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Interannual variability of pteropod shell weights in the high-CO₂ Southern Ocean

**D. Roberts¹, W. R. Howard¹, A. D. Moy^{1,2}, J. L. Roberts^{1,2}, T. W. Trull^{1,3,4},
S. G. Bray¹, and R. R. Hopcroft⁵**

¹Antarctic Climate and Ecosystems Cooperative Research Centre, Hobart, 7001, Tasmania, Australia

²Australian Antarctic Division, Department of the Environment, Water, Heritage and the Arts, Channel Highway, Kingston, 7050, Tasmania, Australia

³Marine and Atmospheric Research, Commonwealth Scientific and Industrial Research Organisation (CSIRO), Castray Esplanade, Hobart, 7000, Tasmania, Australia

⁴Institute of Antarctic & Southern Ocean Studies, University of Tasmania, Hobart, 7001, Tasmania, Australia

⁵Institute of Marine Science, Univ. of Alaska Fairbanks, Fairbanks, Alaska 99775-7220, USA

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Correspondence to: D. Roberts (d.roberts@utas.edu.au)

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Abstract

Anthropogenic inputs of CO₂ are altering ocean chemistry and may alter the role of marine calcifiers in ocean ecosystems. CO₂ emissions over the coming centuries may produce changes in ocean pH not seen for millions of years. Laboratory evidence has shown decreased calcification in some species of coccolithophores, foraminifera, corals and pteropods in response to CO₂ enrichment. However, in situ observations of calcification in marine organisms are limited, especially for the aragonitic pteropods. This group of pelagic molluscs are likely to be more sensitive to changes in carbonate chemistry than calcite producers such as foraminifera and coccolithophores. Here we present observations of pteropod shell-weight and flux from 1997–2006 in sediment traps deployed at 47° S, 142° E at 2000 meters below sea surface in the Southern Ocean. A decadal trend of $-1.17 \pm 0.47 \mu\text{g yr}^{-1}$ ($P=0.02$) in mean shell weight in the pteropod *Limacina helicina antarctica* form *antarctica* suggests a small but detectable reduction in calcification. Gaps in the data make it difficult to state with certainty the significance of the trend. However, this data set represents the first attempt to estimate interannual variations in pteropod calcification and establish a benchmark against which future impacts of ocean acidification may be detected. Contributions of *Limacina helicina antarctica* morphotypes to the total pteropod flux were also reduced over the decade. We suggest these small though discernible trends are due to changing carbonate chemistry in the Subantarctic, as other oceanographic variables show no clear decadal trends. With CO₂ continuing to enter the ocean such impacts on pteropods and other marine calcifiers could result in changes to the distribution of species and the structure of Southern Ocean ecosystems.

1 Introduction

The oceans have absorbed about one-third of the total anthropogenic CO₂ released into the atmosphere (Sabine et al., 2004). The addition of CO₂ to seawater lowers both

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pH and the concentration of dissolved carbonate ions ($[\text{CO}_3^{2-}]$) needed by calcifying organisms for their shells (Fabry et al., 2008) such as coccolithophores (Riebesell et al., 2000; Zondervan et al., 2001), foraminifera (Spero et al., 1997; Bijma et al., 1999, 2002), corals (Gattuso et al., 1998; Kleypas et al., 1999; Gattuso and Buddemeier, 2000) and pteropods (Orr et al., 2005). In response to continued CO₂ emissions and the resulting decrease in ocean pH and $[\text{CO}_3^{2-}]$, calcification rates of some marine organisms could decrease by up to 50% by the end of the century (Sabine et al., 2004). However, such impacts have not been observed so far in situ (IPCC, 2007) especially in high-latitude regions likely to experience the earliest large-scale shifts in ocean carbonate chemistry (Fabry et al., 2008).

The Southern Ocean is a substantial sink for atmospheric CO₂, taking up a large proportion of the anthropogenic carbon in the global oceans (Sabine et al., 2004). We deployed the first of a series of sediment traps at 2000m below the sea surface at 47° S, 142° E in the Southern Ocean (Fig. 1) in 1997/1998 to capture a multiyear series of marine calcifiers falling through the water column (Bray et al., 2000; Trull et al., 2001). The fate of aragonite calcifiers in the Southern Ocean is of particular concern, especially as global carbon cycle models suggest that polar-regions will be the first to experience $[\text{CO}_3^{2-}]$ below aragonite saturation (Orr et al., 2005; Royal Society, 2005; McNeil and Matear, 2008). As aragonite is less stable than calcite, the other main form of biogenic calcium carbonate (CaCO₃) (Mucci, 1983), aragonite producers are likely to respond to ocean acidification more markedly than calcite producers.

One major group of aragonite producers is the thecosomatous (shelled) pteropods: planktonic gastropods (Lalli and Gilmer, 1989). As the only group of pelagic aragonite producers, pteropod production and dissolution play important roles in the upper-ocean alkalinity cycle (Betzer et al., 1984; Byrne et al., 1984; Gangstø et al., 2008). One of the most common pteropods of the Southern Ocean, *Limacina helicina antarctica* (Fig. 2a), has a geographic range that extends from the Subtropical Front to the Antarctic coast (van der Spoel and Dadon, 1999). Two intra-specific morphotypes of this common Southern Ocean pteropod have been identified: *Limacina helicina antarctica* forma

antarctica (Fig. 2b), dominant in Antarctic waters between Antarctica and the Polar Front, and *Limacina helicina antarctica* forma *rangi* (Fig. 2c), found more commonly in Subantarctic waters north of the Antarctic Circumpolar Current (van der Spoel and Dadon, 1999). Both morphotypes were collected in our sediment trap series.

5 We use mean whole pteropod shell weight as a measure of calcification in these aragonite producers. This approach has been used in studies of planktonic foraminifera, where clear correlations between shell weights and $[\text{CO}_3^{2-}]$ in seawater have been observed (Bijma et al., 2002). Our investigation represents the first attempt to estimate interannual variations in in situ pteropod calcification and establish a bench-
10 mark against which future impacts of ocean acidification in the Southern Ocean may be detected.

2 Methods

2.1 Sediment trap deployments and sample retrieval

15 A McLane 21-cup sediment trap was first deployed to a depth of 2000 m at 47° S, 142° E in 1997/1998 (Fig. 1), and sediment traps have been recovered from the same site in 1999/2000, 2000/2001, 2003/2004 and 2005/2006 to date. The conical sediment trap collects particles sinking through the ocean to a 0.5 m² surface area into individual cups prepared with buffered and poisoned solutions that are open for periods varying between 5 and 60 days (Supplementary Table 1 <http://www.biogeosciences-discuss.net/5/4453/2008/bgd-5-4453-2008-supplement.pdf>). The 1997/1998 to 2000/2001 traps were filled with unfiltered deep seawater from the region (collected at 1200 m depth, 49° S, 153° E), which was treated with sodium chloride (5 g l⁻¹) to increase solution density, sodium tetraborate (1 g l⁻¹) as a pH buffer and mercuric chloride (3 g l⁻¹) as a preservative (Bray et al., 2000; Trull et al., 2001). All trap cups from 2001/2002 on-
20 wards used filtered surface seawater in place of the unfiltered seawater and included strontium chloride to address dissolution of acantharian skeletons (Beers and Stewart,

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1970). The pH of all recovered sediment trap cup solutions was measured upon retrieval (all ranged between 8.0 and 8.8) and samples sieved through a 1 mm screen to eliminate the larger motile plankton fraction. Samples were subsequently split into ten aliquots for further analyses using a rotating splitter (McLane, Inc.).

5 2.2 Pteropod shell weights and mass flux

Pteropod aliquots (two <1 mm splits) were soaked in a 3% hydrogen peroxide solution buffered with sodium tetraborate for one hour to dissolve organic matter, washed with deionized water buffered with sodium tetraborate and sieved through a 150 μm screen (King and Howard, 2003). The resulting 150 μm –1 mm size fraction was used to determine mean pteropod shell weights for each sediment trap cup recovered. We focus on pteropods within the 150 μm –1 mm size fraction herein, as pteropods in this size fraction tend to dominate *Limacina helicina* populations (Fabry, 1989; Collier et al., 2000) and are likely to be most sensitive to changes in carbonate chemistry (Byrne et al., 1984; Honjo et al., 2008). Pteropods may be digested or dissolved before they reach the sediment traps so we assume our samples represent a minimum estimate of pteropod flux at the depth of the sediment trap.

Whole pteropods (pitted or fragmented shells were not included in our analyses) were picked from dried aliquots, identified and enumerated. *Limacina helicina antarctica* (Fig. 2a) was the most common pteropod retrieved in the sediment trap series. These shells were separated into morphotypes according to van der Spoel and Dadon's (1999) separation of taxa (Fig. 2b, c), weighed in batches per cup for each season retrieved using a Mettler Toledo microbalance (precision=0.1 μg) and mean shell weights per morphotype per cup per trap calculated (Fig. 3a, c; Supplementary Table 1 <http://www.biogeosciences-discuss.net/5/4453/2008/bgd-5-4453-2008-supplement.pdf>). Flux weighted mean shell weights per morphotype (Fig. 3b, d; Table 1) were calculated from sediment trap pteropod shell (Fig. 4a; Table 2) and mass (Fig. 4b; Table 3) flux to remove bias generated by collection time differences and allow interannual comparisons.

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2.3 Statistical analyses

As a result of non-uniform cup sampling periods (varying between 5 and 60 days), limited sample sizes and our batch-weighting approach we are unable to quantify within-sample error distributions or characterize seasonal variability. Accordingly, non-parametric statistical tests were employed to detect interannual trends in shell weight for either morphotype as these tests make no implicit assumptions about underlying distributions. Using a two-tailed Spearman rank-correlation coefficient test (Anderson et al., 1981) we estimate an interannual shell weight trend ($P=0.14$) for forma *antarctica* only (Table 4a). The Spearman rank-correlation coefficient test does not take into account possible within-sample correlations or allow quantification of the magnitude of trends. To quantify the trend in forma *antarctica* shell weight we assumed normality and applied a weighted least-squares regression (Davies and Goldsmith, 1972) to estimate a slope of $-1.17 \pm 0.47 \mu\text{g yr}^{-1}$ ($P=0.02$) (Table 4b). Note that the shell weight for 2005/2006 is based on a single shell. However, our estimates of trends in the data are insensitive to removal of this data point. Without this final data point, the estimated linear trend is -1.19 ± 0.49 ($P=0.02$). Similarly, without the final data point the Spearman rank-correlation coefficient is only slightly changed ($P=0.12$).

Spearman rank-correlation coefficient tests were also used to detect interannual trends in sediment trap pteropod shell and mass flux (Table 5) and to investigate correlations between forma *antarctica* shell weights and sea surface temperature (SST) and chlorophyll-*a* concentrations in the Subantarctic (Table 6).

2.4 Biogeochemical trends

One objective of this study was to seek to identify environmental variables responsible for the observed changes in mean *Limacina helicina antarctica* forma *antarctica* shell weights. We examined decadal-scale changes in both physical (temperature) and ecological (primary production) parameters at 47°S , 142°E from 1997 to 2006 by linearly interpolating twelve-month averaged sea surface temperatures (SST) (Smith and

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Reynolds, 1997) and chlorophyll-*a* concentrations (Chl-*a*) (SeaWiFS, 2008) (Fig. 5a,b). In addition, we sought to estimate changes in carbonate chemistry of the water masses the pteropods inhabit from discrete carbonate chemistry measurements made in 1995 and 2001 (Fig. 5c). Average mixed-layer (top 100 m) [CO₃²⁻] was calculated from World Climate Research Programme Climate Variability and Predictability Program (CLIVAR) and World Ocean Circulation Experiment (WOCE) SR3 transects between Tasmania and Antarctica on voyages AA9404 (Tilbrook and Rintoul, 1995) and AA0301 (Tilbrook et al., 2001). Average [CO₃²⁻] was calculated from total alkalinity, total carbon dioxide, temperature, pressure, salinity, phosphate and orthosilicate using the CO2Sys Excel macro (version 1.02)(Lewis and Wallace, 1998) and constants from Mehrbach et al. (1973) as modified by Dickson and Millero (1987). Aragonite solubility was calculated from the equation of Mucci (1983) that includes pressure adjustments K_{sp} following Ingle (1975). Pre-industrial mixed-layer [CO₃²⁻] of $\sim 193 \mu\text{mol kg}^{-1}$ was estimated by adding $38 \mu\text{mol kg}^{-1}$ to modern mixed-layer [CO₃²⁻], based on estimates of anthropogenic CO₂ inventories in the Subantarctic Southern Ocean in this sector (Sabine et al., 2004; Feely et al., 2004).

3 Results and discussion

The two morphotypes of *Limacina helicina antarctica* show different shell weight trends in our nine-year sediment trap series. There is an interannual linear shell weight trend for forma *antarctica* of $-1.17 \pm 0.47 \mu\text{g yr}^{-1}$ ($P=0.02$) (Fig. 3a; Table 4). For a constant shell size distribution and shell flux, this change in shell weight is equivalent to a reduction in calcification of $\sim 35\%$ (Fig. 3b). If this rate of shell weight decrease is valid and is sustained, *Limacina helicina antarctica* forma *antarctica* may be unable to sustain a shell by 2020. We do not find the same trend in shell weight for *Limacina helicina antarctica* forma *rangi* (Fig. 3c, d; Table 4) but both morphotypes show a decrease in flux contributions to the sediment traps from 1997/1998 to 2005/2006 (Fig. 4, Ta-

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ble 5). Total pteropod flux in our sediment trap series ranges from 2.84 mg m⁻² day⁻¹ in 1997/1998 to 0.30 mg m⁻² day⁻¹ in 2005/2006 (Table 3). Maximum flux was recorded in the first year of sediment trap collection (0.77 mg m⁻² day⁻¹) and the contribution of pteropod aragonite in that year is between 0.02 and 0.92% of the total PIC flux (Trull et al., 2001). Estimates of CaCO₃ flux in Ross Sea sediment traps (a large proportion of which is *Limacina helicina* in southern Ross Sea traps) are much greater than in this study (Collier et al., 2000) (Table 7). However, our Subantarctic pteropod fluxes are similar to those from sediment traps deployed in the deep Arctic Ocean (Fram Strait – 2000 m and Bear Island – 1700 m) in 1984/1985 (Meinecke and Wefer, 1990) where maximum flux estimates were 0.51 and 0.37 mg m⁻² day⁻¹ respectively and the pteropods *Limacina helicina* and *Limacina retroversa* collectively account for 1.7% and 0.4% of the total CaCO₃ flux to the Arctic Ocean traps (Table 7)(though these fluxes include the >1 mm size fraction).

When looking for a causal mechanism for the rate of shell weight loss in *Limacina helicina antarctica* forma *antarctica* shell weights we found no correlation (Table 6) between this morphotype and either SST (Fig. 5a) or Chl-*a* (Fig. 5b) over the past decade. We determined average mixed-layer (upper 100 m) [CO₃²⁻] has changed from 155 μmol kg⁻¹ in 1995 to 146 μmol kg⁻¹ in 2001 (Fig. 5c), implying a reduction in the saturation state for the mineral aragonite (expressed by the index Ω_{aragonite}) of

~−0.2/decade. This is consistent with other estimates of decadal-scale carbonate saturation decrease due to anthropogenic CO₂ uptake in this region (McNeil et al., 2001; Matear and Lenton, 2008). We suggest the most likely explanation for the shell weight loss observed in *Limacina helicina antarctica* forma *antarctica* is a reduction in [CO₃²⁻] in the Subantarctic Southern Ocean over the past decade. The intra-specific differences in shell weight trends between *Limacina helicina antarctica* forma *antarctica* and *Limacina helicina antarctica* forma *rangi* may be due to differences in their calcification response to changes in carbonate chemistry. The two forms of *Limacina helicina antarctica* are morphologically and ecologically distinct so distinct physiological responses in calcification are plausible.

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Alternatively, the differences in shell-weight trends may be explained by differential aragonite loss due to dissolution in the water column. The sediment trap in this study was deployed at a depth below the aragonite saturation horizon (ASH) so any pteropods falling into the trap would have been sinking through water corrosive to aragonite (Feely et al., 2002). As aragonite is more soluble in seawater than calcite (Mucci, 1983; Gehlen et al., 2005), aragonite producers will be first affected by changes in the saturation horizon. Our sediment trap samples were collected at 2000 m below the sea surface, 800 m below the Sub-Antarctic Southern Ocean's present average ASH depth of ~1200 m (Fig. 1c), and some pteropods would be likely to experience dissolution. Hence, an alternative hypothesis may be that reduced aragonite saturation is not yet inhibiting shell growth but accelerating dissolution during export to the sediment traps. To address this, we apply a semi-quantitative index of pteropod dissolution, based on shell opacity, and originally developed for the congeneric taxon *Limacina inflata* in the Atlantic (Gerhardt and Henrich, 2001), to the *Limacina helicina antarctica* shells in this study. We see signs of dissolution in 30–40% of the forma *antarctica* shells and in 50–70% of the forma *rangi* shells but there is no apparent trend in opacity for either morphotype over the last decade. As we see typically ~25% more dissolution in forma *rangi* yet no systematic shell weight change in this morphotype collected in the sediment trap series we suggest that dissolution is unlikely to be the main causal mechanism for the shell weight trend observed in forma *antarctica*.

Our observations of pteropod shell weights in the Southern Ocean indicate that there is still much to learn about aragonite calcifiers' responses to the acidifying conditions in ocean ecosystems. Recent experiments on the coccolithophore *Emiliana huxleyi* (Iglesias-Rodriguez et al., 2008) reveal potential differences in calcification response to high-CO₂ environments among morphotypes of that species. Such intra-specific differences may explain the differences in trends for the two morphotypes of *Limacina helicina antarctica*. Differential responses to elevated CO₂ conditions may result in competitive advantages that could drive ecosystem shifts (Fabry, 2008). Identifying in situ biological responses of Southern Ocean pteropods and other organisms will

require a continuous sustained sampling program in concert with targeted laboratory experiments to further elucidate responses to increasing ocean CO₂.

4 Conclusions

Our observations represent the first attempt to estimate interannual variations in pteropod calcification and establish a benchmark against which future impacts of ocean acidification may be detected. The changes in high-latitude seawater chemistry anticipated by the end of the century could alter the structure and biodiversity of high-latitude ecosystems, with impacts on multiple trophic levels (Orr et al., 2005). Though, as yet, the implications of these likely impacts are not clear, we know that pelagic molluscs can be important calcifiers in the Southern Ocean (Royal Society, 2005) and act as food sources and grazers in the Antarctic food web (Lalli and Gilmer, 1989; Seibel and Dierssen, 2003; Hunt et al., 2008). South of the Antarctic Polar Front pteropods dominate the export flux of CaCO₃ (Collier et al., 2000) and *Limacina helicina antarctica* replaces krill at times as the dominant Southern Ocean zooplankton group (Lalli and Gilmer, 1989). The production of carbonate by pteropods may also be a modulator of the efficiency of biological particulate carbon transfer to the interior of the ocean (Byrne et al., 1984). Finally, the production and dissolution of aragonite is a constraint on models of the impact of ocean acidification on pelagic ecosystems and on marine alkalinity-cycle feedbacks (Gangstø et al., 2008). As the small but discernable decadal variability we document here may represent an emerging trend we recommend closer monitoring of the Southern Ocean ecosystem for further effects on these pelagic snails, and other, marine calcifiers.

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Table 1. Sediment trap deployment, duration (# days), total number of whole shells collected per trap (n), shell flux (# shells m⁻² d⁻¹), mean and flux weighted mean shell weight (μg) for *Limacina helicina antarctica* forma *antarctica* and *Limacina helicina antarctica* forma *rangi* from 1997/1998 to 2005/2006 at 47° S, 142° E.

<i>Limacina helicina antarctica</i> forma <i>antarctica</i>					
Sediment Trap	Duration (# days)	n (#shells)	trap flux (#shells m ⁻² day ⁻¹)	mean shell weight (μg)	flux weighted mean shell weight (μg)
1997/1998	153	53	84.7	13.9	16.3
1999/2000	405	3	3.0	17.2	17.2
2000/2001	385	11	10.3	12.0	11.9
2003/2004	378	29	20.7	10.6	11.4
2005/2006	312	1	0.7	10.6	10.6
<i>Limacina helicina antarctica</i> forma <i>rangi</i>					
1997/1998	153	25	41.2	35.1	25.0
1999/2000	405	78	23.7	32.0	30.7
2000/2001	385	35	32.8	42.6	19.9
2003/2004	378	13	9.3	34.7	33.4
2005/2006	312	7	4.7	35.1	33.6

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Table 2. *Limacina helicina antarctica* morphotypes and total pteropod shell flux per sediment trap (shells $\text{m}^{-2} \text{d}^{-1}$) from 1997/1998 to 2005/2006 at 47° S, 142° E. *Limacina helicina antarctica* morphotype calculations are based on the number (n) of sediment trap cups containing those species. Total flux is based on the number (n) of sediment trap cups containing any pteropod species.

<i>Limacina helicina antarctica</i> forma <i>antarctica</i> flux						
Sediment Trap	n	Minimum	Mean	Maximum	StdDev	Total
1997/1998	8	2	11	31	10	84.7
1999/2000	3	1	1	1	0	3.0
2000/2001	7	1	1	3	1	10.3
2003/2004	9	1	2	7	2	20.7
2005/2006	1	1	1	1	–	0.7
<i>Limacina helicina antarctica</i> forma <i>rangi</i> flux						
1997/1998	7	1	6	14	5	41.2
1999/2000	12	1	2	4	1	23.7
2000/2001	11	0.2	3	18	5	32.8
2003/2004	8	1	1	3	1	9.3
2005/2006	3	1	2	3	1	4.7
Total pteropod flux						
1997/1998	17	1	8	32	9	141.2
1999/2000	18	1	3	5	1	49.7
2000/2001	16	1	7	35	11	113.7
2003/2004	10	1	3	8	2	32.9
2005/2006	3	1	2	4	2	6.7

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Table 3. *Limacina helicina antarctica* morphotypes and total pteropod mass flux per sediment trap ($\text{mg m}^{-2} \text{d}^{-1}$) from 1997/1998 to 2005/2006 at 47°S , 142°E . *Limacina helicina antarctica* morphotype calculations are based on the number (n) of sediment trap cups containing those species. Total flux is based on the number (n) of sediment trap cups containing any pteropod species.

<i>Limacina helicina antarctica</i> forma <i>antarctica</i> flux						
Sediment Trap	n	Minimum	Mean	Maximum	StdDev	Total
1997/1998	8	0.02	0.17	0.75	0.24	1.38
1999/2000	3	0.01	0.02	0.03	0.01	0.05
2000/2001	7	0.01	0.02	0.04	0.01	0.12
2003/2004	9	0.01	0.03	0.10	0.03	0.24
2005/2006	1	0.01	0.01	0.01	–	0.01
<i>Limacina helicina antarctica</i> forma <i>rangi</i> flux						
1997/1998	7	0.01	0.15	0.33	0.11	1.03
1999/2000	12	0.01	0.06	0.16	0.05	0.73
2000/2001	11	0.004	0.06	0.21	0.06	0.63
2003/2004	8	0.01	0.04	0.08	0.03	0.31
2005/2006	3	0.02	0.05	0.07	0.03	0.16
Total pteropod flux						
1997/1998	17	0.01	0.16	0.77	0.18	2.84
1999/2000	18	0.01	0.08	0.19	0.05	1.42
2000/2001	16	0.004	0.10	0.62	0.15	1.69
2003/2004	10	0.01	0.07	0.16	0.06	0.73
2005/2006	3	0.03	0.10	0.21	0.10	0.30

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Table 4a. Spearman rank-correlation coefficient test of mean shell weight trend with time for *Limacina helicina antarctica* forma *antarctica* and *Limacina helicina antarctica* forma *rangii* from 1997/1998 to 2005/2006 at 47° S, 142° E.

<i>Limacina helicina antarctica</i> forma <i>antarctica</i>	
Number of samples (<i>n</i>)	28
Alpha level ($\alpha/2$)	0.1
Spearman rank correlation coefficient	-0.285
Spearman rank correlation coefficient critical value (at $\alpha/2$)	-0.247
Significance Level (<i>P</i>)	0.14
<i>Limacina helicina antarctica</i> forma <i>rangii</i>	
Number of samples (<i>n</i>)	41
Alpha level ($\alpha/2$)	0.1
Spearman rank correlation coefficient	0.036
Spearman rank correlation coefficient critical value (at $\alpha/2$)	0.203
Significance Level (<i>P</i>)	0.77

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Table 4b. Weighted least squares regression of mean shell weight trend with time for *Limacina helicina antarctica* forma *antarctica* from 1997/1998 to 2005/2006 at 47° S, 142° E.

<i>Limacina helicina antarctica</i> forma <i>antarctica</i>	
Number of samples (<i>n</i>)	28
Alpha level ($\alpha/2$)	0.1
Slope of regression (<i>b</i>)	-1.17
Variance of slope (s^2)	0.22
Significance Level (<i>P</i>)	0.02

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Table 5. Spearman rank-correlation coefficient test of trend in pteropod flux (shells $\text{m}^{-2} \text{d}^{-1}$ and $\text{mg m}^{-2} \text{d}^{-1}$) from 1997/1998 to 2005/2006 at 47°S , 142°E .

<i>Limacina helicina antarctica</i> forma <i>antarctica</i> flux		
	shells $\text{m}^{-2} \text{d}^{-1}$	$\text{mg m}^{-2} \text{d}^{-1}$
Number of samples (<i>n</i>)	28	28
Alpha level ($\alpha/2$)	0.1	0.1
Spearman rank correlation coefficient	-0.391	-0.525
Spearman rank correlation coefficient critical value (at $\alpha/2$)	0.193	0.193
Significance Level (<i>P</i>)	0.04	0.01
<i>Limacina helicina antarctica</i> forma <i>rangi</i> flux		
	shells $\text{m}^{-2} \text{d}^{-1}$	$\text{mg m}^{-2} \text{d}^{-1}$
Number of samples (<i>n</i>)	41	41
Alpha level ($\alpha/2$)	0.1	0.1
Spearman rank correlation coefficient	-0.403	-0.344
Spearman rank correlation coefficient critical value (at $\alpha/2$)	0.158	0.158
Significance Level (<i>P</i>)	0.01	0.03
Total pteropod flux		
	shells $\text{m}^{-2} \text{d}^{-1}$	$\text{mg m}^{-2} \text{d}^{-1}$
Number of samples (<i>n</i>)	65	65
Alpha level ($\alpha/2$)	0.1	0.1
Spearman rank correlation coefficient	-0.005	-0.149
Spearman rank correlation coefficient critical value (at $\alpha/2$)	0.125	0.125
Significance Level (<i>P</i>)	0.69	0.23

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Table 6. Spearman rank-correlation coefficient test of correlation between *Limacina helicina antarctica* forma *antarctica* shell weights, sea surface temperature (SST) and chlorophyll-*a* (Chl-*a*) concentrations from 1997/1998 to 2005/2006 at 47° S, 142° E.

	SST (°C)	Chl- <i>a</i> (mg m ⁻³)
Number of samples (<i>n</i>)	28	28
Alpha level ($\alpha/2$)	0.1	0.1
Spearman rank correlation coefficient	0.025	-0.183
Spearman rank correlation coefficient critical value (at $\alpha/2$)	0.247	0.203
Significance Level (<i>P</i>)	0.90	0.34

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Table 7. Total pteropod flux ($\text{mg m}^{-2} \text{d}^{-1}$) comparisons between this study and others. Calculations are made on the number of sediment trap cups (n) that successfully captured material.

Sediment Trap Location	Duration	Depth (m)	n	Min	Mean	Max	StdDev
Subantarctic Southern Ocean ^a	1997–2006	2000	64	0.004	0.11	0.77	0.13
Northern Ross Sea Southern Ocean ^b	1996–1998	200	14	0.400	12.85	42	12.24
Northern Ross Sea Southern Ocean ^b	1996–1998	460	10	4.200	20.78	41	12.65
Southern Ross Sea Southern Ocean ^b	1996–1998	206	14	0.100	19.39	155	41.49
Southern Ross Sea Southern Ocean ^b	1996–1998	465	21	0.100	36.46	340	82.50
Southern Ross Sea Southern Ocean ^b	1996–1998	481	19	0.100	21.12	150	37.35
Fram Strait Arctic Ocean ^c	1984–1985	2000	5	<0.100	0.19	0.51	0.17
Bear Island Arctic Ocean ^c	1984–1985	1700	7	0.020	0.12	0.37	0.13
Lofoten Basin Norwegian Sea ^c	1983–1984	2761	8	0.130	6.45	18.39	7.15

^a this study: fluxes given are for pteropods in the size fraction $150 \mu\text{m}$ – 1 mm .

^b Collier et al. (2000): fluxes given are for total CaCO_3 in the size fraction $<1 \text{ mm}$. A large proportion of the CaCO_3 flux in the southern trap series is accounted for by pteropods. Mean and standard deviation values were calculated from tables in Collier et al. (2000).

^c Meinecke and Wefer (1990): fluxes given are for pteropods in the size fraction $100 \mu\text{m}$ – 3 mm . Mean and standard deviation values were calculated from figures in Meinecke and Wefer (1990).

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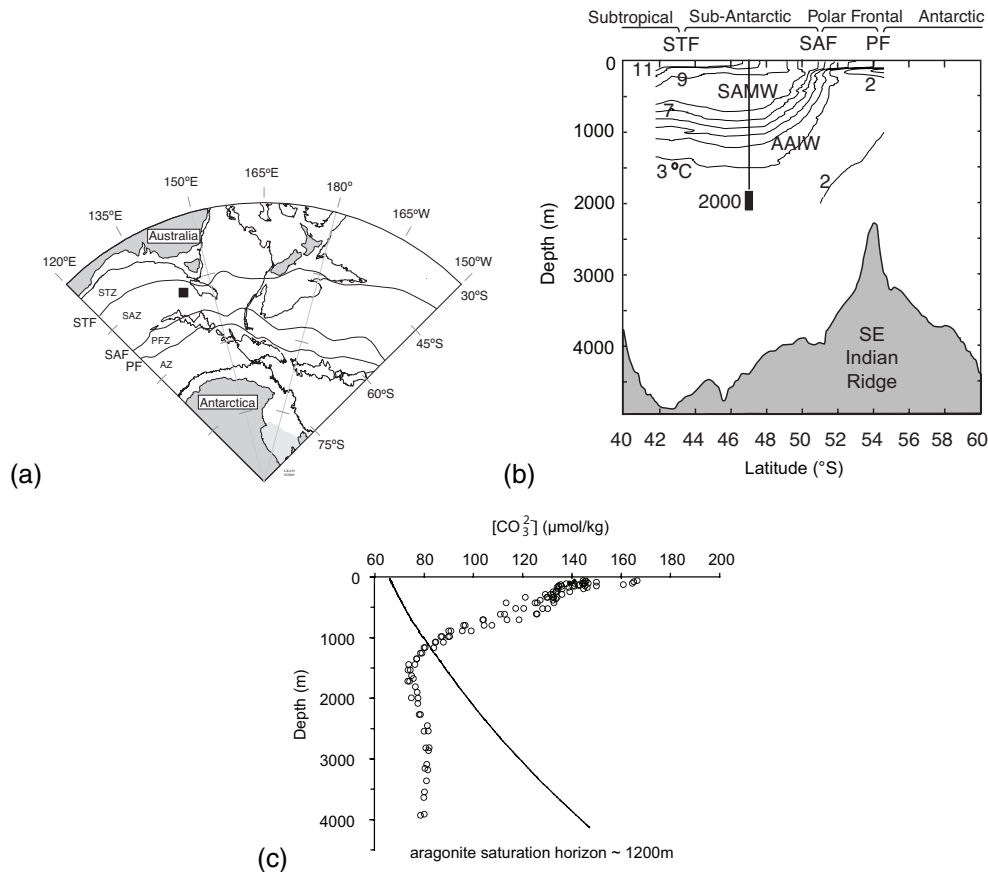


Fig. 1. (a) Sediment trap mooring location (filled square) at 47° S, 142° E. (b) Sediment trap mooring depth (2000 m), late austral summer temperature section and sea floor bathymetry in relation to the oceanographic fronts and zones of the Southern Ocean along ~142° E for the first sediment trap deployment (1997/1998). (c) CLIVAR/WOCE-SR3 vertical profile of [CO₃²⁻] between 46° S and 48° S from voyage AA0301 in 2001 (open circles) and aragonite solubility (solid line). The aragonite saturation horizon occurs at ~1200 m. STF, Sub-Tropical Front; SAF, Sub-Antarctic Front; PF, Polar Front; SAMW, Sub-Antarctic Mode Water; and AAIW, Antarctic Intermediate Water.

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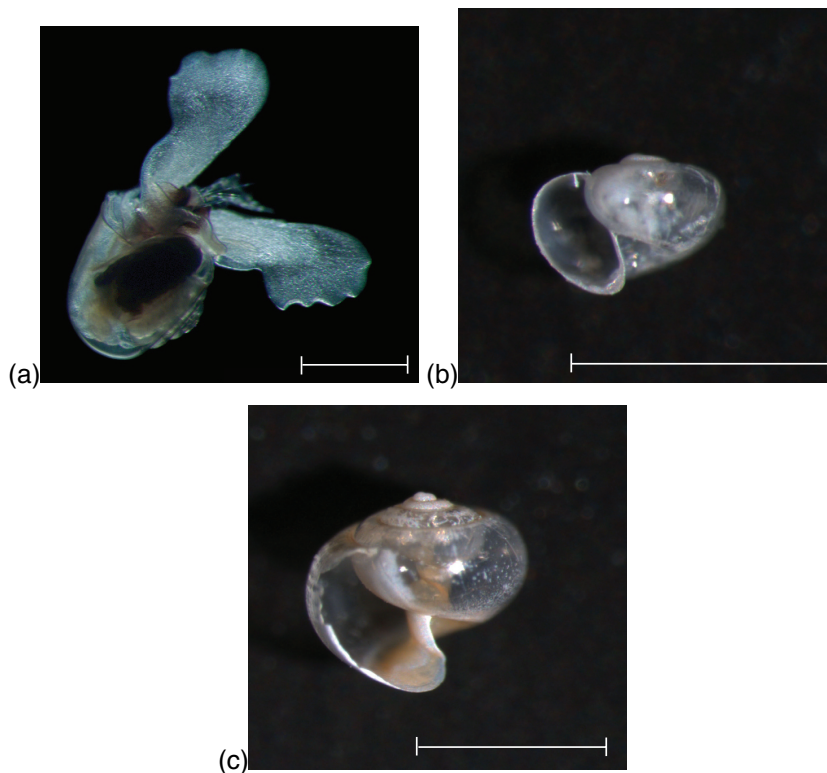


Fig. 2. (a) A living *Limacina helicina antarctica* pteropod collected and photographed aboard the *Umitaka Maru* during the 2008 International Polar Year (IPY) Collaborative East Antarctic Marine Census (CEAMARC) expedition. (b) A typical *Limacina helicina antarctica* forma *antarctica* shell. This shell collected from 2000 m at 47° S, 142° E in the 1997/1998 sediment trap (cup #16). (c) A typical *Limacina helicina antarctica* forma *rangi* shell. This shell collected from 2000 m at 47° S, 142° E in the 1999/2000 sediment trap (cup #1). All scale bars=1 mm.

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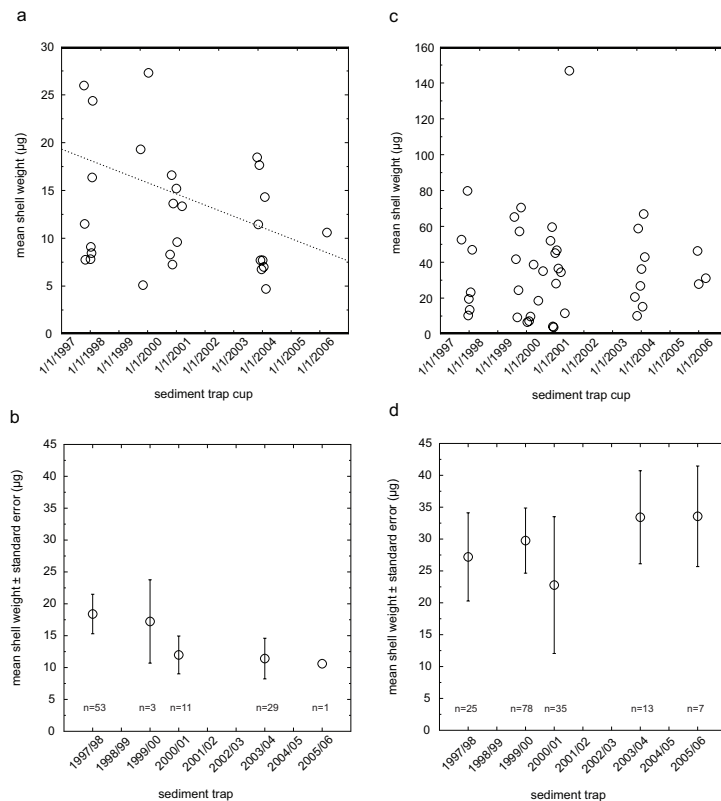


Fig. 3. (a) *Limacina helicina antarctica* forma *antarctica*: a linear decrease in mean shell weight of $1.17 \pm 0.47 \mu\text{g yr}^{-1}$ ($P=0.02$) is seen since 1997/1998. Note that the shell weight for 2005/2006 is based on a single shell. However, our estimates of trends in the data are insensitive to removal of this data point. Without this final data point, the estimated linear trend is -1.19 ± 0.49 ($P=0.02$). (b) *Limacina helicina antarctica* forma *antarctica*: flux weighted mean shell weight \pm standard error per sediment trap. Note there is no standard error estimate for the 2005/2006 shell weight data as it represents a single shell. (c) *Limacina helicina antarctica* forma *rangi*: no significant trend is seen for this morphotype's mean shell weight since 1997/1998. (d) *Limacina helicina antarctica* forma *rangi*: flux weighted mean shell weight \pm standard error per sediment trap.

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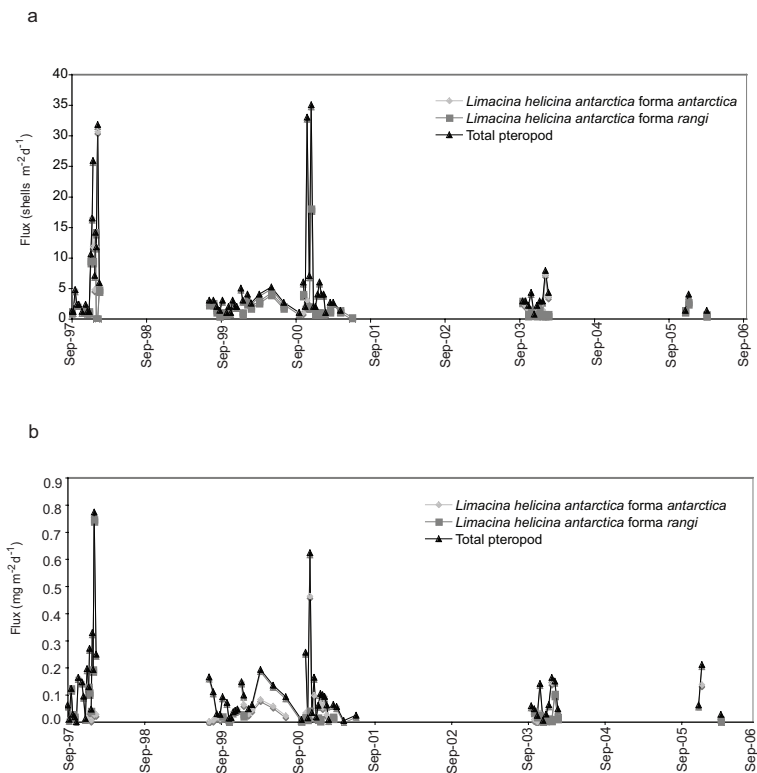


Fig. 4. (a) Flux (shells $\text{m}^{-2} \text{d}^{-1}$) of *Limacina helicina antarctica* morphotypes and total pteropods (150 μm –1 mm) at 2000 m below sea surface from the 47° S, 142° E moored sediment trap series. (b) Mass flux ($\text{mg m}^{-2} \text{d}^{-1}$) of *Limacina helicina antarctica* morphotypes and total pteropods (150 μm –1 mm) at 2000 m below sea surface from the 47° S, 142° E moored sediment trap series.

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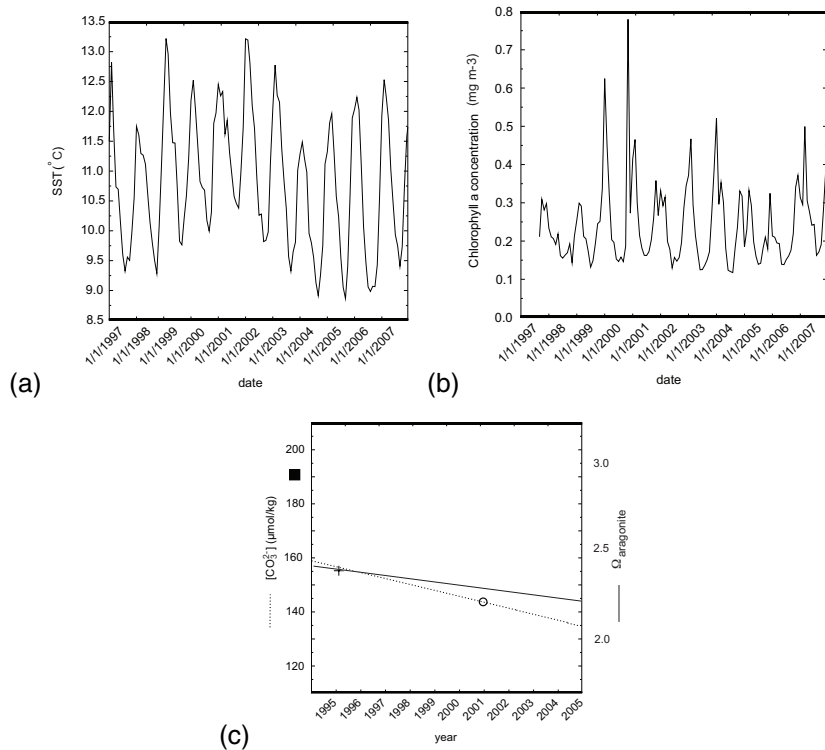


Fig. 5. (a) Twelve month averaged sea surface temperature ($^{\circ}\text{C}$) from 1997 to 2007 at 47°S , 142°E . (b) Twelve month averaged chlorophyll-*a* concentration (mg m^{-3}) from 1997 to 2007 at 47°S , 142°E . Discrete average mixed-layer (top 100 m) $[\text{CO}_3^{2-}]$ at 47°S , 142°E from CLIVAR/WOCE-SR3 voyage AA9404 in 1995 (cross) and AA0301 in 2001 (open circle). Estimated pre-industrial surface water $[\text{CO}_3^{2-}]$ (filled square) is also shown ($\sim 193 \mu\text{mol kg}^{-1}$) (calculated from Feely et al., 2004; Sabine et al., 2004). Decadal trends in $[\text{CO}_3^{2-}]$ (dashed line) and $\Omega_{\text{aragonite}}$ (solid line) are extrapolated from the discrete $[\text{CO}_3^{2-}]$ measurements above and McNeil et al. (2001) respectively.

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