smaller plankton, is therefore a key trophic component (Sabatini and Álvarez Colombo, 2001; Sabatini et al., 2004, 2012; Antacli et al., 2014a,b).

The hydrographic structure of this region has been described extensively from historical observations (Guerrero and Piola, 1997; Bianchi et al., 1982, 2005) and numerical simulations indicate a strong influence of circulation on the spatial distribution of water properties (Palma et al., 2008). Three water masses primarily defined by salinity reflect the dominant circulation patterns, i.e., Magellan Strait water (MSW), Subantarctic shelf water (SASW) and Subantarctic water (SAW). Local circulation is driven by large freshwater inflows, high tidal amplitudes, westerly winds and the strong influence of the Malvinas Current flowing northwards along the shelf-break (Palma et al., 2008; Matano et al., 2010; Palma and Matano, 2012). The contrast between the MSW with the SASW generates the Magellan salinity front, a middle shelf front that extends parallel to shore along most of the study area. The sharpest horizontal gradient of salinity occurs offshore and corresponds to the shelf-break front, which forms from the contrast of SASW with cold and dense SAW. Small tidal, estuarine-plume fronts related to freshwater discharges onto the shelf are also present at short distance from shore (Sabatini et al., 2004). Frontal dynamical interaction generates a cross-shelf circulation that is probably related to the inflow of nutrient-rich waters from offshore. This enrichment mechanism may be essential for the productivity of the inner and middle shelf system (Matano et al., 2010).

Given the importance of salinity in determining the structure and distribution of water masses in the region, it is worth considering that the effects of global warming on Patagonia temperature are predicted to be larger than the global mean (IPCC, 2014) and glaciers, which are a major source of freshwater into the ocean, are melting fast (Rignot et al., 2003; Schneider et al., 2007). Projections suggest also a rise in annual rainfall (IPCC, 2014), and surface runoff is anticipated to intensify as consequence of increasing drainage of continental rivers along the

coast of southern Patagonian (Pasquini and Depetris, 2007). These circumstances emphasize the significance of studies focused on plankton-hydrographic linkages in the region, which is besides geographically and oceanographically connected with the southeastern Pacific and Southern Ocean (Lara et al., 2010; Matano et al., 2010).

Previous work in the study area has been mostly restricted to summer/fall and thus little is known about the seasonality of zooplankton communities. After the pioneering surveys conducted in the late 70s over the entire Argentine Sea which covered roughly an annual cycle (e.g., Carreto et al., 1981; Ramírez, 1981) and the overall patterns of zooplankton biomass described earlier by Sabatini and Álvarez Colombo (2001), this is actually the first time that seasonal data on the southern Patagonian shelf are reported from cruises carried out during spring, summer and late winter in 2005–2006.

Results from the first of these cruises showed that the spatial patterns of mesozooplankton in early spring were distinctly defined across-shelf, with typical communities that mirrored the distribution of water masses and fronts to a significant degree (Sabatini et al., 2012). After these findings, it was suggested that the distribution of mesozooplankton assemblages in waters off southern Patagonia was likely determined by niche adaptation. To investigate this hypothesis, here we used multivariate analysis to determine the distribution patterns of mesozooplankton during the three sampling periods, and examined on the seasonal scale whether the community structure is related to the typical water masses of the southern Patagonian shelf. Present results will further contribute with baseline information regarding the seasonality of zooplankton dynamics in relation to hydrography before major environmental changes may take place in the region.

2. Material and methods

2.1. Sampling

Mesozooplankton communities were investigated during three surveys conducted to the southern Patagonian shelf (47°–55°S) in early spring (GEF 01, October 2005), late summer (GEF 02, March

2006) and late winter (GEF 03, September 2006). In the course of the three cruises sampling was carried out along five transects across shelf: a) off Puerto Deseado (PD) at ca. 47°S, b) off San Francisco de Paula (SFP) at ca. 50°S, c) in middle Grande Bay (GB) at 51°S, d) off the Magellan Strait (MAG) at ca. 53°S, and e) off Tierra del Fuego approaching the Burdwood Bank (BUR) at ca. 54°S (Fig. 1).

At all stations continuous profiles of temperature, salinity and fluorescence were recorded with a Sea-Bird 911 CTD, and a Sea Tech/Seapoint fluorometers mounted onto the CTD in GEF 01 and GEF 03. Fluorescence profiles were not obtained in GEF 02. An exhaustive description of CTD sampling and analysis procedures used for data processing can be found elsewhere (Charo and Piola, 2014). Niskin bottles were used to collect samples for the measurement of chlorophyll *a* (total and <5 µm); these data were reported somewhere else (e.g., Segura et al., 2013) but will be used here to characterize the

seasonal progress of phytoplankton over the study area as proxy of food availability for copepods.

Zooplankton collection was performed with a Motoda sampler, 60 cm mouth diameter with a 200 µm mesh size net mounted on a frame with a closing mechanism (Motoda, 1969). The sampler was towed obliquely at ca. 1.5–2 kts within two strata below and above the depth of maximum fluorescence (or selected depths when the water column was homogeneous or the fluorescence sensor was not available) (Table 1). Larger and faster-swimming zooplankton such as euphausiids, amphipods and chaetognaths were surely undersampled because of the low retrieving speed of this type of sampler (Sameoto et al., 2000). Hence, their occurrence in the samples was assumed to be proportional to their actual abundance, and thus large non-copepod taxa were treated separately from copepods in terms of relative abundance. Filtered volumes were estimated by a digital flowmeter

Table 1
Zooplankton sampling conducted in the southern Patagonian shelf during cruises R/V ARA “Puerto Deseado” (GEF 01–October 2005, GEF 02–March 2006 and GEF 03–September 2006). Sampling dates, times and towing depths. (MDA, Motoda sampler).

| GEF 01 – early spring | | | | | GEF 02 – late summer | | | | GEF 03 – late winter | | | |
|-----------------------|----|----------|------------|------------------------|----------------------|----------|------------|------------------------|----------------------|----------|-------------------------|--------------------|
| Transect | EG | Date | Local time | Strata depth (MDA) | EG | Date | Local time | Strata depth (MDA) | EG | Date | Local time | Strata depth (MDA) |
| PD | 38 | 16/10/05 | 21:18 | 0–15 50–15 | 24 | 16/03/06 | 01:05 | 0–30 100–30 | 15 | 10/09/06 | 14:25 | 0–25 130–25 |
| | 41 | 17/10/05 | 07:30 | 0–15 35–15 | 25 | 16/03/06 | 03:40 | 0–30 70–30 | 16 | 10/09/06 | 17:09 | 0–30 130–30 |
| | 42 | 17/10/05 | 10:16 | 0–15 50–15 | 26 | 16/03/06 | 08:51 | 0–25 80–25 | 17 | 10/09/06 | 19:25 | 0–20 110–20 |
| | 43 | 17/10/05 | 13:42 | 0–15 40–15 | 27 | 16/03/06 | 12:13 | 0–30 60–30 | 21 | 11/09/06 | 05:18 | 0–25 110–25 |
| | 47 | 18/10/05 | 02:20 | 0–10 35–10 | 29 | 16/03/06 | 18:19 | 0–30 90–30 | 22 | 11/09/06 | 08:01 | 0–20 75–25 |
| | 49 | 18/10/05 | 08:34 | 0–10 30–10 | 31 | 16/03/06 | 23:27 | 0–25 60–25 | 23 | 11/09/06 | 10:47 Only one level | 0–25 |
| SFP | 50 | 19/10/05 | 08:26 | 0–20 40–20 | 34 | 18/03/06 | 07:17 | 0–25 80–25 | No sampling | | | |
| | 51 | 19/10/05 | 11:26 | 0–20 30–20 | 36 | 18/03/06 | 11:25 | 0–25 60–25 | | | | |
| | 52 | 19/10/05 | 14:42 | 0–15 25–15 | 37 | 18/03/06 | 13:47 | 0–30 60–30 | | | | |
| MAG | 53 | 20/10/05 | 06:27 | 0–10 40–10 | 51 | 25/03/06 | 14:47 | 0–20 60–20 | 39 | 19/09/06 | 05:38 | 0–35 120–35 |
| | 54 | 20/10/05 | 10:47 | 0–15 40–15 | 52 | 25/03/06 | 17:50 | 0–30 70–30 | 41 | 19/09/06 | 11:08 | 0–30 100–30 |
| | 55 | 20/10/05 | 14:36 | 0–20 60–20 | 53 | 25/03/06 | 20:55 | 0–30 90–30 | 42 | 19/09/06 | 14:30 | 0–30 90–30 |
| | 56 | 20/10/05 | 17:53 | 0–20 60–20 | 54 | 25/03/06 | 23:50 | 0–30 100–30 | 43 | 19/09/06 | 17:19 | 0–30 70–30 |
| | 57 | 20/10/05 | 21:47 | 0–30 60–30 | 55 | 26/03/06 | 02:52 | 0–30 100–30 | | | | |
| BUR | 58 | 21/10/05 | 08:46 | 0–20 40–20 | 43 | 22/03/06 | 18:30 | 0–20 80–20 | 34 | 18/09/06 | 08:44 | 0–20 47–20 |
| | 60 | 21/10/05 | 16:33 | 0–20 60–20 | 45 | 22/03/06 | 23:26 | 0–30 90–30 | 36 | 18/09/06 | 14:30 | 0–45 120–45 |
| | 61 | 21/10/05 | 20:30 | 0–20 Failed | 47 | 23/03/06 | 04:00 | 0–30 30–100 | | | | |
| GB | | | | | 48 | 23/03/06 | 06:00 | 0–30 80–30 | | | | |
| | 68 | 23/10/05 | 00:36 | 0–20 40–20 | 38 | 19/03/06 | 01:14 | 0–30 100–30 | 45 | 20/09/06 | 04:15 | 0–30 75–30 |
| | 69 | 23/10/05 | 03:35 | 0–25 50–25 | 39 | 19/03/06 | 04:35 | 0–30 100–30 | 46 | 20/09/06 | 07:05 | 0–30 100–30 |
| | 71 | 23/10/05 | 15:30 | 0–20 50–20 | 41 | 19/03/06 | 18:28 | 0–30 Only one level | 47 | 20/09/06 | 09:49 | 0–30 100–30 |
| | 72 | 23/10/05 | 18:48 | 0–15 80–15 | 42 | 19/03/06 | 22:23 | 0–30 Failed | 48 | 20/09/06 | 12:44 | 0–30 100–30 |
| | 74 | 23/10/05 | 22:28 | 0–15 40–15 | | | | | 50 | 20/09/06 | 17:38 | 0–30 120–30 |
| | 75 | 24/10/05 | 01:44 | 0–20 Only one level | | | | | | | | |

placed in the mouth of the sampler. Samples were preserved in buffered 5% formaldehyde–seawater solution. Sampling was undertaken at different times of the day depending on the cruise general schedule (Table 1). As a consequence, some animals may have been deeper than sampled in the water column because of diel vertical migration, mainly at deep locations.

2.2. Zooplankton analysis

Considering the importance of copepods in the bulk of mesozooplankton, samples were enumerated in a number of successive aliquots (Postel et al., 2000) until at least 200 adults or late copepodid stages C4–5 were classified to species and all other zooplankton taxa occurring in the subsample were counted. A total of 700–1000 individuals per sample were regularly enumerated. Where possible zooplankton were identified to the species level and developmental stage. Taxonomic classification was mainly based on Ramírez (1970a,b, 1971, 1973) and Boltovskoy (1981, 1999). Dominant copepods were staged and sexed after Bradford et al. (1988), Heron and Bowman (1971) and Hulsemann (1991). Early copepodid stages C1–3 other than *Drepanopus forcipatus* were not classified but pooled together and broken down into either small or large sized calanoid species; mainly *Ctenocalanus* + *Clausocalanus* were included in the former category and mainly Calanidae in the latter.

Mesozooplankton abundances (individuals m^{-3}) were integrated either within each of the two sampled strata or for the whole sampled column (individuals m^{-2}) by the trapezoidal method. Differences in the community composition between the upper and lower layers were examined separately for each cruise by one-way analyses of similarity (ANOSIM) on Bray–Curtis similarity matrices obtained after double-root transformation of species/taxa integrated abundances (PRIMER software package version 5.2.9, Clarke and Warwick, 1994). Community differences between sampled layers were not significant for any sampling period (GEF 01, Global $R = -0.015$, $p < 0.68$; GEF 02, Global $R = -0.020$, $p < 0.71$; GEF 03, Global $R = -0.007$, $p < 0.48$), and then all subsequent analyses were applied to depth-integrated abundances estimated for the entire sampled column (Table 1).

For the sake of comparison across seasons, the dependence of depth-integrated abundances on towing depth (Table 1) was removed by standardizing the values as:

$$\text{Abundance}_{\text{STDZ}} = \text{ind } m^{-2} (Z_{\text{Av}} / Z_{\text{Obs}})$$

where Z_{Av} is the average sampled depth over all sampling stations across the three cruises and Z_{Obs} is the actual towing depth at each station. This way, we can remove the biases in abundance due only to changes in sampling depth, making thus comparable all quantitative data.

To identify the dominant species an index of importance (I) was calculated as the average between the relative abundance and the frequency of occurrence of a given species/taxon in all the samples (after Morales et al., 2010).

2.3. Assessment of the relationship between mesozooplankton communities and water masses

Water masses in the southern Patagonian shelf are distinguished by their saline content, i.e., Magellan Strait Water (MSW, $S < 33.4$), Subantarctic Shelf Water (SASW, $33.4 < S < 34.0$) and Subantarctic Water (SAW, $S > 34.0$) (Bianchi et al., 1982; sensu Palma et al., 2008). In order to test the hypothesis of niche adaptation to water masses as a major driver of mesozooplankton distribution off southern Patagonian, the stations belonging to each of the three water masses were first defined as a priori groups for the three seasons, and multivariate analyses performed afterwards for these groupings (Clarke and Warwick, 1994). Sampling sites were assigned to a given water mass by comparison of

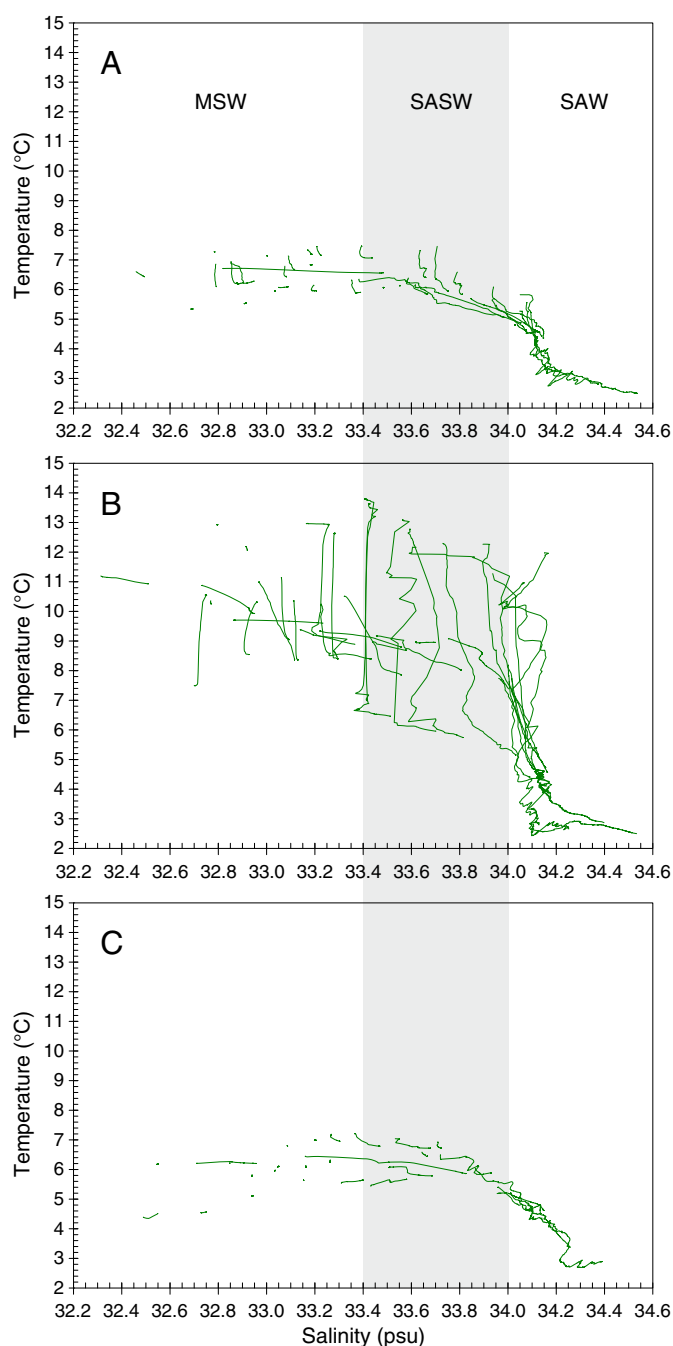


Fig. 2. Southern Patagonian shelf. Seasonal TS diagrams during the three sampling periods: early spring, GEF 01 (A), late summer, GEF 02 (B) and late winter, GEF 03 (C). MSW = Magellan Strait Water; SASW = Subantarctic Shelf Water; and SAW = Subantarctic Water.

the TS profile at each station with the combined TS overlay plot of each of the three cruises/seasons (Fig. 2). At a few biological sampling stations, where two water masses were overlapping one on top another, the station was allocated to the vertically dominant water mass. Significant differences in community structure across water masses and seasons were then tested by two-way crossed analysis of similarity (ANOSIM) and their relationships assessed by MDS ordination (non-metric multi-dimensional scaling). The stress (s) value in MDS reflects how well the ordination summarizes the observed distances among the samples, i.e., $s < 0.05$, excellent representation, $s < 0.2$, adequate ordination and $s > 0.3$, arbitrary ordination (Clarke and Warwick, 1994). Both procedures above were applied on Bray–Curtis similarity

matrices after double-root transformation of the entry data, i.e., depth-standardized species/taxa abundances integrated over the water column. This transformation produces a down-weighting of the abundant species,

allowing not only the mid-range but also the rarer species to exert some influence on the calculation of similarity (Clarke and Warwick, 1994). SIMPER routines (species/taxa contribution) were carried out to identify

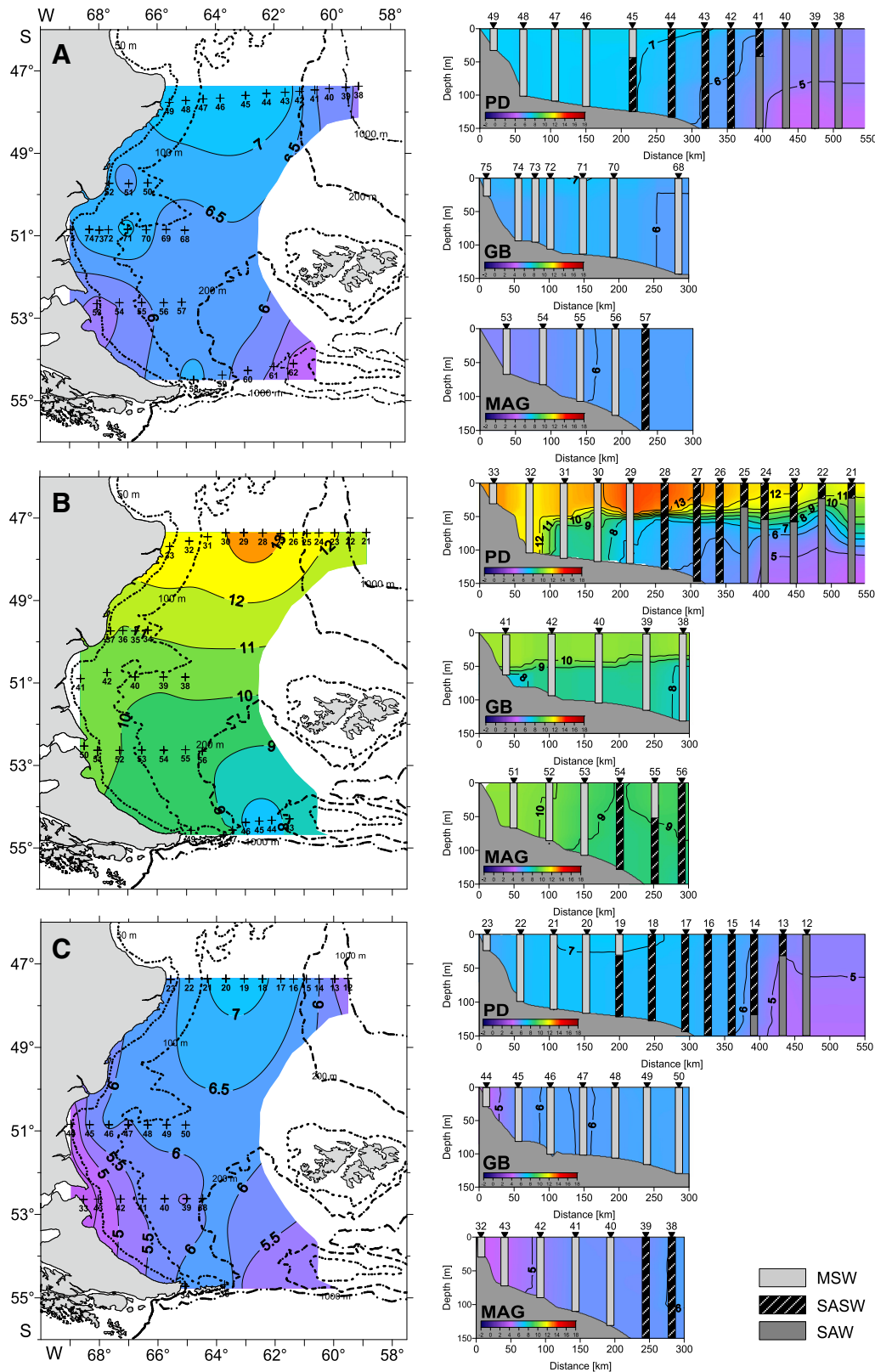


Fig. 3. Surface and vertical thermal structure over the southern Patagonian shelf in early spring 2005 (A), late summer 2006 (B) and late winter 2006 (C). PD, Puerto Deseado transect at 47°S; GB, Grande Bay transect at 51°S; MAG, Magellan Strait transect at 55°S. Vertical bars represent the distribution of the three water mass types in the water column. MSW = Magellan Strait Water; SASW = Subantarctic Shelf Water; and SAW = Subantarctic Shelf Water.

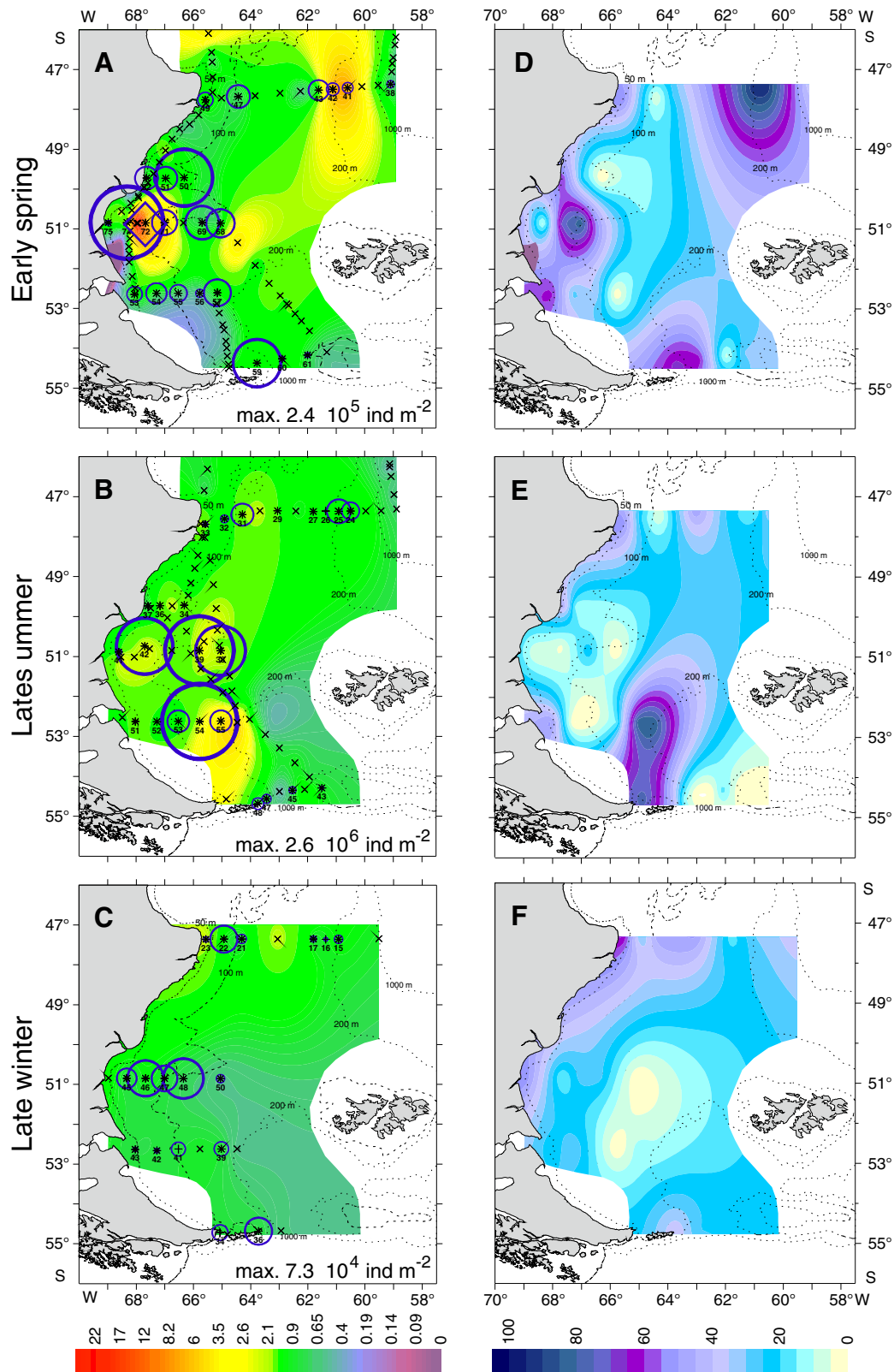
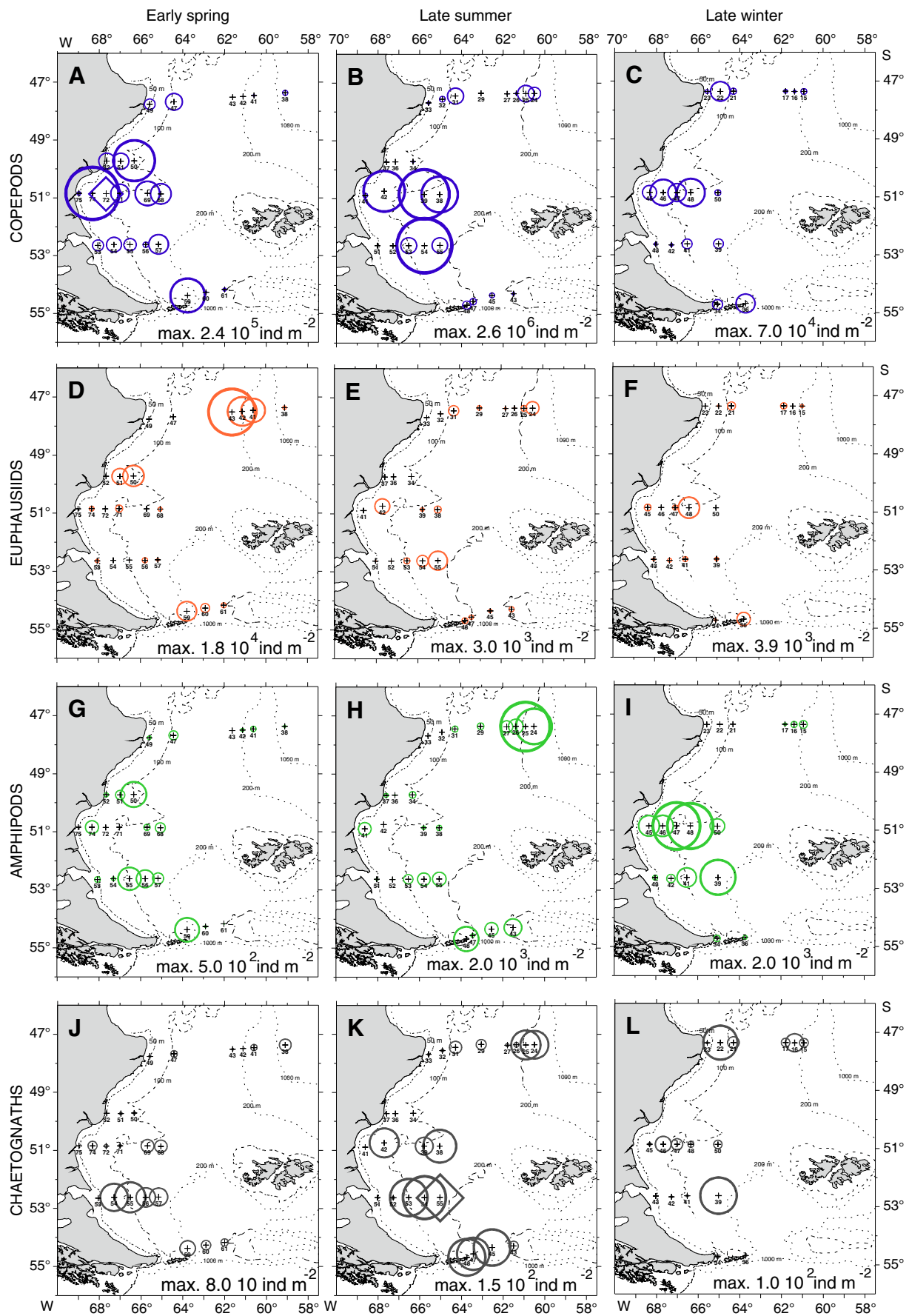


Fig. 4. Seasonal patterns of (standardized) total mesozooplankton abundance (STD_z in m^{-2}) overlapped on surface concentration of chlorophyll *a* (total, $mg\ m^{-3}$ and $>5\ \mu m$ size-fraction, %) over the study area. Early spring, GEF 01 (A, D), late summer, GEF 02 (B, E) and late winter, GEF 03 (C, F). Note the different orders of magnitude recorded during summer in particular (4B). In 4A, the diamond symbol denotes the relatively huge abundance recorded at St 72 (ca. 900,000 $ind\ m^{-2}$; out of the scale illustrated with open circles, max. 240,000 $ind\ m^{-2}$).

typical species proper of each water mass as well as those ones accounting for major differences among mesozooplankton assemblages across seasons. Typical species, i.e., those that occurred at a consistent abundance

at most locations within a water mass, were recognized from relatively larger ratios between the species' contribution to the average similarity within a group (SIM) and the standard deviation (SD) of their



contribution (SIM/SD). Those species primarily responsible for the discrimination among water masses assemblages were identified from the average dissimilarity and standard deviation ratios (DISS/SD) (Clarke and Gorley, 2001).

3. Results

3.1. Seasonal thermal structure and water masses

The heat content in water masses was closely related to the typical mid-latitude alternation of seasons, showing a large thermal amplitude from the highest temperatures in late summer (heat gain) to the lowest ones in winter (heat loss). The area was sampled at the onset of stratification during the first cruise conducted in early spring (GEF01), as denoted by low surface mean temperature (6–7 °C) and weak, not yet well established thermoclines (Fig. 3A). The heat gain in the surface layer during summer creates strong thermoclines over the northern portion of the study area, while southward of ca. 51°S the intense tidal mixing and advection prevent stratification. Thus, at the end of summer when the second cruise was carried out (GEF 02), vertical gradients were maximal at the northernmost transect (PD, ca. 13 °C surface, 7 °C bottom) and decreased with increasing latitude (GB, ca. 10 °C surface, 8 °C bottom) until complete disappearance at the southernmost portion of the surveyed area (MAG) (Fig. 3B). Because the heat that is lost during winter has not been recovered yet by early spring, the sea surface temperature and vertical structure during the late winter cruise (GEF03) proved to be rather similar to conditions found at the beginning of spring 2005 (GEF01), except for the influence of a colder water tongue from the Magellan Strait flowing northwards along the coast up to about 51°S and the spreading of the Malvinas Current onto the shelf at the outermost stations along the PD transect (Fig. 3C). Otherwise, sea surface temperature during both cruises showed a smooth latitudinal gradient from ca. 7 °C in the northern area to ca. 6 °C to the south.

The distribution of TS properties over the study area across all the sampling periods demonstrates clearly that salinity is conservative, while temperature is seasonally variable (Fig. 2). This is the reason for the classification of water masses on the basis of their distinct salinities in this region of the SW Atlantic. The same typical water masses were indeed present off southern Patagonia during the three surveys: the MSW was situated nearshore, the SASW in the middle-shelf, and the SAW influenced the deep stations far offshore (Fig. 3). Due to the absence of a strong saline stratification in the water column, the three water masses typically show a large vertical expansion, and two of them may overlay one on top another at some locations offshore (Fig. 3A–C, PD section). The meridional and vertical extent of water masses over the study area was best represented along the PD transect, which prolonged along >500 km from shore to the slope. A relatively larger expansion offshore of the SASW was evident during late summer (GEF 02), when it occupied the upper layers of the water column in areas located far from shore along the PD transect, and showed also a large spatial development offshore the MAG transect (Fig. 3B, PD and MAG sections). In particular, inclined vertical isotherms at St 54 on this transect show an upwelling of SASW at that point and, as a result, a lens of MSW stayed isolated on top the SASW at the nearby St 55. High Chl *a* values were associated with this mesoscale structure (cf. Fig. 4B). Across all sampling periods, the MSW occurred alongshore extending about 300 km cross-shelf (Fig. 3A, B, C, GB section).

3.2. Spatial and seasonal variation of chlorophyll *a* concentration

Chlorophyll *a* (Chl *a*) concentration at sea surface ranged 0.42–28.6 mg m⁻³ throughout the three sampling periods (Fig. 4A–C), with maximum and minimum values recorded during the early spring and late winter cruises, respectively. While most measurements over the shelf (64%) presented values between ca. 0.8 and 2.0 mg m⁻³, the distribution of surface Chl *a* differed markedly among seasons. In spring and summer, chlorophyll patterns were somehow patchy, and hence indicative of fairly confined algal blooms. In contrast, at the end of winter concentrations were much lower and homogeneously distributed over the shelf (1.0 mg m⁻³ on average). Values were distinctly high in the Grande Bay area, in early spring in particular (28.6 mg m⁻³) but also at the end of summer, though to a much lesser extent (2.4–2.6 mg m⁻³). In spring, two other high Chl *a* patches were located offshore southeast Grande Bay (4.6 mg m⁻³) and at ca. 47°S on the shelf-break (7.7 mg m⁻³), while at the end of summer relatively higher values were recorded only in the area offshore and southwards the Magellan Strait near the slope (4.2 mg m⁻³).

In spring, the contribution of the >5 µm size fraction to total Chl *a* (Fig. 4D) was high particularly near the shelf-break at 47°S, with values between ca. 2–8 mg m⁻³ representing 74–95% of total concentration, and over the mid-outer area of Grande Bay (73–85%). The occurrence of large-sized phytoplankton was less important over almost the entire shelf at the end of summer, except for the spot of maximum Chl *a* where the contribution of the >5 µm size fraction was 78–84% (Fig. 4E). In late winter the contribution of this fraction was consistently low (on average 30%) over the whole area (Fig. 4F).

3.3. Mesozooplankton abundance and composition

Total mesozooplankton abundance (STD_z ind m⁻²) in the southern Patagonian shelf peaked at the end of summer, attained its minimum in winter and showed intermediate values in early spring (Fig. 4A–C). Abundances increased about 2.5-fold from the beginning of spring (max 9.0 10⁵ ind m⁻²) to late summer (max 2.6 10⁶ ind m⁻²), and then decreased at least two orders of magnitude in winter (max 7.3 10⁴ ind m⁻²). Although seasonal differences in abundance were striking, the spatial distribution of mesozooplankton maintained fairly similar patterns, with relatively higher concentrations occurring mainly in Grande Bay and surroundings, and decreasing either northwards or southwards of the study area.

All through the three seasons copepods represented >70–80% of total mesozooplankton over most of the shelf. Therefore, their numbers ruled overall the abundance patterns of the whole community (Fig. 5A–C). The relative contribution of non-copepod taxa to total abundance was on average seasonally steady: euphausiids, 30–50%; amphipods, 20–35%; chaetognaths, 5–10%; others, 15–25%. The distribution of these groups was seasonally and spatially variable. Euphausiids varied both across and along shelf, with the highest values recorded in spring at the northernmost stations near the shelf-break, while their abundance was much lower in summer and at the end of winter over most of the shelf (Fig. 5D–F). Amphipods were widely distributed in shelf and slope waters at variable concentration; minimum numbers were recorded in early spring and maximum ones in late winter, for the most part concentrated in the mid-outer area of Grande Bay (Fig. 5G–I). Chaetognaths occurred overall more abundantly southwards in the surveyed area, with

Fig. 5. Seasonal (standardized) abundance of mesozooplankton major groups (STD_z ind m⁻²). Copepods (A–C), euphausiids (D–F), amphipods (G–I), chaetognaths (J–L). Left vertical panels: early spring, GEF 01; middle vertical panels: late summer, GEF 02; right vertical panels: late winter, GEF 03. Note the different orders of magnitude among groups and across seasons. In 5A, the diamond symbol denotes the relatively much larger copepod abundance recorded at St 72 (900,000 ind m⁻²; out of the scale illustrated with open circles, max. 240,000 ind m⁻²). In 5 K, the diamond symbol refers to the relatively bulky chaetognath population recorded at St 55 (ca. 1000 ind m⁻²; out of the scale illustrated with open circles, max. 150 ind m⁻²).

lowest abundances found in early spring and a less frequent presence in winter; in contrast, values were consistently high at the end of summer, nearby the Magellan Strait and Burdwood Bank in particular (Fig. 5J–L).

The amphipod *Themisto gaudichaudii* – almost entirely represented by juveniles, was the most important species among non-copepod taxa, showing on average a seasonally variable abundance but similarly high relative occurrence through all seasons. Euphausiid eggs and juveniles were the next important (except for eggs being absent in summer), with adults best represented by *Euphausia lucens*, particularly in late summer. Adults of *Euphausia vallentini* and *Thysanoessa* sp. were less significant and seasonally variable. Chaetognath *Sagitta tasmanica* was also important, its presence increasing from spring to winter. *Sagitta gazellae* and *Eukrohnia hamata* were less frequently present (or even absent in winter) and occurred in much lower relative numbers. Lastly, ostracods and salps (*Iasis zonaria* blastozooids) showed a relative lower presence and abundance than the other groups during the three sampling periods, being salps absent in summer (Fig. 6A–C).

3.4. Species-specific copepod patterns

Copepod species best represented through all seasons, in terms of both relative abundance and occurrence, were *D. forcipatus* and *O. helgolandica* (on average 70% and 50% importance, respectively) (Fig. 7A–C). While the former showed a similarly high occurrence but decreasing abundance from spring to winter, the relative presence and numbers of *O. helgolandica* and *Oithona atlantica* increased. *Ctenocalanus vanus*, *Clausocalanus brevipipes* and *Clausocalanus laticeps* and large calanids such as *Calanus australis*, *Calanus simillimus* and *Neocalanus tonsus* were all relatively much less frequent and abundant. The importance of the two former copepods was similar during the three sampling periods, while that of *C. laticeps* decreased with the progress of seasons. The relative importance of *C. australis* and *C. simillimus* increased from spring to summer but decreased to about half at the end of winter. In the latter season *N. tonsus* occurred only occasionally and *O. helgolandica* became on average equally important to *D. forcipatus* (65% importance both) even when the former was surely undersampled by the 200 μ m net (cf. Antaceli et al., 2010). Non-classified Clausocalanidae (*Ctenocalanus* + *Clausocalanus*) and early Calanidae copepodids were relatively more important at the beginning of spring. Much less abundant and occasionally collected species were: *Acartia tonsa*, *Centropages brachiatus*, *Metridia lucens*, *Rhincalanus nasutus*, *Subeucalanus longiceps* and *Calanoides* cf. *patagoniensis* (on average $\leq 5\%$ importance).

D. forcipatus was absolutely dominant whenever present and drove abundance patterns of the whole community over most of the southern Patagonian shelf (Fig. 8A, C, E). This species accounted on average for 98%, 94% and 70% of total copepod abundance in early spring, summer and late winter, respectively. Across all seasons it was most abundantly distributed in the Grande Bay area, attaining maximum numbers in summer ($2.5 \cdot 10^6$ ind m^{-2}); another intense peak was recorded off MAG also in summer. All other species were at least one order of magnitude less abundant than *D. forcipatus* in every season (Fig. 8B, D, F). Of these, *C. vanus* and *C. brevipipes* were secondarily abundant in spring and summer respectively occurring mainly offshore, while *O. helgolandica* was at the end of winter spreading all over the shelf. Among large calanids, *C. australis* was significant in the inner Grande Bay during spring and summer, while *C. simillimus* distributed at offshore sites of the PD, GB and BUR transects mainly during summer. Also in relatively scant quantities, *N. tonsus* C5 was recorded in spring and summer only at the outermost stations along all transects, with maximum numbers found at the end of summer; adult females were collected only twice in late spring (PD–St 38; BUR–St 61) and males were not found.

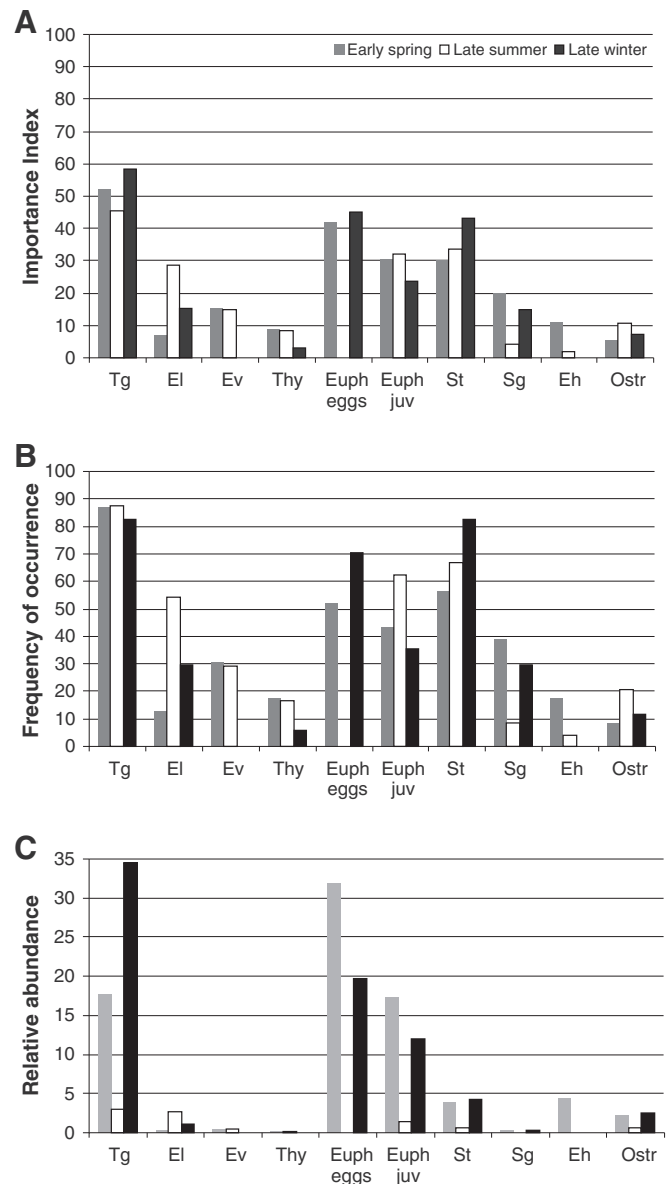


Fig. 6. Seasonal variation in the importance values (A), occurrence frequency (B) and relative abundance (C) of non-copepod taxa. Species/group codes: Tg *Themisto gaudichaudii*, El *Euphausia lucens*, Ev *Euphausia vallentini*, Thy *Thysanoessa* sp., St *Sagitta tasmanica*, Sg *Sagitta gazellae*, Eh *Eukrohnia hamata*, Ostr ostracods.

3.5. Seasonal development of dominant copepod populations

Further general traits in the seasonality of most important copepod species may be inferred from their developmental stage distributions (Fig. 9). Despite its importance through all seasons, the age structure of *O. helgolandica* was not examined because all stages are severely under-represented in plankton collections from 200 μ m nets as we used here (Gallienne and Robins, 2001; Antaceli et al., 2010); individuals were thus not staged but quantified collectively.

In early spring the *D. forcipatus* population was overall dominated by late copepodids C4 and C5 and adult females (on average 41% and 34% respectively). Rather, a different age structure characterized the sites in GB where this copepod was most abundantly distributed. The high numbers recorded and the presence of a significant proportion of adult males (10%) along with some young copepodids C1–3 would suggest that *D. forcipatus* was actively reproducing in that area (Fig. 9A). In turn, by late summer its population was mostly composed of lipid-storing copepodids C4–5 (on average 52% over the

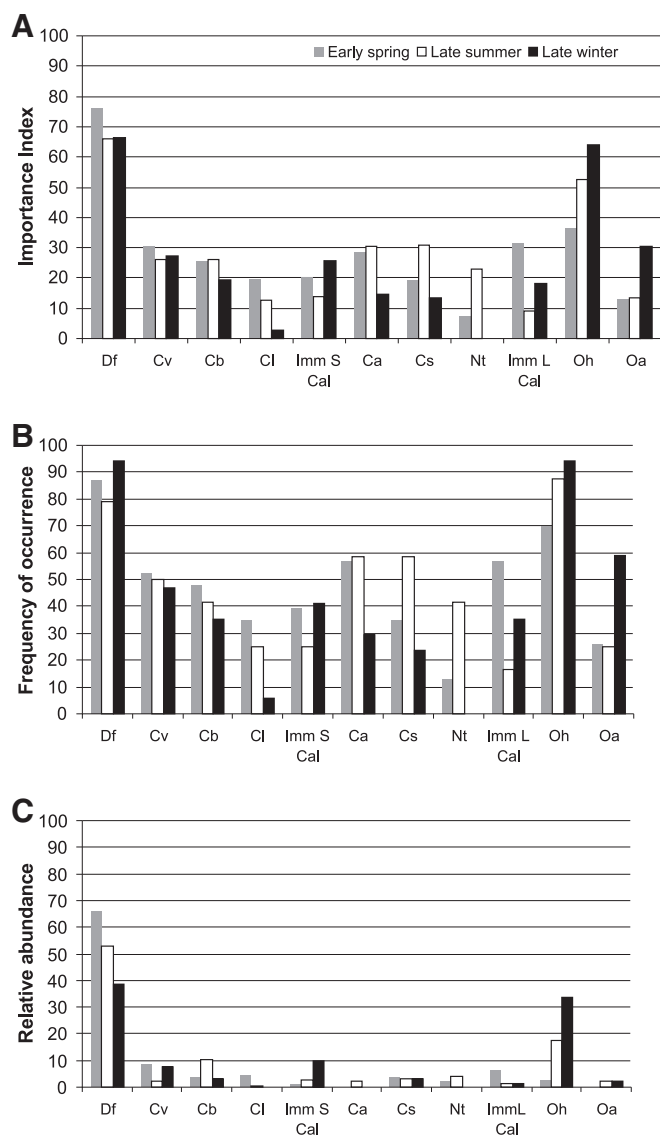


Fig. 7. Seasonal variation in the importance values (A), occurrence frequency (B) and relative abundance (C) of only most important copepod species. Species/group codes: Df *Drepanopus forcipatus*, Cv *Ctenocalanus vanus*, Cb *Clausocalanus brevipes*, Cl *Clausocalanus laticeps*, Ca *Calanus australis*, Cs *C. simillimus*, Nt *Neocalanus tonsus*, Oh *Oithona helgolandica*, Oa *Oithona atlantica*, Imm S Cal and Imm L Cal include pooled non classified Clausocalanidae (*Ctenocalanus* + *Clausocalanus*) and Calanidae early copepodids, respectively.

entire region but up to 95–98% at locations with the highest concentrations, i.e., GB and off MAG), a few early copepodids and almost no adults (Fig. 9B). Although at the end of winter the *D. forcipatus* concentrations were the lowest, the occurrence of relatively large numbers, mainly of adults and copepodids C1–3, in GB and coastal waters to the north would suggest that this species was slowly beginning to reproduce thereby while no activity was still apparent southwards (Fig. 9C).

Being a species proper of the mid-outer shelf, *C. brevipes* occurred more abundantly at the outer stations of most transects and to the south of the study area. Thus, it showed a different spatial pattern than *D. forcipatus* but similar seasonal reproductive traits, as surmised from a comparable progress in the age structure of its population with time, i.e., reproducing at the end of winter and early spring followed by the rise of a large population but declining reproductive activity in late summer (Fig. 9D–F).

C. vanus was overall similarly distributed to *C. brevipes* and its abundance was also comparable in spring and winter but about one order of magnitude lower in summer. The seasonal development of its

population age structure, and eventually its major reproductive events, were somehow parallel to both *C. brevipes* and *D. forcipatus* (Fig. 9G–I). Unlike the latter species, the presence of younger copepodids C1–3 of the two former was significant only southwards and mainly at the end of summer and late winter (Fig. 9P–R).

Active reproduction of the large calanoid *C. australis*, mainly in Grande Bay and northern coastal waters during early spring and late summer respectively, is suggested by the significant occurrence of early copepodids, high numbers of adult females and a few males (Fig. 9J, K, P). At the end of summer, on the opposite, the presence of a likely aging, not-reproducing population of *C. australis* in Grande Bay and southwards would be apparent from the occurrence of many C5 carrying well-developed oil sacs and adult females (together summing up on average >90%), as well as the complete absence of young stages. Maximum concentrations were recorded in inner waters of Grande Bay during this season. At the end of winter *C. australis* was probably starting slowly to reproduce in that same area, as suggested by its lowest seasonal population numbers but dominated by young copepodids C3–4 (on average 65%) (Fig. 9L, R).

Unlike its above congener, *C. simillimus* was distributed over the outer shelf being most abundant at the outermost stations of the PD transect and to the south of the study area (BUR mainly). Maximum numbers were recorded in late summer and minimum in late winter, when this copepod was hardly present southwards (BUR) but occurred noticeably at outer stations northwards (PD). *C. simillimus* would start reproducing at the beginning of spring and it would continue until the end of summer mainly in the MAG and BUR area, as suggested by the age structure of its population (Fig. 9M, P, Q).

3.6. Mesozooplankton communities and water masses

The MDS ordination based on Bray–Curtis similarity matrices of seasonal abundance of mesozooplankton taxa yielded a satisfactory allocation of sampling stations (stress = 0.12–0.14) which was in close correspondence with the geographical distribution of water masses over the southern Patagonian shelf (Fig. 10).

Community differences among water masses (a priori groupings) maintained throughout the three sampling periods and changed significantly but little from season to season (ANOSIM, Table 2). The structure of the SAW and MSW zooplankton communities overlapped to some extent but was clearly different ($R = 0.69$, $p < 0.01$), while those proper of the SASW and MSW masses were barely separable ($R = 0.37$, $p < 0.01$) and differences were not significant between the SAW and SASW assemblages.

In particular, St 41 in early spring (Fig. 10A, PD transect) and Sts 24 and 25 in late summer (Fig. 10B, PD transect) were allocated a priori to the vertically prevailing SAW water mass, although the upper layers down to ca. 30–60 m were occupied by SASW (cf. Fig. 3A, B). Thus, it is unsurprising that the mesozooplankton community structure at these stations turned out to be closer to those that were occupied only by SAW (Fig. 10A, B, MDS ordinations). Similarly, St 55 in late summer was hydrologically assigned to the dominant SASW, although a lens of MSW was present in the upper layer (cf. Fig. 3B, MAG transect). This is in good agreement with the resulting placement of St 55 in the MDS ordination, which was closely related to the MSW assemblage (Fig. 10B).

With varying occurrence and abundance throughout seasons, typical species of the MSW were adults and late copepodids of *D. forcipatus*, copepodids C5 and adult females of *C. australis* and the amphipod *T. gaudichaudii*. The SASW was characterized by copepodids C4–5 of *D. forcipatus*, females and late copepodids of *C. brevipes*, *C. vanus* and *C. simillimus*, the cyclopoids *O. helgolandica* and *O. atlantica*, *T. gaudichaudii*, the chaetognath *S. tasmanica* and euphausiid juveniles. Most of the latter species were also typical of the SAW assemblage, and in consequence these two water masses were not significantly different. Actually, differences in population development and abundance

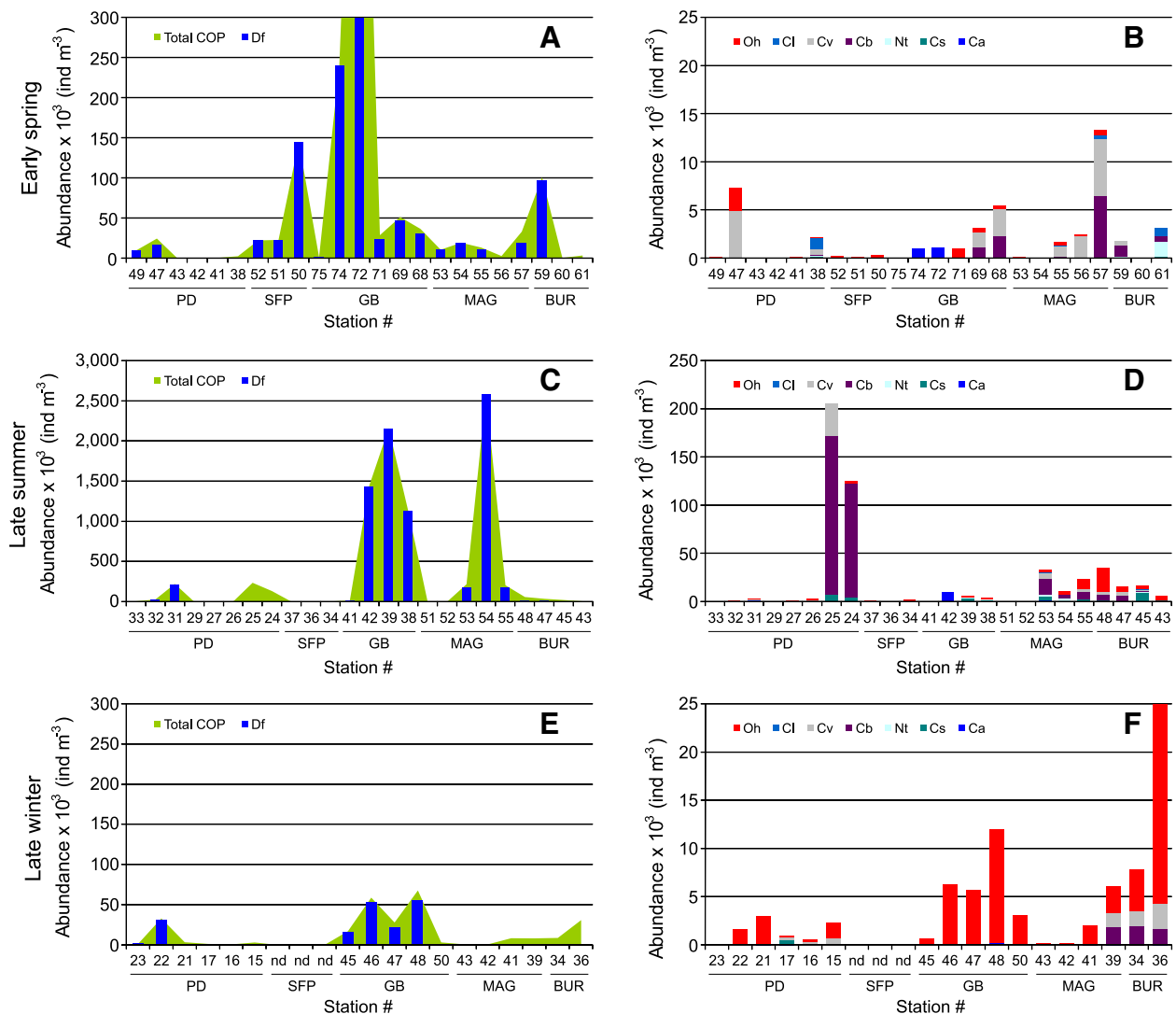


Fig. 8. Seasonal variation of copepod species composition and abundance off southern Patagonia. Early spring, GEF 01 (A–B), late summer, GEF 02 (C–D) and late winter, GEF 03 (E–F). Species codes: Df *Drepanopus forcipatus*, Ca *Calanus australis*, Cs *Calanus simillimus*, Nt *Neocalanus tonsus*, Cb *Clausocalanus brevipes*, Cv *Ctenocalanus vanus*, Cl *Clausocalanus laticeps*, Oh *Oithona helgolandica*. In 8A, values at St 72 are out of scale: max copepods (COP), 884×10^3 ind m^{-3} and *D. forcipatus* (Df), 883×10^3 ind m^{-3} . Note the different orders of magnitude recorded during summer in particular.

of typical species were more important than species composition in defining the assemblages (Table 3).

Some of the species/taxa mentioned above plus a few others listed in Table 4 occurred in consistently distinct abundances across water masses, and thus they were as well good discriminating species between zooplankton assemblages. Discriminating species among water masses varied overall throughout seasons. *D. forcipatus*, *C. simillimus*, *Subeucalanus longiceps* and *S. gazellae* accounted for differences in early spring, while *C. brevipes*, *C. simillimus* and *T. gaudichaudii* did it in late summer. At the end of winter, late copepodids of *D. forcipatus*, adult females of *C. vanus* and *Oithona* spp. were distinctly represented in the MSW and SASW communities.

4. Discussion

4.1. Seasonality

The results obtained in this study from three cruises conducted in spring and summer 2005 and late winter 2006 over the southern Patagonian shelf indicated an annual development of plankton communities typical of cold temperate regions, with a clear seasonal signal in

mesozooplankton abundance long after the spring phytoplankton bloom. General trends are in agreement with early findings from six regional surveys conducted in the late 1970s, which to date comprised the only available seasonal dataset for the region (Carreto et al., 1981; Ramírez, 1981).

Spring progress of plankton populations is not uniform across the whole Patagonian shelf and at a given time populations in the north are generally in a more advanced state of development than further south (Fig. 11). South of 47°S, satellite images taken in spring through autumn (October 2005 to March 2006) showed two separate extensive phytoplankton blooms occurring in the inner area of Grande Bay and to the north of the Malvinas Islands, the former spreading N–NE in coincidence with the predominant mean flow and the latter propagating downstream the Malvinas Current along the shelf-break, as it has been shown in other satellite studies in the area (Rivas et al., 2006; Romero et al., 2006; Dogliotti et al., 2014). Zooplankton abundance can be similarly enhanced during austral summer, particularly in the Grande Bay area (e.g., Sabatini and Álvarez Colombo, 2001; Sabatini et al., 2004; Sabatini, 2008). Mesozooplankton and in situ Chl *a* data here fit well the overall picture. In early spring and late summer, spots of high zooplankton abundance (either copepods or euphausiids)



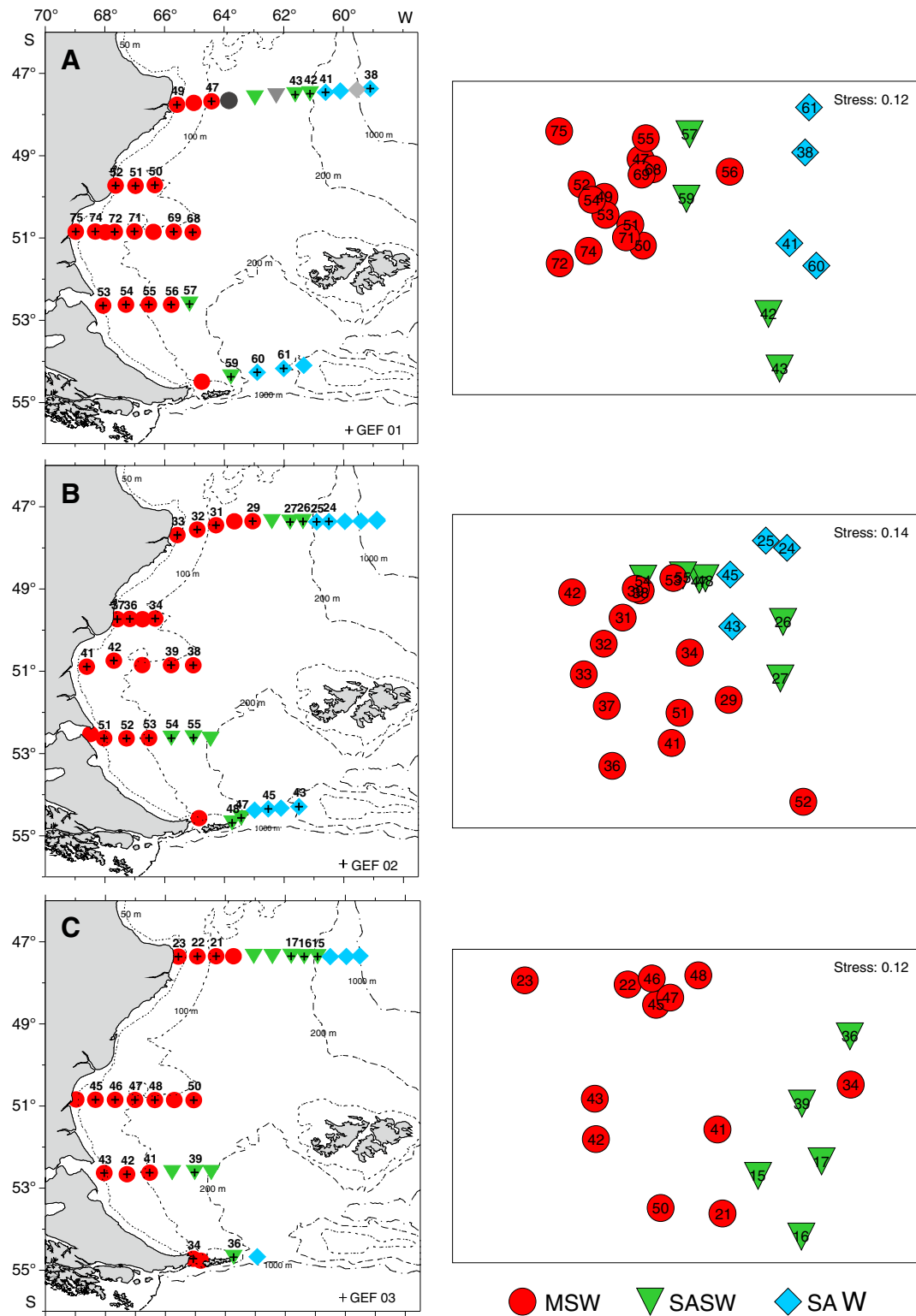


Fig. 10. Location of stations allocated *a priori* to each of the three water masses (MSW, Magellan Strait Water; SASW, Subantarctic Shelf Water; SAW, Subantarctic Water) and MDS ordinations based on Bray–Curtis similarity matrices of depth-integrated mesozooplankton abundances. Same symbols identify sampling sites corresponding to water masses in both the maps and mesozooplankton MDS plots.

were recorded overall in areas of increased Chl *a* concentration, while in winter both Chl *a* and zooplankton were the lowest (Fig. 4). The dinoflagellate *Prorocentrum minimum* and the diatom *Thalassiosira cf. oceanica* were respectively blooming in Grande Bay and offshore Puerto Deseado near the slope, in coincidence with the highest spring Chl *a*

values (Sabatini et al., 2012). In contrast, by the end of summer phytoplankton was dominated by small sized forms – mainly *Synechococcus* spp. and picophytoplankton, and to a lesser extent diatoms (*Fragilariopsis* sp., *Lennoxia* sp.), cryptophytes and *Pyramimonas* sp. (Silva et al., 2015), all of them likely below the optimal size for

Table 2

Seasonal mesozooplankton community structure. Analysis of similarities among waters mass assemblages off southern Patagonian for the three cruises (ANOSIM tests, two-way crossed analysis). SAW = Subantarctic Water; SASW = Subantarctic Shelf Water; and MSW = Magellan Strait Water.

| Differences between water masses (averaged across all seasons)Factor: water masses (Fig. 10)Global R: 0.46; significance level: 0.001 | |
|---|--------|
| Groups | R |
| SAW, SASW | 0.05 |
| SAW, MSW | 0.69** |
| SASW, MSW | 0.37** |
| Differences between seasons (averaged across all water masses)Factor: seasons (Fig. 10)Global R: 0.18; significance level: 0.001 | |
| Groups | R |
| Spring, summer | 0.22** |
| Spring, winter | 0.14* |
| Summer, winter | 0.14* |

* $P \leq 0.05$.

** $P \leq 0.01$.

efficient copepod feeding (ca. 10–14 μm ; e.g., Berggreen et al., 1988). High zooplankton numbers recorded at the end of the austral

summer (March 2006), mainly in Grande Bay, probably reflect seasonal development of copepods as they comprised ca. 80% of total mesozooplankton across all sampling periods. At this time of the year the peak of reproduction of many species is past and their populations achieve maximum abundance (Figs. 8 and 9). Mesozooplankton seemed to respond to the increasing availability of potential autotrophic food starting in early spring (October) in Grande Bay as shown by a coherent spatial pattern of decreasing Chl $a > 5 \mu\text{m}$ in late summer (March), which may be reflecting copepod consumption in the time course of subsequent generations developing with the progress of the productive season (Fig. 4; Fig. 11). In accordance, Antacli et al. (2014b) reported that feeding by females of copepods *D. forcipatus* and *C. australis* in Grande Bay at the beginning of spring 2005 was about 6–8 times greater than during previous summer 2004, when pico- and nanoeukariotes were prevailing. Copepod abundance in summer was also very high to the south of the study area at stations offshore the Magellan Strait. Besides small food particles, potential food of relatively larger size was available there (dinoflagellates *Prorocentrum* sp., *Karenia* sp.), while at inshore stations a *Phaeocystis* bloom was taking place (Akselman, unpublished data). As a result zooplankton was found to be extremely low. This is not an unusual finding. Low or inefficient feeding and/or egg production rates with consequently drastic decreases in copepod abundance is generally documented for *Phaeocystis* spp. (Schoemann et al., 2005 and references

Table 3

Seasonal average depth-integrated abundance (STD_2 and m^{-2}) of most important mesozooplankton contributors to the average similarity within each of the three water-masses occurring over the southern Patagonian shelf. Names and values in bold refer to typical species of each water mass (i.e., those showing relatively larger SIM/SD, not shown) and to their highest average abundances during each sampling period, respectively (SIMPER analysis).

| Species/taxon | Magellan strait water | | | Subantarctic shelf water | | | Subantarctic water | | |
|--|--------------------------------|--------------------------------|--------------------------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|--------------------------|
| | Spring N = 15 Sim = 51.5 | Summer N = 14 Sim = 19.4 | Winter N = 12 Sim = 32.8 | Spring N = 4 Sim = 32.1 | Summer N = 6 Sim = 29.2 | Winter N = 4 Sim = 36.9 | Spring N = 4 Sim = 39.2 | Summer N = 5 Sim = 35.1 | Winter No sampling |
| <i>Drepanopus forcipatus</i> 1–3 | 1038 | 11,932 | 2049 | 0 | 6,699 | 0 | 0 | 0 | |
| <i>Drepanopus forcipatus</i> 4–5 | 48,006 | 345,649 | 3832 | 8695 | 453,379 | 121 | 4 | 79 | |
| <i>Drepanopus forcipatus</i> F | 44,806 | 12,036 | 8760 | 16,728 | 2597 | 115 | 6 | 61 | |
| <i>Drepanopus forcipatus</i> M | 4725 | 151 | 354 | 3559 | 278 | 0 | 0 | 0 | |
| <i>Ctenocalanus vanus</i> 4–5 | 275 | 363 | 47 | 601 | 519 | 227 | 67 | 1394 | |
| <i>Ctenocalanus vanus</i> F | 413 | 198 | 83 | 684 | 944 | 263 | 83 | 7254 | |
| <i>Ctenocalanus vanus</i> M | 161 | 0 | 14 | 273 | 0 | 11 | 2 | 0 | |
| <i>Clausocalanus brevipes</i> 4–5 | 0 | 300 | 124 | 433 | 2117 | 497 | 0 | 31,510 | |
| <i>Clausocalanus brevipes</i> F | 168 | 818 | 25 | 1136 | 1989 | 174 | 33 | 39,551 | |
| <i>Clausocalanus brevipes</i> M | 33 | 18 | 16 | 340 | 100 | 33 | 132 | 37 | |
| <i>Clausocalanus laticeps</i> 4–5 | 0 | 0 | 0 | 0 | 0 | 0 | 294 | 0 | |
| <i>Clausocalanus laticeps</i> F | 8 | 8 | 0 | 104 | 170 | 10 | 223 | 599 | |
| <i>Clausocalanidae</i> n.i. copepodids | 223 | 61 | 556 | 421 | 3100 | 902 | 3 | 1095 | |
| <i>Centropages brachiatus</i> | 0 | 23 | 52 | 0 | 1293 | 13 | 0 | 187 | |
| <i>Calanus australis</i> 5 | 45 | 527 | 12 | 0 | 33 | 3 | 0 | 0 | |
| <i>Calanus australis</i> F | 93 | 330 | 4 | 0 | 97 | 3 | 0 | 0.5 | |
| <i>Calanus australis</i> M | 2 | 3 | 1 | 0 | 8 | 0 | 0 | 0 | |
| <i>Calanus simillimus</i> 5 | 0.6 | 282 | 0 | 29 | 259 | 7 | 5 | 2364 | |
| <i>Calanus simillimus</i> F | 0.2 | 310 | 0 | 9 | 271 | 88 | 28 | 2793 | |
| <i>Calanus simillimus</i> M | 0.1 | 2 | 0 | 4 | 46 | 16 | 43 | 366 | |
| <i>Neocalanus tonsus</i> 5 | 0 | 294 | 0 | 4 | 496 | 3 | 366 | 0 | |
| <i>Neocalanus tonsus</i> F | 0 | 0 | 0 | 0 | 0.5 | 0 | 59 | 0 | |
| <i>Calanidae</i> n.i. copepodids | 556 | 30 | 36 | 54 | 0.6 | 171 | 76 | 152 | |
| <i>Subeucalanus longiceps</i> | 0 | 4 | 0 | 34 | 4 | 0 | 28 | 0 | |
| <i>Metridia lucens</i> | 0 | 131 | 0 | 0 | 73 | 0 | 0 | 7846 | |
| <i>Oithona helgolandica</i> | 346 | 604 | 3186 | 142 | 7379 | 5135 | 20 | 3542 | |
| <i>Oithona atlantica</i> | 11 | 0.7 | 33 | 94 | 87 | 341 | 2 | 459 | |
| <i>Themisto gaudichaudii</i> | 116 | 27 | 424 | 153 | 190 | 233 | 8 | 897 | |
| <i>Sagitta tasmanica</i> | 14 | 0 | 13 | 7 | 216 | 30 | 3 | 0 | |
| <i>Sagitta gazellae</i> | 0.2 | 0.2 | 0.1 | 2 | 2 | 2 | 3 | 13 | |
| Crustacea larvae | 216 | 304 | 323 | 0 | 0 | 338 | 9 | 0 | |
| Euphausiid eggs | 289 | 0 | 411 | 6593 | 0 | 321 | 986 | 0 | |
| Euphausiid larvae | 182 | 16 | 46 | 671 | 87 | 90 | 480 | 466 | |
| <i>Euphausia vallentini</i> | 0.1 | 0 | 0 | 3 | 0 | 0 | 5 | 0 | |
| <i>Euphausia lucens</i> | 0 | 254 | 1 | 0 | 546 | 17 | 0 | 5340 | |
| <i>Thysanoessa</i> spp. | 0 | 7 | 0 | 0 | 5 | 1 | 2 | 18 | |
| Ostracods | 0 | 0 | 0 | 0 | 45 | 15 | 0 | 1481 | |
| <i>Iasis zonaria</i> | 0 | 0 | 5 | 0 | 0 | 3 | 0 | 0 | |

Table 4
Average depth-integrated abundance (STD_z and m^{-2}) of species primarily responsible for the dissimilarity between mesozooplankton assemblages proper of each water-mass across seasons (relatively larger DISS/SD ratios in SIMPER analysis, not shown).

| Species/taxon | Early spring | | Late summer | | Late winter | |
|----------------------------------|----------------------------|---------------------------|----------------------------|---------------------------|----------------------------|------|
| | MSW vs SASW Diss = 69.6 | MSW vs SAW Diss = 81.0 | MSW vs SASW Diss = 80.8 | MSW vs SAW Diss = 90.3 | MSW vs SASW Diss = 73.5 | |
| <i>Drepanopus forcipatus</i> 4–5 | | 48,006 4 | | | 3832 | 121 |
| <i>Drepanopus forcipatus</i> F | | 44,806 6 | | | | |
| <i>Drepanopus forcipatus</i> M | | 4725 0 | | | | |
| <i>Ctenocalanus vanus</i> F | | | | | 83 | 263 |
| <i>Clausocalanus brevipus</i> F | | | 818 1.989 | | | |
| <i>Calanus simillimus</i> 5 | 0.6 29 | | 282 260 | | | |
| <i>Calanus simillimus</i> F | | | | 310 2793 | | |
| <i>Calanidae</i> n.i. copepodids | | | | | 36 | 171 |
| <i>Subeucalanus longiceps</i> | | 0 28 | | | | |
| <i>Oithona helgolandica</i> | | | | | 3186 | 5135 |
| <i>Oithona atlantica</i> | | | | | 33 | 341 |
| <i>Themisto gaudichaudii</i> | | | | 27 897 | | |
| <i>Sagitta gazellae</i> | | 0.2 3 | | | | |

therein). Poor fecundity resulting from a diet on these algae may inhibit the increase of copepod populations during blooms (Turner et al., 2002). Due to the locally restricted but massive occurrence of ctenophores at the end of summer, mesozooplankton was also almost absent in the coastal area to the north of Grande Bay (SFP). By late winter, mesozooplankton numbers were still very low although an incipient recovery of some populations appeared to be proceeding in the Grande Bay area, as shown by the emergence of young developmental stages in a few species, e.g., *D. forcipatus*, *C. australis* (Fig. 9C and 9L), *T. gaudichaudii* (Fig. 5I), and *S. tasmanica* (Sotelo et al., 2011). Concurrent food resources were low and predominantly small sized: mainly *Synechococcus* spp., picophytoeukariotes, small diatoms *Minidiscus* spp. (Silva et al., 2015), and microplanktonic aloricate ciliates (Santoferrara et al., 2011). It is likely that the limited ongoing calanoid activity we recorded in late winter was being fuelled partially by reserves, as we have found recurrently that late lipid-rich copepodids build up most of the population of dominant species during the previous temporal window, i.e., at the end of summer (Fig. 9B and K here; Sabatini, 2008; Antacli et al., 2014b). However, aloricate ciliates and heterotrophic dinoflagellates may also play a role in sustaining copepod populations at the end of the winter (Santoferrara et al., 2011).

Species composition was roughly similar across all sampling periods but the relative abundance and occurrence of species in most cases showed marked seasonal changes mainly related to their life histories (Figs. 6 and 7). In addition to the major anticipated components for the inner and mid shelf, i.e., *D. forcipatus*, *O. helgolandica*, *C. australis* and the amphipod *T. gaudichaudii*, other small clausocalaniids (*C. vanus* and *Clausocalanus* spp.) and epipelagic seasonal migrants such as *C. simillimus*, *N. tonsus*, *S. longiceps* and *M. lucens* were recorded in the outer shelf near the slope, being the latter species strongly related to the overall drift northwards of subantarctic waters (Ramírez, 1981; Ramírez and Sabatini, 2000).

Our findings here for *D. forcipatus* and *C. australis* round out other studies in the region indicating that both copepods were reproducing in early spring during the *Prorocentrum* bloom (Antacli et al., 2014b). Coincidental with their highest seasonal abundance after the population development throughout spring and summer, the two species were, in contrast, hardly reproducing at the end of summer and preparing to overwinter (Sabatini et al., 2000; Sabatini, 2008; Antacli et al., 2014b). Clausocalaniids other than *D. forcipatus* followed the same time course but they prospered and peaked in dissimilar areas suggesting a differentiation in their ecological niches. At the lowest mesozooplankton numbers recorded in late winter, the cyclopoid *O. helgolandica* was either

equally or relatively much more important than any co-occurring calanoid (Figs. 7 and 8F), probably because of inadequate food conditions for the latter. Closely related species to the ones present in the southern Patagonian shelf are known to be either cruising (*Clausocalanus furcatus*) or feeding-current feeders (*Pseudocalanus* sp., *Calanus helgolandicus*) that detect non-motile prey by near-field mechanoreception (Gonçalves and Kiørboe, 2015). It is likely that *D. forcipatus* is a current-feeding feeder, similarly to their northern vicariant *Pseudocalanus* spp. In contrast, *Oithona* species are characterized as ambush feeders (Kiørboe and Visser, 1999) that feed on relatively large motile prey, which they perceive hydromechanically (Svensen and Kiørboe, 2000; Saiz et al., 2014). Besides, they seem to satiate at low food concentrations (Lampitt and Gamble, 1982). The current-feeding mode is suitable for relatively abundant prey of small size and limited motility (Tiselius et al., 2013) such as those we found in spring and summer, when *D. forcipatus* was absolutely dominant over most of the study area (Fig. 8). On the contrary, *Oithona* feeding strategy may imply an advantage over *Drepanopus* and other calanoids during poor food conditions in late winter. Otherwise, *D. forcipatus* stays as the most abundant key copepod over the southern Patagonian shelf, even if sampling is conducted with a fine-mesh (66 μm) net (Antacli et al., 2014a). Its particularly great abundance in the study area is only comparable to records in the Georgias del Sur (South Georgia) shelf ecosystem, where it also displays a patchy distribution (e.g., Ward, 1989; Ward and Shreeve, 1999; Atkinson et al., 2001). As in some other copepod species, aggregating in swarms may offer proximity to mates, reduction of predation and maintenance of position in a favorable habitat (Ambler, 2002).

Life cycles of the above mentioned seasonally migrating species are largely unknown in the study area. Yet, they are well documented for other subantarctic ecosystems and usually involve reproduction and feeding of early juveniles in summer and less active, lipid storing older stages, with arrested or reduced activity in winter, often at depth (Atkinson et al., 2012 and references therein). Accordingly, late copepodids and adult females of *C. simillimus* were found in significant densities only at the end of summer mainly over the outer shelf near the slope, which is highly influenced by the spreading of the neighboring Malvinas Current. *N. tonsus* in particular is an ontogenetically vertical migrant that spawns in deep water at the end of winter, the nauplii molt while making their way up to surface waters, developing into advanced copepodids. They feed in the upper layer during spring and summer and at the end of summer the copepodids descend to deep waters, where they enter a resting stage. At the end of winter they emerge as adults, ready to breed

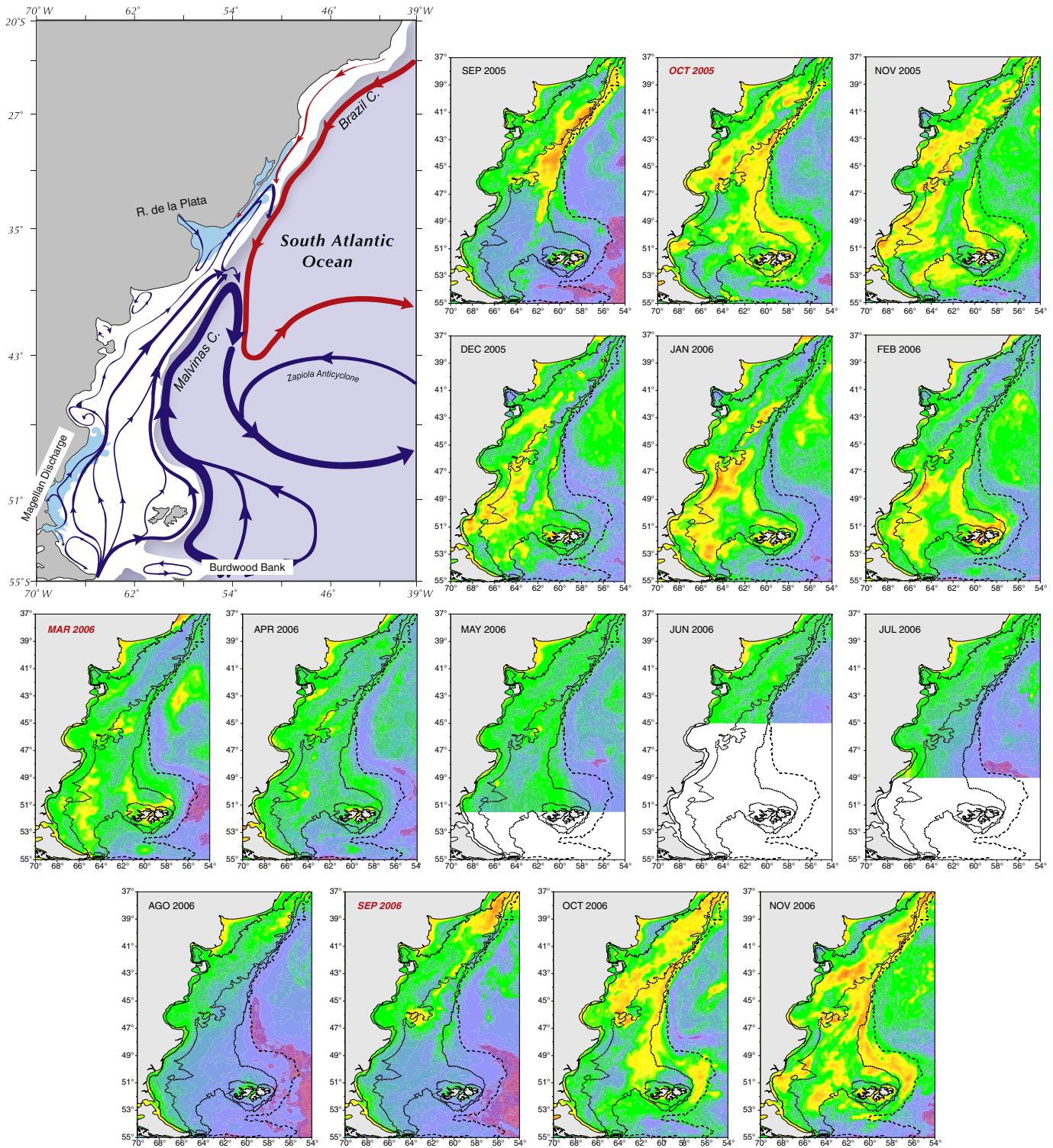


Fig. 11. General overview of the physics in the southwestern Atlantic region and time course of satellite ocean color images during the sampling period. The upper left inset is a schematic figure of the depth-averaged circulation in the region (modified after [Matano et al., 2010](#)). Monthly composites of climatological chlorophyll-*a* concentration (mg m^{-3}) were mapped from averaged MODIS data, 4 km resolution, for the September 2005–November 2006 period. Satellite ocean color data were obtained from <http://oceancolor.gsfc.nasa.gov/cgi/L3>. Months of cruises when mesozooplankton sampling for this study was accomplished are in italics.

(Bradford-Grieve, 2001). Consequently, we found its copepodids C5 in spring and summer only at the outermost stations along all transects. Since only the upper water column was sampled at deep locations offshore, depending on the season, a proportion of the population of seasonally migrant species may have been overwintering below the level sampled by the net.

The different population structures we found in most copepod species at northerly and southerly stations are likely highlighting the importance of temperature besides food, which, despite seasonal warming/cooling, displays a clear latitudinal gradient over the southern Patagonian shelf (Fig. 2). The effect of low temperatures on development and growth rates may cause differences in the

phenology of dominant species (Mackas et al., 2012; Ward and Atkisson, 2012).

The seasonal amphipod pattern here was not the one we expected from previous surveys, i.e., mostly large sized *T. gaudichaudii* peaking in late summer in the Grande Bay area and adjacent waters (Sabatini and Álvarez Colombo, 2001; Padovani et al., 2015). Rather, we recorded the highest numbers in the same area but in late winter, being almost exclusively a population comprised of small juveniles. Differences are likely the result of using here a low speed sampler 200 μm mesh size, while sampling in the above mentioned studies was carried out with a fast towing Nackthai sampler (Nellen and Hempel, 1969) with 390 or 500 μm nets, which is suitable for collecting larger, fast swimming individuals.

The chaetognath *S. tasmanica* probably reproduces continuously in the study area as indicated by the presence of juveniles across the three sampling periods. This species peaked at the end of summer coinciding with a high (copepod) prey availability while in late winter mature individuals were few. Numbers of *E. hamata* and *S. gazellae* were much lower and mature animals were not recorded suggesting that they reproduce out of the surveyed area (Sotelo et al., 2011).

4.2. Spatial distribution and water masses

In confirmation of previous findings in early spring, we found that water masses over the southern Patagonian shelf encompass distinctive mesozooplankton assemblages that extend across seasons (Fig. 10). In this system, most of the shelf is dominated by a distinct low salinity surface plume ($S < 33.4$) that is associated with the discharges from the Magellan Strait (MSW) while the outer shelf is highly influenced by the cold and saline ($S > 34$) Subantarctic water (SAW) of the boundary Malvinas Current (Bianchi et al., 1982; Palma et al., 2008). Correspondingly, the MSW and SAW mesozooplankton communities were found to be clearly different, while boundaries between the former and the SASW assemblage appeared less definite. This middle shelf water mass is a relatively fresh (S 33.4–34) variant of Subantarctic water that is injected into the region through the Le Maire Strait, the Cape Horn and the shelf break (Palma et al., 2008). As the SASW and SAW masses are so closely related in origin, it is not unexpected that the differences between their associated communities were not statistically significant (Table 2). The dissimilarity among water mass assemblages actually increased with increasing cross-shelf geographical distance (Table 4).

Numerical simulations indicate that the Magellan discharge affects the overall shelf circulation in southern Patagonia (Palma et al., 2008; Palma and Matano, 2012) (Fig. 11). The limits of the Magellan plume (MP) extend both downstream and upstream of the Magellan Strait, the cross-shelf width is larger at Grande Bay and shrinks approaching 47°S. The plume generates a region of weak currents in the inner shelf to the north of the strait and a southward recirculation gyre with increased coastal currents. In the middle shelf there is a northward flow current of intermediate speed ($> 1.5 \text{ cm s}^{-1}$), which intensifies over the outer shelf because of the spreading of the neighboring Malvinas Current. The influence of the Malvinas Current and strong tidal forcing on the local frontal dynamics produces additionally a cross-shelf circulation pattern characterized by onshore intrusions, downwelling and subsequent upwelling of dense and nutrient-rich Subantarctic waters. These effects seem to strengthen in the Grande Bay area and are likely introducing further nutrients into the region (Sánchez et al., 1995; Sabatini et al., 2004; Matano et al., 2010). Therefore, in the broad area influenced by the MP, where low current flows dominate ($< 0.5 \text{ cm s}^{-1}$), the extensive MSW community was present, with abundances that were markedly higher than in the other two water masses, particularly in spring to summer. It seems likely that a significant proportion of production can be retained over the inner shelf, particularly in the Grande Bay area and northwards, at temporal scales that allow for the in situ development of primary and secondary producers.

The differences between the MSW and SASW mesozooplankton assemblages were related to changes in the dominance of a few shared species, rather than to a distinct taxonomic composition, although average abundances of shared taxa were often considerably lower in the latter (Table 3). Reasons for this may be related to the increasing current speeds beyond the 100 m isobath (Palma and Matano, 2012), where advection may play a dominant role. The middle shelf SASW community that juxtaposes approximately the Magellan salinity front may be characterized as an ecotone-type assemblage, i.e., to some extent related to the MSW community but with a strong contribution of species proper of the SAW (Table 4). Because of the wide extension of the continental shelf off Southern Patagonian, the latter community was much less represented in the surveyed area, occurring only near the shelf-break either at the northern- or southernmost transects (Fig. 10).

As we found here, mesozooplankton distribution boundaries and water masses are regularly at the same time consistent with regions of semi-closed circulation, or at least intermittent return flows, that allow species to persist within a suitable habitat (Ward et al., 2003, 2007; Miller and Wheeler, 2012; Pepin et al., 2015). Hence, the relationship with the notion of niche adaptation (Hutchinson, 1959) is straightforward. Water masses defined by TS diagrams and the associated circulation patterns create a combination of physical and biological conditions adequate for individuals of each species to tolerate the physical environment, obtain energy and nutrients, and avoid predators. The whole set of requirements of species determine where they can live and how abundant they can be at any place. Therefore, their adaptation to the entire range of the fairly stable conditions of a water mass certainly represents an evolutionary advantage (Miller and Wheeler, 2012).

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