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Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: Forcings, characteristics and implications for lower trophic levels

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ABSTRACT

The Southern Ocean is known to have warmed considerably during the second half of the 20th century but there are few locations with data before the 1950s. In addition, assessments of change in this region are hampered by the strong seasonal bias in sampling, with the vast majority of data collected during the austral summer. However, oceanographic measurements near South Georgia span most of the last century, and we here consider almost year-round data from this location over an 81-year period (1925–2006). We observe significant warming between the early and late 20th century, with differential warming between summer and winter months and an indication that late 20th century summer temperatures peaked ~6 days earlier. To quantify the long-term warming trend in this highly variable data, a mixed model utilising a Residual Maximum Likelihood (REML) method was used. Over the 81-year period, a mean increase of ~0.9 °C in January and ~2.3 °C in August was evident in the top 100 m of the water column. Warming diminished below 100 m and approached 0 at 200 m. Thus the long-term warming around South Georgia is substantial—more so than documented previously for the circumpolar warming of the Southern Ocean. We examine potential causal effects of this trend, including local atmospheric and cryospheric change, the influence of upstream waters and the role of coupled modes of climate variability such as El Niño/Southern Oscillation and the Southern Annular Mode (SAM). It is likely that all of these play a part in the observed temperature increase. However, the role of the SAM is strongly indicated, via its likely role in the circumpolar warming trend in the Southern Ocean, and also by the atypical response of the South Georgia region to changes in heat fluxes associated with the SAM. Furthermore, the combination of a regional decline in ice extent and strong upstream warming likely explains a significant part of the strong seasonal variation apparent in the warming trend. In addition, we consider the implications that long-term warming has for South Georgia's lower trophic levels. For *Euphausia superba*, at their northern limit, we find a significant negative relationship between summer South Georgia water temperatures and mean summer density of *E. superba* across the southwest Atlantic sector of the Southern Ocean. Simple abundance and growth rate relationships with our long-term temperature data appear to show declining habitat suitability for *E. superba*. In contrast, the warming trend is likely to favour other macro- and mesozooplankton species that occupy the more northerly parts of the Antarctic Circumpolar Current, and it is likely to promote phytoplankton growth.

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1. Introduction

The circumpolar Southern Ocean is known to have warmed considerably during the second half of the 20th century, with temperature increases larger than those of the global ocean as a whole (e.g. Levitus et al., 2000, 2005; Gille, 2002, 2008). The causes of this warming are not yet fully understood, but suggestions include changes in the atmosphere–ocean heat fluxes, changes in the location of the fronts of the Antarctic Circumpolar Current (ACC), acceleration and southward shifting of the subtropical circulation, and changes in the poleward flux of heat associated with oceanic mesoscale eddies (e.g. Fyfe and Saenko, 2005; Fyfe, 2006; Meredith and Hogg, 2006; Cai, 2006; Cai and Cowan, 2007; Fyfe et al., 2007; Gille, 2008; Hogg et al., 2008). Many of these proposed mechanisms have anthropogenic processes at their origin, with the strengthening of the westerly winds over the Southern Ocean commonly implicated (e.g. Thompson and Solomon, 2002; Cai, 2006).

Warming in the Southern Ocean is not spatially uniform (Gille, 2008), but there are comparatively few locations where multi-decadal temperature trends can be reliably quantified. This is a consequence of the paucity of observational data from this region; even today, the region is grossly under-sampled compared with the other major oceans, because of its remoteness and inhospitable nature.

A further restriction on our understanding of temperature changes in the Southern Ocean derives from the strong seasonal bias of *in situ* measurements. The vast majority of measurements from ships are made during the austral summer, and whilst recent advances in technology (e.g. satellites, autonomous floats) have enabled year-round coverage, the time series of such measurements are still short compared with the multi-decadal characteristic of the circumpolar warming trends (Gille, 2002). Year-round, *in situ* measurements are exceedingly rare and are most valuable.

South Georgia, at the northeastern edge of the Scotia Sea in the Atlantic sector of the Southern Ocean (Fig. 1a), is one of the few regions where a long series of *in situ* oceanographic measurements exists and where quantifications of the long-term changes in ocean properties can be attempted. South Georgia sits within the eastward flow of the ACC (Fig. 1a) and is subject to changes of both local and remote cause (Murphy et al., 2007; Meredith et al., *in press*). To the west of South Georgia the Antarctic Polar Front (APF) crosses the North Scotia Ridge (NSR) before resuming its generally eastward flow to the north of the island (Moore et al., 1999). The Southern ACC Front (SACCF) approaches South Georgia from the southwest and loops anticyclonically around its eastern flank before retroflecting eastwards near the Northwest Georgia Rise (NGR; Orsi et al., 1995; Thorpe et al., 2002; Meredith et al., 2003).

Variations in ocean temperature and salinity in the vicinity of South Georgia were documented by Deacon (1977), who summarised earlier results from the *Discovery Investigations* (e.g. Deacon, 1933, 1937) and discussed causal factors. He detailed seasonal change, identified a northwest–southeast temperature gradient between the APF and the SACCF, and documented warm years and cold years that he associated with ice coverage further south (see also Mackintosh, 1972). (Although Deacon used earlier nomenclature when referring to the ACC fronts, for clarity we use here the modern terminology throughout.) Furthermore, he linked surface water temperatures to air temperature recorded at Grytviken, situated about mid-way along the island's northern coast (Fig. 1b), and suggested there was an overall trend to a warmer climate by $\sim 0.5^\circ\text{C}$ between 1925 and 1937.

Whitehouse et al. (1996a) correlated environmental variability at South Georgia with fast-ice duration to the south but suggested that both were related to basin-scale environmental factors as opposed to a simple cause and effect. Subsequently, interannual variability and

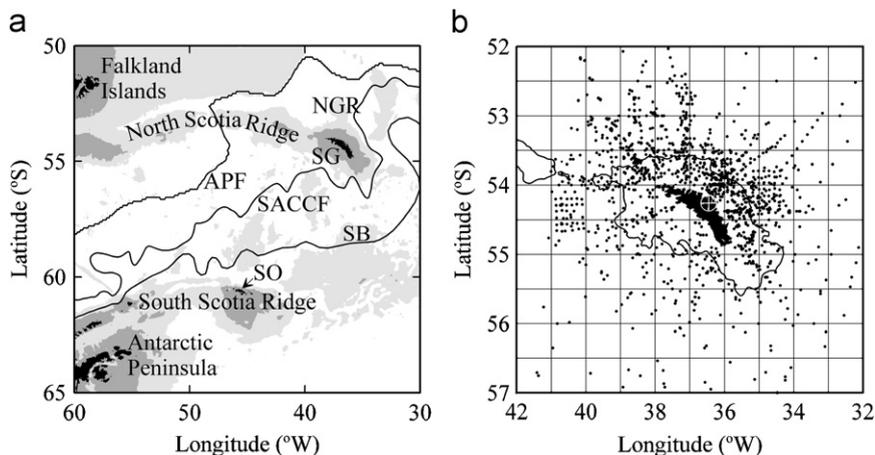


Fig. 1. (a) The Scotia Sea region showing the locations of South Georgia (SG), the Northwest Georgia Rise (NGR), the North Scotia Ridge, the South Scotia Ridge and the South Orkney Islands (SO) and mean positions of the Antarctic Polar Front (APF; Moore et al., 1999), the Southern Antarctic Circumpolar Current Front (SACCF; Thorpe et al., 2002) and the Southern Boundary of the Antarctic Circumpolar Current (SB; Orsi et al., 1995). The pale and dark grey shading is delineated by the 2000 and 500 m isobaths. (b) The study site, profile locations and modelling grid box. The 500 m isobath is marked as a solid black line and the location of Grytviken is indicated (⊕).

anomalous warming have been linked with El Niño events (Trathan and Murphy, 2003), and Meredith et al. (2005) have shown that variability associated with ENSO (the El Niño/Southern Oscillation phenomenon) can affect South Georgia far more rapidly than described previously. Meredith et al. (in press) discussed in detail the processes that control the transmission of ENSO signals to South Georgia and found that complex interactions across the South Pacific and, in particular, close to the western Antarctic Peninsula were key. They also found that variability associated with the Southern Hemisphere Annular Mode (SAM; Thompson and Wallace, 2000) controlled surface temperatures at South Georgia.

The pelagic ecosystem of South Georgia is exceptionally productive. The island's phytoplankton blooms regularly produce chlorophyll *a* (chl-*a*) concentrations $> 10 \text{ mg m}^{-3}$ and may be sustained for 4 months or more (Korb et al., 2004). They seed the ocean for hundreds of kilometres downstream and are associated with the highest predicted carbon export production in the Southern Ocean (Schlitzer, 2002). This enhanced primary production (Gilpin et al., 2002; Korb and Whitehouse, 2004) supports a rich food web that is also a valuable commercial resource (Atkinson et al., 2001).

In this paper, we have compiled a dataset from the South Georgia region that includes Deacon's measurements along with more recent British Antarctic Survey data and various other data from a variety of investigations that took place in the intervening period. This sequence of data covers 81 years, the longest ocean temperature time series yet compiled for the Southern Ocean. We concentrate on temperature changes, since possible changes in salinity are harder to robustly determine and quantify because of uncertainties surrounding the earlier salinity measurements. We consider and quantify changes to the seasonal cycle and the long-term warming trend for the period of data coverage. In addition, we consider the implications that long-term warming has for South Georgia's lower trophic levels.

2. Methods

2.1. The dataset

We defined our study site as the waters around the island of South Georgia between latitude 52°S and 57°S and between longitude 32°W and 42°W . We examined data held by the British Oceanographic Data Centre (BODC), Liverpool, UK, which included that collected during the *Discovery Investigations* (1925–1938) and miscellaneous cruises (1957–1984) along with British Antarctic Survey (BAS) measurements (1980–2006). The dataset comprised 1596 depth profiles that were predominantly collected during January (503), February (326), March (180), August (105), November (139) and December (236) with fewer measurements available for April (38), May (6), July (3), September (28) and October (32) and none for June.

Most BAS measurements were by high-resolution Conductivity–Temperature–Depth (CTD) profiler, whereas

the majority of BODC data were collected with water bottles. Gille (2008) conducted an intercomparison of temperature records from different sources and found discrepancies between CTD data and that from certain other methods (most notably expendable bathythermographs). However, bottle data were deemed suitable for use in trend analysis, and we use them here for this purpose. To account for the different depth resolutions of CTD and bottle data, we here consider narrow depth ranges (e.g. 0–10 m) to optimise the datasets' compatibility. The earlier datasets recorded depth in metres and temperature in $^{\circ}\text{C}$. Again, for compatibility, we have used these parameters from the BAS dataset, rather than pressure and potential temperature. This study focuses on the surface and near-surface layers of the ocean around South Georgia, for which temperature and potential temperature are practically equivalent.

Many of the surveys on which the data were collected emanated from the island, particularly from the northern coast where whaling stations were based during the *Discovery Investigations* and scientific bases were sited in more recent years (Fig. 1b). To compensate for geographical bias in our dataset we superimposed a grid over our study area and included a grid reference in our regression models (see Section 3.1).

In this paper, we make use of a Southern Annular Mode (SAM) index, obtained from the Climate Prediction Center of the National Centers for Environmental Prediction (NCEP). Monthly values were used, obtained from: <http://www.cpc.ncep.noaa.gov/>. We also use sea surface temperature (SST) data produced by Reynolds et al. (2002), obtained from the National Oceanographic and Atmospheric Administration Climate Diagnostics Center. The data are optimum interpolation SST values, produced on a 1-degree grid using *in situ* and satellite SST, plus SST simulated by sea-ice cover.

2.2. Statistical treatment

Temporal trends were initially examined with General Linear Models (GLMs). However, these were inadequate for a more comprehensive analysis of the data that was inevitably temporally and spatially skewed. To analyse the long-term temperature change for each month, several different sources of random variation needed to be incorporated: variation between samples within grid boxes in the same year; variation between annual changes in different grid boxes; variation between years (about the long-term). To allow for these additional sources of variation, we used a model with additional random effects. Suppose that the temperature for the *k*th observation in the *i*th grid box, in the *j*th year is denoted by y_{ijk} . The model is then written as follows:

$$y_{ijk} = m + g_i + b_j + a_j + g a_{ij} + \varepsilon_{ijk},$$

where m is an overall mean, g_i denotes a fixed effect for the *i*th grid box (a deviation from the mean) and b is the slope in the linear time trend. The remaining terms are random effects for years (a_j), a grid box \times year interaction ($g a_{ij}$), and residual variation between replicates within

boxes and years (ε_{ijk}). The random effects are assumed to vary independently and follow normal distribution with mean zero and variances V_a , V_{ga} and V_e . This mixed model contains both fixed (systematic) effects and more than one random effect. This approach uses a Residual Maximum Likelihood (REML) method to obtain estimates of the fixed effects (plus standard errors) and the variances of the random effects and overcomes the problem of pseudoreplication, which arises in the application of a GLM to responses that are not independent.

A plausible model for the periodic seasonal pattern of temperature was a cosine curve:

$$y = A + B \cos \left[\frac{2\pi(t - C)}{365} \right],$$

where t denotes time measured in days from the start of the year. (Consideration of leap years separately does not affect results.) For $B > 0$ there is a maximum of $A+B$ at $t = C$ and a minimum at $t = C+365/2$. The parameter A is the average daily temperature, and B measures the amplitude of the seasonal pattern.

3. Results

3.1. Spatial gradient

The main subject of this study is temporal variability. However, it is first necessary to address the spatial gradient across the study area and make allowance for it in the analysis of temporal trends. Across our entire study site from the northwest to the southeast, there was a highly significant temperature gradient ($p < 0.001$) for near-surface (0–10 m) waters. Deacon (1977) illustrated this temperature gradient for average values between 0 and 50 m waters around South Georgia during January and February 1930. We have replotted Deacon's data (Fig. 2) and, although modern contouring software draws the isotherms somewhat differently than Deacon did in his original hand-drawn illustration, the data consistently show two important features of water temperature around South Georgia.

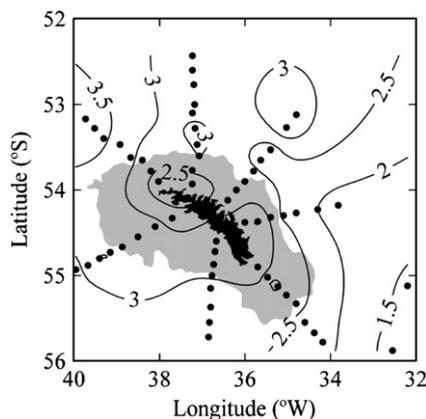


Fig. 2. Station locations (●) and average 0–50 m water temperature (°C) around South Georgia during January and February 1930, originally detailed by Deacon (1977). The dark grey shading is delineated by the 500 m isobath.

Firstly, the northwest to southeast gradient is obvious, and upon consideration of an additional two stations to the southeast, a range of $> 2^\circ\text{C}$ across the domain is evident. The orientation of this gradient is a consequence of the northward diversion of the predominantly eastward-flowing ACC, so that the usual north–south temperature gradients associated with this part of the ACC are rotated counter-clockwise as they pass South Georgia. Additionally, the colder temperatures associated with water from south of the SACCF are evident east of the 2.5°C isotherm. It is critical to allow for this substantial spatial range of temperatures at South Georgia when contemplating temporal trends. By using a grid reference (see Section 2) in all of our subsequent models, we have compensated for this source of variability.

3.2. Seasonality

The seasonal variation of near-surface (0–10 m) water temperatures was fairly small with an average summer to winter difference between 3 and 4°C (Fig. 3). A comparison of pre-1939 and post-1956 data indicates a substantial difference between early and late 20th century temperatures. Furthermore, although the amplitudes of the two periods' fitted curves are not statistically different ($p = 0.56$), there is clearly differential warming between summer and winter months. The minimum pre-1939 temperature is -1.07°C (S.E. = 0.09) compared with 0.25°C (S.E. = 0.08) for post-1956: a difference of 1.32°C (S.E. = 0.13, $z = 10.5$, $p < 0.001$). The maximum pre-1939 value is 2.67°C (S.E. = 0.05) compared with 3.41°C (S.E. = 0.06) for post-1956: a difference of 0.74°C (S.E. = 0.08, $z = 9.1$, $p < 0.001$). In addition, there is an indication that the post-1956 temperature peak occurs 5.8 days earlier than the pre-1939 (S.E. = 2.91, $z = 1.98$, $p = 0.05$).

3.3. Long-term trend

The differential warming between summer and winter months is evident if we consider the long-term trend

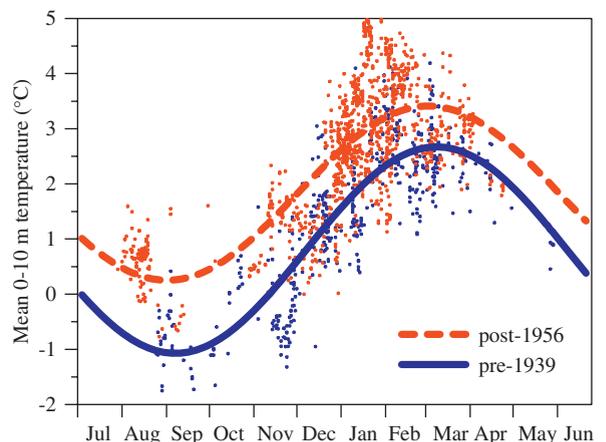


Fig. 3. Seasonal distribution of mean 0–10 m temperature (°C).

in near-surface waters between 1925 and 2006 (Fig. 4). The regression lines represent months for which we had adequate data (May, June, July and October are excluded), with those for winter lying below those for summer. The lowest regression line in Fig. 4 represents September, whereas the top-most line represents February. Between these two, the regression lines generally follow a seasonal order, as expected from the temperature trend in Fig. 3. The regression lines' convergence with time illustrates the seasonal warming anomaly with winter slopes far steeper than summer. However, these slopes do not take into consideration spatial and temporal variability or the sampling bias detailed above. To accommodate these factors we have used a REML model.

Linear trends were estimated for a series of depth ranges and months for which we had sufficient data to allow the estimation of variance components (Table 1).

Our depth ranges are restricted by the sampling frequency used with water bottle collected data. Even so, the estimates are fairly robust. The amount of warming was generally uniform throughout the top 100 m of the water column, below which it diminishes substantially between 100 and 150 m and approaches 0 at 200 m. The January and August profiles indicate the differential seasonal warming (Fig. 5), with a mean summer increase of $\sim 0.9^\circ\text{C}$ in the top 100 m compared with $\sim 2.3^\circ\text{C}$ in winter. Also, there is some indication that a small degree of warming may have occurred below 200 m, but our dataset is inadequate to estimate this with any accuracy.

4. Discussion

Our dataset indicates significant warming throughout the top 100 m of the ocean in the vicinity of South Georgia.

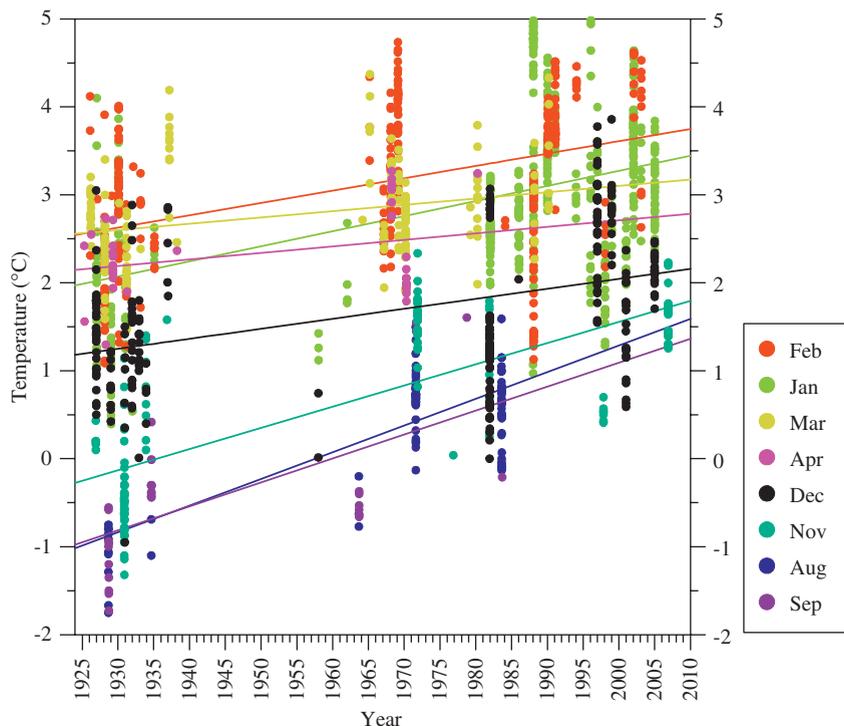


Fig. 4. Long-term monthly trend for mean 0–10 m temperature ($^\circ\text{C}$) between April 1924 and November 2006.

Table 1

Monthly temperature increase in $^\circ\text{C}$ (S.E.) between 0 and 200 m from the REML model over the 81-year period between 1925 and 2006

Depth range (m)	January	February	March	April	August	September	November	December
0–10	0.92 (0.36)	1.12 (0.41)	0.90 (0.51)	0.90 (0.68)	2.29 (0.68)	2.28 (1.35)	0.88 (0.69)	1.19 (0.39)
21–30	1.05 (0.39)	1.24 (0.45)	1.06 (0.55)	0.30 (1.09)	2.37 (0.49)	2.27 (1.35)	0.88 (0.62)	1.45 (0.37)
41–50	0.99 (0.41)	0.77 (0.45)	1.10 (0.48)	0.20 (1.10)	2.33 (0.69)	–	0.97 (0.54)	1.33 (0.37)
71–80	0.79 (0.43)	0.78 (0.33)	1.40 (0.45)	0.79 (0.71)	2.34 (0.54)	1.24 (1.41)	0.92 (0.49)	1.06 (0.42)
91–100	0.78 (0.37)	0.70 (0.30)	1.45 (0.37)	1.17 (0.73)	2.14 (0.67)	2.86 (1.81)	1.09 (0.44)	0.74 (0.32)
141–150	0.36 (0.20)	0.14 (0.18)	0.92 (0.34)	–	0.99 (0.52)	–	0.74 (0.33)	0.35 (0.14)
191–200	0.15 (0.15)	–0.17 (0.18)	0.03 (0.36)	–0.08 (0.39)	–	–	–	0.25 (0.17)

Estimates with a significant slope ($p < 0.05$) are shown in bold.

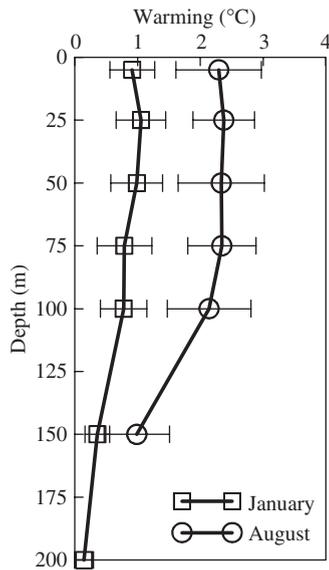


Fig. 5. Penetration of surface warming for January and August. Estimates (plus standard error bars) are from the REML model.

Overall, a simple regression of near-surface (0–10 m) temperatures with year indicates an increase of $\sim 1.54^\circ\text{C}$. When spatial and temporal variations are incorporated in the model, this equates to a skewed warming of $\sim 0.9^\circ\text{C}$ over the January months and $\sim 2.3^\circ\text{C}$ for August (Table 1). These warmings are thus very significant, exceeding even the strong warming of the near-surface circumpolar Southern Ocean noted by Gille (2008). The changes we have seen around South Georgia are unlikely to be purely local or restricted to the upper ocean, but instead reflect changes in the coupled atmosphere/ocean/ice system on a range of scales. Here we provide evidence of contemporaneous atmospheric and cryospheric changes in the South Georgia system and examine broader-scale forcings for likely causal mechanisms.

4.1. Local atmospheric change

Local monthly air temperature data are available for Grytviken, South Georgia, from January 1905 until the present day (BAS data, available at: <http://www.antarctica.ac.uk/met/READER/>). The dataset has two major gaps in the time series, between March 1982 and March 1984 and between January 1989 and April 2001. The Grytviken site is within a deep, sheltered fjord so is not an ideal location for assessing atmospheric temperatures in relation to the surrounding ocean. However, over the 102-year span of the measurements, significant warming has occurred ($+0.65^\circ\text{C}$, S.E. = 0.33, $t = 1.97$, $p < 0.05$). This equates to an increase of $\sim 0.51^\circ\text{C}$ for the 81 years covered by our ocean dataset: 1°C less than our overall seawater increase. A detrended correspondence analysis between Grytviken air temperature and near-surface (0–10 m) ocean temperature (considering both concurrent and time-lagged data) indicated significant ($p < 0.001$) coupling of local atmospheric and ocean temperatures.

However, even the greatest monthly air temperature increases between 1925 and 2006 (0.6 – 1.0°C between December and March) were substantially less than the surface ocean trend. Furthermore, the difference between air and ocean warming was far greater for the months between April and November, when the mean air temperature increase was $\sim 0.4^\circ\text{C}$ (see Table 1). Given that the atmospheric warming is consistently less than the observed ocean warming, that the seasonal variations of the temperature trends are so different, and considering the much greater heat capacity of the ocean compared with the atmosphere, this is evidence that the ocean changes we are seeing are not simply passive responses to the locally-warming atmosphere, but that other factors are also involved.

4.2. Local cryospheric change

As part of the *Discovery Investigations*, Mackintosh and Herdman (1940) compiled closed pack-ice data (i.e. sufficiently closed to bar the progress of a ship) from the early 20th century to show seasonal variation of ice extent across the Southern Ocean. The authors caution that theirs is a preliminary assessment of a complex and variable phenomenon. Nevertheless, they documented a maximum northwards ice extent that occurred between July and October and approached within 200 km of South Georgia. Exceptionally, the pack-ice extended north of the island. The ice retreated to its minimum extent at about the South Scotia Ridge ($\sim 62^\circ\text{S}$) during February and March. Recent satellite data (National Oceanic and Atmospheric Agency/National Centers for Environmental Prediction (NOAA/NCEP) indicates that the average northern extent of 15% ice concentration is to within 325 km of South Georgia, with “closed” pack-ice further south. Furthermore, the average minimum pack-ice extent is well to the south of the South Scotia Ridge. This suggests a general situation of greater ice influence near South Georgia in the *Discovery* era.

Fast-ice duration records from the South Orkney Islands (Fig. 1a) present further evidence of a long-term decline in sea-ice in the Scotia Sea. Murphy et al. (1995) present fast-ice duration data for much of the 20th century and relate their data to large-scale ice dynamics. They demonstrate links between fast-ice duration at the South Orkneys and regional variability in sea-ice extent, and they document a nonlinear decline in sea-ice (see their Fig. 3). It appears that a rapid decline in fast-ice duration, and potentially extent, occurred about mid-way through the 20th century—coincidental with the gap in our water temperature data (see Fig. 4).

The pre-satellite sea-ice record for the Scotia Sea is sparse and fragmented, and we cannot directly relate our seawater warming data to the decline in sea-ice. However, the two are clearly linked by the cyclical nature of the interdependence of seawater temperature on sea-ice formation and melt. The key point in this process is that waters that are subject to a melt/freeze cycle will show a smaller seasonal range in temperature than those that are not. Given the known changes in sea-ice extent in the

vicinity of South Georgia during the 20th century, this could explain a significant part of the seasonality in the observed ocean temperature trend. In particular, the long-term decrease in ice extent during winter implies warmer ocean conditions during this season, and indeed the ocean temperature trend we derive is strongest in winter.

4.3. *The influence of upstream waters*

Upstream of South Georgia in the southern part of the ACC flow is the western Antarctic Peninsula (WAP), where ocean temperatures have warmed considerably in recent years. Meredith and King (2005) documented a summertime increase of $\sim 1.25^\circ\text{C}$ at the WAP since the 1950s, predominantly in the upper 100 m of the water column. Water from the vicinity of the WAP takes ~ 6 months to reach South Georgia as part of the general ACC flow (Ichii et al., 1998); therefore, summer ocean conditions at the WAP will be transferred to some extent to winter conditions at South Georgia. As this water flows across the Scotia Sea, there will be heat exchange with the atmosphere; thus the winter warming at South Georgia via this process will be less than the observed summer warming at the WAP. Consequently, the WAP ocean warming certainly cannot account for all of the observed warming at South Georgia, but it may be a significant contributor. In particular, it may contribute to the extremely strong wintertime warming that we have seen in the ocean around South Georgia, hence explaining some of the season difference in the warming trends here.

4.4. *The impact of coupled modes of climate variability*

The South Georgia system is influenced strongly by physical forcing, and the role of El Niño/Southern Oscillation (ENSO) has been described previously (Trathan and Murphy, 2003; Meredith et al., 2005, *in press*). In recent decades, ENSO has shown more El Niño events compared with La Niña events, potentially inducing long-term changes in the ocean here. However, while the response at South Georgia is complex, it is unlikely that this would explain the warming we have observed. In particular, the near-instantaneous response of surface temperature at South Georgia to an El Niño event is typically one of cooling (Meredith et al., *in press*), and while there are lagged effects that subsequently may raise ocean temperatures, there are no indications that these would exceed the initial cooling effect. Conversely, the SAM is on a multi-decade rising trend (Thompson and Solomon, 2002), and it seems highly likely that this would give a warming trend at South Georgia (Meredith et al., *in press*).

The intensification of the SAM in recent decades has been associated with stronger, southward-shifted westerly winds over the Southern Ocean (Thompson and Solomon, 2002). Various studies have investigated the effect of this change in the wind field on the subtropical circulation and the ACC (e.g. Cai, 2006; Cai and Cowan, 2007), and it has been hypothesised that the ACC could accelerate and shift southwards in response; this is consistent with the behaviour of coarse-resolution

coupled climate models (e.g. Oke and England, 2004; Fyfe, 2006; Cai and Cowan, 2007). Were the real ACC to show such a response, this would bring warmer water southward, and an apparent warming at a fixed location would result; this is one of the theories that has been proposed to explain the observed warming of the Southern Ocean (e.g. Gille, 2008). However, coarse resolution ocean models typically have poor representations of the ACC's interaction with complex bathymetric regions within the Southern Ocean. While the ACC might be susceptible to a shift southwards over abyssal plains, in places characterised by rugged bathymetry (like the Scotia Sea and around South Georgia) the ACC is strongly constrained by the shape of the underlying seabed. In a recent comparison of early and late 20th century hydrography, Ward et al. (*in press*) concluded that the present path of the SACCF close to South Georgia was nearly identical to that measured during 1926/1927. Therefore, while a southward shift of the ACC might be a feasible explanation of the warming seen in some sectors of the Southern Ocean (Gille, 2008), it seems unlikely that the observed warming of South Georgia's waters can be attributed to such a shift.

Other theories that relate to the impact of the increasing SAM on ocean temperatures are more likely to be relevant to the observed warming around South Georgia. Fyfe et al. (2007) noted that the rising trend of the SAM could be associated with increased atmosphere-to-ocean heat flux, with consequent warming of the ocean. A further factor is that the stronger westerly winds associated with the increasing SAM will initially accelerate the ACC (Meredith et al., 2004), but this extra energy is subsequently cascaded to smaller (mesoscale) spatial scales via baroclinic instability (Meredith and Hogg, 2006). Mesoscale eddies in the Southern Ocean are responsible for a poleward heat flux, and recent eddy-resolving model studies show that increasing the eddy activity here results in an increased heat flux, and ultimately a circumpolar warming of the surface waters that is comparable to that observed (Hogg et al., 2008).

It is important to note that the "footprint" of the SAM-induced temperature response is unusual in the Scotia Sea around South Georgia. Fig. 6 (reproduced from Meredith et al., *in press*) shows the spatial pattern of the correlation of the SAM with remotely sensed surface temperature over the Southern Ocean (The correlations are lagged by 1 month for this plot since this is when the temperature response is clearest). It can be seen that, for much of the domain of the ACC (between $\sim 50^\circ\text{S}$ and 70°S), the response of an increase in the SAM is a near-instantaneous, short-term cooling of the ocean surface (blue shading in Fig. 6). This is a direct response of the northward Ekman transport pushing colder surface waters further north and hence producing a cooling effect at a fixed location. The warming effect due to the enhancement to the eddy field discussed above occurs some years after this (~ 3 – 4 years later), and it is this delayed eddy-induced warming that Meredith and Hogg (2006) and Hogg et al. (2008) have proposed may explain a significant proportion of the circumpolar Southern Ocean warming.

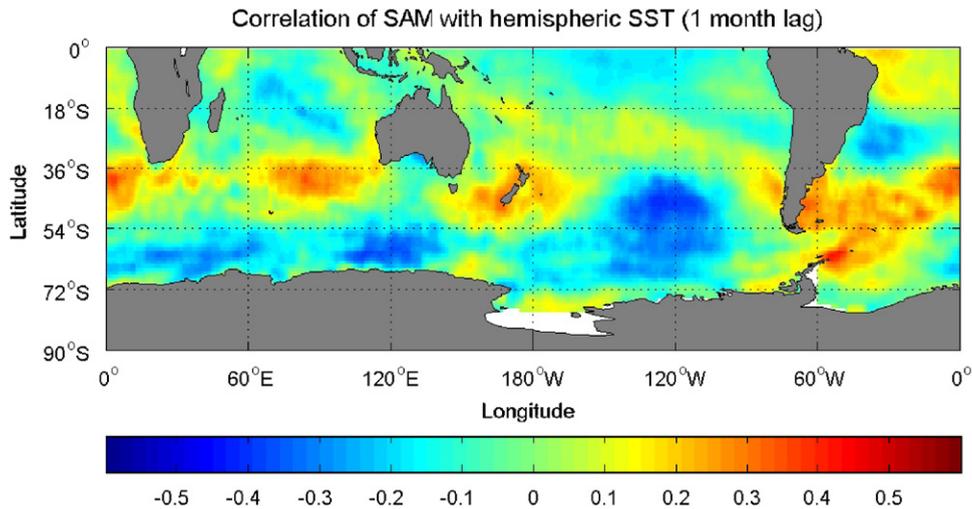


Fig. 6. Spatial pattern of the correlation of monthly Southern Hemisphere sea surface temperatures with the Southern Annular Mode (SAM) index. Red colours denote an increase in surface temperature in response to a positive change in the SAM, blue colours the reverse. Correlations are shown for a 1-month lag, which gives the clearest ocean temperature response to the SAM. Note the positive correlations around South Georgia and the Scotia Sea, unlike the negative correlations around most of the rest of the ACC's path in the Southern Ocean. From Meredith et al. (in press).

However, the region around South Georgia and the Scotia Sea is one that shows a near-instantaneous warming in response to a positive change in the SAM (red shading in Fig. 6), unlike the cooling observed for the rest of the circumpolar band in which it sits. This is a consequence of the atmosphere-to-ocean heat flux response to the SAM being anomalous in this region, with each of the sensible heat flux, latent heat flux and net radiative flux combining to give a strong positive heat flux into the ocean here for a positive SAM (e.g. Sengupta and England, 2006). This nature of response means that the upward trend in the SAM is likely to have at least two warming effects on the ocean around South Georgia: one near-instantaneous due to the strong positive heat flux response (as reflected in the sea surface temperatures in Fig. 6) and the second delayed by a number of years (the latter associated with increased eddy activity). Consequently, the upward trend in the SAM is likely to result in stronger temperature increases around South Georgia than might be expected elsewhere in the Southern Ocean, and this very likely explains a significant proportion of the very high magnitude of the warming trend that we have observed here with *in situ* data.

4.5. Implications for lower trophic levels

Polar environments are characterised by low and seasonally fairly stable temperatures relative to temperate latitudes (Fig. 3). Consequently, polar ectotherms tend to be stenothermal, with poor ability to tolerate even modest increases in temperature (Peck et al., 2004). In a study of high Antarctic marine benthos, Peck et al. (2004) showed that the onset of anaerobic metabolism (a sub-lethal effect) resulted from an increase in water temperature to only 2 °C. These authors predicted that a 2 °C rise in sea

temperature could cause population or species removal from the Southern Ocean. However, these experiments were conducted at the Antarctic Peninsula, at a site where the seasonal range in water temperatures is substantially less than we observed at South Georgia. The ~0.9 °C increase in summer temperature that we observed needs to be interpreted in the context of the lower latitude of South Georgia relative to more extreme marine environments.

Has the temperature increase last century been associated with a change within the lower trophic levels? Unlike the higher trophic levels there are very few time series for phyto- or zooplankton spanning more than 20 years. One exception is *Euphausia superba* (Antarctic krill, hereafter “krill”). This major species showed a significant decrease across the whole SW Atlantic sector during the period 1976–2003 (Atkinson et al., 2004). Their analysis was restricted to equivalent net samplers, but by introducing a standardisation procedure (Atkinson et al., 2008) to improve comparability across net sampling methods, the *Discovery* era krill densities across the SW Atlantic (30–70 °W) were found to be similar to the high values of the late 1970s and early 1980s. In Fig. 7 we have plotted these standardised krill densities (arithmetic mean density per summer season based on all sampling stations between 30°W and 70°W) against mean South Georgia surface seawater temperature for that season.

The relationship between these two variables is negative and significant ($p = 0.015$), and it has two important implications. First, it supports the veracity of these independently derived datasets, both on temperature and krill density. This is because they show a relationship that has been predicted to exist, based on an observed link between the breeding performance of krill-dependent predators and sea temperature (Trathan et al., 2006; Murphy et al., 2007). In other words the fact

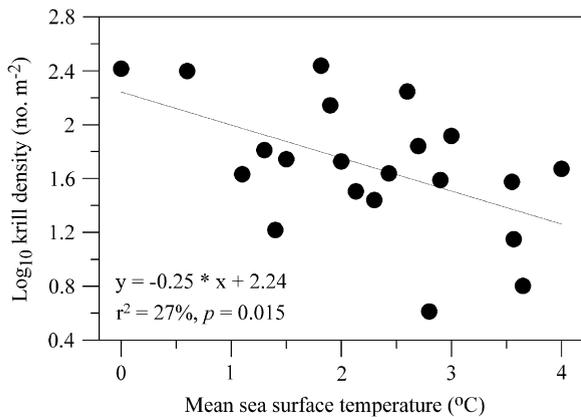


Fig. 7. Relationship between mean summer (October–April) krill density across the SW Atlantic sector, south of the APF and between 30°W and 70°W, and mean sea surface (0–10 m) temperature values from South Georgia for the same summer season. The krill data (no. postlarvae m⁻²) are based on KRILLBASE (Atkinson et al., 2008), and each point represents one summer season ($n = 21$, spanning 1928–2003) during which >50 stations were sampled.

that we observe this relationship means that the respective datasets must be capturing the inter-annual variability reasonably well. The second point concerns the large spatial scale of the krill component of this relationship, as it integrates all krill observations across the whole SW Atlantic sector. This implies that we are observing coherent, ocean basin-scale effects, rather than a local phenomenon. Again this large-scale concordance has been suggested before (Trathan and Murphy, 2003; Atkinson et al., 2004; Murphy et al., 2007). These independent sets of data provide further evidence in support, and show for the first time a link between krill density and temperature that spans several decades.

Krill are a stenothermal, cold-water species, predominantly inhabiting the seasonal sea-ice zone. South Georgia is near their warmest, northern limit, and is the only krill habitat near the APF (Atkinson et al., 2008). Experiments made near the island and across the Scotia Sea were used to develop empirical models relating krill growth to water temperature, food and body length (Atkinson et al., 2006). Krill were found to grow fastest at colder water temperatures (~0.5 °C) than typify South Georgia in summer, and growth here appears to be possible only because of the region's predictable and enhanced food supply (Atkinson et al., 2006). For a 40 mm long krill with 1 mg chl-*a* m⁻³ food, this model would predict a daily growth rate of 0.155 mm d⁻¹ for pre-1939 maximum summer temperatures (2.67 °C; Fig. 3) and 0.115 mm d⁻¹ for post-1956 maximum summer temperatures (3.41 °C). Converting this length growth to mass (Atkinson et al., 2006) would give a pre-1939 growth rate of 1.52% d⁻¹ and a post-1956 growth rate of 1.12% d⁻¹, or 73% of the early rate for equivalent food and size of krill.

However, it is important not to over-interpret the abundance and growth rate relationships as direct causative effects from temperature. Other co-variants such as ice cover also need to be considered. Atkinson et al. (2004) showed a negative relationship between ice

cover (extent and duration) and krill densities within the SW Atlantic sector, and that is possibly related to years of enhanced ice cover increasing recruitment success of krill (Siegel and Loeb, 1995).

While it appears that the increase in temperature could have had some adverse effect on krill in late summer, this “temperature penalty” will vary in severity according to food (phytoplankton) quantity, and it is possible that food may increase with elevated temperatures. Primary production in the Southern Ocean is controlled by a variety of factors that include grazing (e.g. Weber and El-Sayed, 1985; Weber et al., 1986; Banse, 1994), light availability (e.g. Sakshaug and Holm-Hansen, 1986; Tilzer et al., 1986), the availability of micronutrients (e.g. Martin et al., 1990; de Baar et al., 1995; Boyd et al., 2007) and in some more northern regions, such as South Georgia, silicic acid availability (Whitehouse et al., 2008). Additionally, phytoplankton growth may be promoted by elevated temperature. There is little direct evidence of a link between *in situ* seawater temperature and algal biomass (e.g. Holm-Hansen et al., 2004), but this is not true for *in vivo* experimental work. Indeed the work of Tilzer et al. (1986) and Smith and Harrison (1991) showed that most Southern Ocean phytoplankton are psychrotolerant, not psychrophilic, with temperature optima for growth and photosynthesis in excess of the water temperatures typically encountered.

Within the Southern Ocean, South Georgia is one of several regions where large algal blooms occur annually (Whitehouse et al., 1996b, 2000; Korb and Whitehouse, 2004; Korb et al., 2004). South Georgia's blooms occur largely to the northwest of the island in the Georgia Basin and are constrained to the north by the APF. In recent years, seawater temperatures >5 °C have been recorded in the Georgia Basin (e.g. Korb et al., 2005). In a study of natural phytoplankton populations near South Georgia, Reay et al. (2001) suggested that a 1–2 °C temperature increase could result in significantly higher growth rates and nitrate use. Indeed, anomalously cold seasons (e.g. 1981/1982) were characterised by delayed and low primary production, while warmer seasons (e.g. 1985/1986) tended to be more productive (Whitehouse et al., 1996a). Elsewhere, in the high-nutrient, low-chlorophyll waters of the subarctic Pacific, a large bloom formed in response to iron additions where water temperatures rose from 5 to 8 °C during the study (Takeda and Tsuda, 2005). These observations, together with onboard incubations, led the investigators to conclude that the bloom had formed in response to the combined effect of temperature and iron (Noiri et al., 2005). Given the generally favourable nutrient and light conditions at South Georgia, it is feasible that warmer waters enhance further one of the largest phytoplankton blooms and predicted carbon sinks in the Southern Ocean (Schlitzer, 2002; Korb and Whitehouse, 2004; Korb et al., 2004).

Within the mesozooplankton the temperature dependence of physiological functions such as copepod fecundity, embryonic development, growth and mortality is apparent from many studies (e.g. Ward and Shreeve, 1998; Hirst and Kiørboe, 2002; Hirst and Bunker, 2003; Bunker and Hirst, 2004; Ward and Hirst, 2007). Temperature

increases of 1–2 °C would act to increase fecundity and decrease development times by varying amounts, but such relationships are in many cases also influenced by factors such as food availability and body mass, and so ultimately temperature-influenced food chain effects will also be important. South Georgia lies in the ACC, and there is a balance around the island between advected zooplankton populations and locally generated production (Atkinson et al., 2001; Ward et al., 2002, 2007). Populations may therefore reflect warming processes of broadly the same order occurring upstream of South Georgia (see Meredith et al., in press).

A recent study (Ward et al., in press) compares plankton data collected around South Georgia by *Discovery Investigations* in December 1926 and January 1927 with similar surveys undertaken recently (1996–2004). Although no significant differences emerged, abundance was lowest during the 1926/1927 survey, and the cold water copepod *Calanus propinquus* was more abundant during the earlier survey. The authors caution that such change may be due to sampling artefacts, but subtle changes may have occurred and their detection is hampered by the absence of a time-series. Responses of plankton communities to warming trends in the North Atlantic Ocean over recent decades have been described by Beaugrand et al. (2002), who report significant changes in the distribution of plankton communities that appear related to increasing trends in northern hemisphere temperature and the North Atlantic Oscillation. A northward extension of > 10° of latitude of warm-water species was associated with a decrease in the number of cold-water species observed east of 20°W. The zooplankton assemblage at South Georgia comprises a variety of species with a wide spectrum of optimal temperatures (Atkinson and Sinclair, 2000). Any warming trend in the Southern Ocean is likely to favour those species that occupy the more northerly parts of the ACC and that may extend their ranges southwards. Unfortunately, the relative paucity of historical data makes the scale of such change exceedingly difficult to assess adequately.

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References

- Atkinson, A., Sinclair, J.D., 2000. Zonal distribution and seasonal vertical migration of copepod assemblages in the Scotia Sea. *Polar Biology* 23, 46–58.
- Atkinson, A., Whitehouse, M.J., Priddle, J., Cripps, G.C., Ward, P., Brandon, M.A., 2001. South Georgia, Antarctica: a productive, cold water, pelagic ecosystem. *Marine Ecology Progress Series* 216, 279–308.
- Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432, 100–103.
- Atkinson, A., Shreeve, R.S., Hirst, A.G., Rothery, P., Tarling, G.A., Pond, D.W., Korb, R., Murphy, E.J., Watkins, J.L., 2006. Natural growth rates of Antarctic krill (*Euphausia superba*): II. Predictive models based on food, temperature, body length, sex and maturity stage. *Limnology and Oceanography* 51, 973–987.
- Atkinson, A., Siegel, V., Pakhomov, E.A., Rothery, P., Loeb, V., Ross, R.M., Quetin, L.B., Schmidt, K., Fretwell, P., Murphy, E.J., Tarling, G.A., Fleming, A.S., 2008. Oceanic circumpolar habitats of antarctic krill. *Marine Ecology Progress Series* 362, 1–23.
- Banase, K., 1994. Grazing and zooplankton production as key controls of phytoplankton production in the open ocean. *Oceanography* 7, 13–20.
- Beaugrand, G., Reid, P.C., Ibanez, F., Lindley, J.A., Edwards, M., 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296, 1692–1694.
- Boyd, P.W., Jickells, T., Law, C.S., Blain, S., Boyle, E.A., Buesseler, K.O., Coale, K.H., Cullen, J.J., de Baar, H.J.W., Follows, M., Harvey, M., Lancelot, C., Levasseur, M., Owens, N.P.J., Pollard, R., Rivkin, R.B., Sarmiento, J., Schoemann, V., Smetacek, V., Takeda, S., Tsuda, A., Turner, S., Watson, A.J., 2007. Mesoscale iron enrichment experiments 1993–2005: synthesis and future directions. *Science* 315, 612–617.
- Bunker, A.J., Hirst, A.G., 2004. Fecundity of marine planktonic copepods: global rates and patterns in relation to chlorophyll *a*, temperature and body weight. *Marine Ecology Progress Series* 279, 161–181.
- Cai, W.J., 2006. Antarctic ozone depletion causes an intensification of the southern ocean super-gyre circulation. *Geophysical Research Letters* 33, L03712.
- Cai, W.J., Cowan, T., 2007. Trends in Southern Hemisphere circulation in IPCC AR4 models over 1950–99: ozone-depletion vs. greenhouse forcing. *Journal of Climate* 20, 681–693.
- Deacon, G.E.R., 1933. A general account of the hydrology of the South Atlantic Ocean. *Discovery Reports* 7, 171–238.
- Deacon, G.E.R., 1937. The hydrology of the Southern Ocean. *Discovery Reports* 15, 1–124.
- Deacon, G.E.R., 1977. Season and annual variations in water temperature and salinity near South Georgia 1925–1937. Institute of Oceanographic Sciences, Report no. 49, Unpublished manuscript.
- de Baar, H.J.W., de Jong, J.T.M., Bakker, D.C.E., Löscher, B.M., Veth, C., Bathmann, U., Smetacek, V., 1995. Importance of iron for plankton blooms and carbon dioxide drawdown in the Southern Ocean. *Nature* 373, 412–415.
- Fyfe, J.C., 2006. Southern Ocean warming due to human influence. *Geophysical Research Letters* 33, L19701.
- Fyfe, J.C., Saenko, O.A., 2005. Human-induced changes in the Antarctic Circumpolar Current. *Journal of Climate* 18, 3068–3073.
- Fyfe, J.C., Saenko, O.A., Zickfeld, K., Eby, M., Weaver, A.J., 2007. The role of poleward intensifying winds on Southern Ocean warming. *Journal of Climate* 20, 5391–5400.
- Gille, S.T., 2002. Warming of the Southern Ocean since the 1950s. *Science* 295, 1275–1277.
- Gille, S.T., 2008. Decadal-scale temperature trends in the southern hemisphere Ocean. *Journal of Climate*, early online release. doi:10.1175/2008JCLI2131.1.
- Gilpin, L.C., Priddle, J., Whitehouse, M.J., Savidge, G., Atkinson, A., 2002. Primary production and carbon uptake dynamics in the vicinity of South Georgia—balancing carbon fixation and removal. *Marine Ecology Progress Series* 242, 51–62.
- Hirst, A.G., Bunker, A.J., 2003. Growth in marine planktonic copepods: global rates and patterns in relation to chlorophyll *a*, temperature and body weight. *Limnology and Oceanography* 48, 1988–2010.
- Hirst, A.G., Kiørboe, T., 2002. Mortality in marine planktonic copepods: global rates and patterns. *Marine Ecology Progress Series* 223, 179–199.
- Hogg, A.McC., Meredith, M.P., Blundell, J.R., Wilson, C., 2008. Eddy heat flux in the Southern Ocean: response to variable wind forcing. *Journal of Climate* 21, 608–620.
- Holm-Hansen, O., Naganobu, M., Kawaguchi, S., Kameda, T., Krasovski, I., Tchernyshkov, P., Priddle, J., Korb, R., Brandon, M., Demer, D., Hewitt, R.P., Kahru, M., Hewes, C.D., 2004. Factors influencing the distribution, biomass, and productivity of phytoplankton in the Scotia Sea and adjoining waters. *Deep-Sea Research, Part II* 51, 1333–1350.
- Ichii, T., Katayama, K., Obitsu, N., Ishii, H., Naganobu, M., 1998. Occurrence of Antarctic krill (*Euphausia superba*) concentrations in the vicinity of the South Shetland Islands: relationship to environmental parameters. *Deep-Sea Research, Part I* 45, 1235–1262.

- Korb, R.E., Whitehouse, M., 2004. Contrasting primary production regimes around South Georgia, Southern Ocean: large blooms versus high nutrient, low chlorophyll waters. *Deep-Sea Research, Part I* 51, 721–738.
- Korb, R.E., Whitehouse, M.J., Ward, P., 2004. SeaWiFS in the southern ocean: spatial and temporal variability in phytoplankton biomass around South Georgia. *Deep-Sea Research, Part II* 51, 99–116.
- Korb, R.E., Whitehouse, M.J., Thorpe, S.E., Gordon, M., 2005. Primary production across the Scotia Sea in relation to the physico-chemical environment. *Journal of Marine Systems* 57, 231–249.
- Levitus, S., Antonov, J.I., Boyer, T.P., Stephens, C., 2000. Warming of the world oceans. *Science* 287, 2225–2229.
- Levitus, S., Antonov, J.I., Boyer, T.P., 2005. Warming of the world ocean, 1955–2003. *Geophysical Research Letters* 32, L02604.
- Mackintosh, N.A., 1972. Life cycle of Antarctic krill in relation to ice and water conditions. *Discovery Reports* 36, 1–94.
- Mackintosh, N.A., Herdman, H.F.P., 1940. Distribution of the pack-ice in the Southern Ocean. *Discovery Reports* 19, 285–296.
- Martin, J.H., Gordan, R.M., Fitzwater, S.E., 1990. Iron limitation in Antarctic waters. *Nature* 345 (6271), 156–158.
- Meredith, M.P., Hogg, A.M., 2006. Circumpolar response of Southern Ocean eddy activity to changes in the Southern Annular Mode. *Geophysical Research Letters* 33, L16608.
- Meredith, M.P., King, J.C., 2005. Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophysical Research Letters* 32, L19604.
- Meredith, M.P., Watkins, J.L., Murphy, E.J., Cunningham, N.J., Wood, A.G., Korb, R., Whitehouse, M.J., Thorpe, S.E., Vivier, F., 2003. An anticyclonic circulation above the Northwest Georgia Rise, Southern Ocean. *Geophysical Research Letters* 30, 2061, doi:10.1029/2003GL018039.
- Meredith, M.P., Woodworth, P.L., Hughes, C.W., Stepanov, V., 2004. Changes in the ocean transport through Drake Passage during the 1980s and 1990s, forced by changes in the Southern Annular Mode. *Geophysical Research Letters* 31, L21305.
- Meredith, M.P., Brandon, M.A., Murphy, E.J., Trathan, P.N., Thorpe, S.E., Bone, D.G., Chernyshkov, P.P., Sushin, V.A., 2005. Variability in hydrographic conditions to the east and northwest of South Georgia, 1996–2001. *Journal of Marine Systems* 53, 143–167.
- Meredith, M.P., Murphy, E.J., Hawker, E.J., King, J.C., Wallace, M.I. On the interannual variability of ocean temperatures around South Georgia, Southern Ocean: forcing by El Niño/Southern Oscillation and the Southern Annular Mode. *Deep-Sea Research II*, in press, doi:10.1016/j.dsr2.2008.05.020.
- Moore, J.K., Abbott, M.R., Richman, J.G., 1999. Location and dynamics of the Antarctic Polar Front from satellite sea surface temperature data. *Journal of Geophysical Research* 104, 3059–3073.
- Murphy, E.J., Clarke, A., Symon, C., Priddle, J., 1995. Temporal variation in Antarctic sea-ice: analysis of a long term fast-ice record from the South Orkney Islands. *Deep-Sea Research, Part I* 42, 1045–1062.
- Murphy, E.J., Trathan, P.N., Watkins, J.L., Reid, K., Meredith, M.P., Forcada, J., Thorpe, S.E., Johnston, N.M., Rothery, P., 2007. Climatically driven fluctuations in Southern Ocean ecosystems. *Proceedings of the Royal Society B* 274, 3057–3067.
- Noiri, Y., Kudo, I., Kiyosawa, H., Nishioka, J., Tsuda, A., 2005. Influence of iron and temperature on growth, nutrient utilization ratios and phytoplankton species composition in the western subarctic Pacific Ocean during the SEEDS experiment. *Progress in Oceanography* 64, 149–166.
- Oke, P.R., England, M.H., 2004. Oceanic response to changes in the latitude of the Southern Hemisphere subpolar westerly winds. *Journal of Climate* 17, 1040–1054.
- Orsi, A.H., Whitworth III, T., Nowlin Jr., W.D., 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Research, Part I* 42, 641–673.
- Peck, L.S., Webb, K.E., Baily, D.M., 2004. Extreme sensitivity of biological function to temperature in Antarctic marine species. *Functional Ecology* 18, 625–630.
- Reay, D.S., Priddle, J., Nedwell, D.B., Whitehouse, M.J., Ellis-Evans, J.C., Deubert, C., Connelly, D.P., 2001. Regulation by low temperature of phytoplankton growth and nutrient uptake in the Southern Ocean. *Marine Ecology Progress Series* 219, 51–64.
- Reynolds, R.W., Rayner, N.A., Smith, T.N., Stokes, D.C., Wang, W., 2002. An improved in situ and satellite SST analysis of climate. *Journal of Climate* 15, 1609–1625.
- Sakshaug, E., Holm-Hansen, O., 1986. Photoadaptation in Antarctic phytoplankton: variations in growth rate, chemical composition and P versus I curves. *Journal of Plankton Research* 8, 459–473.
- Schlitzer, R., 2002. Carbon export fluxes in the Southern Ocean: results from inverse modeling and comparison with satellite-based estimates. *Deep-Sea Research, Part II* 49, 1623–1644.
- Sengupta, A., England, M., 2006. Coupled ocean-atmosphere-ice response to variations in the Southern Annular Mode. *Journal of Climate* 19, 4457–4486.
- Siegel, V., Loeb, V., 1995. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Marine Ecology Progress Series* 123, 45–56.
- Smith, W.O., Harrison, W.G., 1991. New production in polar-regions—the role of environmental controls. *Deep-Sea Research A* 38, 1463–1479.
- Takeda, S., Tsuda, A., 2005. An in situ iron-enrichment experiment in the western subarctic Pacific (SEEDS): introduction and summary. *Progress in Oceanography* 64, 95–109.
- Thompson, D.W.J., Solomon, S., 2002. Interpretation of recent southern hemisphere climate change. *Science* 296, 895–899.
- Thompson, D.W.J., Wallace, J.M., 2000. Annular modes in the extratropical circulation. Part I: Month-to-month variability. *Journal of Climate* 13, 1000–1016.
- Thorpe, S.E., Heywood, K.J., Brandon, M.A., Stevens, D.P., 2002. Variability of the southern Antarctic Circumpolar Current front north of South Georgia. *Journal of Marine Systems* 37, 87–105.
- Tilzer, M.M., Elbrachter, M., Gieskes, W.W., Beese, B., 1986. Light-temperature interactions in the control of photosynthesis in Antarctic phytoplankton. *Polar Biology* 5, 105–111.
- Trathan, P.N., Murphy, E.J., 2003. Sea surface anomalies near South Georgia: relationships with the Pacific El Niño regions. *Journal of Geophysical Research* 108.
- Trathan, P.N., Murphy, E.J., Forcada, J., Croxall, J.P., Reid, K., Thorpe, S.E., 2006. Physical forcing in the southwest Atlantic: ecosystem control. In: Boyd, I.L., Wanless, S., Camphuysen, C.J. (Eds.), *Top Predators in Marine Ecosystems*, vol. 12. pp. 28–45.
- Ward, P., Hirst, A.G., 2007. *Oithona similis* in a high latitude ecosystem: abundance, distribution and temperature limitation of fecundity rates in a sac spawning copepod. *Marine Biology* 151, 1099–1110.
- Ward, P., Shreeve, R., 1998. Egg hatching times of Antarctic copepods. *Polar Biology* 19, 142–144.
- Ward, P., Whitehouse, M.J., Meredith, M.P., Murphy, E.J., Shreeve, R.S., Korb, R.E., Watkins, J.L., Thorpe, S.E., Woodd-Walker, R., Brierley, A.S., Cunningham, N., Grant, S.A., Bone, D.G., 2002. The Southern Antarctic Circumpolar Current Front: physical and biological coupling at South Georgia. *Deep-Sea Research, Part I* 49, 2183–2202.
- Ward, P., Whitehouse, M., Shreeve, R., Thorpe, S., Atkinson, A., Korb, B., Pond, D., Young, E., 2007. Plankton community structure south and west of South Georgia (Southern Ocean): links with production and physical forcing. *Deep-Sea Research, Part I* 54, 1871–1889.
- Ward, P., Meredith, M.P., Whitehouse, M.J., Rothery, P. The summertime plankton community at South Georgia (Southern Ocean): comparing the historical (1926/27) and modern (post 1995) records. *Progress in Oceanography*, in press.
- Weber, L.H., El-Sayed, S.Z., 1985. Spatial variability of phytoplankton and the distribution and abundance of krill in the Indian sector of the Southern Ocean. In: Siegfried, W.R., Condy, P.R., Laws, R.M. (Eds.), *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin, pp. 284–293.
- Weber, L.H., El-Sayed, S.Z., Hampton, I., 1986. The variance spectra of phytoplankton, krill and water temperature in the Antarctic Ocean south of Africa. *Deep-Sea Research* 33, 1327–1343.
- Whitehouse, M.J., Priddle, J., Symon, C., 1996a. Seasonal and annual change in seawater temperature, salinity, nutrient and chlorophyll *a* distributions around South Georgia, South Atlantic. *Deep-Sea Research, Part I* 43, 425–443.
- Whitehouse, M.J., Priddle, J., Trathan, P.N., Brandon, M.A., 1996b. Substantial open-ocean phytoplankton blooms to the north of South Georgia, South Atlantic, during summer 1994. *Marine Ecology Progress Series* 140, 187–197.
- Whitehouse, M.J., Priddle, J., Brandon, M.A., 2000. Chlorophyll/nutrient characteristics in the water-masses to the north of South Georgia, Southern Ocean. *Polar Biology* 23, 373–382.
- Whitehouse, M.J., Korb, R.E., Atkinson, A., Thorpe, S.E., Gordon, M., 2008. Formation, transport and decay of an intense phytoplankton bloom within the High Nutrient Low Chlorophyll belt of the Southern Ocean. *Journal of Marine Systems* 70, 150–167.