Interannual to diurnal variability in the near-surface scattering layer in Drake Passage

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Backscattering strength was estimated from 127 shipboard surveys with an acoustic Doppler current profiler (ADCP) made during Drake Passage transits from 1999 to 2004. The backscattering strength is used to determine the characteristics of the near-surface scattering layer, which south of the Southern Antarctic Circumpolar Current Front (SACCF) is dominated by Antarctic krill (Euphausia superba). Diel vertical migration in the upper 150 m was the dominant variability observed in any single transect. When averaged over depth, there was a well-defined annual cycle in backscattering strength, with a factor of four increase from a late-winter minimum to a spring-summer maximum over a period of four months, followed by a more gentle decline during late summer and autumn. In addition, there were significant differences in scattering strength north and south of the Polar Front (PF) on both seasonal and interannual time-scales. The average summer maximum to the north of the PF was more than twice the maximum to the south, but the winter minima were about the same. On interannual time-scales, scattering strength south of the PF displayed a negative linear trend primarily attributable to a fourfold decrease in backscattering strength south of the SACCF. No significant long-term trend in the scattering strength north of the SACCF was observed.

Keywords: acoustic backscatter, Drake Passage, long-term changes, regional variations, seasonal variations, Southern Ocean, vertical migration.

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Introduction

Beginning with the study of Flagg and Smith (1989), many investigators have utilized the echo intensity measured by acoustic Doppler current profilers (ADCPs) to examine the distribution and variability of scattering layers in the ocean (e.g. Heywood et al., 1991; Zhou et al., 1994; Ashjian et al., 1998; Brierley et al., 2006). For ADCPs operating at frequencies between 150 and 300 kHz, the primary scatterers are zooplankton, and in these studies, significant correlations were found between backscattering strength estimated from the ADCP and zooplankton abundance estimated from net tows. Although coincident net tows are required to relate scattering strength to biomass directly, the backscatter may be useful in its own right to characterize the scattering layer and to guide biological sampling. The data can give valuable insights into depth distributions, vertical migration behaviours, and even life cycles of dominant backscatterers (Heywood, 1996; Tarling et al., 2001; Cottier et al., 2006).

This study presents a unique time-series of backscattering strength estimated from an uncalibrated, hull-mounted shipboard ADCP installed on the Antarctic supply vessel ARSV “Laurence M. Gould” (LMG) in September 1999 (Chereskin et al., 2000). The LMG is the principal supply vessel for Palmer Station, Antarctica, and it crosses Drake Passage 2–4 times per month (Figure 1). As of January 2005, 127 transects of ocean currents and acoustic backscatter had been collected. Unfortunately, no routine net sampling is conducted from the LMG within Drake Passage, although a number of long-term biological-sampling programmes have been conducted in the coastal waters surrounding the west Antarctic Peninsula from the LMG and other vessels (e.g. Smith et al., 1995; Hofmann et al., 2002; Hewitt et al., 2003; Quetin and Ross, 2003). Because the LMG transducer is uncalibrated, the backscattering-strength time-series presented in this study is relative to an unknown constant, as in the study by Heywood et al. (1991). However, as all cruises used the same transducer, operating under uniform conditions, the relative changes in backscatter over time and space are well-resolved even if the absolute level cannot be determined. Measurements made over a 6-year period, 1999–2004, are used to characterize the scattering layer in Drake Passage, its annual cycle, and interannual variability.

Methods

The vessel sails from Punta Arenas, Chile, and follows a fairly set track over the Patagonian shelf from the Straits of Magellan to the tip of Tierra del Fuego; within Drake Passage the tracks form a fan, spreading south and east (Figure 1). The typical steaming speed is 5 m s⁻¹, and the Drake crossing (1000 km) takes about two days, crossing the Polar Front (PF) about mid-passage. Though irregular in space and time, the LMG dataset provides a time-series of highly resolved (<5 km spatial resolution) backscattering strength sampled continuously along the 127 tracks shown in Figure 1. The ship crosses Drake Passage in all seasons, but the temporal coverage is slightly denser in the austral winter because

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of good data is less, depth is centred at 418 m, although the typical maximum depth collected. The first depth is centred at 26 m, and the maximum is also indicated.

2004. The open square marks the 53.55 LMG Drake Passage transits from September 1999 to December 1998; Urick, 1983): Passage transects using the following equation (RD Instruments, Harding, 1993). The recorded dataset comprises 300-s averaged profiles of currents and 4-beam averaged AGC levels. The depth of the transducer is 6 m, the “blank-after-transmit” interval is 8 m, and the depth bin is 8 m. In all, 50 profiles of current and 4-beam averaged AGC levels. The depth bin is 8 m. In all, 50

Figure 1. Map of Drake Passage region. The grey shading indicates depths <1000 m; land is shown in black. Grey dotted lines mark 127 LMG Drake Passage transits from September 1999 to December 2004. The open square marks the 53.55’S site on the Patagonian shelf transit. Black dashed lines enlose study regions north and south of the Southern Antarctic Circumpolar Current Front (SACCF). Black solid lines mark the mean positions of the Subantarctic Front (SAF), PF, and SACCF as determined from climatology by Orsi et al. (1995). The location of Elephant Island (EI) is also indicated.

The LMG does quick turnarounds to Palmer Station (four crossings per month), whereas in summer, the ship tends to stay south for up to one month to support research in the Peninsula area (two crossings per month). Biannually, there is a one-month break for a shipyard period, usually in August.

The transducer, a 153.6 kHz RD Instruments (RDI) narrowband ADCP, is installed in a sonar pod that deflects the ice and bubble-laden boundary layer. The ADCP is nominally configured to transmit a 16-m pulse along four acoustic beams orientated at 30° with respect to the vertical and equally spaced in azimuth. As part of the signal processing for currents, the received echo intensity is maintained at constant amplitude by an automatic-gain-control (AGC) loop (Flagg and Smith, 1989; Chereskin and Harding, 1993). The recorded dataset comprises 300-s averaged profiles of currents and 4-beam averaged AGC levels. The depth of the transducer is 6 m, the “blank-after-transmit” interval is 8 m, and the depth bin is 8 m. In all, 50 × 8-m depth bins were collected. The first depth is centred at 26 m, and the maximum depth is centred at 418 m, although the typical maximum depth of good data is less, ∼300 m.

Backscattering strength (S_b) in dB referenced to [m × 4π]−1 was calculated as a function of depth and latitude for all Drake Passage transsects using the following equation (RD Instruments, 1998; Urick, 1983):

\[
S_b = 10 \log_{10} \left[ \frac{4.47 \times 10^{-20} K_2 K_3 (T_x + 273)(10^{K_1 (E - E_s)/10} - 1) R^2}{c P K_1 10^{-2 a K_1/10}} \right]. 
\]

where

\[ R = \frac{B + (P - D)/4 + nD/4}{\cos(\theta) 4.17 \times 10^5}, \]  

\[ \frac{c}{1475.1}. \]

The AGC or echo intensity (E) was measured in counts (0–256) with \( E_s \), the reference level or noise count, estimated from examining the constant level measured at the end of the profile in deep water, \( E_s = 18 \). Echo-intensity counts relative to the noise level were converted from internal logarithmic units to dB using the conversion factor \( K_1 = 0.436 \text{ dB per count} \). This factor depends on the temperature of the electronics chassis, which is located in a climate-controlled laboratory maintained at ~19°C. The conversion factor varies by only 0.34% per °C, and hence a variation in temperature of a few degrees is a relatively small source of error. Ocean sound speed, \( c \), was calculated as a function of water temperature \( T_x \) at 153.6 kHz, a salinity of 34.15, and a pH of 8 appropriate for seawater (Ainslie and McCollm, 1998). \( P \) is the pulse length (16 m). Two variables that would be determined from a system calibration are \( K_1 \), the power (in W) transmitted into the water, and \( K_2 \), a dimensionless system noise factor. RDI no longer provides factory calibrations for narrowband systems, and therefore nominal values \( K_1 = 10 \) and \( K_2 = 2 \) were used here. Hence, the calculated \( S_b \) is relative rather than absolute. \( K_1 = 4.17 \times 10^5 \) is a frequency-dependent, system constant (RD Instruments, 1998). The slant range, \( R \), to depth bin \( n \) was calculated from

\[ 5 \text{Sv}\]
at 53.55°S is typical (Figure 2). The variability is due to non-exact repeating ship tracks and to the coarse resolution in determining the depth of the maximum amplitude from the 8-m water-track bin. The hypothesis of zero trend is valid at 99% confidence, and only 8% of the variance is explained by a linear fit. The standard deviation is \( \pm 1 \) dB, and the standard error in the mean is \( \pm 0.1 \) dB. We conclude that the transducer is stable to \( \pm 1 \) dB.

The major fronts of the Antarctic Circumpolar Current (ACC), the Subantarctic Front (SAF), the PF, and the Southern ACC Front (SACCF) are potentially important in structuring zooplankton communities in Drake Passage, because they are water-mass boundaries and are associated with strong, vertically coherent velocity jets. Orsi et al. (1995), hereafter referred to as O95, determined the front locations using climatological hydrographic data (Figure 1). Within Drake Passage, high-resolution repeat observations made from the LMG of upper-ocean temperature using expendable bathythermographs (XBTs) (Sprintall, 2003), and surface-layer currents from the ADCP (Lenn et al., 2007) have been used to refine the mean front locations. The mean SAF as determined from XBT and ADCP data lies north of the O95 location and closely follows the 1000-m bathymetric contour of the Patagonian shelf break (Lenn et al., 2007). Hence, the bulk of our data lie south of the SAF. The mean PF as determined from XBT and ADCP data is similar in orientation and location to O95 but on average lies \( \pm 50 \) km to the north of it (Lenn et al., 2007). To examine differences in backscattering strength north and south of the PF, the O95 PF location was determined for each transect. On cruises where XBT observations were made, we also determined the synoptic PF location. The SACCF determined from ADCP observations is in good agreement with the O95 location (Lenn et al., 2007). Most of the LMG tracks lie west of the Shackleton Fracture Zone, where O95 indicates a distinct northward meander (Figure 1) that complicates finding a unique SACCF crossing on some transects. To examine differences in backscattering strength north and south of the SACCF, the data were binned into a pair of regions enclosed by dashed lines in Figure 1 encompassing roughly equal numbers of observations.

### Results

Figure 3 shows a single section from a northbound crossing in March 2000, and Figure 4 shows a typical sequence from the crossings made in 2001 (Table 1). The intersection of the mean O95 PF with each transect is indicated (Figures 3–6). Also indicated is the time of day, to assess the importance of diel vertical migration (DVM), a known behaviour in which zooplankton descend to greater depths to escape predation during daylight and ascend to feed at night (e.g. Bollens et al., 1991; Wilson and Firing, 1992; Ashjian et al., 1998; Lenn et al., 2003). Daytime and night-time were determined from calculating the times of sunrise and sunset at 65°W, 60°S.

A clear example of a daytime descending layer is seen during lg0003 (Figure 3). North of the PF, the daytime layer has an \( S_0 \) level of about \(-87 \) dB and descends from 26 m to a depth of 150 m. A descending daytime layer is also observed to the south of the PF, but there the \( S_0 \) level is weaker, about \(-94 \) dB. By night, the overall backscatter level is higher, but distinct layers are not readily discernible. The maximum profiling depth is greater at that time of day because of deep scatterers that rise to lie within the ADCP’s range. Note, for example, the very pronounced night-time scattering layer south of the PF, in the depth range 150–350 m (Figure 3). In general, the diurnal variation in \( S_0 \) is one of the most striking features of the observations, and the features described for lg0003 can be seen in most other transects (Figure 4).

Seasonal modulation of the diurnal cycle is also readily apparent. The day/night difference is most notable in winter, when nights are long and the daytime minimum in \( S_0 \) level routinely reaches the minimum level contourled, \(-115 \) dB (Figure 4). In summer, in addition to shorter nights, the overall mean \( S_0 \) level is higher. The night-time deep-scattering maximum also seems to have seasonal variability. It first appears on the southern boundary of Drake Passage in late summer (e.g. lg0003 in Figure 3 and lg0103 in Figure 4) and subsequently is seen at progressively more northerly latitudes through autumn and winter, and is in evidence on the northern boundary of Drake Passage in spring (lg0108a in Figure 4). This deep night-time signal occurs in all sampled years.

Depth-averaged \( S_0 \) was examined to define the boundaries between regions with different characteristic \( S_0 \) levels (Figures 5 and 6). \( S_0 \) was averaged from the first recorded bin, at 26 m, to 154 m. The cut-off depth is a depth of consistently good returns that includes DVM of the surface scattering layer, except for the upper 26 m, but excludes the deeper scattering layer that is only sampled at night. Comparison of the depth-averaged signal with a fixed level of \(-100 \) dB (Figures 5 and 6) illustrates that the...
The overall signal level is higher in summer than other seasons. The most significant changes in $S_v$ level in any given transect occur at sunrise and sunset. Also apparent is the tendency for higher $S_v$ in the coastal regions at both the northern and southern boundaries of Drake Passage.

To examine the annual cycle, monthly averages of $S_v$, averaged in depth to 154 m and in latitude across the Drake Passage, were calculated. Figure 7 compares the annual cycles for the individual years (2000–2004) and the 6-year mean (1999 only partially sampled). Errors in the mean are standard errors. A spring...
transition is readily apparent, with $S_v$ increasing by an average of 6 dB from August to November, typically within 2 months. The spring-summer maximum erodes gradually through summer and autumn, reaching a minimum in late winter (August). July 2001 had the lowest monthly $S_v$ level; in 2004, the first half of the year had normal levels, but the spring maximum was anomalously low, by about 2 dB.

Synoptic PF crossings were examined for the subset of cruises (26) where XBT observations were made, and to avoid confusing geographical variability with DVM, the crossing did not coincide with local sunrise or sunset. No significant gradient in $S_v$ was observed. However, despite the lack of any abrupt change at the PF, there were quantifiable differences in $S_v$ to the north and

Table 1. Dates of Drake Passage transects in 2001.

<table>
<thead>
<tr>
<th>Cruise</th>
<th>Southbound</th>
<th>Northbound</th>
</tr>
</thead>
<tbody>
<tr>
<td>0101a</td>
<td>4–6 February 2001</td>
<td>13–14 February 2001</td>
</tr>
<tr>
<td>0103</td>
<td>20–23 March 2001</td>
<td>10–12 April 2001</td>
</tr>
<tr>
<td>0104</td>
<td>22–24 April 2001</td>
<td>1–4 June 2001</td>
</tr>
<tr>
<td>0108</td>
<td>22–24 September 2001</td>
<td>29 September – 1 October 2001</td>
</tr>
<tr>
<td>0108a</td>
<td>8–10 October 2001</td>
<td>18–19 October 2001</td>
</tr>
<tr>
<td>0108b</td>
<td>28–30 October 2001</td>
<td>9–11 November 2001</td>
</tr>
<tr>
<td>0109</td>
<td>4–6 December 2001</td>
<td>24–26 December 2001</td>
</tr>
</tbody>
</table>

Figure 5. Depth-averaged (26–154 m) $S_v$ on transects made during the first half of 2001 (Table 1). The horizontal line marks $-100$ dB and is coloured grey/black to mark day/night, respectively. Each curve is offset by $-30$ dB from the one above. The filled triangle marks the mean location of the PF (Figure 1 and Orsi et al., 1995).

Figure 6. Depth-averaged (26–154 m) $S_v$ on transects made during the second half of 2001 (Table 1). The horizontal line marks $-100$ dB and is coloured grey/black to mark day/night, respectively. Each curve is offset by $-30$ dB from the one above. The filled triangle marks the mean location of the PF (Figure 1 and Orsi et al., 1995).

Figure 7. Comparison of annual cycles of $S_v$ for individual years, averaged in depth and latitude across Drake Passage irrespective of time of day. Coloured curves with symbols are individual years (see legend). The black curve is the 6-year average annual cycle, with standard errors shown as vertical bars.
South of it (Figures 8 and 9). Averages of depth-averaged $S_v$ north of the O95 PF were higher during summer in all years compared with averages of $S_v$ south of it (Figure 8a). Because of potential bias from the diurnal cycle, the calculation was repeated using only night-time data (Figure 8b) (note that although this removes bias attributable to diel migration, it also reduces the spatial sampling by 50%). The patterns are robust, with the northern Drake Passage consistently higher than the southern Drake Passage.$S_v$ averaged over the northern Drake Passage is $\sim$5 dB higher than the southern Drake Passage during summer (Figure 8). The only times when northern Drake Passage $S_v$ levels drop to levels within 1–2 dB of those observed south of the PF are at the end of winter, when levels everywhere are at a seasonal low (Figure 9). The average winter minima north and south of the PF are about the same, differing by an amount comparable with the standard error in the mean (Figure 8).

In order to examine interannual variability, anomaly time-series were calculated. Four such series were considered: north/south of the PF using all and night-time-only data in turn. In each case, the anomaly was relative to the 6-year monthly means of the respective time-series. South of the PF, the backscatter anomaly has a negative trend, significant at 99% confidence, of $-0.04$ dB per month, corresponding to a twofold (3 dB) decline over 6 years (Figure 10). The percentage of the variance in the anomalies explained by the linear fit is 28% ($r^2 = 0.28$). North of the PF, not shown, the sign of the slope was not significantly different from zero.

The data south of the PF were binned further into a pair of regions on either side of the SACCF (Figure 1). Two series were considered: north and south of the SACCF, respectively, using all data. In each case, the anomaly is defined relative to the 6-year monthly mean of the region. The results indicate that there is a significant (99% confidence, $r^2 = 0.30$) negative trend south of the SACCF of $-0.08$ dB per month, corresponding to a 6 dB decline over 6 years (Figure 11b). North of the SACCF the fit is not significant (Figure 11a). Hence, the decline south of the PF can be further isolated to south of the SACCF.

Figure 8. (a) Comparison of mean annual cycle of $S_v$ north and south of the PF. The black curve is the 6-year mean for all of Drake Passage (DP), as shown in Figure 7. The dashed/dash-dot curve is the 6-year mean to the north/south of the PF, respectively. (b) The same as (a), using only night-time data.

Figure 9. Monthly time-series of $S_v$, averaged in depth and latitude, irrespective of time of day. The solid/dashed curve is the average over all data to the north/south of the PF, respectively.

Figure 10. Monthly anomaly in $S_v$ south of the PF. The anomaly is defined relative to the 6-year monthly mean for (a) all data south of the PF (dash-dot curve in Figure 8a), and (b) night-time data south of the PF (dash-dot curve in Figure 8b). The slope of the least squares fit in dB per month is given as the 99% confidence interval with 56 degrees of freedom.
Figure 11. Monthly anomaly in $S_r$ north and south of the SACCF. The anomaly is defined relative to the 6-year monthly mean for (a) north of the SACCF, (b) south of the SACCF. The slope of the least squares fit in dB per month is given as the 99% confidence interval with 56 degrees of freedom. The regions north/south of the SACCF are shown in Figure 1.

Discussion

Backscattering strength estimated from 127 shipboard ADCP surveys made during all seasons over a 6-year period was used to examine variability in the scattering layer in the upper 300 m of Drake Passage. Each Drake Passage crossing took about two days, and DVM was the dominant variability observed in any single transect. A shallow scattering layer descended to ~150 m during the day. At night, there was an increase in overall backscatter level and an increase, to about 300 m, in the depth range profiled, consistent with the ascent and dispersion of scatterers from below the daytime-profiling range.

There was a well-defined annual cycle in depth-averaged backscatter, with the average scattering strength increasing by a factor of four from a late-winter minimum to a spring-summer maximum over a period of four months, followed by a more gentle decline during late summer and autumn. In addition, there were significant differences in scattering levels north and south of the PF. Backscattering strength in the northern Drake Passage was consistently higher than that in the southern Drake Passage in all months, especially in summer. The average summer maximum backscatter level north of the PF was more than twice the maximum level south of the PF, but the winter minima were about the same. Interannual variability was also observed, with a fourfold decrease in backscatter south of the SACCF over six years.

Species composition

A comprehensive net-sampling campaign was carried out in the Atlantic sector of the Southern Ocean by the “Discovery” expeditions in the first part of the last century (Kemp and Bennet, 1929). From those samples, Mackintosh (1934) categorized the following species as “abundant”: the calanoid copepods, Calanus acutus, C. propinquus, and Rhincalanus gigas, the euphausiids Euphausia superba and Thysanoessa spp., the thecosome pteropod Limacina balea (now called L. retroversa australis), and the Chaetognatha. Other species that fell under the “numerous” category were Euphausia frigida and L. helicina, and the hyperiid amphipod Themisto gaudichaudii. Euphausia triacantha and E. vallentini were noted as being abundant in patches to the north of the PF. There have been very few recent net-catch surveys carried out in the north of the Drake Passage. One of the most comprehensive carried out in the southern Drake Passage in recent times was by Ward et al. (2004), who found patterns of abundance in accord with those reported by Mackintosh (1934), with calanoid copepods being the most abundant organisms, followed by Limacina helicina. Most other recent net-sampling surveys in Drake Passage have only covered the very southern extremity (Piatkowski, 1989; Siegel, et al., 2002; Hewitt et al., 2003), where E. superba frequently dominates zooplankton biomass.

Crustaceans <5 mm will have a weak target strength at 150 kHz ($< -110$ dB, Stanton et al., 1994; Greene et al., 1998), making it unlikely that the calanoid copepods contribute to backscattering patterns observed in the present study. Euphausiids are larger (10–60 mm) and have a higher target strength at 150 kHz (Buchholz et al., 1995; Tarling et al., 2001). Although thecosome pteropods such as L. helicina and L. retroversa australis are comparatively small (10–20 mm; van der Spool and Dodon, 1999), their hard aragonite shells make them a very efficient scatterer of sound (Stanton et al., 1994). Measured as echo-energy per unit biomass, the scattering strength of thecosomes was 60 times that of a euphausiid at 200 kHz (Stanton et al., 1994). Per individual, a euphausiid would have a target strength at 150 kHz of around $-80$ dB, whereas that of a thecosome pteropod would be around $-90$ dB (Tarling et al., 2001). The respective target strengths and abundances of euphausiids and thecosome pteropods make them the most likely contributors to the backscatter patterns observed in this study.

Vertical distribution and DVM

DVM in scattering layers was frequently observed in the present study. Euphausiids such as Thysanoessa spp. and E. triacantha are noted for their pronounced DVM behaviour. The former migrates vertically between 150 m and the surface over a diel cycle (Hardy and Gunther, 1935; Piatkowski et al., 1994), whereas the latter may reside as deep as 500 m by day before migrating to the surface layers at night (Baker, 1959; Piatkowski et al., 1994). The DVM behaviour of E. superba is more erratic, with some swarms showing a regular DVM cycle and others hardly ever migrating vertically (Hardy and Gunther, 1935; Eversen, 1983). Godlewksa (1996) reports that E. superba can migrate vertically between the surface and 250 m, and Demer and Hewitt (1995) reported that the biomass of E. superba peaked at the two depths of 12.5 m and 62.5 m. Hardy and Gunther (1935) provide one of the only considerations of vertical migration of L. helicina, which occupied depths of around 100 m by day, and around 20 m at night. With respect to the acoustic patterns observed in the present study, it is likely that the scattering layer migrating from the surface layer at night to around 100–150 m by day (Figure 3) consists of a combination of euphausiids and pteropods. The euphausiid E. triacantha may be partly responsible for some of the scattering layers ascending from greater depths.

Some of the transects, especially those carried out in winter, showed evidence of a deep scattering layer, usually below 300 m. Myctophids have frequently been identified as the main
that the population will increase in both abundance and individual
juveniles developing into adults to spawn the new generation
Limacina
tality increases during the challenging winter (Siegel, 2000a, b).
will oscillate over the course of the year as recruitment into the
distribution.
course of the year; and second, seasonal change in vertical
depth-averaged backscatter tended to be higher in the north of the
transect than the south, but note that the deep-scattering layer was
excluded from this calculation. This trend agrees with patterns
observed in the “Discovery” expedition net catches taken along a
similar transect line, with the relative quantity of plankton being
between 20 and 100 times higher in the northern part than in
the south (Mackintosh, 1934). Ward et al. (2004) found that
copepods as well as Limacina and Thysanoessa were particularly
abundant towards the north of the region, although they did not
sample beyond the PF. The abundance of E. triacanth a also
peaks around the PF (Baker, 1959), which may increase backscatter
to the north even further. At the northern side of the PF, it is
likely that euphausiids and thecosome pteropods become even
more abundant, especially E. vallentini and L. retroversa australis.
The abundance of the former is demonstrated by the fact that it is
the main component in the diet of many Subantarctic higher
predators (Ridoux, 1988). The latter reaches concentrations of
between 67 and 1000 individuals m\(^{-2}\) (Boltskovskoy, 1971a, b;
Dadon, 1990a, b), orders of magnitude greater than typical
concentrations of the dominant congener to the south of the PF,
L. helicina (Ward et al., 2004).
Seasonal trends in backscatter
A prominent feature in the backscattering patterns in all of the
years studied in the present investigation was the large seasonal
oscillation in biomass, with a peak in summer and a trough in
winter. This is likely to result from two major processes: first,
recruitment and mortality of individuals in populations over the
course of the year; and second, seasonal change in vertical
distribution.
In the first case, euphausiids in this region display multiyear life
cycles, meaning that the adults persist for a number of years and
population numbers are relatively stable. However, the numbers
will oscillate over the course of the year as recruitment into the
adult population peaks during the productive summer and mor-
tality increases during the challenging winter (Siegel, 2000a, b).
Limacina
normally has a 1-year life cycle, with overwintering
juveniles developing into adults to spawn the new generation
before dying in autumn (Gannefors et al., 2005). This means that the
population will increase in both abundance and individual
body size over the course of summer. The combination of these
effects will increase backscatter in line with our observations.
The second major process, seasonal change in vertical distri-
bution, occurs when certain species enter a state of diapause and
descend to depths beyond 1000 m during the winter (Schnack-Schiel, 2001). At present, most examples of this beha-
viour have been established for calanoid copepods, although
Southern Ocean euphausiids are likely to be exemplars also.
Reports of seasonal horizontal migrations have mostly been
restricted to E. superba. Here, spawning females migrate to the
outer shelf to spawn in summer and return to the shelf to spend
the winter under ice (Siegel, 1988, 2000a; Nicol, 2006). This
would mean that they would no longer be observed along the
respective survey tracks during winter, so decreasing backscatter
along its southern fringes.
Interannual decline in backscatter
The present study found there to be a significant decline in back-
sscatter south of the PF over the six years of observation, peaking in
1999 and dropping to the lowest levels in 2006. Most notably, the
largest decline was seen south of the SACCF, where the biomass is
dominated by E. superba (Siegel, 1988). Euphausia superba goes
through peaks and troughs of biomass over a 6–8-year cycle (Hewitt et al., 2003; Quetin and Ross, 2003), believed to result from
the influence of environmental factors on larval recruitment
(Quetin and Ross, 2003). At the Peninsula, for instance, Siegel
(1988) put forward the theory that recruitment of larvae was
large when the extent of ice reached its maximum. Quetin and
Ross (2003) found that larval recruitment was good in years
when conditions were around their average for the region. Patterns in the timing and extent of ice formation have been cor-
related with El Niño cycles (Kwok and Comiso, 2002), although
the exact mechanisms remain unclear (Turner, 2004).
In respect of the pattern observed in the present study, it is
possible that 1999 corresponds with the start of a 6–8-year recruit-
ment cycle, such that a decline in krill biomass is observed over the
period of study. Hewitt et al. (2003) documented a peak in krill
density in 1997/1998 and then a decline through 1999. However, they also observed krill biomass to increase in 2000
and again in 2004, contrary to present observations. This suggests
either that the LMG transect is not sampling the same krill popu-
lation as that described by them or that the significant decline in
backscatter observed over the six-year study period is being
caused by different organisms. At present, it is impossible to dis-
tinguish between these two scenarios.
It is notable in this regard that populations of planktivorous
higher predators (e.g. Adelie penguins, Pygoscelis adeliae) at
nearby islands have been declining over a number of years
(Forcada et al., 2006). Such planktivorous predators have the
capacity to switch between prey items to buffer against the episodic
cycles of abundance in their prey species over shorter time-scales,
ensuring that their population sizes remain relatively stable
(Forcada et al., 2005). Long-term declines in population size
point to a more significant environmental shift. The fact that
both planktivores and acoustic backscatter have declined over
similar periods suggests that the wider zooplankton community
is currently in a phase of decline in this region of the Southern
Ocean. This is especially true in regions where Antarctic krill
dominate, for example south of the SACCF. Such a decline may
be a result of recent warming trends in the surface waters of this
region (Meredith and King, 2005) as well as the changing ice dynamics (Vaughan et al., 2003).

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