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Spatial variation in seabed temperatures in the Southern Ocean: Implications for benthic ecology and biogeography

Andrew Clarke,[1] Huw J. Griffiths,[1] David K. A. Barnes,[1] Michael P. Meredith,[1] and Susie M. Grant[1]

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[1] The Antarctic seabed has traditionally been regarded as cold and thermally stable, with little spatial or seasonal variation in temperature. Here we demonstrate marked spatial variations in continental shelf seabed temperature around Antarctica, with the western Antarctic Peninsula shelf significantly warmer than shelves around continental Antarctica as a result of flooding of the shelf by Circumpolar Deep Water from the Antarctic Circumpolar Current. The coldest shelf seabed temperatures are in the Weddell Sea, Ross Sea, and Prydz Bay as a consequence of seasonal convection associated with strong air-sea heat fluxes and sea-ice formation. These waters constitute the dense precursors of Antarctic Bottom Water, and can descend down the adjacent slope to inject cold water into the Southern Ocean deep sea. Deep sea seabed temperatures are coldest in the Weddell Sea and are progressively warmer to the east. There is a distinct latitudinal gradient in the difference between seabed temperatures on the shelf and in the deep sea, with the deep sea warmer by up to ~2 K at high latitudes and colder by ~2 K around sub-Antarctic islands. These differences have important consequences for benthic ecology and biogeography, understanding the evolutionary history of the Antarctic marine biota, and the impact of regional climate change.

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1. Introduction

[2] The Southern Ocean is the coldest marine environment on Earth. While some areas have traditionally been regarded as thermally highly stable (for example McMurdo Sound [*Littlepage*, 1965], but see *Hunt et al.* [2003]), others exhibit a seasonal variation in temperature which, though distinct, is small in amplitude by comparison with temperate waters (Signy Island [*Clarke and Leakey*, 1996] and northern Marguerite Bay [*Clarke et al.*, 2008]). The Antarctic benthic thermal environment is thus typically viewed as cold and stable, and one where small seasonal or spatial differences in temperature probably have little ecological relevance.

[3] Two recent developments have focused renewed attention on the thermal environment of Antarctic benthos. The first has been the demonstration of a distinct warming in the upper layer waters to the west of the Antarctic Peninsula and also around South Georgia in the southwest Atlantic sector of the Southern Ocean. In the Bellingshausen Sea surface waters have shown a highly significant warming over more than 1 K since 1955; the magnitude of this warming decreases with depth and is negligible at 100 m [*Meredith and King*, 2005]. A longer data series is available for South Georgia (1925 to date), and this reveals a significant warming between the early and late 20th century. During this period there has been a mean increase in the temperature of the top 100 m of the water column of ~2.3 K in August (austral winter) and ~0.9 K in January (austral summer), with peak summer temperatures occurring ~6 days earlier in more recent decades [*Whitehouse et al.*, 2008].

[4] The second has been the discovery that some Antarctic marine organisms are highly sensitive to quite small increases in temperature [*Peck*, 2002; *Peck et al.*, 2004]. While these experimental investigations typically involve rates of temperature increase that are rapid compared with seasonal change or long-term secular warming, they do suggest that quite small changes in ambient temperature may have serious consequences for Antarctic benthos (but see *Barnes and Peck* [2008]). To put these observations in context we need a clearer idea of the environmental setting. Here we report an analysis of seabed temperatures over the Antarctic continental shelf, continental slope and deep sea of the Southern Ocean. We highlight several features of the spatial variability in seabed temperature which, while being known to physical scientists, have important ecological and evolutionary implications that have been previously under-appreciated.

1.1. Oceanographic Context

[5] The Antarctic continental shelf is unusually deep. Large areas are below 500 m, with glacial gullies extending

[1]Biological Sciences Division, British Antarctic Survey, NERC, Cambridge, UK.

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in places to depths of over 1000 m; this compares with a mean depth of continental shelves elsewhere of <100 m [*Walsh*, 1988]. The unusual depth of the continental shelves around Antarctica is caused by two principal factors: isostatic depression resulting from the enormous mass of continental ice, and scouring of surficial sediments as the ice sheet extended over the continental shelf during previous glacial maxima. This scouring has also produced an unusual profile for the shelf, which is often deeper close to the continent, and shallower toward the shelf break. Bathymetric profiles indicate that the boundary between the continental shelf and slope around Antarctica varies from around 500–600 m in some locations, to around 900–1000 m in others; the transition also varies from sharply defined to more gentle. In order to simplify the analyses, we use the 1000 m isobath to define the boundary of the continental shelf (as was used in previous biogeographical analyses [*Clarke and Johnston*, 2003; *Clarke et al.*, 2007a, 2007b]). The transition from continental slope to abyssal plain is typically at around 3000 m.

[6] The benthic environment of all continental shelves is influenced strongly by interaction with the overlying water column. The shallow depth of most non-Antarctic continental shelves means that the seasonal mixed layer can reach the seabed, and hence interact directly with the benthic environment. The Antarctic continental shelves are very different in that, with the exception of shallow nearshore areas, the seabed lies well below the mixed layer, which in the western Antarctic Peninsula area can extend to 150 m [*Meredith et al.*, 2004; *Clarke et al.*, 2008]. However, in regions such as the Weddell and Ross Seas, intense seasonal air-sea fluxes and ice production generates very dense cold water that drives deep convection in autumn and winter to the bottom of the shelf [*Fahrbach et al.*, 1995]. This dense shelf water can convect down the continental slope in key locations, entraining warmer, more saline, water from intermediate depths as it descends. This is one of the key processes that leads to the formation of Antarctic Bottom Water (AABW) in regions such as the Weddell Sea and Ross Seas (see *Whitworth et al.* [1998] for a review). Such seasonal downslope convection has also been detected to the north of Elephant Island [*Meredith et al.*, 2003], which lies beyond the northernmost extension of mainland Antarctic and is separated from the continental shelf of western Antarctic Peninsula by the deep waters of Bransfield Strait.

[7] The uppermost waters over the continental shelf are typically very variable in both temperature and salinity, because of interaction with the atmosphere and cryosphere. Traditionally termed Antarctic Surface Waters (AASW), they typically cool and gain salt from sea-ice formation as summer moves into winter, then warm and freshen from winter to summer as a result of insolation and ice melt [*Klinck*, 1998]. The spring melt of surface ice can lead to strong stratification with relatively warm surface layers in summer; this seasonality is seen down to depths ~100 m [*Meredith et al.*, 2004]. The creation of a relatively warm and fresh surface layer during summer leads to isolation of the remnant of the cold winter mixed layer from the atmosphere. This can result in a subsurface temperature minimum, traditionally referred to as Winter Water (WW) [*Mosby*, 1934].

[8] Whereas the coasts of the Weddell and Ross Seas are separated from the Antarctic Circumpolar Current (ACC) by large regional gyres, at the edge of the western Antarctic Peninsula (WAP) continental shelf, the waters of the ACC lie immediately adjacent to the slope. This proximity is significant, since it means that waters from the ACC can intrude directly onto the continental shelf in forms that are much less modified than elsewhere around the continent; glacially carved canyons are believed to be especially important in this context [*Klinck*, 1998; *Hofmann and Klinck*, 1998; *Dinniman and Klinck*, 2004]. Of prime importance is Circumpolar Deep Water (CDW), the water mass that occupies the middle levels of the ACC. This is usually divided into upper (shallower) and lower components (UCDW and LCDW, respectively), with UCDW being characterized by a maximum in potential temperature, relatively high-nutrient contents, and a low oxygen content [*Hofmann et al.*, 1996; *Meredith et al.*, 2004]. Incursions of UCDW are important in bringing heat and nutrients onto the continental shelf. Over the period 1993 to 2002, UCDW flooded large areas of the WAP continental shelf in most years, and this appears to be a reasonably consistent feature of shelf oceanography in this region [*Ducklow et al.*, 2007]. These features can be seen very clearly in the representative conductivity-temperature-depth (CTD) cast from Marguerite Bay in summer (Figure 1 (left)). Here a warm summer surface layer (~1°C) overlies the remnant WW which exhibits a temperature minimum of −1.61°C at a depth of 71 m. Water below the WW is significantly warmer, and from ~300 m to the seabed the temperature is uniformly relatively warm (>+1°C).

1.2. Regional Differences Around America

[9] In contrast, a CTD cast from the Weddell Sea shelf (Figure 1 (right)) shows a quite different thermal structure. Here the summer surface waters are much colder than to the west of the Antarctic Peninsula, and the deeper waters below ~100 m are uniformly cold. The Weddell Gyre that separates the ACC from the continental shelf in this region means that any intrusions of CDW that influence the Weddell Sea do so in a highly modified form. CDW that penetrates into the Weddell Gyre is typically termed Warm Deep Water (WDW) and is significantly cooler than CDW in the ACC. As a result of this, and the seasonal deep convection associated with the very strong atmosphere-ocean heat fluxes and ice production in this area, the thermal environment of the Weddell Sea shelf seabed is dominated by shelf waters with temperatures much lower than in the WAP, and which are typically around freezing point [*Carmack*, 1990].

[10] CTD profiles from the Antarctic continental shelf can be highly variable depending on season, proximity to ice shelves, and the presence or absence of intrusions at intermediate depths of warmer water. Nevertheless the two representative CTD traces shown here (Figure 1) demonstrate the strong differences between the western Antarctic Peninsula continental shelf, where the seabed is warmed by relatively unmodified CDW, and much of the rest of the Antarctic continental shelf, where it is not. They also illustrate that there are marked regional differences in the temperature of the seabed on the Antarctic continental shelf, differences that may have strong ecological consequences.

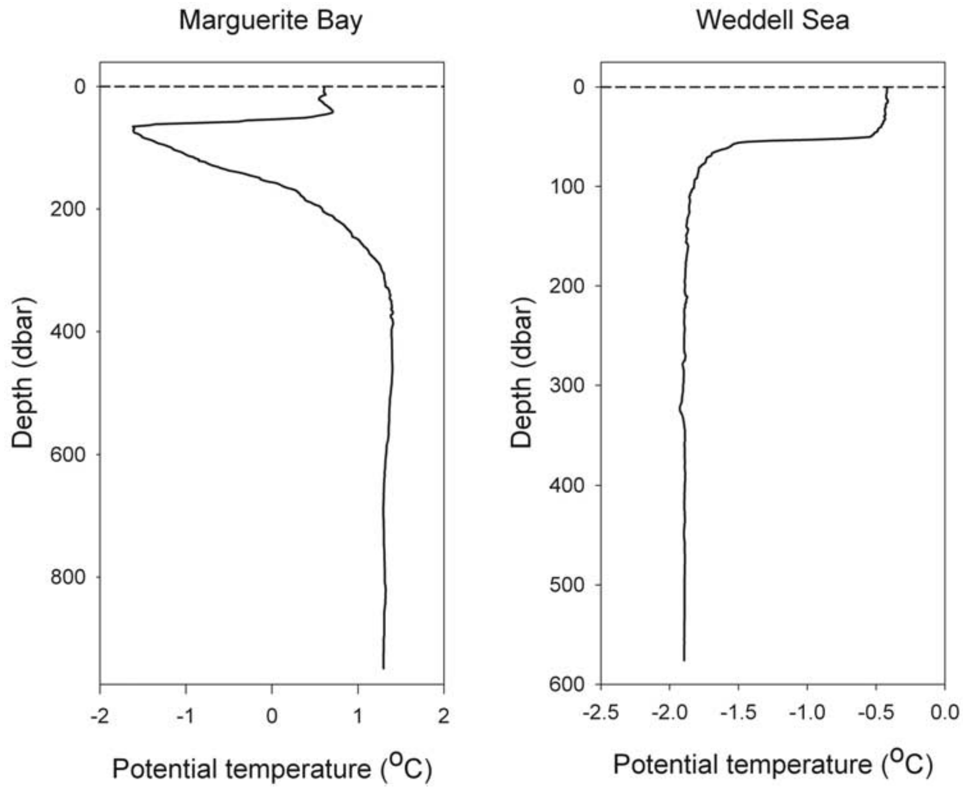

Figure 1. Representative CTD casts from the continental shelf around Antarctica. (left) Marguerite Bay in summer (18° 54.07′S, 70° 20.75′W, 18 February 2006) and (right) the Weddell Sea shelf in summer (74° 26.77′S, 59° 01.28′W, 1 February 1998).

These spatial variations and their ecological consequences are explored in this paper.

2. Materials and Methods

[11] Data were taken from the World Ocean Atlas 2005, a data product of the Ocean Climate Laboratory of the U.S. National Oceanographic Data Centre (http://www.nodc.noaa.gov/OC5/WOA05/pr_woa05.html). Data were global mean annual ocean in situ temperature data interpolated into 33 standard vertical intervals (depth ranges) at a 1° spatial resolution, and were overlaid onto a bathymetry grid (ETOPO1) [*Amante and Eakins*, 2008]. Temperature data then were extracted where the depth range coincided with the bathymetry of the seafloor at that location to create a seafloor data set. Potential sources of error here include poorly known bathymetry, or a sparse spatial coverage of temperature data. The initial maps were therefore reviewed, and where inconsistences were noted, bathymetric and seabed temperature data were updated in the light of more recent knowledge [e.g., *Jenkins and Jacobs*, 2008]. Potential temperature was calculated according to the UNESCO equation of state for seawater and ITS-90. A nearest neighbor interpolation was then used to create a seafloor temperature grid for both in situ and potential temperature in ArcGIS. While this grid is unable to resolve in detail the relatively small-scale topographic features that can be responsible for CDW or WDW reaching shelf regions, or dense waters leaving the shelf, the intention here is to investigate the larger-scale variation in seabed temperature. For statistical analysis each 1° box was assigned a mean depth and temperature (both in situ and potential). Each box was also classified on the basis of mean depth as shelf (0–1000 m), slope (1000–3000 m) or deep sea (>3000 m). All statistical analyses were undertaken using Minitab (v15).

3. Results

3.1. Continental Shelf

[12] The large-scale spatial distribution of potential seabed temperature on the Antarctic continental shelf is shown in Figure 2. The coldest seabed temperatures are found nearshore in the larger embayments such as the Weddell Sea, Ross Sea and Prydz Bay, as a consequence of seasonal convection of dense surface waters and interaction with the adjacent ice shelves. In all three cases, seabed temperatures are warmer toward the edge of the shelf, as the shelf waters are warmed by interaction with other water masses.

[13] As noted above, the Weddell Gyre means that any CDW that reaches the Weddell Sea continental shelf from the ACC does so only in a highly modified form (WDW). Furthermore the deep waters of the Weddell Sea shelf are also strongly influenced by very cold water produced by interaction of shelf water with the underside of floating ice shelves [*Weiss et al.*, 1979] together with the generation of cold dense water in polynyas and during the formation of sea ice. The large embayments of the Ross Sea and Prydz Bay also have very cold bottom temperatures.

[14] In contrast to the shelves around continental Antarctica, the western Antarctic Peninsula (WAP) shelf is distin-

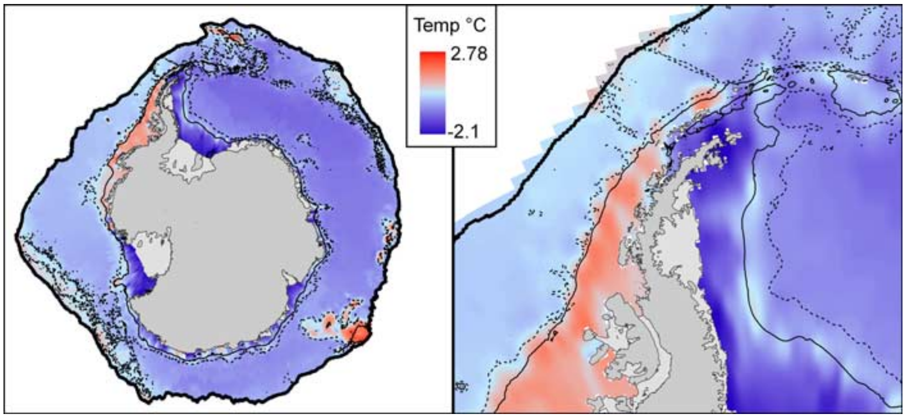

Figure 2. Spatial distribution of bottom (seabed) potential temperatures around Antarctica. (left) Circumpolar distribution of seabed temperature, emphasizing the colder temperatures on shelves closer to the ice shelves and the warmer temperatures of abyssal water in an eastward (clockwise) direction. (right) Detail for the Antarctic Peninsula, emphasizing the areas where shelves are warmed by CDW from the ACC. Note the marked contrast between the Bransfield Strait and the outer shelf at the northern end of the Antarctic Peninsula. The 1000 and 3000 m isobaths are shown, and data extend to the mean position of the Antarctic Polar Front.

guished by its markedly warmer bottom temperatures. These warmer seabed temperatures extend from the outer shelf at the South Shetland Islands to the north, to the nearshore areas of the Bellingshausen and Amundsen Seas (Figure 2 (left)). The majority of the continental shelf in this sector is kept warm by the influence of the UCDW from the ACC, and the marked difference in shelf seabed temperature this induces can be seen in the comparison with the two major embayments (Weddell Sea, Ross Sea) and the shelf around continental Antarctica (everywhere else) (Figure 3 (left)). The median temperature of the WAP shelf seabed is ~2 K warmer than either the Weddell Sea and Ross Sea shelves, and ~1.5 K warmer than the shelves of continental Antarctica; these differences are statistically significant (ANOVA, sector as fixed factor: $F(3, 583) = 66.6$, $p < 0.001$).

[15] Although the seabed temperatures of the WAP continental shelf are generally warm, they do exhibit important variability at smaller scales (Figure 2 (right)). At the northern end of the Antarctic Peninsula there is a region of very low seabed temperatures in Bransfield Strait between the peninsula and the South Shetland Islands, caused by a cold water entering from the Weddell Sea [*Hofmann et al.*, 1996]. Outside the South Shetland Islands, between the archipelago and the edge of the continental shelf there appears to be a mixture of warm and cool water. There is also an apparent cool region to the west of the Wilkins Ice Shelf, Alexander Island, between Charcot Island and Latady Island (Figure 2 (right)). Given that CDW is believed to flood the entire continental shelf in the WAP area [*Ducklow et al.*, 2007; *Jenkins and Jacobs*, 2008], and is a key supply of heat to melt ice shelves, we believe that these two anomalously cool areas are artifacts related to errors in bathymetry or paucity of direct measurement and that further data will reveal a more uniform distribution of warm temperatures from CDW flooding the entire WAP continental shelf.

[16] The water column temperature field over the continental shelf deepens westward (anticlockwise), with the isotherms deeper over the Amundsen Sea shelf than over

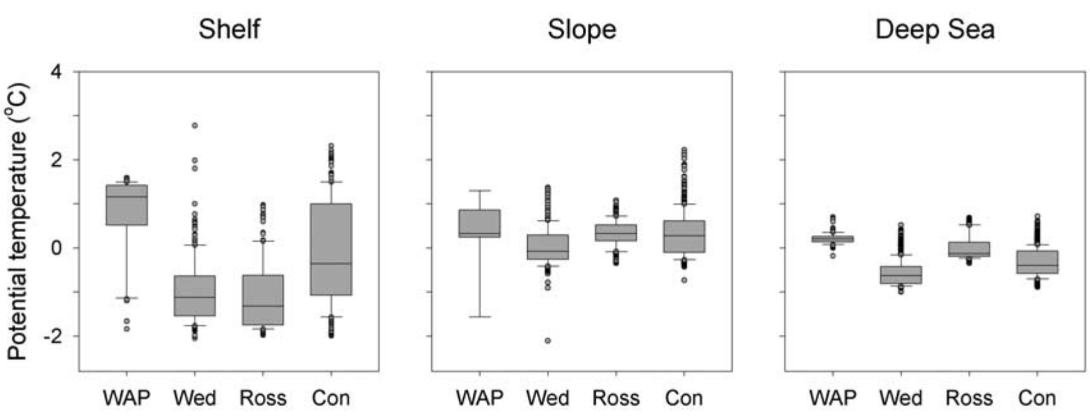

Figure 3. Box plots summarizing seabed potential temperatures for the continental shelf (0–1000 m), the continental slope (1000–3000 m) and the deep sea (>3000 m). Data are shown separately for the western Antarctic Peninsula, the Weddell Sea, the Ross Sea, and the remainder of continental Antarctica.

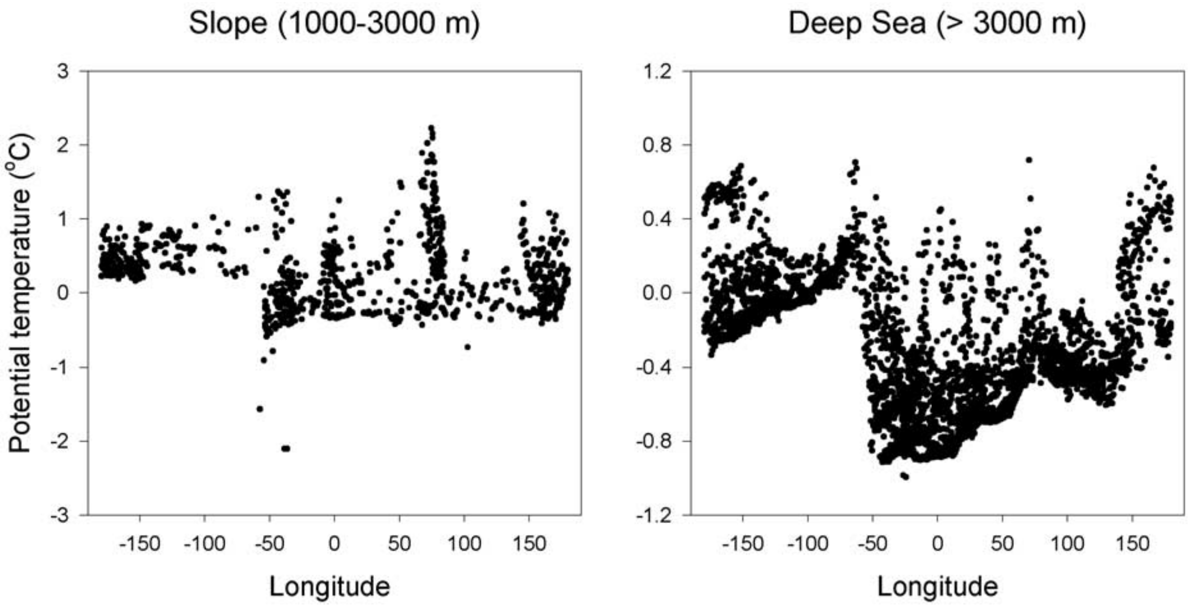

Figure 4. Longitudinal (circumpolar) distribution of seabed potential temperature for the continental slope (1000–3000 m) and deep sea (>3000 m) in the Southern Ocean. By convention eastern longitudes are positive and western longitudes are negative.

the shelves of the WAP or Bellingshausen Sea [*Giulivi and Jacobs*, 1996]. As a result, areas of shallow shelf may intrude into colder water. Although the Amundsen Sea is very difficult of access because of multiyear ice, and hence has relatively few data compared with shelves elsewhere in Antarctica, present data would suggest that the seabed temperature here is more variable spatially than in the WAP and Bellingshausen Sea shelves to the east.

3.2. Deeper Water Seabed Temperatures

[17] The continental slope around Antarctica is bounded by the edge of the shelf, here defined by the 1000 m isobath, and the start of the abyssal plain at 3000 m depth. It forms a relatively steep and narrow zone around Antarctica, and has a median potential temperature close to 0°C everywhere (Figure 3 (middle)). Despite the low spatial variability in slope temperatures evident from Figure 3 (middle), the differences between sectors are statistically significant ($F(3, 861) = 21.3$, $p < 0.001$).

[18] The seabed temperature of the Southern Ocean deep sea (depths greater than 3000 m) is far less variable than either the shelf or slope seabed, but does exhibit significant differences spatially (Figure 3 (right)). Again, the region adjacent to the WAP exhibits the warmest seabed temperatures, with the Weddell Sea coldest and other areas intermediate (Figure 3 (right)). These differences are statistically highly significant (ANOVA, sector as fixed factor, $F(3, 4096) = 563$, $p < 0.001$). A striking feature of the seabed temperature of the deep sea around Antarctica is that the coldest water is located in the Weddell Sea, and that AABW is progressively warmer in an eastward (clockwise) direction (Figure 2 (left)). This pattern can be seen clearly when deep sea seabed temperatures are plotted as a function of longitude (Figure 4). The eastern coast of the Antarctic Peninsula at around longitude 60°W defines the westernmost limit of the coldest water and proceeding eastward (clockwise) the coldest temperatures are warmer by ∼0.28 K per 90° of longitude. It is notable that this pattern does not appear to be strongly influenced by very cold shelf water elsewhere around Antarctica (Figures 2 and Figure 4 (right)). There is also an increase in abyssal seabed temperature with distance from the bottom of the continental slope, as at all longitudes the coldest waters are those closest to the bottom of the slope.

3.3. Latitudinal Variation

[19] Although much of the coastline of continental Antarctica is effectively zonal in orientation, there are a few areas where the coast runs meridionally, and hence latitudinal variations in temperature might be expected. These include the Antarctic Peninsula (both west and east coasts), and Victoria Land. If the island groups that lie south of the Polar Front are included in the analysis, then these provide further latitudinal spread. Comparison of the bottom temperature for continental shelf, slope and deep sea habitats reveals significant differences in latitudinal patterns (Figure 5). Shelf seabed temperatures are highly variable, but there is a consistent trend for the coldest bottom temperatures to be at the highest latitudes. In addition, seabed temperatures around the lower-latitude island groups are consistently warmer than for the Antarctic continent itself (Figure 5 (left)). For the shelf data overall there is a highly significant relationship between bottom temperature and latitude $F(2, 586) = 283.3$, $p < 0.001$).

[20] Slope temperatures exhibit less variability, but there is again a distinct trend for bottom temperatures to increase with decreasing latitude, though only below ∼65°S; at higher latitudes there is an indication of a tendency for the reverse trend with slope temperatures at ∼75°S slightly warmer than those at ∼65°S (Figure 5 (middle)). This plot shows two groups of outliers. Two grid boxes at 77.5°S (36.5°W and 38.5°W) have seabed potential temperatures

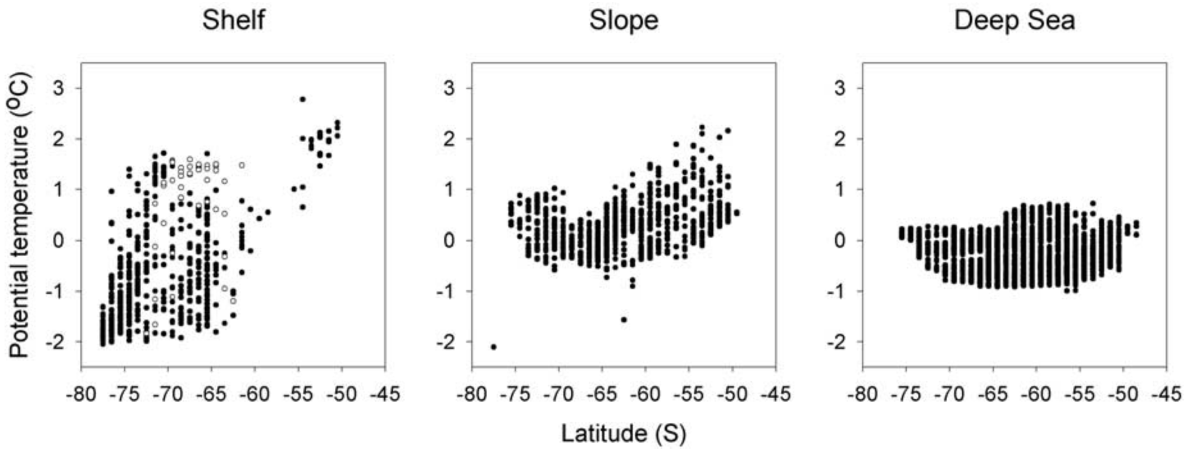

Figure 5. Latitudinal distribution of seabed potential temperatures in Antarctica. (left) The continental shelf (0–1000 m), (middle) the continental slope (1000–3000 m), and (right) the deep sea (>3000 m) out to the mean position of the Antarctic Polar Front.

∼−2°C. This is colder than the surface freezing point, and hence indicates waters that have been cooled under pressure through interaction with the nearby ice shelves in the Weddell Sea prior to descending from the shelves in convective plumes. The group of cold outliers between 60 and 65°S all come from the continental slope at the northern end of the Antarctic Peninsula, a region where downslope convection of cold water has previously been detected [*Meredith et al.*, 2003]. Such downslope convection undoubtedly occurs in other regions around Antarctica, but the spatial extent of the convecting plumes is small and, combined with likely seasonality in their activity, leads to their being unrepresented in the hydrographic database. For the data set overall the relationship between bottom temperature and latitude is significant ($F(2, 212) = 64.8$, $p < 0.001$), though the distribution of residuals indicates that a linear model is not a good fit to the data. The data for the deep sea are the least variable, and show no significant variation with latitude ($F(2, 4534) = 0.82$).

4. Discussion

[21] This analysis highlights a number of aspects of the spatial and depth distribution of bottom temperatures that are not in themselves novel, but which have to date not been integrated into discussions of the ecology or physiology of Antarctic benthic organisms. The most notable of these is the striking difference between the thermal environment of the continental shelf seabed to the west of the Antarctic Peninsula, and that of the shelves around continental Antarctica. Also important in an ecological context are the latitudinal cline in shelf seabed temperatures, and in the thermal gradient between the shelf and deep sea seabed environments. In attempting to evaluate the ecological implications of spatial variability in seabed temperature, it is important to consider in situ rather than potential temperature. This is because the physiological processes in organisms are affected by both thermodynamic temperature and hydrostatic pressure. Whereas thermodynamic temperature influences reaction rates primarily through kinetic effects, pressure exerts a significant influence through differences in molar volumes between reactants and products, and the changes in molar volume and hydration which occur during ligand binding, catalysis and product release [*Hochachka and Somero*, 2002]. Aspects of Antarctic benthic ecology that merit discussion in the context of the spatial variability of bottom temperature include physiological constraints, biogeography, the evolutionary history of the benthic fauna, and the potential impact of future climate change.

4.1. Physiological Constraints

[22] Over 150 years of oceanographic investigations have established that the fauna of the Antarctic continental shelf is rich and diverse, fully comparable with many temperate regions and even some nonreef warm water habitats [*Arntz et al.*, 1997; *Clarke and Johnston*, 2003]. While the relative abundance of different groups differs from warmer waters, in general all the major groups of organisms are present. There are however a few taxa that are low in diversity relative to lower latitudes; these include molluscs, decapod crustaceans and both teleost and cartilaginous fish. Although the low temperature of the Southern Ocean has often been invoked to explain such patterns, in very few cases can we be certain that temperature is the key factor. Perhaps the best example is that of brachyuran crabs, whose absence from the Southern Ocean appears to be the result of an inability to maintain ionic balance at low temperatures [*Frederich et al.*, 2001]. Although this physiological constraint excludes brachyuran crabs completely from the Antarctic continental shelf, a more subtle constraint is where a species has a life history that includes a growth stage that is particularly sensitive to temperature. A good example here would be anomuran lithodid crabs, where careful experimental work has shown that the larval development in the sub-Antarctic *Paralomis granulosa* requires temperatures greater than ∼+1°C [*Anger et al.*, 2003]. If this physiological limitation is general for lithodids, it would thus confine these anomuran crabs almost completely to deeper water in the Southern Ocean, where the ACC keeps the bottom temperature sufficiently high [*Klages et al.*, 1995; *Thatje et al.*, 2008]. On most of the Antarctic continental shelf seabed temperatures are too cold; the only exception here would be the western Antarctic Peninsula

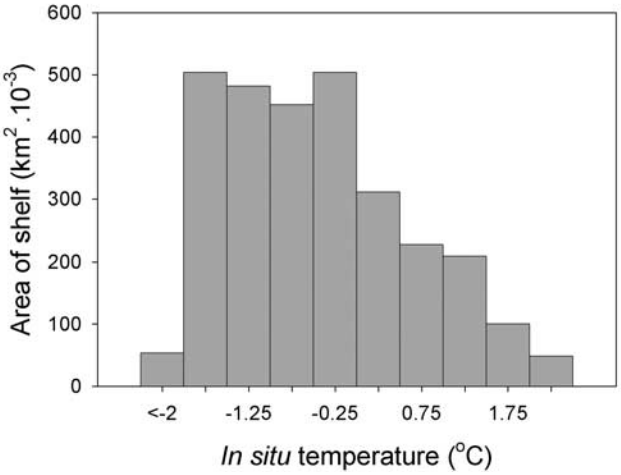

Figure 6. Histogram showing area of continental shelf with different mean seabed in situ temperatures.

where one might expect that, assuming all other ecological requirements are met, lithodid crabs might survive. On sub-Antarctic islands such as South Georgia, where shelf seabed temperatures are warmer, lithodids are found in shallow water. However, their near absence from the shallowest waters at South Georgia (where seabed temperatures are the warmest in the Southern Ocean) indicates that other factors are also important in determining their distribution.

[23] Although seabed temperatures on the continental shelf can be close to the in situ freezing point, this is not a problem for benthic marine invertebrates. This is because they have body fluids whose osmolarity (though not ionic composition) is similar to that of seawater. The situation is very different in teleost fish, whose body fluids are dilute. As a result the freezing point of teleost blood is above −1°C, and Antarctic teleosts synthesize a suite of antifreeze proteins to prevent growth of ice nuclei [*DeVries*, 1983]. While teleost fish need antifreeze to live on most of the continental shelves around Antarctica (Figure 2), there are significant areas where, at least at present-day temperatures, the threat of freezing is nonexistent (Figure 6). These areas amount to ∼13% of the shelf, roughly $3.8.10^5$ km^2, and all are to the west of the Antarctic Peninsula (Figure 2). The warmer lower water column in these areas might allow teleost fish without antifreeze to survive on the shelf, or in the overlying waters, producing a very different ichthyofauna from elsewhere around Antarctica.

[24] Warmer seabed temperatures will also influence patterns of microbial organic matter decomposition and remineralisation processes in the bottom sediments. Microbial processes can be very sensitive to temperature [*Pomeroy and Deibel*, 1986] and while there is also a complex interaction with substrate concentration [*Pomeroy and Wiebe*, 2001; *Mincks et al.*, 2005; *Smith et al.*, 2006], it is possible that the variation in seabed temperatures may lead to differences in sediment remineralisation dynamics and carbon sequestration between the shelves of the western Antarctic Peninsula and elsewhere around Antarctica.

4.2. Biogeography and Bioregionalisation

[25] Temperature has long been regarded as a key abiotic factor determining the distribution of organisms [*Gaston*, 2003]. Although the absolute range of spatial variation in seabed temperatures found across Antarctic benthic habitats is small, there is increasing evidence that several aspects of the physiology, ecology and behavior of Antarctic marine organisms can be highly sensitive to temperature. These include crustacean moulting rate [*Quetin et al.*, 1994], embryonic development rate [*Pearse et al.*, 1991; *Stanwell-Smith and Peck*, 1998; *Peck et al.*, 2006], and a range of types of locomotor activity [*Peck*, 2002; *Peck et al.*, 2004]. These recent results suggest the possibility that the spatial variations in bottom temperature we report here may have consequences for the nature and diversity of benthic assemblages.

[26] The broadest-scale comparison would obviously be that between the warm shelf of the western Antarctic Peninsula with the very much colder shelves (by ∼3 K) of the Weddell and Ross Seas. An intriguing feature of this comparison is that Bransfield Strait in the northernmost parts of the WAP shelf is isolated from the direct influence of the ACC by the South Shetland islands, as a result this area has low seabed temperatures, comparable with those in the Weddell Sea (Figure 2). We can use this intriguing pattern to make some simple predictions. The first is that if the nature of Antarctic benthic assemblages is strongly influenced by mean seabed temperature, then we would expect the benthic fauna of the western Antarctic Peninsula continental shelf from Anvers Island south to Alexander Island to be quite distinct from that of the Weddell Sea, Ross Sea or East Antarctic continental shelves, and also distinct from that of the Bransfield Strait. It is most unlikely that the nature of Antarctic benthic assemblages are a function solely of mean temperature, for variability and occasional extreme values will also be important. There is also the confounding problem that other key habitat features will covary with temperature (for example cold areas near ice shelves will be subject to quite different sediment input and primary production than shallow areas close to predominantly rocky shores). Nevertheless, the simple prediction based on temperature alone gives us a starting point.

[27] We tested this prediction using data from the Southern Ocean molluscan database [*Griffiths et al.*, 2003]. We queried the database for gastropod and bivalve molluscs known from four broad regions: the WAP (confining this to those sections of the WAP with warm seabed temperatures), the Weddell and Ross Seas, and the continental shelf of East Antarctica. Bray-Curtis similarities calculated from presence/absence data only were used to cluster the samples according to similarity. The topology of the overall patterns for gastropods and bivalves were remarkably similar (Figure 7), and while there are many factors other than temperature that will affect faunal similarities, the deepest node in both groups is that separating the WAP samples from the colder shelves elsewhere in Antarctica.

[28] This simple analysis thus suggests that despite the very small absolute range of seabed temperatures in the Southern Ocean, spatial variations in temperature may be an important factor in governing the distribution of Antarctic organisms and hence the composition of benthic assemblages. The spatial distribution of seabed temperatures in the northern WAP shelf would thus lead to a prediction that the benthic assemblages of the Bransfield Strait, where the seabed is very cold because of the influence of water from

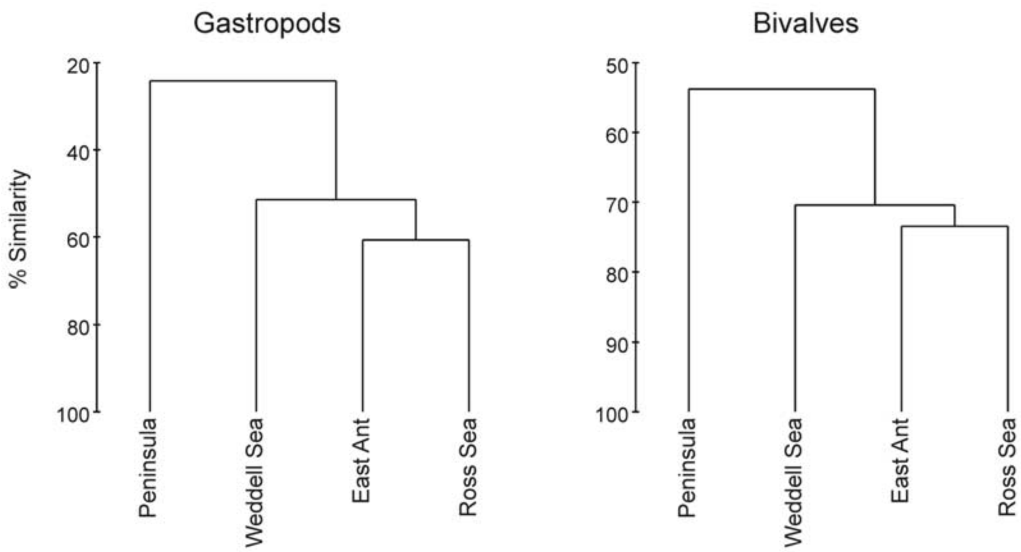

Figure 7. Bray-Curtis similarities for molluscan assemblages from the continental shelf of the central western Antarctic Peninsula, Weddell Sea, Ross Sea, and East Antarctica. Data for gastropods and bivalves plotted separately.

the Weddell Sea, should be different from those of the shelf at the same latitude but outside the South Shetland Islands, which is warmed by CDW. There are few studies of the benthic fauna of the Bransfield Strait, particularly to the north where the influence of Weddell Seawaters would be expected to be greatest, but preliminary data do suggest marked differences between the fauna of Bransfield Strait and the continental shelf outside the South Shetland Islands [*Arnaud et al.*, 2001; *San Vicente et al.*, 2007]. There is an increasing interest in the development of an objective classification of provinces or bioregions within the global ocean [*Longhurst*, 1998; *Spalding et al.*, 2007], and also recently within Antarctica itself [*Beaman and Harris*, 2005; *Grant et al.*, 2006]. The analyses reported here indicate that seabed temperature will be an important factor to include in any regionalisation of the continental shelf around Antarctica.

4.3. Evolutionary History

[29] A persistent theme in discussions of both the evolutionary history of the Antarctic benthic fauna has been migration between the deep sea, the continental slope and the shelf [*Menzies et al.*, 1973; *Wilson*, 1980; *Brandt*, 1992; *Gage*, 2004]. Frequently this has been based on the assumption that there has been no thermal barrier to such migration, or more specifically that the similarity of temperatures between the Antarctic shelf and the deep sea has allowed such migration [*Lipps and Hickman*, 1982].

[30] Our analysis indicates that there is a strong latitudinal gradient in the difference between shelf and deep seabed in situ temperatures, with the deep sea warmer by ~2 K at the highest latitudes, around zero for much of the main shelf around Antarctica, and cooler by ~2 K for island groups closer to the Polar Front (Figure 8). The thermal sensitivity demonstrated recently for some marine ectotherms living at polar temperatures [*Peck*, 2002; *Peck et al.*, 2004] suggests that such migration may well have required physiological adjustment for the differences in temperature as well as pressure. It is thus possible that physiological limitations may have restricted migration to areas where the temperature difference between shelf and deep water is minimal, or to have prompted genetic differentiation (and in some cases speciation) in the new populations. These possibilities are, of course, somewhat at variance with the assumption underpinning the original suggestions, which was that migration would have been easier at high latitudes because there were no thermal barriers to overcome.

4.4. Climate Change

[31] The atmosphere above the western Antarctic Peninsula is currently undergoing one of the fastest rates of regional climate change on earth [*King*, 1994; *King and Harangozo*, 1998]. Recently a very strong rate of oceanographic warming has been detected in the Bellingshausen Sea [*Meredith and King*, 2005]. While this warming is confined to the surface and near-surface waters, and hence affects only the shallower benthic habitats, it has focused attention on how Antarctic marine organisms will respond to continued regional climate change. It has also been suggested that there may be an increased upwelling of CDW and a stronger penetration onto the shelf in the Bellingshausen and Amundsen Sea regions, possibly as a consequence of stronger wind forcing over the Southern Ocean [*Thoma et al.*, 2008].

[32] One of the ways in which organisms may respond to climatic change is to shift biogeographic range and examples have been widely reported [*Parmesan and Yohe*, 2003; *Parmesan*, 2006]. However, such a response requires that there is somewhere suitable for the organisms to move to. In the case of marine organisms, a shift in biogeographic range is seen most often when there is a more or less continuous habitat that runs effectively parallel to the climate gradient, such as in California [*Barry et al.*, 1995; *Sagarin et al.*, 1999] or NW Europe [*Mieszkowska et al.*, 2006, 2007]. Where would benthic organisms move in a warming Antarctica, given that they are adapted to very low temperatures

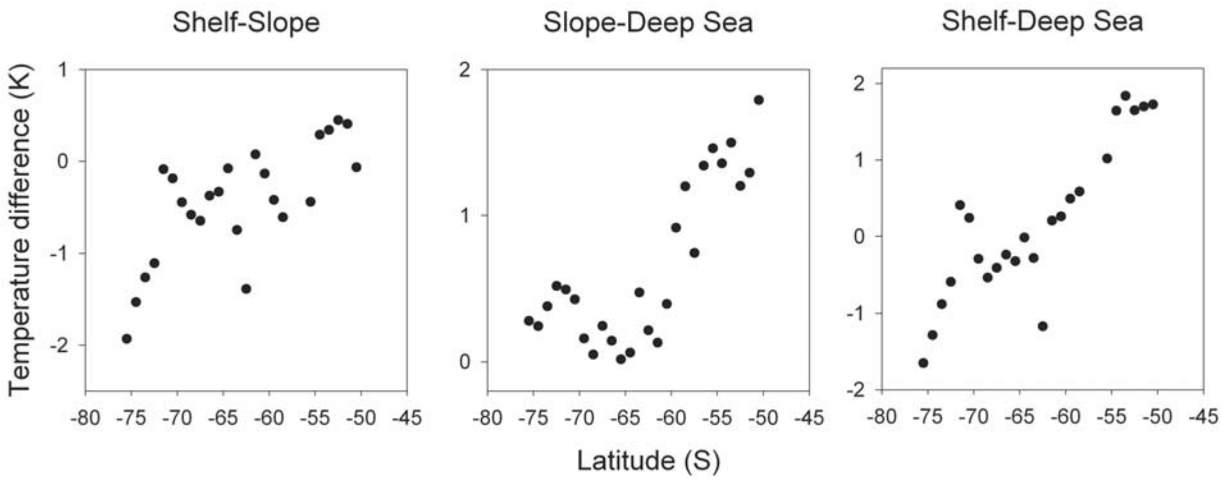

Figure 8. Latitudinal gradients in the difference between in situ seabed temperatures on the continental shelf and deeper water. Data pooled by 1° bins of latitude. The (left) difference between shelf and slope, (middle) difference between shelf and deep sea, and (right) difference between the shelf and the deep sea.

and many appear to be particularly sensitive to small increases in temperature? The only significant meridional coastlines are the Antarctic Peninsula and Victoria Land, but in neither case is there a simple gradient in bottom temperatures from high to low latitudes. Indeed, along the western Antarctic Peninsula seabed temperature is warmest in the middle, and colder both to the north and south (Figure 2b).

[33] The present scenario of warming surface waters along the western Antarctic Peninsula, coupled with a thermally stable shelf around continental Antarctica, indicates that, for the moment, the range of any stenothermal polar organisms currently found on the western Antarctic Peninsula shelf could contract to the shelf around the continent. If these shelves themselves start to warm, then the only refuge is the continental slope and deep water, assuming that organisms can adjust to the differences in temperature and pressure. For organisms living on the warmer shelves around the island groups such as South Georgia, the only potential shifts would be into deep water (which here are colder than the shelves), or a shift southward either along the Scotia arc, or directly across the Scotia Sea. To be achieved by larval dispersal this would require dispersal across the powerful mean flow of the ACC; the alternative would be a mechanism for adults to disperse by island hopping.

[34] Although the ACC marks a strong biogeographic barrier, the Southern Ocean is not as isolated as might appear. Recent data have shown that zooplankton and larvae cross the Polar Front in both directions, principally through eddies [*Clarke et al.*, 2005; *Barnes et al.*, 2006]. This indicates that the major factor preventing establishment of alien taxa in Antarctica is likely to be the ability to establish. The arrival of nonnative marine taxa in Antarctica may be facilitated by increasing human activities [*Lewis et al.*, 2003], and the likelihood of such taxa becoming established will be higher in those areas where thermal conditions are most similar to the native range. The warmer seabed temperatures of the WAP shelf, the marked oceanographic warming of near-surface waters in the Bellingshausen and Amundsen Seas, and the high incidence of human activities mark the Antarctic Peninsula as the most likely place for nonnative marine taxa to become established.

5. Concluding Remarks

[35] We have demonstrated marked spatial variability in seabed temperature around Antarctica and more widely across the Southern Ocean, that indicates the primary influence of large-scale physical oceanographic processes. The spatial variability in continental shelf seabed temperature has major implications for the assemblage composition (and hence bioregionalisation) of the benthic fauna. Latitudinal gradients in the difference between shelf and deep sea seabed temperatures have powerful implications for understanding both past evolutionary history and the potential impact of future climate change.

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References

Amante, C., and B. W. Eakins (2008), ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis, http://www.ngdc.noaa.gov/mgg/global/global.html, Natl. Geophys. Data Cent. Boulder, Colo.

Anger, K., et al. (2003), Larval and early juvenile development of *Paralomis granulosa* reared at different temperatures: Tolerance of cold and food limitation in a lithodid crab from high latitudes, *Mar. Ecol. Prog. Ser.*, *253*, 243–251, doi:10.3354/meps253243.

Arnaud, P. M., et al. (2001), Species diversity and assemblages of macrobenthic Mollusca from the South Shetland islands and Bransfield Strait (Antarctica), *Polar Biol.*, *24*, 105–112, doi:10.1007/s003000000183.

Arntz, W. E., et al. (1997), Antarctic marine biodiversity: An overview, in *Antarctic Communities: Species, Structure and Survival*, edited by B. Battaglia et al., pp. 3–14, Cambridge Univ. Press, Cambridge, U. K.

Barnes, D. K. A., and L. S. Peck (2008), Vulnerability of Antarctic shelf biodiversity to predicted regional warming, *Clim. Res.*, *37*, 149–163, doi:10.3354/cr00760.

Barnes, D. K. A., et al. (2006), Incursion and excursion of Antarctic biota: Past, present and future, *Glob. Ecol. Biogeogr.*, *15*, 121–142, doi:10.1111/j.1466-822X.2006.00216.x.

Barry, J. P., et al. (1995), Climate-related, long-term faunal changes in a California rocky intertidal community, *Science*, *267*, 672–675, doi:10.1126/science.267.5198.672.

Beaman, R. J., and P. T. Harris (2005), Bioregionalisation of the George V Shelf, east Antarctica, *Cont. Shelf Res.*, *25*, 1657–1691, doi:10.1016/j.csr.2005.04.013.

Brandt, A. (1992), Origin of Antarctic Isopoda (Crustacea, Malacostraca), *Mar. Biol.*, *113*, 415–423, doi:10.1007/BF00349167.

Carmack, E. C. (1990), Large-scale physical oceanography of polar oceans, in *Polar Oceanography. Part A: Physical Science*, edited by W. O. Smith, pp. 171–222, Academic, San Diego, Calif.

Clarke, A., and N. M. Johnston (2003), Antarctic marine benthic diversity, *Oceanogr. Mar. Biol.*, *41*, 47–114.

Clarke, A., and R. J. G. Leakey (1996), The seasonal cycle of phytoplankton, macronutrients, and the microbial community in a nearshore Antarctic marine ecosystem, *Limnol. Oceanogr.*, *41*, 1281–1294.

Clarke, A., et al. (2005), How isolated is Antarctica?, *Trends Ecol. Evol.*, *20*, 1–3, doi:10.1016/j.tree.2004.10.004.

Clarke, A., et al. (2007a), How well do we know the Antarctic marine fauna?: A preliminary study of macroecological and biogeographical patterns in Southern Ocean gastropod and bivalve molluscs, *Divers. Distrib.*, *13*, 620–632, doi:10.1111/j.1472-4642.2007.00380.x.

Clarke, A., et al. (2007b), Climate change and the marine ecosystem of the western Antarctic Peninsula, *Philos. Trans. R. Soc. London Ser. B*, *362*, 149–166, doi:10.1098/rstb.2006.1958.

Clarke, A., et al. (2008), Seasonal and interannual variability in temperature, chlorophyll and macronutrients in northern Marguerite Bay, Antarctica, *Deep Sea Res. Part II*, *55*, 1988–2008, doi:10.1016/j.dsr2.2008.04.035.

DeVries, A. L. (1983), Antifreeze peptides and glycopeptides in cold-water fishes, *Annu. Rev. Physiol.*, *45*, 245–260, doi:10.1146/annurev.ph.45.030183.001333.

Dinniman, M. S., and J. M. Klinck (2004), A model study of circulation and cross-shelf exchange on the west Antarctic Peninsula continental shelf, *Deep Sea Res. Part II*, *51*, 2003–2022, doi:10.1016/j.dsr2.2004.07.030.

Ducklow, H. W., et al. (2007), Marine pelagic ecosystems: The west Antarctic Peninsula, *Philos. Trans. R. Soc. London Ser. B*, *362*, 67–94, doi:10.1098/rstb.2006.1955.

Fahrbach, E., et al. (1995), Formation and discharge of deep and bottom water in the northwestern Weddell Sea, *J. Mar. Syst.*, *53*, 515–538.

Frederich, M., et al. (2001), Distribution patterns of decapod crustaceans in polar areas: A result of magnesium regulation?, *Polar Biol.*, *24*, 719–723, doi:10.1007/s003000100270.

Gage, J. D. (2004), Diversity in deep-sea benthic macrofauna: The importance of local ecology, the larger scale, history and the Antarctic, *Deep Sea Res. Part II*, *51*, 1689–1708, doi:10.1016/j.dsr2.2004.07.013.

Gaston, K. J. (2003), *The Structure and Dynamics of Geographic Ranges*, 266 pp., Oxford Univ. Press, Oxford, U. K.

Giulivi, C., and S. Jacobs (1996), Profiling the South Pacific Antarctic continental shelf, *Antarct. J. U. S.*, *31*, 103–104.

Grant, S. M., et al. (2006), *Bioregionalisation of the Southern Ocean: Report of the Experts Workshop (Hobart, September 2006)*, World Wildlife Fund Australia, Sydney, N. S. W., Australia.

Griffiths, H. J., et al. (2003), SOMBASE—Southern Ocean Mollusc Database: A tool for biogeographic analysis in diversity and ecology, *Org. Divers. Evol.*, *3*, 207–213, doi:10.1078/1439-6092-00079.

Hochachka, P. W., and G. N. Somero (2002), *Biochemical Adaptation: Mechanism and Process in Physiological Evolution*, 466 pp., Oxford Univ. Press, Oxford, U. K.

Hofmann, E. E., and J. M. Klinck (1998), Thermohaline variability of the waters overlying the west Antarctic Peninsula continental shelf, in *Ocean, Ice and Atmosphere: Interactions at the Antarctic Continental Margin*, *Antarct. Res. Ser.*, vol. 75, edited by S. S. Jacobs and R. F. Weiss, pp. 67–81, AGU, Washington, D. C.

Hofmann, E. E., et al. (1996), Water mass distribution and circulation west of the Antarctic Peninsula and including Bransfield Strait, in *Foundations for Ecological Research West of the Antarctic Peninsula*, *Antarct. Res. Ser.*, vol. 70, edited by R. M. Ross et al., pp. 61–80, AGU, Washington, D. C.

Hunt, B. M., et al. (2003), Annual warming episodes in seawater temperatures in McMurdo Sound in relationship to endogenous ice in notothenioid fish, *Antarct. Sci.*, *15*, 333–338, doi:10.1017/S0954102003001342.

Jenkins, A., and S. Jacobs (2008), Circulation and melting beneath George VI Ice Shelf, Antarctica, *J. Geophys. Res.*, *113*, C04013, doi:10.1029/2007JC004449.

King, J. C. (1994), Recent climate variability in the vicinity of the Antarctic Peninsula, *Int. J. Climatol.*, *14*, 357–369, doi:10.1002/joc.3370140402.

King, J. C., and S. A. Harangozo (1998), Climate change in the western Antarctic Peninsula since 1945: Observations and possible causes, *Ann. Glaciol.*, *27*, 571–575.

Klages, M., et al. (1995), Stone crabs close to the Antarctic Continent: *Lithodes murrayi* Henderson, 1888 (Crustacea; Decapoda; Anomura) off Peter 1 Island (68°51′S, 90°51′W), *Polar Biol.*, *15*, 73–75, doi:10.1007/BF00236128.

Klinck, J. M. (1998), Heat and salt changes on the continental shelf west of the Antarctic Peninsula between January 1993 and January 1994, *J. Geophys. Res.*, *103*, 7617–7636.

Lewis, P. N., et al. (2003), Marine introductions in the Southern Ocean: An unrecognized hazard to biodiversity, *Mar. Pollut. Bull.*, *46*, 213–223, doi:10.1016/S0025-326X(02)00364-8.

Lipps, J. H., and C. S. Hickman (1982), Origin, age and evolution of Antarctic and deep-sea faunas, in *Environment of the Deep Sea*, edited by W. G. Ernst and J. G. Morris, pp. 256–324, Prentice Hall, Englewood Cliffs, N. J.

Littlepage, J. L. (1965), Oceanographic observations in McMurdo Sound, Antarctica, *Antarct. Res. Ser.*, *5*, 1–37.

Longhurst, A. (1998), *Ecological Geography of the Sea*, 398 pp., Academic, San Diego, Calif.

Menzies, R. J., et al. (Eds.) (1973), *Abyssal Environment and Ecology of the World Oceans*, 488 pp., John Wiley, New York.

Meredith, M. P., and J. C. King (2005), Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century, *Geophys. Res. Lett.*, *32*, L19604, doi:10.1029/2005GL024042.

Meredith, M. P., et al. (2003), Downslope convection north of Elephant Island, Antarctica: Influence on deep waters and dependence on ENSO, *Geophys. Res. Lett.*, *30*(9), 1462, doi:10.1029/2003GL017074.

Meredith, M. P., et al. (2004), Impact of the 1997/98 ENSO on upper ocean characteristics in Marguerite Bay, western Antarctic Peninsula, *J. Geophys. Res.*, *109*, C09013, doi:10.1029/2003JC001784.

Mieszkowska, N., et al. (2006), Changes in the range of some common rocky shore species in Britain—A response to climate change?, *Hydrobiologia*, *555*, 241–251, doi:10.1007/s10750-005-1120-6.

Mieszkowska, N., et al. (2007), Long-term changes in the geographic distribution and population structures of *Osilinus lineatus* (Gastropoda: Trochidae) in Britain and Ireland, *J. Mar. Biol. Assoc. U. K.*, *87*, 537–545, doi:10.1017/S0025315407053799.

Mincks, S. L., et al. (2005), Persistence of labile organic matter and microbial biomass in Antarctic shelf sediments: Evidence of a sediment "food bank," *Mar. Ecol. Prog. Ser.*, *300*, 3–19, doi:10.3354/meps300003.

Mosby, H. (1934), The waters of the Atlantic Antarctic Ocean, in *Scientific Results of the Norwegian Antarctic Expedition, 1927–1928*, vol. 11, edited by J. Dybwad, pp. 1–131, Norw. Acad. of Sci. and Lett., Oslo.

Parmesan, C. (2006), Ecological and evolutionary responses to recent climate change, *Annu. Rev. Ecol. Syst.*, *37*, 637–669, doi:10.1146/annurev.ecolsys.37.091305.110100.

Parmesan, C., and G. Yohe (2003), A globally coherent fingerprint of climate change impacts across natural systems, *Nature*, *421*, 37–42, doi:10.1038/nature01286.

Pearse, J. S., et al. (1991), Reproduction of Antarctic benthic marine invertebrates: Tempos, modes and timing, *Am. Zool.*, *31*, 65–80.

Peck, L. S. (2002), Ecophysiology of Antarctic marine ectotherms: Limits to life, *Polar Biol.*, *25*, 31–40, doi:10.1007/s003000100308.

Peck, L. S., et al. (2004), Extreme sensitivity of biological function to temperature in Antarctic marine species, *Funct. Ecol.*, *18*, 625–630.

Peck, L. S., et al. (2006), Metabolism and development in pelagic larvae of Antarctic gastropods with mixed reproductive strategies, *Mar. Ecol. Prog. Ser.*, *318*, 213–220.

Pomeroy, L. R., and D. Deibel (1986), Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters, *Science*, *233*, 359–361, doi:10.1126/science.233.4761.359.

Pomeroy, L. R., and W. J. Wiebe (2001), Temperature and substrates as interactive limiting factors for marine heterotrophic bacteria, *Aquat. Microb. Ecol.*, *23*, 187–204, doi:10.3354/ame023187.

Quetin, L. B., et al. (1994), Krill energetics: Seasonal and environmental aspects of the physiology of Euphausia superba, in *Southern Ocean Ecology: The BIOMASS Perspective*, edited by S. Z. El-Sayed, pp. 165–184, Cambridge Univ. Press, Cambridge, U. K.

Sagarin, R. D., et al. (1999), Climate-related change in an intertidal community over short and long time scales, *Ecol. Monogr.*, *69*, 465–490.

San Vicente, C., et al. (2007), Biodiversoty and structure of the suprabenthic assemblages from South Shetland islands and Bransfield Strait, Southern Ocean, *Polar Biol.*, *30*, 477–486, doi:10.1007/s00300-006-0206-6.

Smith, C. R., et al. (2006), A synthesis of bentho-pelagic coupling on the Antarctic shelf: Food banks, ecosystem inertia and global climate change, *Deep Sea Res. Part II*, *53*, 875–894, doi:10.1016/j.dsr2.2006.02.001.

Spalding, M. D., et al. (2007), Marine ecoregions of the world: A bioregionalization of coastal and shelf areas, *BioScience*, *57*, 573–583, doi:10.1641/B570707.

Stanwell-Smith, D. P., and L. S. Peck (1998), Temperature and embryonic development in relation to spawning and field occurrence of larvae of 3 Antarctic echinoderms, *Biol. Bull.*, *194*, 44–52, doi:10.2307/1542512.

Thatje, S., et al. (2008), Encounter of lithodid crab *Paralomis birsteini* on the continental slope off Antarctica, samples by RoV, *Polar Biol.*, *31*, 1143–1148, doi:10.1007/s00300-008-0457-5.

Thoma, M., et al. (2008), Modelling Circumpolar Deep Water intrusions on the Amundsen Sea continental shelf, Antarctica, *Geophys. Res. Lett.*, *35*, L18602, doi:10.1029/2008GL034939.

Walsh, J. J. (1988), *On the Nature of Continental Shelves*, 520 pp., Academic, San Diego, Calif.

Weiss, R. F., et al. (1979), Geochemical studies of the Weddell Sea, *Deep Sea Res. Part I*, *26*, 1093–1120, doi:10.1016/0198-0149(79)90059-1.

Whitehouse, M. J., et al. (2008), Rapid warming of the ocean around South Georgia, Southern Ocean, during the 20th century: Forcings, characteristics and implications for lower trophic levels, *Deep Sea Res. Part I*, *55*, 1218–1228.

Whitworth, T., et al. (1998), Water masses and mixing near the Antarctic Slope Front, in *Ocean, Ice and Atmosphere: Interactions at the Antarctic Continental Margin*, *Antarct. Res. Ser.*, vol. 75, edited by S. S. Jacobs and R. F. Weiss, pp. 1–17, AGU, Washington, D. C.

Wilson, G. D. (1980), New insights into the colonization of the deep sea: Systematics and zoogeography of the Munnidae and the Pleurogoniidae *comb. nov.* (Isopoda; Janiroidea), *J. Nat. Hist.*, *14*, 215–236.

D. K. A. Barnes, A. Clarke, S. M. Grant, H. J. Griffiths, and M. P. Meredith, Biological Sciences Division, British Antarctic Survey, NERC, Madingley Road, Cambridge CB3 0ET, UK. (accl@bas.ac.uk)