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Effects of the physical properties of water masses on microbial activity during an Ice Shelf Water overflow in the central Ross Sea

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Abstract: During the 1997–98 Italian Expedition to Antarctica a five-day mesoscale experiment was carried out on the continental shelf-break in the central Ross Sea. This area is oceanographically characterized by shelf/slope interactions, through intense mixing processes, between the Circumpolar Deep Water (CDW) and the Ice Shelf Water (ISW), coming from beneath the Ross Ice Shelf and spilling over the shelf edge. The export of dense shelf waters is of crucial importance not only for the mass balance of the basin, but also for carbon export from the upper layers into the abyssal ones. The study investigated how the ISW interactions with the CDW may influence bacterial metabolism during an ISW downslope event. In particular, what effect does this have on the bacterial activities related to the utilization and transformation of the organic carbon substrate (ectoenzymatic activities, carbon production, growth rate) within the ISW and the CDW cores? Our data show that in the CDW the metabolic response was to increase the biomass and enzymes were less active due to a higher nutritional value for the substrate. In the ISW the bacterial metabolic activity shifted towards degradative processes. These results suggest differences in the quality of the organic carbon pool with a greater concentration of labile organic matter in the CDW and of low-degradable compounds in the ISW. The use of microbial parameters seems to be very promising in the evaluation of the carbon export during mixing processes, when the refractory fraction of the organic carbon pool might play a key role.

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Introduction

The processes of dense water formation at high latitudes drive the global deep circulation (Gordon 1986). The Weddell Sea dense waters make the largest contribution to the production of Antarctic Bottom Waters (AABWs) (Gill 1973, Foster & Carmack 1976, Foster *et al.* 1987), but the Ross Sea seems to play a crucial role in the ventilation of the Pacific Ocean (Jacobs *et al.* 1970, Locarnini 1994).

Two shelf waters can be found in the Ross Sea: the Ice Shelf Water (ISW) and the High Salinity Shelf Water (HSSW). Changes in the hydrological properties of the shelf waters could strongly influence the rates of formation and characteristics of the AABWs, originating from the mixing between the Circumpolar Deep Water (CDW) coming from the open Ross Sea and the waters at the shelf-break (Locarnini 1994).

The ISW, characterized by temperatures lower than the surface freezing point, has two cores, the Shallow ISW (SISW) and the Deep ISW (DISW), located at different depths inside the water column due to their different density (Jacobs *et al.* 1979, 1985). Once formed beneath the Ross Ice Shelf (RIS), the ISW flows northward as a super-cold water tongue and migrates to the shelf-break, descending as a shelf-break gravity current, aided by friction and any topographical channelling counteracting the geostrophic tendency for along-slope flow (Whitehead 1987, Huthnance 1995, Shapiro & Hill 1997). The ISW outflow is an impulsive phenomenon (Bergamasco *et al.* 2002a) and on the continental slope this dense water mixes with the ambient water masses, in particular with the CDW core (Locarnini 1994), contributing to the AABWs formation.

The down-slope processes are important for ocean-shelf exchange of physical and biological properties, in particular for the export of carbon and suspended material from continental shelves to the deep ocean (Huthnance 1995).

The assessment of hydrolytic activity of microbial enzymes is a useful approach to describe the main patterns and rates of organic matter exploitation (Christian & Karl 1995). Heterotrophic microbes use extracellular enzymes deployed on cell surfaces to obtain nutrients from the pool of organic matter. It can be hypothesized that bacteria activate these enzymes because molecules greater than 600 Da (Weiss *et al.* 1991) are too large to pass through the outer membrane and therefore they must be enzymatically hydrolyzed outside the cell. Their action mediates the generation of small assimilatable products, which can drive microbial growth and therefore are directly related to bacterial productivity and biomass. In the Ross Sea, it has recently been shown that bacterial production is controlled by carbon availability (Carlson *et al.* 1998, 2000) and below

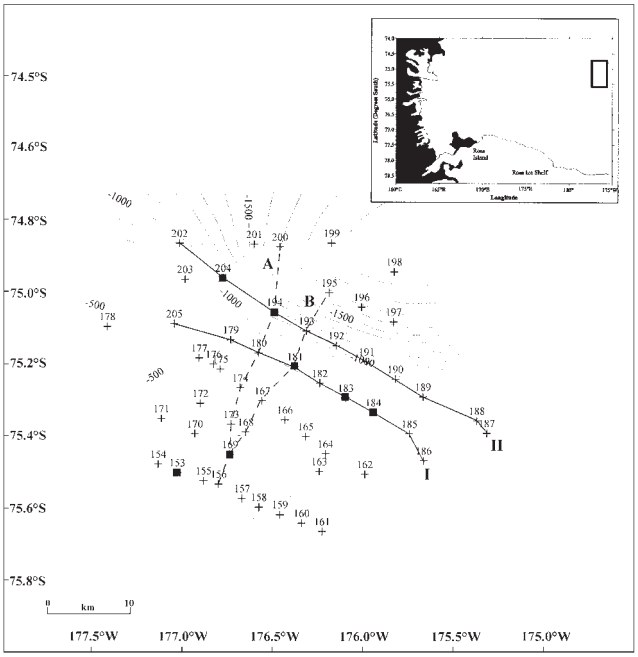

Fig. 1. Map of the 53 hydrological casts of the mesoscale experiment. The biological stations are indicated by black squares. The solid lines (I and II) indicate two along slope sections study, while the dashed lines (A and B) two cross slope sections.

150 m, where DOC is always near zero, the bacterial carbon demand was satisfied by decomposition of some part of the vertical POC flux (Ducklow *et al.* 2001). The qualitative composition of POC vertically exported is closely related to the phytoplankton community structure and therefore water masses of different origin are characterized by different POC pools.

This paper presents the analysis of the physical and biological data acquired during a five-day mesoscale experiment (15–20 February 1998), carried out in the framework of the 1997–98 summer synoptic cruise of the CLIMA Project of the Italian PNRA. The focus of this high resolution survey was the investigation of the interactions between the ISW and the CDW on the shelf-slope break in the central Ross Sea. The physical structure of the water column at some selected sections allowed us to detect the presence of the CDW and the ISW in this area. Moreover, it demonstrated the occurrence of an ISW overflow event, shown by the presence of waters with temperatures in the range of the ISW down to 1200 m on the continental slope and already discussed in Bergamasco *et al.* (2002b). In characterizing the effects of downslope processes on the export of organic carbon, our intention is to demonstrate that the microbial metabolism inside ISW and CDW is different and clearly related to the origin of each water mass. Bacterial ectoenzymatic activities are used as a proxy for organic matter composition.

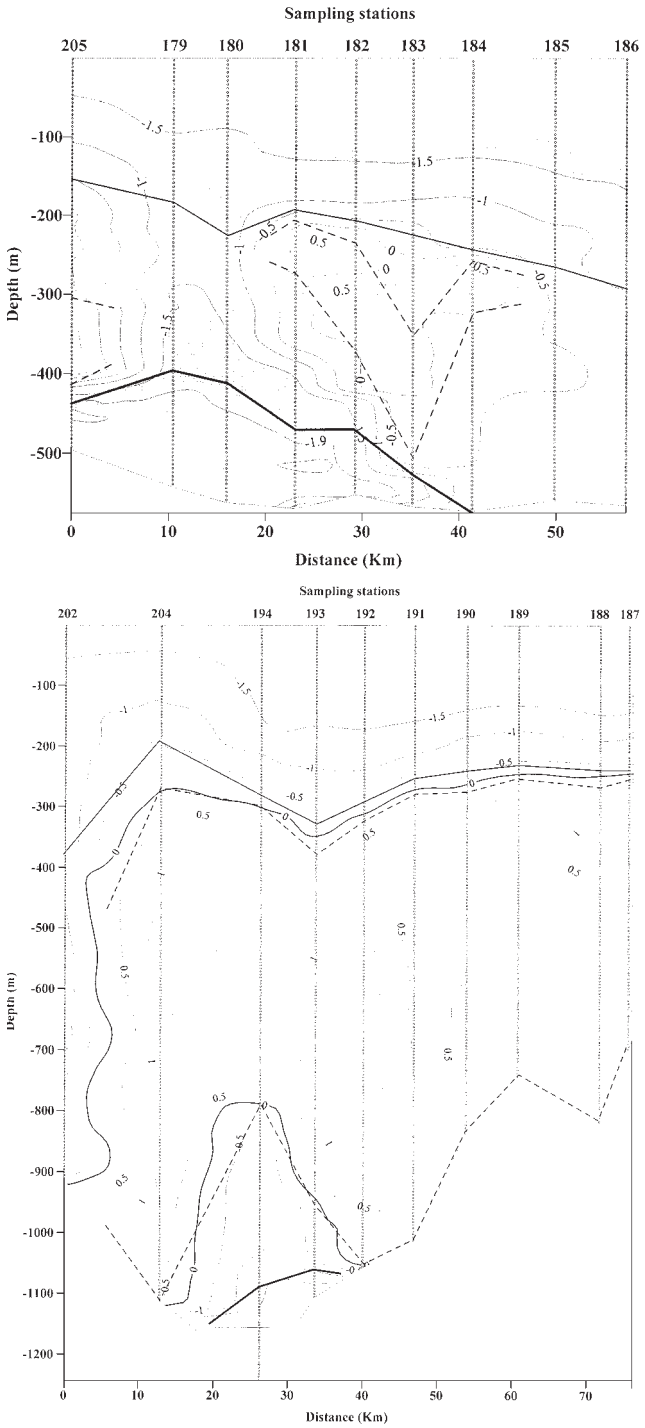

Fig. 2. Temperature distribution along **a.** section I, **b.** section II. Solid line = AASW lower limit, dashed lines = CDW upper and lower limit, thicker solid line = ISW upper limit.

Materials and methods

The hydrological measurements were acquired using a CTD (Sea-Bird Electronics 9/11 Plus) with a sampling frequency of 24 Hz (see Fig. 1 for sampling position). The CTD sensors were used to measure temperature, conductivity,

pressure, oxygen, fluorescence, light transmission and pH. Temperature and conductivity sensors were calibrated before and after the cruise at the Saclant Undersea Research Centre of La Spezia (Italy), but *in situ* calibrations were also performed using reversing thermometers and a laboratory salinometer.

Seawater samples, representative of the CDW and the ISW cores, were collected at selected depths by means of the 12 litre Niskin bottles of the CTD rosette sampler. The biological analyses were carried out immediately on board the ship.

Bacterial counts were performed by epifluorescence microscopy after staining the cells with 4,6-diamidino-2-phenyl indole (DAPI) (Porter & Feig 1980). After filtration with black polycarbonate filters (Nuclepore), the bacteria were stained and stored in Petri dishes on board. They were kept frozen at -20°C, until they were microscopically analysed in Italy.

Ectoenzymatic activities were assayed on board using fluorogenic substrate analogues (Hoppe 1983, 1993) derived from 7-amino-methyl-coumarin (AMC) and 4-methyl-umbelliferone (MUF). Protease activity was assayed as the hydrolysis rate of leucine-AMC. ß-D-glucosidase, lipase and alkaline phosphatase were assayed using MUF-ß-D-glucosidase, MUF-oleate and MUF-phosphate, respectively. Enzyme activities measured by means of fluorogenic substrates were expressed in terms of the rate of MUF or AMC production. The substrates were added to 5 ml samples at 20 µM final concentration and incubated for 6 h in the dark at room temperature (max. dev. ± 2°C). All samples were run in triplicate with 0.2 µm filtered and boiled seawater as controls. The fluorescence of MUF and AMC hydrolysed from the model substrates was measured using a Shimdtzu RF-1501 spectral fluorometer (364 nm excitation and 455 nm emission). Standard solutions of MUF and AMC were used to calibrate the fluorometer.

Bacterial production was estimated on board by incorporation of ^{3}H[thymidine] at *in situ* temperatures (-2°C to 0°C) according to the method of Fuhrman & Azam (1982). Thymidine incorporation was converted into bacterial production using conversion factors of Ducklow *et al.* (1999) established for the Ross Sea bacterial communities (8.6×10^{17} cells mol^{-1}). Carbon content of bacterial cells was taken as 1.87×10^{8} µgC per cell (Lochte *et al.* 1997).

Specific bacterial growth rates (µ) were estimated from the production/biomass ratio. Statistical comparisons were performed using an ANOVA test.

The physical characterization of the investigation area was obtained through a classical θ/S analysis. Three water types were identified: the Antarctic Surface Water (AASW), the CDW and the ISW. The temperature and salinity values characterizing these water masses were used to define the three vertices of a triangle ideally superimposed on the

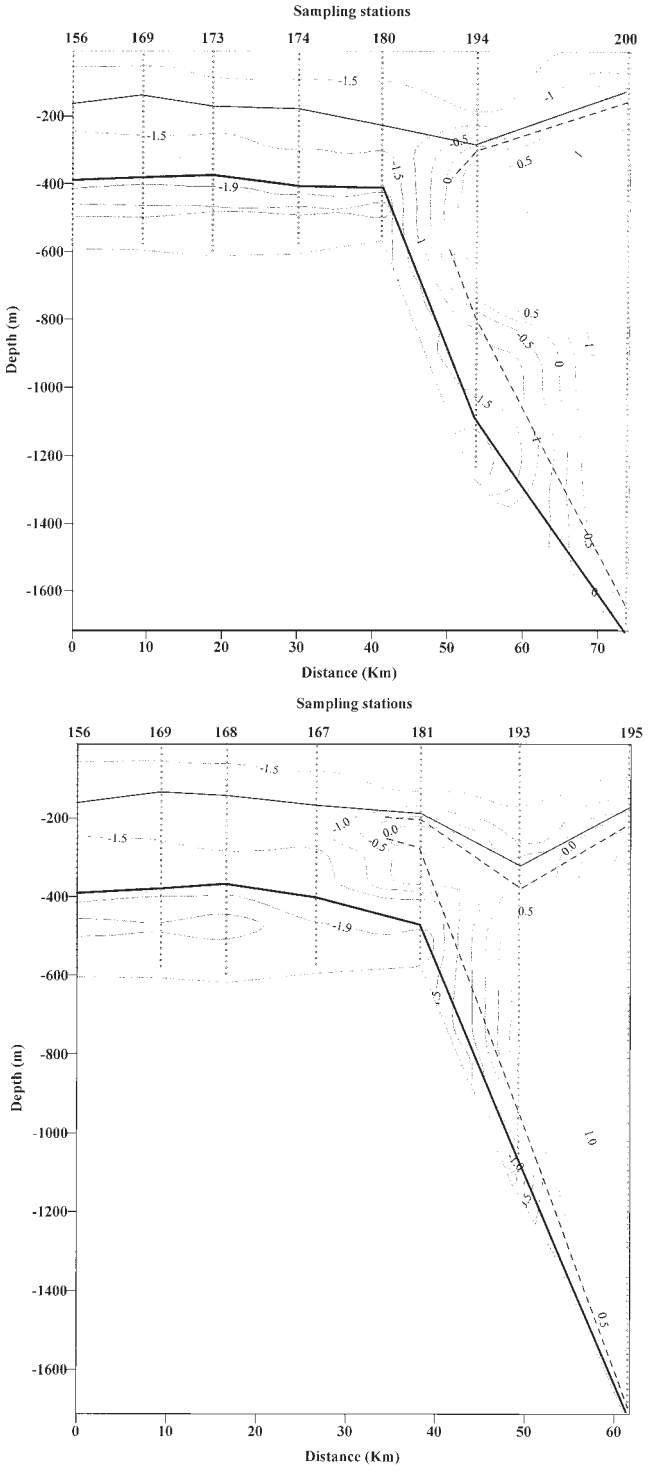

Fig. 3. Temperature distribution along **a.** section A, **b.** section B. Solid line = AASW lower limit, dashed lines = CDW upper and lower limit, thicker solid line = ISW upper limit.

cumulative θ/S diagram. The computation of the distance between a generic point inside the triangle (identifying the temperature and salinity values of a particular water type) and the vertices (representing, respectively, the temperature

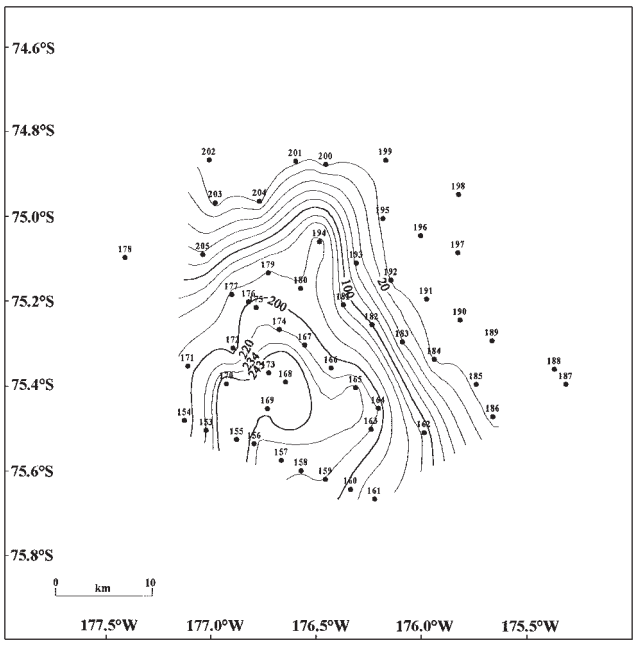

Fig. 4. Map of the ISW layer thicknesses on the water column when the ISW percentage is higher than 50%.

and salinity values of the AASW, the CDW and the ISW) gave the percentage of AASW, CDW and ISW present at that point. Thus, a rough estimate of the upper and lower limits of the AASW, the CDW and the ISW through the water column was obtained.

The temperature distribution along the sections considered was computed through objective analysis (Bretherton *et al.* 1976, Roemmich 1983).

Results

Hydrological data analysis

The temperature distribution along two E–W (Fig. 2a & b) and two S–N (Fig. 3a & b) sections is presented. The location of the sections is indicated in Fig. 1, where it can be seen that the central stations of sections I and II define an ideal alignment axis with south–north orientation.

In all figures the superimposed lines represent, respectively, the AASW lower limit (solid line), the CDW upper and lower limit (dashed lines) and the ISW upper limit (thicker solid line). These limits correspond to over 50% of the aforementioned water types.

Table I. Bacterial carbon production (BCP), bacterial abundance (BA) and specific growth rate (U) inside the ISW and CDW water samples. Average values and standard deviations are reported.

	BCP (μgC l^{-1} d^{-1})	BA (10^8 cell l^{-1})	U (d^{-1})
ISW	0.03 ± 0.01	3.4 ± 1.2	0.006 ± 0.001
CDW	0.05 ± 0.02	3.1 ± 1.1	0.010 ± 0.003

The along shelf sections (Fig. 2) clearly show the ISW and the CDW presence in the area investigated. The ISW is progressively confined on the eastern side of the sections, going from south (Fig. 2a) to north (Fig. 2b) according to the ideal alignment axis. It is particularly interesting that the core of modified ISW at station number 194 has a bottom layer temperature of about -1.95°C (Fig. 2b). This is the experimental evidence of the ISW overflow event on the continental slope at about 1200 m depth (Fig. 2b).

The CDW signature (T > 0.5°C) is clear in the eastern and central part of section I (Fig. 2a) and dominates the whole water column (Fig. 2b) from about 300 m to about 900 m depth.

The two cross shelf sections (Fig. 3) have a very similar structure characterized by the presence of the ISW tongue (T < -1.95°C) on the shelf (Fig. 3a & b), the penetration of the Warm Core (T ≅ -1.0°C) of the CDW on the shelf-break (see in particular Fig. 3b) and the strong signal of the CDW (T > 1.0°C) on the continental slope (Fig. 3a & b).

Both plots show a modified ISW overflow, respectively, at about 1200 m depth at cast 194 (Fig. 3a) and at about 1100 m depth at cast 193 (Fig. 3b). In the latter case, the event is weaker and more localized in space.

The ISW path in the whole investigation area is well represented in Fig. 4 that shows the ISW layer thickness, when the ISW percentage inside the water column is over 50%.

The super-cold water tongue spreads from the shelf (southernmost stations) controlled by topography and it is identified by the greater thickness in layers (highest values in Fig. 4). The ISW core corresponds to a layer of 243 m. The ISW signature becomes less intense and the layer is thinner away from the shelf (see lower values in Fig. 4), but it is still present on the slope at station 194, where we detected the ISW overflow event shown in Fig. 3a.

Table II. Values (mean and standard deviation) of the ectoenzymatic activities of lipase, phosphatase, aminopeptidase and β-glucosidase. AMP/GLU indicates the ratio between aminopeptidase and β-glucosidase. Each value represents the mean ± the standard deviation of 10–15 determinations. Statistical differences between the two water masses were determined by means of the analysis of variance (the asterisk indicates *P*-values < 0.05).

	Lipase (nM h^{-1})	Phosphatase (nM h^{-1})	Aminopeptidase (nM h^{-1})	Glucosidase (nM h^{-1})	AMP/GLU
ISW	103.14 ± 34.55	388.02 ± 152.03	47.07 ± 35.10	32.26 ± 19.30	1.46
CDW	52.27* ± 12.35	213.34 ± 85.55	5.79* ± 1.35	77.15* ± 23.54	0.08

Table III. Values (mean and standard deviation) of the ectoenzymatic activities of lipase and aminopeptidase at station 153.

# CAST	Sampling depth	Lipase (nM h^{-1})	Aminopeptidase (nM h^{-1})
153	230 m (CDW)	52.82 ± 44.74	7.32 ± 1.98
	465 m (ISW)	148.40 ± 54.74	84.29 ± 31.70

Biological data analysis

Biological data are related to some hydrological casts selected as representative of specific water masses, namely the ISW and the CDW. In Table I, we report bacterial carbon production (BCP), bacterial abundance (BA), and specific growth rate (U) data in the ISW and CDW water samples. The mean value and standard deviation are indicated for each parameter. Bacterial abundances (BA) ranged between 1.5 and 6.5 × 10^8 cell l^{-1}, with means of 3.4 × 10^8 cell l^{-1} and 3.1 × 10^8 cell l^{-1} in the ISW and CDW samples, respectively.

Bacterial production (BCP), calculated from thymidine incorporation rates, decreased slightly in the ISW samples, ranging from 0.027 to 0.10 in the CDW and from 0.009 to 0.06 µgC l^{-1} d^{-1} in the ISW. Bacterial specific growth rates (U) in the CDW layer were of the order of 0.01 d^{-1}. The lowest growth rates recorded in the bottom layer (ISW) were 0.006 d^{-1}.

Table II summarizes the values (average and standard deviation) of the ectoenzymatic activities. Activity differences between water masses were tested by means of the analysis of variance (*P*-value < 0.05).

Phosphatase was the highest among all enzymatic activities, ranging between 59.39 and 597.84 nmol l^{-1} h^{-1}. We did not observe any significant difference between the two water masses for this activity. Lipase and aminopeptidase activities were significantly higher in the deeper samples. They ranged from 66.8 to 148.4 nmol l^{-1} h^{-1} (vector x symbol here = 103.1 ± 34.5) and from 16.3 to 84.3 nmol l^{-1} h^{-1} (X = 47.1 ± 25.1), respectively. Lipase and aminopeptidase were a hundred times more active in ISW than in CDW and this is particularly true where the ISW layer was thicker (see Fig. 4 and Table III) as at stations 153 and 169, located on the shelf inside the ISW core. In the CDW core lipase and aminopeptidase were less active, reaching average values of 52.3 ± 12.3 nmol l^{-1} h^{-1} (34.4 ± 68.5 nmol l^{-1} h^{-1}) and 5.8 ± 1.3 nmol l^{-1} h^{-1} (4.0 ± 7.3 nmol l^{-1} h^{-1}), respectively. On the contrary, ß-glucosidase reaches maximum values in the CDW core, ranging from 46.8 to 182.2 nmol l^{-1} h^{-1} (X = 117.8 ± 53.1 nmol l^{-1} h^{-1}). Hydrolysis rates of ß-glucosidase (from 15.5 to 53.3 nmol l^{-1} h^{-1}; X = 32.3 ± 19.3) were lowest in the deeper water mass.

Discussion

This work presents the results of the physical and biological analyses of the interactions between the ISW and the CDW, detected at the shelf-slope in the central Ross Sea in the late 1998 summer. The ISW, coming from below the RIS, flows northward and, at the shelf-break, spills over the continental slope, mixing with the CDW. The complex mechanisms connected to these overflow events are an important component of the AABWs formation process; so it is fundamental to study the dynamics of water mass interactions at the shelf-slope border.

In this context, the hydrological sections presented here, clearly identify two regions, characterized by the presence of the ISW (on the shelf) and the CDW (on the continental slope), respectively. These two regions are defined by different hydrological and dynamical features, but they are connected at the shelf-break through intense mixing processes, controlled by friction, entrainment and topographic channelling.

The super-cold water tongue spread from the shelf, where the thickness of the ISW layer was greater, to the continental slope, reaching station 194. The presence of water temperatures in the range of the ISW at this station at about 1200 m depth represented the "link" between the two domains described above and gave the experimental evidence of the overflow event on the continental slope. Microbial community data contributed to a clear identification of the ISW and the CDW water masses.

Bacterial abundance did not significantly differ between the two water masses. The order of magnitude (3 x 10^8 cell l^{-1}) was similar to values previously reported (Hodson *et al.* 1981, Ducklow *et al.* 2001) in deep samples from the same area. In the Antarctic regions the bacterial vertical distribution is usually more or less homogeneous under the euphotic zone in both the central Ross Sea (Ducklow *et al.* 2001) and Bellinghausen Sea (Pedrós-Alió *et al.* 2002).

Although bacterial biomass attained relatively high levels, production rates were undeniably low in both water masses, confirming the observations of Carlson *et al.* (1998) and Ducklow *et al.* (2001). By way of comparison, mean ^{3}H-thimidine incorporation rates in the ISW and the CDW fell inside the pool of data reported by Ducklow *et al.* (2001) during six cruises in the upper 50 m layer. Despite the similar BA, in the CDW core BCP was significantly higher than in the ISW waters.

Numerous reports suggest that a considerable fraction of bacteria is in some kind of dormant state or is inhibited by low substrate availability rather than by low temperatures. Exceptionally high bacterial production has been reported in the Arctic Ocean, even under the sea ice (Rich *et al.* 1997), perhaps here in response to large river inputs of DOC that cannot occur in the Antarctic regions. Our data suggest that more accessible concentrations of labile organic matter were present in the CDW water mass carrying essentially biogenic debris and organic matter (Budillon *et al.* 1999). Ectoenzymatic activity provides important indications of the organic matter flux through bacteria, as well as of the quantity and quality of the organic matter available to

heterotrophs. Our data on enzymatic activities confirm the presence, in the CDW, of available substrate. Aminopeptidase activity was very low and phosphatase showed a decrease in activity from the ISW to the CDW. The behaviour of these two enzymes might indicate that in the latter water mass nitrogen and phosphorus were largely available, probably due to remineralization processes. Their availability inhibited the production and the activity of enzymes. In the Southern Ocean, nitrogen recycling from sinking organic material is more rapid than carbon recycling (Treguer *et al.* 1990). In the CDW core, the utilization of carbon sources followed different patterns: the glucosidase activity reached the highest values, while lipase activity was significantly lower than in the ISW. Kirchman *et al.* (2001) showed a very low concentration of dissolved sugars in Antarctic deep waters (> 200 m) with glucose contents equal to those observed in the labile organic pool. In fact, the spring refractory pool of sugars in surface waters was enriched in glucose. This difference in glucose yields probably reflects the different sources of dissolved sugars in the surface layer (suspended, recently produced POM) versus the deep layer (sinking "old" detrital POM). The limited availability of dissolved glucose induces bacteria to produce β-glucosidase and the resulted molecules are immediately assimilated by the cells. The high nutritional quality of the carbohydrate pool in the CDW was confirmed by the relatively low aminopeptidase/β-glucosidase ratio. Lipids represented only another carbon source since lipid-carbon in this region is the largest component in intermediate and deep waters (Fabiano *et al.* 1993) of the sinking POM.

The deeper ISW, younger than the CDW, was probably depleted in nitrogen, due to the relatively recent uptake by photothrops at the surface, and bacteria showing a higher proteolitic activity are the only heterotrophic organisms able to exploit nitrogen compounds of proteins. It is well known that aminopeptidases are not strictly specific, thus allowing exploitation of a wide range of proteic material. Christian & Karl (1993) detected surprisingly high aminopeptidase activities in the shelf and oceanic waters of the Antarctic Circumpolar Current. The ISW mass was also depleted in phosphorous. In fact, phosphatase activity was the most active enzyme. The major carbon source was represented by lipids and hydrolysis rates of macromolecules were very high, whereas the glucosidase activity was low. The aminopeptidase/β-glucosidase ratio was high confirming the low nutritional quality of the carbohydrate pool.

The quality of organic matter available in the two water masses sampled was probably very different and induced different patterns of bacterial metabolic activity. In the CDW metabolic activity was devoted to increasing the biomass as confirmed by the higher BCP rates detected in this water mass, and enzymes were less active due to the higher nutritional value of the substrate. In the deeper ISW, metabolic bacterial activity shifted towards degradative processes.

The evaluation of bacterial metabolic activities for studying the different nutritional compositions of water masses seems very promising. In the future, we would like to test these microbial parameters as a biological proxy, comparable in terms of resolution times with physical parameters, enabling us to identify not only the spatial dimension of some specific hydrological events (e.g. ISW spill), but possibly also the sources and ages of different water masses.

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