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Is there a distinct continental slope fauna in the Antarctic?

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ABSTRACT

The Antarctic continental slope spans the depths from the shelf break (usually between 500 and 1000 m) to ~3000 m, is very steep, overlain by 'warm' (2–2.5 °C) Circumpolar Deep Water (CDW), and life there is poorly studied. This study investigates whether life on Antarctica's continental slope is essentially an extension of the shelf or the abyssal fauna, a transition zone between these or clearly distinct in its own right. Using data from several cruises to the Weddell Sea and Scotia Sea, including the ANDEEP (ANtarctic benthic DEEP-sea biodiversity, colonisation history and recent community patterns) I–III, BIOPEARL (BIOdiversity, Phylogeny, Evolution and Adaptive Radiation of Life in Antarctica) 1 and EASIZ (Ecology of the Antarctic Sea Ice Zone) II cruises as well as current databases (SOMBASE, SCAR-MarBIN), four different taxa were selected (i.e. cheilostome bryozoans, isopod and ostracod crustaceans and echinoid echinoderms) and two areas, the Weddell Sea and the Scotia Sea, to examine faunal composition, richness and affinities. The answer has important ramifications to the link between physical oceanography and ecology, and the potential of the slope to act as a refuge and resupply zone to the shelf during glaciations.

Benthic samples were collected using Agassiz trawl, epibenthic sledge and Rauschert sled. By bathymetric definition, these data suggest that despite eurybathy in some of the groups examined and apparent similarity of physical conditions in the Antarctic, the shelf, slope and abyssal faunas were clearly separated in the Weddell Sea. However, no such separation of faunas was apparent in the Scotia Sea (except in echinoids). Using a geomorphological definition of the slope, shelf-slope-abyss similarity only changed significantly in the bryozoans. Our results did not support the presence of a homogenous and unique Antarctic slope fauna despite a high number of species being restricted to the slope. However, it remains the case that there may be a unique Antarctic slope fauna, but the paucity of our samples could not demonstrate this in the Scotia Sea. It is very likely that various ecological and evolutionary factors (such as topography, water-mass and sediment characteristics, input of particulate organic carbon (POC) and glaciological history) drive slope distinctness. Isopods showed greatest species richness at slope depths, whereas bryozoans and ostracods were more speciose at shelf depths; however, significance varied across Weddell Sea and Scotia Sea and depending on bathymetric vs. geomorphological definitions. Whilst the slope may harbour some source populations for localised shelf recolonisation, the absence of many shelf species, genera and even families (in a poorly dispersing taxon) from the continental slope indicate that it was not a universal refuge for Antarctic shelf fauna.

1. Introduction

A restriction of species to confined depth ranges has been one of the most globally consistent patterns found in faunal sampling of continental shelves, slopes and abyssal plains (Rex, 1981; Tyler and Zibrowius, 1992; Carney, 2005). While the details and causes of this zonation remain to be determined, it is generally thought that the shelf and slope are populated by largely distinct suites of species (e.g., Blake and Narayanaswamy, 2004). However this may be partly due to continental shelf faunas being much better known and studied (Gage and Tyler, 1991; Clarke and Johnston, 2003). Data on slope and abyssal faunal similarity, however, are scarce, which makes the assessment of faunal differences across depths in most taxonomic groups problematic. Abyssal plains occur below the continental rise and above trenches, usually defined as between 3000 and 6000 m (Smith et al., 2008), and cover more than half the planet's surface. The abyss seems to have relatively little topographic complexity and low disturbance

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levels (compared to the shelf). Particulate organic carbon (POC) flux is weak and probably drives very low abundance and biomass levels (e.g., Rex et al., 2006). Great debate remains about the number of species that inhabit abyssal regions and how they coexist (e.g., Grassle and Maciolek, 1992).

The slope may link shelf and abyssal faunas (Gage and Tyler, 1991), but it resembles neither in environmental features. Turbidites frequently cascade down the slope into the abyss, probably commonly triggered by fluid flow, earthquakes or shallow gas coupled with oversteepening (e.g., Sultan et al., 2004). Although the steepness of the slope reduces accumulation of POC, it enhances nutrient transport to deeper sills (Isla et al., 2005). Biomass and faunal densities can be locally high, where phytodetritus cascades down canyons (Schlacher et al., 2007). Despite many adverse conditions, the slope may harbour the oldest marine fauna, as sea level changes and ice sheets expelled fauna from shelves and the abyss has often been anoxic (e.g., Jacobs and Lindberg, 1998). Therefore, the slope potentially represents a source for recolonisation of the shelf or the abyss following catastrophic events, such as deep-sea anoxia or ice grounding and scouring on the shelf during glacial episodes (Brey et al., 1996; but see Thatje et al., 2005).

The nature of the seabed around Antarctica contrasts strongly to other areas. Benthic communities on the shelves have undergone major periodic eliminations by advancing grounded ice cover (during glaciations) but also geomorphologic boundaries of shelf, slope and abyss lack simple bathymetric demarcation. The Antarctic continent is depressed by a massive ice sheet, and surrounding shelves are thus anomalously deep and typically vary from 500 to 800 m (Clarke, 2003). Whilst ice-mediated disturbance is probably the major influence on the structure and richness of life on polar shelves, sedimentation, quality and quantity of food input or changes in oxygen concentrations may be driving factors on the slope (Levin, 2003; Barnes and Conlan, 2007). Long topographic and oceanographic isolation has led to a highly endemic Antarctic shelf fauna (~50–80%, see Arntz et al., 1997). In contrast, below slope depths the Southern Ocean is well connected to other oceans, potentially enabling strong faunal exchange (Brandt et al., 2007). Connectivity at slope depths would seem to be intermediate and restricted to three main areas: the Scotia arc, Kerguelen plateau and Macquarie ridge. As water temperature is relatively uniform, thermal barriers are mostly absent, which may have aided faunal movement between the shelf, slope and abyss and led to wide eurybathic distributions in some taxa (Brey et al., 1996). Despite the importance as a potential refuge for polar biodiversity during glaciations, few studies have investigated the ecology of Antarctic slope environments, and those which have, focussed on single groups or higher taxonomic levels (Herman and Dahms, 1992; Kaiser et al., 2007; Aldea et al., 2008). In the current study we attempt to determine the nature of benthic faunal transitions across the Antarctic shelf, slope and abyss and to evaluate that transition relative to the unique characteristics of the Southern Ocean using data for cheilostome bryozoans, isopod and ostracod crustaceans and echinoid echinoderms in the Scotia Sea and Weddell Sea.

Both, high faunal eurybathy (Brey et al., 1996) and relatively homogenous environmental conditions across depths in the Southern Ocean would suggest enhanced faunal linkages between shelf, slope and abyssal faunas. So, the null hypothesis was that there is no significant difference between species assemblages on the Antarctic continental slope and those on the shelf or in the abyss. However, the considerably steeper profile of the slope compared to the shelf and abyss anywhere in the Southern Ocean coupled to likely sediment instability would suggest a different environment and fauna. Thus, the first alternate hypothesis would be that the slope fauna is unique and differs from both shelf and abyssal faunas in the Antarctic. However, there are arguments for regional similarities between shelf, slope and abyssal faunas, such as where past submergent and emergent migrations have occurred between the shelf and the abyss. Reinvasion of the shelf from deeper waters following past coverage of the Antarctic shelf by grounded ice during glacial maxima (Huybrechts, 2002) should support potential similarity. However it has become clear that a few areas remained ice-free during glaciations (e.g., parts of the Weddell Sea, Barnes and Hillenbrand, 2010), leaving pockets of shelf refugia. Such areas have the potential to be much more distinct across depths than areas which have been reinvaded from greater depths. So our second alternate hypothesis is that the slope differs from the shelf/abyssal in some taxa or in some areas but not in others (e.g., areas where the shelf was completely covered by ice during the last glacial maximum vs. areas where shelf refugia were present).

2. Material and methods

2.1. Study area

The Scotia Sea (~54–62°S and 27–57°W) is bordered by the Scotia ridge to the north and south and the South Sandwich forearc to its east. It opens westwards to the Drake Passage. Shelves and slopes of the Scotia arc are characterised by surrounding archipelagos and seamounts of differing, continental and volcanic, origins, topography (e.g., in terms of depths of the shelf break, steepness of the slope) and geological and glaciological history. Shelves across the Scotia Sea are unusually shallow (e.g., shelf break at Elephant Is.: 225 m, South Orkney Is.: 500 m and South Georgia: average of 200 m) and range from very narrow in the South Sandwich Is. to 50–150 km at South Georgia (Brandon et al., 1999). From the shelf break the slope rapidly grades into abyssal or even hadal depths (> 6000 m, Smith et al., 2008).

Data on the glaciological history of Scotia Sea locations since the last glacial maximum (LGM) are patchy, and little is known about some archipelagos, such as the South Sandwich Islands. At the South Shetland Islands it has been suggested that ice sheets expanded across the shelf and generally grounded at ~400 m depths (see Anderson et al., 2002). Similarly in the South Orkney Islands ice sheets grounded to at least 250–300 m depths (Bentley and Anderson, 1998), and arguably covered most of the shelf around South Georgia (Graham et al., 2008). The shelf areas around the South Sandwich Islands are very steep and grade straight into slope (see Fig. 1B). Both shelves and slopes are likely to be highly disturbed environments by periodic volcanism and the downward cascading of sediment and ash (Howe et al., 2004).

Scotia Sea shelf and slope waters are dominated by the strong eastward flow of the Antarctic Circumpolar Current (ACC). The lower part of the ACC comprises relatively warm (2–2.5 °C), but highly saline upper and lower CDW and cold and dense Antarctic Bottom Water (AABW) (Orsi et al., 1995). There are places in the Antarctic, where CDW flows across the shelf (e.g., Amundsen and Bellingshausen Sea), but normally it occurs at slope depths. Scotia Sea shelf waters are separated from those in the Weddell Sea by the Weddell–Scotia confluence extending from the tip of the Antarctic Peninsula (South Shetland Islands) across the Southern Scotia Sea, the Powell Basin and South Orkney Islands, to about 30°E (e.g., Patterson and Sievers, 1980). The Scotia Sea and Weddell Sea abyss is connected via AABW leaving the Weddell Sea through the South Scotia Ridge (Orsi et al., 1995). In some places, AABW modified as Weddell Sea Deep Water and Weddell Sea Bottom Water can also be found at shelf and slope depths, i.e. overflowing the South Orkney plateau (see Naveira Garabato