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Importance of the contribution of *Limacina helicina* faecal pellets to the carbon pump in Terra Nova Bay (Antarctica)

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The understanding of the role of the pteropods *Limacina helicina* in the ecosystem has become of greater interest as the debate on ocean acidification and its consequences for calcifying organisms has increased. Four incubation experiments were carried out in January and February 2006 in Terra Nova Bay Polynya (Ross Sea) to identify the faecal pellets (FPs) produced by *L. helicina*. Mean FP production rates were 6.1 $\pm$ 1.3 and 10.9 $\pm$ 2.1 pellets day^{-1} individual^{-1} in January and February, respectively. FPs produced by *L. helicina* had an oval shape with a more lengthened side. The identification of *L. helicina* faeces allowed us to quantify the amounts of *L. helicina* FPs in the material collected by sediment traps deployed in the same area from 1998 to 2001. We found that *L. helicina* FPs flux ranged from 71 $\times$ 10^3 FP m^{-2} year^{-1} to 362 $\times$ 10^3 FP m^{-2} year^{-1} and reach maximum values in March–April every year. The FPs flux of this organism contributed 19% of the particle organic carbon flux. The carbon pump may be modified if the *L. helicina* population declines as a consequence of the predicted acidification in polar and subpolar waters.

INTRODUCTION

Limacina helicina (Phipps, 1774) is a Thecosome pteropod (shelled pelagic mollusk) with a bipolar distribution and may occur in high densities in polar regions as well as in subpolar waters (Kobayashi, 1974; Lalli and Gilmer, 1989a; Tsurumi *et al.*, 2005). *Limacina helicina* is the exclusive prey item for *Clione limacina* (a shell-less pteropod) and is also an important prey item for a number of other species in Antarctic waters, including whales, myctophid and notothenioid fishes (Pakhomov *et al.*, 1996), which are themselves important components in the diet of penguins and mammals (Davis *et al.*, 1999). *Limacina helicina* is a key component of the ecosystem influencing phytoplankton stocks (Hopkins, 1987), carbon flux (Noji *et al.*, 1997) and dimethyl sulphide levels which in turn influence global climate through ocean–atmosphere feedback loops (Levasseur *et al.*, 1994). Manno *et al.* (Manno *et al.*, 2002, 2004) and Accornero *et al.* (Accornero *et al.*, 2003) showed that *L. helicina* collected by sediment traps represents the dominant taxa in terms of organism abundance in the western Ross Sea and near the Ross Ice Shelf. They hypothesized that these pteropods were most likely responsible for the high faecal flux that followed

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the intense diatom bloom at the end of summer in the Terra Nova Bay (TNB) Polynya (Antarctica). The importance of faecal pellets (FPs) for the export of organic material from the euphotic zone into deeper waters has been demonstrated in several studies (Angel, 1984; Bathmann and Liebezeit, 1986; Fowler *et al.*, 1991; Wexels Riser *et al.*, 2002). Sinking rates of zooplankton FPs are known to be faster than those of phytoplankton cells, and, therefore, these pellets can be a major component in the vertical transport of organic matter to the deep ocean (Honjo, 1976; Komar *et al.*, 1981; Bruland and Silver, 1981). It is generally considered that grazing by microzooplankton and small copepods is an important mechanism for biogenic material retention in the upper water column: sinking rates of their pellets are slow and degradation processes cause recycling before sinking can occur (Dagg *et al.*, 2003). In contrast, large zooplankton contribute mainly to downward flux (Aksnes and Wassmann, 1993; Legendre and Michaud, 1998) because their pellets have higher sinking rates.

Over the last few years, as the ocean acidification debate has increased in intensity, understanding the role of *L. helicina* in the ecosystem has become of greater interest. Orr *et al.* (Orr *et al.*, 2005a, b) predicted that some polar and subpolar surface waters will become undersaturated in aragonite, probably within the next 50 years and the calcifying organisms, particularly shelled pteropods, would be unable to maintain their shells (Legendre and Rivkin, 2005). In the polynya of TNB, Manno *et al.* (Manno *et al.*, 2007) recently described the occurrence of dissolution of the aragonite shells of the pteropod *L. helicina*. In this scenario, the contribution of *L. helicina* pellets to the organic carbon pump of this area could be strongly modified due to the decline of pteropods with increasing ocean acidification.

To our knowledge, FPs of Antarctic *L. helicina* have never been described before. The aim of this study was to identify the FPs produced by *L. helicina* by means of FPs production experiments. Once we had identified the *L. helicina* faeces, we quantified their amounts in material collected by sediment traps from 1998 to 2001 in the same area and we estimated their contribution to the organic carbon pump.

METHOD

FP production experiments

Four experiments (two in January and two in February 2006) were carried out during the XXI Italian Antarctic cruise, at the mooring D station (75°S and 164°E) of the TNB Polynya (Ross Sea) (Fig. 1). Live *L. helicina* were collected by vertical tows from 50 m to the surface with a WP2 net (200 μm mesh) during day hours. For each experiment, three 2 L bottles with four specimens of *L. helicina* were incubated in diminished light for 12 h. Each plastic bottle was equipped with two bottom meshes: the first mesh (200 μm) separated *L. helicina* from FPs to avoid any possible destruction and/or fragmentation of FPs; the second mesh (100 μm) collected faecal material. Bottles were filled with filtered seawater and placed vertically in a flowing seawater incubator. At the end of the incubation, bottles were gently removed from the incubator tank. The nets were cleaned and all specimens of *L. helicina* and FPs recovered were fixed with buffered formaldehyde (4% final concentration). The *L. helicina* selected for the experiments had a shell size between 0.6 and 0.8 mm consistent with the dominant shell size previously collected in the sediment traps. In the laboratory, within two months, pellets were counted under a dissection microscope, classified by morphology and measured using an ocular micrometer with an accuracy of 5 μm (100×). Pellet volume was estimated by equating shapes to standard geometric figures and carbon content was calculated by applying the volume to carbon conversion of 0.0495 mg C mm^{-3} (Gonzalez *et al.*, 1994).

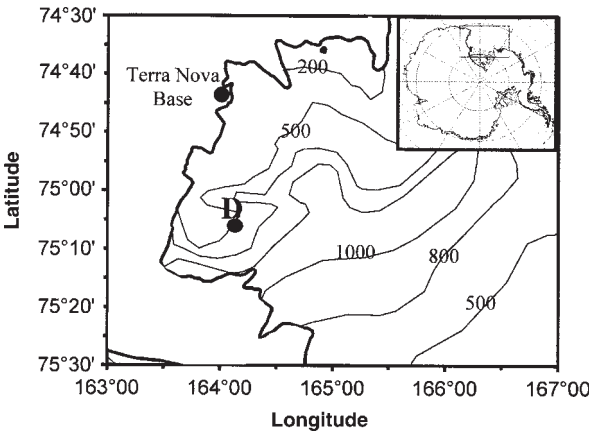

Fig. 1. Location of the study area, near the mooring station D in TNB Polynya (western part of the Ross Sea).

FP content was examined by Scanning Electron Microscope (Hitachi S 520 SEM) for qualitative observations.

Sediment trap sampling and analysis

FPs and specimens of *L. helicina* were collected by a Hydro-Bios Multi Sediment Trap MST 24, provided with 24 receiving cups and a collecting area of 0.6 m^2. The traps were deployed in TNB Polynya (mooring D:

75°06′S, 164°13′E, bottom 998 m). In this study we analysed the samples from the upper trap (180 m depth) from January 1998 to January 2001. Sediment traps were deployed and recovered every year (in total 96 cups collected for the whole period). Sediment trap rotation intervals varied between 4–15 days (sampling frequency was shorter during the high flux period and longer during the low flux period).

Each trap was fitted with a plastic baffle mounted in the opening, to prevent the entrance of large sized organisms. In the receiving cups, 4% buffered formalin-seawater solution was used as preservative. Upon recovery, samples were stored at~2–4°C in the dark until further analysis.

In order to recover the *L. helicina*, the samples were wet-sieved through a 1 mm nylon mesh. *L. helicina* individuals were carefully removed from the <1 mm fraction by hand-picking under a dissecting microscope. Successively the pteropods were counted and classified according to their size. Each sample was then accurately split into a series of replicate fractions, for FPs and particle organic carbon analysis, following the technique of Heussner *et al.* (1990).

Replicates of sediment trap subsamples were allowed to settle in Utermöhl sedimentation chambers and examined using an inverted microscope to identify and enumerate FPs. FP flux (pellets m^{-2} day^{-1}) was calculated using the number of days the trap was deployed and the mouth area of the sediment trap. Twenty pellets from each size class were used to calculate an average volume and carbon flux. To estimate the FP carbon content, the volume of FPs observed in the traps was converted to carbon content using a conversion factor of 0.0495 mg C mm^{-3} (Gonzalez *et al.*, 1994).

The particulate organic carbon (POC) was measured on subsamples filtered onto GFF pre-combusted filters. After 2 N H_3PO_4 and 1 N HCl treatment to remove inorganic carbon, POC was measured by combustion in an elemental analyzer (LECO CS 125).

RESULTS

FP production experiments

FP production rates were calculated as the average of daily FP produced by a single *L. helicina*. Mean FP production rates were 6.1 ± 1.3 and 10.9 ± 2.1 pellets day^{-1} $individual^{-1}$ in January and February 2006, respectively. FP production rates were significantly lower in the experiments carried out in January than in February (Mann–Whitney *U* test, $P < 0.05$) (Fig. 2). FP produced by *L. helicina* had an oval shape (Fig. 3) with a side more lengthened. They were greenish brown and presented a transparent but compact structure. All FPs produced during the experiments had a peritrophic membrane. SEM examination showed that in February pellets were mainly composed of diatoms and dinoflagellates, while in January copepods, nauplii and tintinnids were also present, generally broken into small fragments. FPs differed in size: the largest pellets were produced in February and the smallest in January, consequently mean volume of the single pellets exhibited maximum values in February (44.61×10^4 μm^3) and minimal in January (28.66×10^4 μm^3) (Table I).

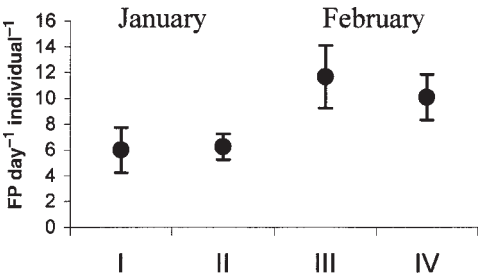

Fig. 2. *Limacina helicina* FP production rate expressed as FP day^{-1} $individual^{-1}$. Experiments were carried out in January (I, II) and February (III, IV) 2006.

Limacina helicina and FP interannual trend

Limacina helicina was the most abundant zooplankton organism collected in our sediment traps. Annual flux (individual m^{-2} $year^{-1}$) was calculated including daily flux (individual m^{-2} day^{-1}) and seasonal contribution of *L. helicina* (monthly flux annual $flux^{-1} \times 100$). The interannual trend of *L. helicina* flux (Fig. 4) showed a large variability (one order of magnitude) ranging from a minimum of 2607 individual m^{-2} $year^{-1}$ (in 1998) to a maximum of 11 300 individual m^{-2} $year^{-1}$ (in 1999). The highest quantity of pteropods was always recovered in late summer–early autumn (March–April). From 68% (2000) to 82% (1998) of the annual flux of *L. helicina* occurred during this period.

On average, 70% of *L. helicina* collected in our sediment traps had a shell diameter between 0.6 and 0.8 mm (Fig. 5). Since the specimens of *L. helicina* used in the FP production experiments had a similar size, we used the results of shape and dimension of *L. helicina* FP to identify the FP of these pteropods in the sediment traps.

Generally, we observed a good conservation state of the oval FP shape without any evident sign of coprorhexy and/or coprophagy. The oval FP annual flux collected by sediment traps ranged from 71×10^3 to 362×10^3 FP m^{-2} $year^{-1}$ (Fig. 6). For all years, minimum and maximum fluxes of oval FP

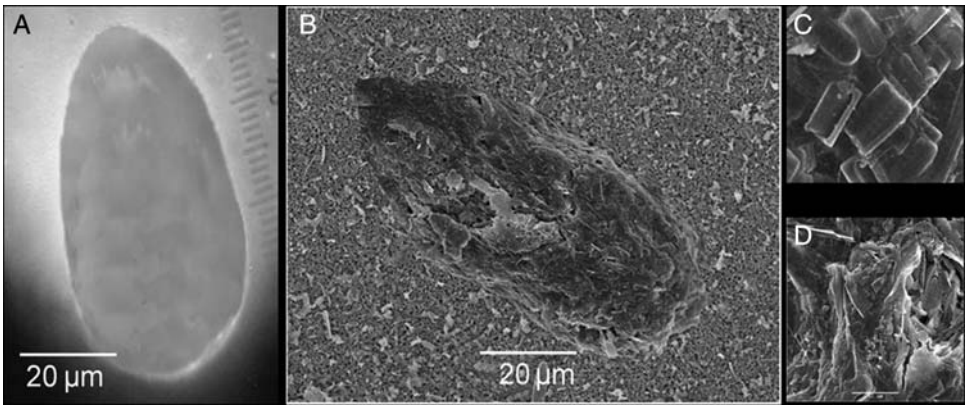

Fig. 3. Digital camera (a) and SEM (b) images of *L. helicina* FPs and details of pellet content during (c) February 2006 (FP were mainly composed of diatoms debris) and (d) January 2006 (FP were mainly composed of organic remains).

Table I: Length (µm), width (µm) and volume (µm^3) mean of FPs produced by L. helicina during the four incubation experiments (two in January and two in February)

	January 2006 (109)[a]	February 2006 (138)[a]
Length mean (µm)	103.5 ± 19.2	120.3 ± 15.9
Width mean (µm)	80.5 ± 15.1	91.3 ± 20.1
Volume mean (µm^3 × 10^4)	28.7 ± 11.9	44.6 ± 18.6

[a]Total number of FPs measured.

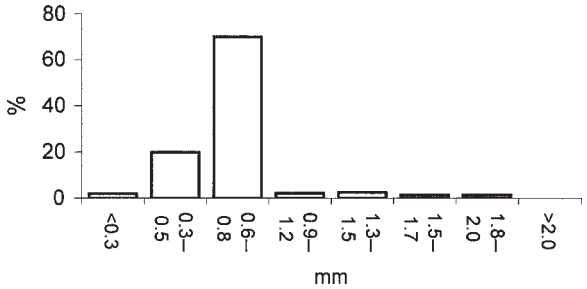

Fig. 5. Percentage (%) of the shell diameter (mm) of the *L. helicina* collected by sediment traps in TNB from 1998 to 2001. A total of 800 individual were measured (200 shells per year).

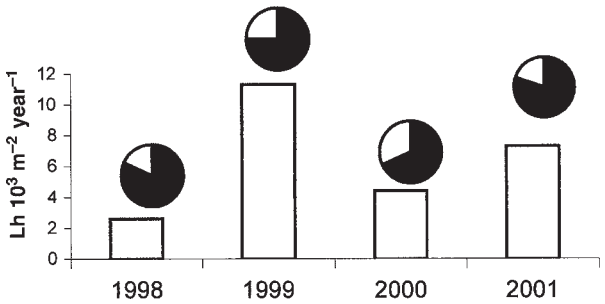

Fig. 4. Multiyear trend of *L. helicina* flux (expressed as *L. helicina* 10^3 m^{-2} year^{-1}) in TNB from 1998 to 2001 (white histograms). The pie charts represent the percentage of *L. helicina* collected in March–April (black slices) and during other months (white slices).

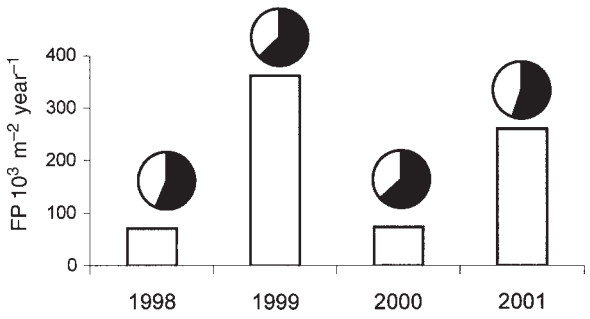

Fig. 6. Multiyear trend of *L. helicina* FP flux (FP*10^3 m^{-2} year^{-1}) in TNB from 1998 to 2001 (white histograms). The pie charts represent the percentage of FPs collected in March–April (black slices) and during other months (white slices).

corresponded to minimum and maximum fluxes of *L. helicina*. Moreover (Fig. 6), the contribution of oval FP was never less than 55% of total FP annual flux during in late summer–early autumn (March–April).

POC multiyear trend and *Limacina helicina* FP contribution

Figure 7 shows the multiyear trend of POC flux from 1998 to 2001. The flux ranged from 511 mg C m^{-2} year^{-1} (2000) to 884 mg C m^{-2} year^{-1} (1999). As for FPs, POC shows higher values when fluxes of *L. helicina* are the highest. *Limacina helicina* FP contributed significantly to the POC in all years, with percentages ranging from 10% (1998) to 30% (1999) and a multiyear average of 19%.

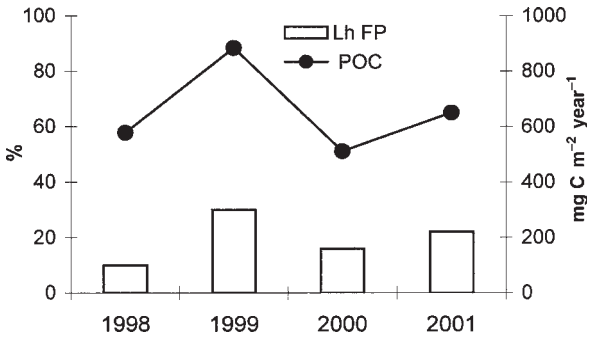

Fig. 7. Multiyear trend of POC flux (mg C m^{-2} year^{-1}) in TNB from 1998 to 2001 (black circles). Contribution (%) of *L. helicina* FPs to the POC (white histograms).

DISCUSSION

Although in the past many authors (Gonzales, 1992; Accornero *et al.*, 2003, Manno *et al.*, 2004) indicated *L. helicina* as the possible major contributor to the production of oval FPs, this study has shown for the first time the production of the oval FP by living *L. helicina* collected in Antarctic waters.

Since it has been observed that *L. helicina* often does not feed under laboratory conditions (Gilmer & Harbison, 1991), the FPs recovered during our experiments are probably the result of the food ingested by the pteropods before their capture. In the TNB Polynya, primary production and phytoplankton biomass largely increas from December to February (Lazzara *et al.*, 1999, Fonda Umani *et al.*, 2002, Saggiomo *et al.*, 2002). Consequently, the higher FP production rate observed in February 2006 is probably related to higher food availability in the late summer. FPs produced in this period were indeed characterized by an important content of phytoplanktonic cells.

Hopkins (Hopkins, 1987) found that *L. helicina* feed exclusively on phytoplankton, while Gilmer and Harbison (Gilmer and Harbison, 1991) observed some diatoms as well as copepods, tintinnids and small pteropods in pteropod stomach. They suggested that *L. helicina* is able to switch from a herbivorous to an omnivorous feeding strategy during the rapid decline in phytoplankton blooms and suggested the hypothesis that only individuals of large sizes (>3 mm) were opportunistic feeders. Since we observed a mixed content (autotrophic and heterorophic prey) in many FPs produced by small pteropods, our results disagree with the hypothesis expressed by Gilmer and Harbison (Gilmer and Harbison, 1991) on the relation between shell size and pteropod diet. Conversely, our observation agree with the findings of Gannefors *et al.* (Gannefors *et al.*, 2005) in the Arctic Ocean which suggested, based on the fatty acid composition, that *L. helicina* is a true omnivore feeding on available particulates, ranging from a phytoplankton based diet in spring and summer to degraded organic material in late autumn and winter.

The late summer–early autumn flux peaks (March–April) of *L. helicina* were often related to the massive mortality of the population probably due to the decline in food availability at the end of the austral summer (Collier *et al.*, 2000; Gardner, 2000; Accornero *et al.*, 2003). This observation let us suppose that, between March and April, *L. helicina* collected in the sediment traps could represent a good estimate of their abundance in the water column before the crash. According to this assumption, we calculated the mean FP contribution of a single individual as a ratio of total oval FP/total *L. helicina* collected by sediment traps between March and April. As a result, we estimated that each *L. helicina* could produce an average of 19 FP day^{-1}. This value is higher than the FP production rates measured in our experiments (6 and 12 FP day^{-1}), probably because of the unnatural laboratory conditions.

In order to calculate the *L. helicina* oval FP flux, we took into account the sediment trap FPs with shape, colour and content similar to the FP observed during the production experiments. Several authors (Cadée *et al.*, 1992; Gonzales, 1992; Marino *et al.*, 1994) have suggested that Ostracoda are also possible producers of oval pellets, together with pteropods. However, Ostracoda contributed less than 1% to the total zooplankton community in the samples collected for FP production. Guglielmo *et al.* (Guglielmo *et al.*, 2007) showed that Ostracoda do not contribute significantly to the TNB zooplankton abundance in the upper 50 m. Additionally, during the whole sediment trap deployment period, when high quantities of oval FP were recovered, few Ostracoda were present (<0.2% of total zooplankton flux). Furthermore, the oval FP and *L. helicina* fluxes showed an analogous trend and the decrease to zero of oval pellet fluxes coincided with sedimentation of only dead pteropods (empty tests). Our results agree with the findings of Accornero *et al.* (Accornero *et al.*, 2003) who analysed the material collected by sediment traps in the TNB from 1995 to 1997. In fact, even during this previous period, *L. helicina* showed a seasonal trend very similar to the FP flux with an enhanced flux in the second half of the summer/early autumn and low fluxes during the winter and spring. On the basis of all those observations, almost all the oval FP collected by sediment traps were considered to be produced by *L. helicina*.

The high abundance of oval pellets in the deep sediment traps (Honjo *et al*, 2000; Accornero *et al.*, 2003; Manno *et al.*, 2004; Pilskaln *et al.* 2004) and their high

sinking rates suggest that they are more resistant to mechanical and microbial degradation than the other faeces (Gonzales, 1992; Cadée *et al*., 1992).

Our results agree with these findings since we observed that *L. helicina* FP did not show evident signs of mechanical and chemical degradation. Hence, *L. helicina* plays a fundamental role in the production of fast and robust FP which significantly contribute to the transport of organic carbon to the deep water (Gonzales, 1992).

As shown in Fig. 7, *L. helicina* FP contributed 19% of the POC (multiyear average). Orr *et al*. (2005a, b) forecasted that some polar and subpolar surface waters will become undersaturated, probably within the next 50 years, with respect to aragonite and as a consequence pteropods may be unable to maintain their shells. Data from sediment traps indicate that empty pteropod shells exhibit partial dissolution as soon as they fall below the aragonite saturation horizon (Honjo *et al*., 2000, Manno *et al*., 2007) and *in vitro* measurements confirm such rapid pteropod shell dissolution rates (Fabry and Deuser, 1991). In a drastic collapse of *L. helicina* scenario due to an increasing of ocean acidification, the loss in the *L. helicina* FP contribution to the total organic carbon flux could be significant, especially during the late summer–early autumn when *L. helicina* FP are generally dominant in the sediment traps.

Accornero *et al*. (Accornero *et al*., 2003) showed that the "soft part" of *L. helicina* (collected by sediment traps in TNB) contributed 53% to the annual POC (annual average). Therefore, estimating the *L. helicina* organic carbon fluxes as the sum of FP plus *L. helicina* soft part, this organism could contribute up to 72% of the total organic carbon export.

Limacina helicina is the dominant zooplanktonic organism collected by sediment traps not only in TNB but also in several other areas of the Ross Sea (Hecq *et al*., 1999; Manno *et al*., 2002, Accornero *et al*., 2003). A recent review on the pteropods in the Southern Ocean ecosystem (Hunt *et al*, 2008) underlined in terms of density, biomass, trophic role and contribution to the organic carbon flux that these organisms are important components of the Southern Ocean. Moreover, shelled pteropods can reach densities of 1000–10 000 individuals m^{-3} in high-latitude areas (Bathmann *et al*., 1991) contributing 17 and 53% of the total zooplankton communities in the Weddell Sea (Boysen-Ennen and Piatkowski 1988) and South Georgia (Pakhomov *et al*., 1997), respectively, as well as in the Arctic (Falk-Petersen *et al*., 1999). We estimated only the contribution in terms of organic carbon export by soft tissues and FP but have to keep in mind that the eventual disappearance of this organism will also impact the carbonate pump by diminishing the CO_2 uptake to build their shells, thus causing a significant increase in CO_2 partial pressure in the Antarctic waters.

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