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The macro- and megabenthic fauna on the continental shelf of the eastern Amundsen Sea, Antarctica

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Abstract

In 2008 the BIOPEARL II expedition on board of RRS *James Clark Ross* sailed to the eastern Amundsen Sea Embayment and Pine Island Bay, one of the least studied Antarctic continental shelf regions due to its remoteness and ice cover. A total of 37 Agassiz trawls were deployed at depth transects along the continental and trough slopes. A total of 5,469 specimens, belonging to 32 higher taxonomic groups and more than 270 species, were collected. Species richness per station varied from 1-55. The benthic assemblages were dominated by echinoderms and clearly different to those in the Ross, Scotia and Weddell seas. Here we present the macro- and megafaunal assemblage structure, its species richness and the presence of several undescribed species.

Keywords

biodiversity, abundance, megabenthos, Southern Ocean, Pine Island

1. Introduction

The Amundsen Sea in western Antarctica is in the Pacific sector of the Southern Ocean and is one of the most remote, least explored and most rapidly changing regions of Antarctic waters. Despite being a region with large and prolonged sea ice cover, two extremely productive polynyas, the Amundsen Sea and the Pine Island Bay polynyas, occur in this region (Arrigo et al., 2012; Yager et al., 2012). Based on satellite derived chlorophyll a data, the better studied Amundsen Sea Polynya is the most productive of the Antarctic polynyas (Arrigo and von Dijken, 2003). Over the last 30 years the summer sea ice extent has declined and the opening of the Amundsen Sea Polynya has occured earlier (Yager et al., 2012). During the Austral springe polynyas are locations of significant phytoplankton blooms and intensive sedimentation (Smith and Comiso, 2008; Ducklow et al., 2008); both of which will have an effect on the distributions and abundance of the underlying benthic fauna (Corliss et al., 2009; Sun et al., 2006). To date, the biodiversity and distribution of the benthic fauna in the Amundsen Sea is unstudied, while marine geological and oceanographic cruise activities in the region have increased substantially (Lowe and Anderson, 2003; Jenkins et al., 2004; Thoma et al., 2008; Jacobs et al., 2011). This increased interest follows land-based geophysical research on the West Antarctic Ice Sheet (WAIS) glaciers and the ice streams of Marie Byrd Land showing that these are thinning faster than any other glaciers in Antarctica (Shepherd et al., 2001; Holt et al., 2006). As a result, The Amundsen Sea Embayment is a major drainage basin for the WAIS (Rignot, 1998; Evans et al., 2006). Of particular interest in the recent debate on climate change and sea level rise is how increased melting of the WAIS might lead to its collapse and what the influence on global sea-level rise

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could be (Vaughan, 2008; Bamber et al., 2009). Initial bathymetric investigations of the seafloor topography showed that the continental shelf of the Amundsen comprises several deep troughs and basins which were formed during past ice ages and reach more than 1600 m in depth (Dowdeswell et al., 2006; Noormets et al., 2009; Graham et al., 2010). One of these deep basins is located in Pine Island Bay (Graham et al. 2010) and was a particular focus of attention in this study.

Recent studies on the biogeographic distribution of the Antarctic benthic and pelagic faunas highlight the AS as a completely unsampled region (Linse et al., 2006; Griffiths et al., 2009; Griffiths, 2010). During a geology-focused expedition on RV *Polarstern* in 1994 (Miller and Grobe, 1996) three biological stations were sampled off the Bakutis Coast in the Amundsen Sea using a remote operating vehicle with an underwater video camera and an Agassiz trawl and the observed megafauna analysed (Starmans et al., 1999). In 2008 the British Antarctic Survey (BAS) BIOPEARL II (Biodiversity Dynamics: Phylogeography, Evolution and Radiation of Life) cruise on RRS *James Clark Ross* sampled the benthic animals of the Amundsen Sea Embayment and Pine Island Bay for the first time. The deep shelf basin of Pine Island Bay is of particular interest for evolutionary studies on the survival of benthic fauna on the Antarctic shelf during glacial maxima when ice sheets covered most shelf areas (Barnes and Hillenbrand, 2010). These basins may have acted as refugia for shelf species. Alternatively, the link with the Antarctic Circumpolar Deep Water through the shelf troughs might have supplied the Pine Island Bay basin with deep-sea species since the Last Glacial Maximum (Riehl and Kaiser, 2012). Preliminary identifications of macro- and megafauna collected during the BIOPEARL II cruise found isopod species in this shelf area that had

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only previously been reported from the Antarctic deep sea (Kaiser et al., 2009). Initial investigations on the holothurians and isopods from this region have revealed species new to science from the Amundsen Sea Embayment and Pine Island Bay (Brandt, 2009; O'Loughlin et al., 2010; Riehl & Kaiser, 2012).

The main objective of this study is to describe the benthic assemblage structure in the southern Amundsen Sea collected by Agassiz (AGT) trawl. Species composition and richness will be assessed and compared with those of the Ross, Scotia and Weddell seas.

2. Material and methods

2.1. *Study area*

The main study area was the eastern Amundsen Sea embayment and Pine Island Bay (Fig. 1). Comparative and replicate samples were taken in the southern Bellingshausen Sea and in the adjacent deep sea at the Mary Byrd Seamount (Fig. 1).

The Amundsen Sea Embayment is one of the three major drainage basins for the West Antarctic Ice Sheet (Rignot, 1998; Evans et al., 2006). Several large ice shelves discharge into the Amundsen Sea Embayment and Pine Island Bay, and large parts of the area are covered by perennial sea ice (Graham et al., 2010). The geomorphology of its continental shelf and slope is shaped by the past and recent movement of ice shelf, icebergs and melt-water channels (Dowdeswell et al., 2006; Nitsche et al., 2007; Larter et al., 2009; Noormets et al., 2009; Graham et al., 2010). The seabed topography is characterised by iceberg scours, drainages channels and deep troughs. The main troughs are the Pine Island Troughs West and East, where water depth decreases from around 500 m on the shelf down to 1700 m in the troughs (Fig. 1) (Graham et

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al., 2010). The sedimentology of the Amundsen Sea Embayment has been described by Ehrmann et al., (2011). It is characterised by a high concentration of kaolinite in the clay mineral composition of the surface sediments and a high water content in the upper five centimetres (Ehrmann et al., 2011).

The oceanography of the Amundsen Sea and, in particular, the continental shelf is defined by its prominent water mass, the Antarctic Circumpolar Deep Water (CDW) (Jenkins et al., 2004, 2011; Thoma et al., 2008). The intrusion of warm Circumpolar Deep Water onto the shelf, into over-deepened shelf basins and troughs, leads to temperatures > 3.5°C above freezing point in the Amundsen Sea Embayment and Pine Island Bay (Jacobs et al., 2011). These warmer waters are assumed to increase the melting rate at the base of the floating ice shelves (Rignot et al., 2002; Vaughan, 2008) and in the last decade the presence of the warm CDW has risen there facilitating rapid ice shelf decrease (Jenkins et al, 2010; Jacobs et al., 2011).

2.2. Collection and treatment of samples

A 2 m wide Agassiz trawl (AGT) was deployed at 3 stations in the southern Bellingshausen Sea, 10 stations in the Amundsen Sea slope and shelf and at 2 adjacent deep-sea station during the RRS *James Clark Ross* expedition JR179 BIOPEARL II in February-April 2008 (Figure 1, Table 1). The sampling design on the shelf and slope was per location (BIO1-6) up to three depth intervals (500 m, 1,000 m, 1,500 m; labelled 1-3) were trawled with two (1,500 m; A-B) or three (500 m, 1,000 m, A-C) replicates resulting in the following labels e.g. BIO4-AGT-2B for a 1,000 m (AGT-2) replicate (B) AGT in inner Pine Island Bay (BIO4).

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A total of 37 AGT with an inner net size of 10 mm were taken and the collected benthic fauna was analysed (Table 1). The deployment protocol was standardised to 10 min (500 m) and 15 min (>1,000 m) trawling at 1 knot with 1.5 times cable length to water depth to facilitate comparability between the different trawls. The haul distances were calculated from the time the Agassiz trawl travelled on the ground, while heaving (0.5 m/s) had to be added after the ship stopped and the tension meter of the winch clearly indicated when the AGT left the seabed. Haul length varied from 344 to 1374 metres (Table 1). Species richness and abundance from the stations in the southern Bellingshausen Sea are shown but not included in the analysis of the Amundsen Sea.

When the trawl reached the deck, each sample was sieved through 500 µm Glenammer test sieves. Mega- and larger macrofauna were separated by eye on deck, tissue samples taken for DNA analysis and specimens fixed in 96% ethanol, 4% formaldehyde or frozen at -20°C. The residues in the sieves were fixed in 96% ethanol. After 48 hours fixation at +8ºC the sieve residue was sorted under stereomicroscopes. The taxa of each trawl sample were identified to morphospecies and counts made to determine the abundance and species richness of major taxonomic groups. Species records will be deposited in SCAR-MarBIN (Scientific Committee of Antarctic Research Marine Biodiversity Information Network; www.scarmarbin.be). For faunal analysis, organisms were assigned to one of 32 higher taxonomic groups (Table 2). The phylum Arthropoda was split into the subphyla Chelicerata and Crustacea. To enable comparisons between densities at replicates, the number of individuals and mass were standardised to 1,000 m^2 trawled area hauls and relative abundances were evaluated to compensate for the

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qualitative nature of the AGT data. The times and positions when the AGT reached and left the seafloor were used to calculate trawl length to compensate for the fact that the trawl cannot be closed. Biomass was measured on board as wet weight to within 0.001 kg with marine scales.

Assemblage composition similarity between station replicates was analysed using Jaccard similarities of transformed species presence/absence data (Jaccard, 1902; 1912) and displayed as MDS using PRIMER 6 (Clarke and Warwick, 2001). . The analysis package PRIMER 6 (Clarke and Warwick, 2001) was also used to calculate the estimated number of species using Chao and Jacknife estimators and to analyse the assemblage variability along gradients with ANOSIM and SIMPER and Sigmaplot was used test species richness and adundancetrends by linear regression.

3. Results

The investigations of shelves, slopes and deep sea of the southern Bellingshausen and eastern Amundsen seas, based on 37 AGT catches, yielded 5,469 specimens belonging to 16 phyla, at least 20 classes and more than 270 species (Table 2, 3, Supplement 1). The total collected wet mass was 24.495 kg (Table 1).

3.1. *Taxon richness*

The numbers of species found per station in the southern Bellingshausen Sea and the Amundsen Sea ranged from 1 at station BIO1-AGT-2B to 55 at BIO6-AGT-3C (Figure 2, Table 1). Variability in species numbers between replicates from one station was higher on the shelf (500 m) than in the deeper waters (Figure 2A). Highest species numbers in the Amundsen Sea were found at the 500 m stations in PIB (BIO4-AGT-3) and at the shelf edge of the Amundsen Sea Embayment (BIO6-AGT-3) (Figure 2 B). Species richness varied between

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stations and replicates, increasing with depth at the southern Bellingshausen Sea location (BIO1), but decreasing with increasing depth in the Amundsen Sea (R^2=0.3993, p< 0.0001; Figure 2). The innermost station in PIB yielded the highest species numbers, for an individual replicate (55 species) as well as for the pooled stations (96 species) (Figure 2A, B). The most frequent phylum was Echinodermata, occurring at 35 of the 37 stations, followed by Crustacea (32 stations) Mollusca and Cnidaria (both 31 stations) (Table 2). Regarding species numbers at each replicate, bryozoans were most numerous with 26 species (BIO6-AGT-3C) and 18 species (BIO4-AGT-3B), followed by echinoderms with 19 species (BIO4-AGT-3A) and 18 species (BIO6-AGT-2A) (Table 2). Many other phyla often occurred with a single species only in many of the catches (Table 2). In total 275 taxa have been identified to species level so far, of which 32 species were identified as new to science (Table 3, Supplement A.1). Of these, 128 were singletons (found in one AGT catch only) and 46 doubletons, indicating patchy distributions of species in the ASE and PIB (Supplement A.1). The scaphopod *Dentalium majorinum* Mabille & Rochebrune, 1889 found at 22 stations and the holothurian *Peniagone vignoni* Hérouard, 1901 at 17 stations were present at the most sampled stations (Supplement A.1). Calculations of the estimated number of species using jackknife and chao estimaters based on the species observed in the Amundsen Sea suggests that less than half of the present benthic large macro- and megafauna has been recorded (Figure 3). The Bryozoa with 70 identified species were the most species rich taxon recorded, followed by Ophiuroidea (23 species), Polychaeta (23 species) and Holothuroidea (20 species) (Table 3).

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3.2. *Abundance*

The echinoderms, with 2,980 specimens, were the most abundant taxon in terms of total collected specimen numbers as well as relative abundance at each site (Figure 4A). The next most abundant phyla were Mollusca (616 spec.) and Cnidaria (345 spec.). Apart from the consistent dominance of echinoderms in the Amundsen Sea, the relative abundances of other taxa varied; at some stations polychaetes were of importance (e.g. BIO3-AGT-1C, BIO4-AGT-2B), at others bryozoans (e.g. BIO5-AGT-2B, BIO4-AGT-3B, BIO6-AGT-3C).

Abundances of individuals per 1,000 m^2 ranged from 1.1 (BIO1-AGT-2B) in the southern Bellingshausen Sea, and 2.5 (BIO5-AGT-1B) in Pine Island Bay to 397 (BIO6-AGT-2A) at the upper slope of the Amundsen Sea (Figure 4B). Standardized abundances were highest with ~ 400 ind/1,000 m^2 in two AGT hauls at 1,000 m depth on the Amundsen Sea continental slope (BIO6-AGT-2A & B) followed by the 500 m AGT hauls in Pine Island Bay (Figure 4B) but no trend with depth was observed.

3.3. *Assemblage structure*

The assemblage analysis of the Amundsen Sea stations showed a close grouping of the 500 m stations while the 1,000 m and 1,500 m stations formed a second grouping which can be subdivided into the three areas BIO4, BIO 5 and BIO6 (Figure 5). The two deep-sea stations at the Mary Byrd Seamount in 2000 m and 3000 m depth clearly separate from the shelf and slope stations. The ANOSIM based on the Jaccard resemblance matrix confirmed significant differences between the 500 m stations and the deeper 1,000 and 1,500 m

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stations ($p < 0.001$) based on the factor “depth”, but no significance different was found between the deeper stations (1,000 m and 1,500 m). Analysis of the similarity of the deeper samples (1,000 and 1,500 m) by geographic location (continental slope (BIO6) versus Pine Island Bay troughs (BIO4+5) 1,0001,500station subset found significance differences in the structure of these assemblages ($p<0.001$). The SIMPER analysis on the complete Amundsen Sea assemblage dataset showed an average similarity 29% for the 500 m stations, 17% for the 1,000 m station and 16 % for the 1,500 m and displayed the species most responsible for this (Table 4). The SIMPER analysis on the geographic groupings showing the differences between the stations on the continental slope and the Pine Island Bay troughs is shown in Table 5.

4. Discussion

4.1. *Taxon richness*

This study is based on the first benthic samples to be collected in the eastern Amundsen Sea, and suggests that the higher taxon richness (e.g. phylum, class and order levels) is as high as that of other Antarctic regions (Gambi and Bussotti, 1999; Arntz et al., 2005; Rehm et al., 2006; Linse et al., 2007; Griffiths et al 2008; Cummings et al., 2010). However, the taxonomic composition of the Amundsen Sea benthic fauna is different from the Dumont D’Urville, Weddell and Ross Seas, and the islands in the Scotia Sea. The Amundsen Sea macro- and megafauna collected by this study is comparatively species rich in bryozoans (Barnes and Hillenbrand, 2010), decapods, echinoderms and octopus (this study) whilst poor in bivalves, gastropods, amphipods and isopods (Brandt et al., 1999; Linse et al., 2006). Dimmler et al. (1996) observed a similar composition in the megafauna

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Bakutis Coast region of the Amundsen Sea. The species richness observed in the larger isopods and molluscs in the Amundsen Sea AGT samples is opposite to that observed for smaller macrobenthic isopods and molluscs collected by an epibenthic sledge (EBS) at the same stations in the Amundsen Sea (Kaiser et al., 2009, Moreau et al., 2013). In the decapods, moderate species richness was observed in the Amundsen Sea with four benthic species, the shrimps *Nematocarcinus lanceopes*, *Notocrangon antarcticus* and *Chorismus antarcticus* as well as the lithodid *Neolithes yaldwyni*. For the more intensively sampled Weddell Sea, a total of five benthic shrimp species are recorded with the former three species as well as the two rare deep-water species *Eualus kinzeri* and *Lebbeus antarcticus*, while lithodids are absent (Gorny, 1999). During the intensive sampling of the CEAMARC surveys in Terre Adélie, only two species of benthic decapods, *Nematocarcinus lanceopes* and *Chorismus antarcticus* were collected (Raupach et al., 2010). The tunicate fauna in the Amundsen Sea is less prominent compared with 33 species of ascidians identified from Terre Adélie collected during the French-Australian CEAMARC surveys (Monniot et al., 2011).

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The overall observed species richness (275 species) in Amundsen Sea Embayment and Pine Island Bay is far lower than the overall species richness reported from the eastern Weddell Sea (1,059 species) (Gutt et al., 2000), but different taxonomic groups were identified to species level. When the same taxonomic groups (bivalves, gastropods, polyplacophorans, scaphopods, amphipods, isopods, decapods, pycnogoids, bryozoans, brachiopods, ophiuroids and asteroids) are compared, the species richness in the eastern

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Weddell Sea with 471 species is three times higher than the 153 species observed in the Amundsen Sea. Based on the observed Weddell Sea species richness (Gutt el al., 2000) analyzing only 16 of the 42 stations, Gutt et al. (2003) estimated the number of macrozoobenthic species for the Weddell Sea shelf (2098 - 14358 species) as well as the entire Antarctic shelf (11232 – 17110 species). Their (Gutt et al., 2003) Jack-knife 1&2 and Chao 2 estimations doubled the number of observed species for the Weddell Sea, a result similar to the estimated species richness observed in this study.

The number of species per trawl (1-55) from the AGTs taken in the Amundsen Sea is lower than that reported from other Antarctic shelf regions. On the shelves of localities such as the eastern Weddell Sea or Bouvet Island 46 to 306 species have been reported from trawls taken in 230 – 855 m depth (Arntz et al., 2005, 2006). In the southern Weddell Sea 25 – 112 species were reported in trawls taken in 252 – 1176 m depth (Voβ, 1988). The Amundsen Sea species per trawl numbers are more similar to those observed in AGTs taken in the deep-sea of the Antarctic South Atlantic section, where species numbers ranged from 6 to 148 (Linse et al., 2007). Kaiser et al. (2009) observed an increase of isopod families and genera in the AS from the outer shelf to the inner Pine Island Bay analyzing EBS samples collected at the 500 m stations. They hypothesized that the high taxonomic richness implies evidence for stability in the environment, although the most abundant families were mobile ones that can re-colonize habitats after disturbance events. The greater species richness discovered in the inner Pine Island Bay might be related to the glacial history of the region as Pine Island Bay might have been a refuge for shelf species during glaciations (Barnes and Hillenbrand, 2010) or

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the deep troughs provide higher habitat heterogeneity and niches. The presence of shelf refugia and their importance for re-colonization after glaciations events has been discussed by Thatje et al. (2005; 2008) and Convey et al. (2009). Post et al. (2010) suggested that the current benthic community structure on the George V Shelf, East Antarctica, was recolonized after the LGM from the deep sea as well as the possible shelf refugia on the Mertz and Adélie Banks. The higher species richness might also be linked with the presence of the productive Pine Island Polynya (Arrigo et al*.,* 2012; Mills et al*.,* 2012), as connectivity has been shown between primary production and benthic diversity (Corliss et al*.,* 2009; Sun et al*.,* 2006).

The high number of singleton and doubleton species is an unexpected observation, which could indicate a patchy distribution or rare occurances of species in the Amundsen Sea. Evidence for this patchy distribution is shown by the fact that at each sample location two to three AGT hauls were taken next to each other. The high number of rare occurrences seems not to be caused by the few samples taken in the Amundsen Sea. Kaiser et al. (2009), analyzing the macrobenthic isopods from the 500 m EBS samples in the Amundsen Sea, reported a high rate of undescribed species in the families Desmosomatidae and Nannoniscidae. The geophysical data and sediment core data for the Amundsen Sea suggest that grounded ice extended to the shelf edge during the LGM retreated to the inner shelf by 10 ^{14}C ka BP (Graham et al., 2010). Without underwater video surveys, as done in the George V Shelf and Terre Adélie, we cannot postulate if the scouring marks detected in the geophysical surveys (Graham et al., 2010) are of recent or historical origin, on the age of the fauna collected, or if the observed high

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number of rare species is a result of disturbance. Gutt et al. (2007) showed that different levels of disturbance and biological dynamics affect the mega-benthic assemblages of Terre Adélie in 20 m to 100 m depth. The studies on the impact of ice disturbance on the shallow-waters (5 – 25 m) benthic community structure off Adelaide Island suggested that increased iceberg scouring intensity would result in fewer species and lower abundances and biomass (Smale 2007, 2008). Studying the benthic fauna of the Larsen Ice Shelf 5 and 12 years after its collapse, Gutt et al. (2010) found an impoverished fauna with pioneer species as well as typical Antarctic shelf species.

In an unexplored biogeographic region like the Amundsen Sea, the discovery of undescribed species can be expected; benthic studies on the fauna of the southern Bellingshausen Sea have revealed new fish, crustacean and molluscan species (Garcia Raso et al., 2005, 2008; Eakin et al., 2008; Aldea et al., 2009, 2011). The morphological identifications of the collected benthic fauna has revealed at least 32 undescribed species, with further species being assigned to a species with cf. which requires further detailed morphological and molecular identifications to confirm their species status. A new species already described from the Amundsen Sea is *Acutiserolis poorei* Brandt, 2009 (Brandt, 2009). Specimens of *Promachocrinus kerguelensis* helped to reveal circumpolarity and sympatry of seven lineages in the Southern Ocean with three of these lineages being found in Amundsen Sea (Hemery et al., 2012). Specimens from the lineage D in Amundsen Sea show a strong connectivity between this population and those from the Antarctic Peninsula and the Weddell Sea (Hemery et al., 2012). Molecular COI

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barcoding on Amundsen Sea holothurians has revealed an undescribed species of the genus *Crucella* and also genetic connectivity to the neighbouring Ross Sea (O'Loughlin et al., 2010). Genetic connectivity to the Ross Sea was also suggested for *Pareledone aequipapillae* (Allcock et al., 2011) and to the Weddell Sea for *Benthoctopus* (Strugnell et al., 2011).The Bellingshausen Sea gastropods *Antimargarita powelli* Aldea, Zelaya and Troncoso, 2009 and *Zeidora antarctica* Aldea, Zelaya and Troncoso, 2011 have also been recorded in the Amundsen Sea, suggesting a faunal overlap between these neighbouring regions. The taxonomic assessment of ophiuroid species of the Amundsen Sea has revealed that most species are also found in neighbouring regions (Sands et al., 2012). In the pycnogonids 10 of the 11 species reported from Amundsen Sea are circumpolar and biogeographically group with the continental shelf fauna (Munilla and Soler, 2009, Griffiths et al. 2011). Biogeographic analyses for the other benthic taxa are required to reveal the biogeographic position of the Amundsen Sea.

4.2. *Abundance*

The abundance patterns in the Amundsen Sea Embayment and Pine Island Bay are, as with species richness, dominated by echinoderms. Echinoderms stood out in the soft bottom assemblages in the Amundsen Sea Embayment and Pine Island Bay, irrespective of depth and latitude. In contrast, the soft-bottom assemblages in the Ross Sea (Gambi and Bussotti, 1999), off Anvers Island (Glover et al., 2008) and at Livingston Island (Griffiths et al., 2008) are dominated by polychaetes and bivalves. A dominance of echinoderms has previously been observed for the shelf and upper slopes of Elephant Island, the northern Powell Basin, Southern Thule, Bouvet Island, at the Larsen ice shelves in the Weddell Sea and off the Bakutis Coast in the AS (Arntz et al.,

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2006, Griffiths et al., 2008, Gutt et al., 2010, Starmans, 1997). At South Georgia, Shag Rocks and in the Falkland Trough taxon dominances varied with depth (Griffiths et al., 2008). They reported that at South Georgia, malacostrac crustacea dominated at 200 m in abundance, while at 500 m holothurians and at 1,000 m polychaetes were most abundant and at 1,500 m crustaceans and polychaetes dominated.

Analysing relative macro- and megabenthic abundances in the bathyal and abyssal Weddel Sea Linse et al. (2007) reported differences between individual stations, but revealed no general trend linked with depth or location. Malacostracan crustaceans were most abundant at slope stations and ophiuroids dominated between 3000 and 4500 m while the proportion of bivalves increased with depth. Sponge dominated habitats like those present in the Weddell and Ross seas and Terre Adélie (Arntz et al., 1994; McClintock et al., 2005; Eléaume unpublished) have not yet been found in the Amundsen Sea (Dillmer et al., 1996; this study). Antarctic sponge dominated assemblages are usually found in areas associated with colder Antarctic Bottom Water that is not present on the Amundsen Sea shelf (Olbers et al., 1992). The shallower, near shore habitats off Terre Adélie (20 m to 100 m depth) are dominated by holothurians, polychaetes and ascidians while sponges were rare (Gutt et al., 2007). Video surveys of the megabenthos in the George V Shelf (Dumont d'Urville Sea, East Antarctica) from 117 m to 1175 m revealed dominance of bryozoans, sponges and soft corals (Post et al., 2010) in this area.

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Compared to standardized macrofaunal abundances from shelf and upper slopes of the Weddell Sea based on grab samples (16 – 14483 individuals/m^2), the Amundsen Sea abundances (2.5 – 397 individuals/ 1,000 m^2) are low (Arntz et al., 2005). They show similar abundances to the individual numbers observed in the Scotia Sea at comparable depths (Griffiths et al., 2008) and in the Antarctic deep sea (Linse et al., 2007), which were also obtained by AGT. The trend of decreasing abundance with increasing depth, which has been observed at Antarctic slopes (Piepenburg et al., 2001), was not found at the BIO6- AGT-2 station at 1,000 m on the continental slope, which showed very high abundances. Linse et al. (2007) had reported an increase of macro- and megafaunal abundance with depth in the Powell Basin, while the opposite trend was found off Kapp Norvegia. No information is available on the absolute and relative abundances of the megafauna observed off the Bakutis Coast in the Amundsen Sea as these stations were pooled with the Bellingshausen Sea stations (Starmans et al., 1999).

4.3. *Assemblage structure*

The similarity analysis of the Amundsen Sea revealed faunal assemblage separation by depth. The similar faunal assemblages were found at the outer and inner 500 m stations but differing faunal composition of the 1,000 m and 1,500 m deep stations between the continental slope and inner Pine Island Bay. Overall the similarity patterns of the assemblages were driven by the high number of singletons and doubletons and not the presence of common, shared species. The similarity of the 500 m stations can be explained with the continuous shelf between the continental shelf break and the inner Pine Isalnd Bay throughs. . A comparison of the similarities between only the deeper stations discovered a geographic split between the continental slope samples

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and the Pine Island Bay trough stations indicating different assemblages possibly due to not all species present in the adjacent deep sea being able to reach the inner troughs. The sediments in the studied Amundsen Sea Embayment and Pine Island Bay consisted of soft sediments and hard substrates were absent, so no separation by sediment type was applicable. Gutt et al., (2010) analyzing the benthic fauna of Larsen A/B after the collapse of the ice shelf found clear separation of benthic faunal assemblages by sediment type, distance from former ice shelf edge and water depth. The clear separation of the seamount stations from the shelf and slope stations is not surprising as seamounts typically host highly unique faunas (Rogers, 1994). Analysing the megafauna assemblages based on video surveys in the Amundsen, Bellingshausen and Weddell seas, Starmans (1997) discovered three assemblages in the Weddell Sea based on depth and sediment and two groups in the Bellingshausen and Amundsen seas based on sediment characteristics. Of three stations collected in the Amundsen Sea, two were associated with soft sediments and one with soft sediments containing larger dropstones (Starmans, 1997).

4.3. *Conclusions*

The benthic macro- and megafauna of the eastern Amundsen Sea has been reported for the first time and new benthic species are recorded. While species richness in some taxa, e.g. bivalves and gastropods was low, other taxa like bryozoans, echinoids and ophiuroids was high. The fauna in the deep basins of Pine Island Bay shows some similarities with the fauna of the adjacent continental slope explainable by a connection via the intruding Circumpolar Deep Water. However, these basin communities are not a subset of the continental slope fauna but have their own species composition

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signature. At present the position of the Amundsen Sea within the biogeographic regions of the Southern Ocean is mostly unknown and further analyses are required. The results presented here show shared species with the neighboring regions, the Ross and southern Bellingshausen seas.

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Table legends

Table 1

Details of Agassiz trawl (AGT) stations and replicates of BIOPEARL II. Abbreviations: sBS – southern Bellingshausen Sea, ASE – Amundsen Sea Embayment, PIB – Pine Island Bay, MBS – Mary Byrd Seamount, N – number of specimens, S – number of species

Area	AGT	Station	Date	Depth (m)		Latitute (S)		Longitude (W)		Haul lengths			Biomass
				Start	End	Start	End	Start	End	(m)	N	S	(kg)
sBS	1	BIO1-AGT-1A	27/02/2008	1470	1474	-68.3833	-68.38827	-75.8671	-75.88	1068	61	18	0.039
sBS	2	BIO1-AGT-1B	27/02/2008	1486	1520	-68.3931	-68.39715	-75.8966	-75.9123	1099	32	18	0.039
sBS	3	BIO1-AGT-2A	27/02/2008	939	959	-68.4726	-68.47639	-76.1243	-76.137	879	52	20	0.064
sBS	4	BIO1-AGT-2B	27/02/2008	945	940	-68.4798	-68.48365	-76.1491	-76.1618	918	3	1	0.003
sBS	5	BIO1-AGT-2C	28/02/2008	953	972	-68.4725	-68.47577	-76.1262	-76.1369	839	31	14	0.019
sBS	6	BIO1-AGT-3A	28/02/2008	463	467	-68.5263	-68.53109	-76.1761	-76.1893	804	51	7	0.222
sBS	7	BIO1-AGT-3B	28/02/2008	463	467	-68.5337	-68.53633	-76.1964	-76.2036	538	18	9	0.121
sBS	8	BIO1-AGT-3C	28/02/2008	469	464	-68.5357	-68.533	-76.2017	-76.1944	518	15	7	0.152
ASE	9	BIO3-AGT-1A	04/03/2008	577	596	-71.8104	-71.80735	-106.33	-106.341	639	59	22	0.611
ASE	10	BIO3-AGT-1B	04/03/2008	579	589	-71.8012	-71.79775	-106.295	-106.298	526	37	18	0.051
ASE	11	BIO3-AGT-1C	04/03/2008	582	586	-71.7958	-71.7927	-106.291	-106.295	526	19	9	0.088
PIB	12	BIO4-AGT-1A	06/03/2008	1416	1401	-74.3593	-74.36098	-104.731	-104.708	958	180	21	0.117
PIB	13	BIO4-AGT-1B	06/03/2008	1408	1407	-74.3579	-74.35972	-104.731	-104.709	602	117	17	1.526
PIB	14	BIO4-AGT-2A	05/03/2008	1208	1217	-74.4789	-74.48286	-104.237	-104.219	899	143	33	0.620

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PIB	15	BIO4-AGT-2B	05/03/2008	1037	1191	-74.48	-74.48354	-104.255	-104.239	740	313	30	1.463
PIB	16	BIO4-AGT-2C	05/03/2008	1026	1156	-74.4774	-74.47967	-104.257	-104.239	606	142	38	0.137
PIB	17	BIO4-AGT-3A	06/03/2008	511	501	-74.4099	-74.41291	-104.655	-104.647	526	231	50	2.404
PIB	18	BIO4-AGT-3B	07/03/2008	497	492	-74.3989	-74.40191	-104.63	-104.621	526	305	54	1.205
PIB	19	BIO4-AGT-3C	07/03/2008	499	513	-74.4046	-74.40606	-104.611	-104.605	363	78	37	0.245
PIB	20	BIO5-AGT-1A	08/03/2008	1505	1486	-74.1266	-74.13008	-105.777	-105.757	998	70	13	0.080
PIB	21	BIO5-AGT-1B	08/03/2008	1518	1534	-74.1188	-74.12214	-105.824	-105.804	978	6	5	0.006
PIB	22	BIO5-AGT-2A	09/03/2008	1053	1079	-73.8625	-73.86312	-106.294	-106.277	819	8	4	0.004
PIB	23	BIO5-AGT-2B	09/03/2008	1110	1088	-73.8718	-73.87446	-106.299	-106.281	819	25	12	0.048
PIB	24	BIO5-AGT-2C	09/03/2008	1070	1094	-73.8656	-73.87137	-106.299	-106.291	879	227	13	0.070
PIB	25	BIO5-AGT-3A	10/03/2008	558	552	-73.9749	-73.97853	-107.422	-107.415	526	190	25	4.461
PIB	26	BIO5-AGT-3C	10/03/2008	539	534	-73.9864	-73.98941	-107.39	-107.382	538	162	37	1.923
PIB	27	BIO5-AGT-3D	10/03/2008	544	536	-73.9805	-73.98259	-107.408	-107.403	403	171	40	5.004
ASE	28	BIO6-AGT-1A	13/03/2008	1516	1504	-71.1463	-71.14873	-109.971	-109.989	938	152	19	0.822
ASE	29	BIO6-AGT-1B	13/03/2008	1485	1490	-71.1517	-71.1533	-110.013	-110.031	978	128	23	0.159
ASE	30	BIO6-AGT-2A	12/03/2008	1080	1003	-71.1751	-71.17761	-109.863	-109.878	879	699	32	0.561
ASE	31	BIO6-AGT-2B	12/03/2008	998	985	-71.179	-71.18048	-109.894	-109.91	859	657	28	0.639
ASE	32	BIO6-AGT-2C	12/03/2008	987	970	-71.1821	-71.18392	-109.926	-109.944	828	410	27	0.194
ASE	33	BIO6-AGT-3A	11/03/2008	481	479	-71.3482	-71.34451	-109.998	-109.998	487	237	36	0.684
ASE	34	BIO6-AGT-3B	11/03/2008	481	479	-71.3416	-71.33792	-109.998	-109.998	487	206	31	0.161

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ASE	35	BIO6-AGT-3C	11/03/2008	476	478	-71.3486	-71.34636	-110.006	-110.006	344	263	55	0.317
MBS	36	BIO7-AGT-2000	15/03/2008	2214	2221	-69.2094	-69.21245	-117.519	-117.501	1167	9	8	0.015
MBS	37	BIO7-AGT-3000	15/03/2008	3166	3174	-69.2609	-69.26393	-117.33	-117.327	1374	20	7	0.221

Table 2

Taxon richness of benthic phyla per AGT haul, sorted by presence.

Station	Ctenophora	Hemihordata	Miscellaneous	Chaetognatha	Echiura	Sipunculida	Nemertea	Brachiopoda	Chelicerata	Chordata	Bryozoa	Porifera	Annelida	Cnidaria	Mollusca	Crustacea	Echinodermata
BIO1-AGT-1A								1			6		1	1	2	6	1
BIO1-AGT-1B								1			4		3		1	7	2
BIO1-AGT-2A				1			1		1		5		5	1	1	1	4
BIO1-AGT-2B															1		
BIO1-AGT-2C				1						1	4		2		1	1	4
BIO1-AGT-3A				1							1		1	1			3
BIO1-AGT-3B									1			1		1		1	5
BIO1-AGT-3C											1	1		1	1		3
BIO3-AGT-1A					1	1	1		1	2		1	2	2	1	1	11
BIO3-AGT-1B			1		1	1	1	1	1	1			2	2	1		6
BIO3-AGT-1C						1	1						3	1			3
BIO4-AGT-1A							1	1	1		4		2		2	2	8
BIO4-AGT-1B								1		1			4		5	1	5
BIO4-AGT-2A					1			1	2	1	13		5	3	2	1	4
BIO4-AGT-2B						1		1	1		9	1	4	3	3	1	6
BIO4-AGT-2C					1	1			1	1	15		3	2	4	1	9
BIO4-AGT-3A		1			1	1	1	1		1	11	1	4	2	7		19
BIO4-AGT-3B									2	1	18	1	2	4	6	4	16
BIO4-AGT-3C									4	1	11	1	1	4	4		12
BIO5-AGT-1A							1						3	4	2		3
BIO5-AGT-1B								1					1	1	1		1
BIO5-AGT-2A							1				3						
BIO5-AGT-2B						1		1					4	1	1	1	3
BIO5-AGT-2C					1								4		1	3	4
BIO5-AGT-3A										2		1	1		4	2	15
BIO5-AGT-3C								1	2	3		1	6	4	6	1	13
BIO5-AGT-3D			1					2		2		1	8	2	9	3	11
BIO6-AGT-1A														1	3	6	9
BIO6-AGT-1B	1								1					1	7	3	10
BIO6-AGT-2A				1			1		2			1		1	6	2	18
BIO6-AGT-2B									2				1	1	9	5	10
BIO6-AGT-2C			1								6		1	1	8	2	8
BIO6-AGT-3A								1	2	1		1	2	3	8	4	14
BIO6-AGT-3B								1	1	1		1	4	3	6	1	13

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BIO6-AGT-3C						1	1	1	26	1	4	3	5	5	8
BIO7-AGT-2000	1								2			1		3	1
BIO7-AGT-3000		1									2		1		3

Table 3

Species numbers per phylum

Phylum	Class		Number of species
Nemertea			1
Mollusca	Aplacophora		1
	Bivalvia		18
	Gastropoda		19
	Polyplacophora		2
	Scaphopoda		1
	Cephalopoda	Octopoda	8
Annelida	Polychaeta		23
Sipunculida			1
Echiurida			1
Arthopoda/ Crustacea	Cirripedia		2
	Malacostraca	Amphipoda	8
		Isopoda	16
		Mysidacea	1
		Euphasiacea	1
		Decapoda	3
Arthropoda/Chelicerata	Pycnogonida		11
Tentaculata	Bryozoa		70
	Brachiopoda		3
Echinodermata	Ophiuroidea		26
	Asteroidea		13
	Echinoidea	Echinoida	2
		Cidaroida	5
		Spatangoida	5
		Holasteroida	2
	Crinoidea		5
	Holothuroidea		20
Hemichordata	Hemichordata		1
Chordata	Ascidiacea		4
Echiurida			1
			274

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Table 4

One-ways SIMPER analysis for factor "depth" for all stations.

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Group 500 (Average similarity: 29.59)					
Peniagone vignoni	0.75	1.99	0.98	6.72	6.72
Flabellidae	0.83	1.87	1.33	6.32	13.03
Porifera	0.83	1.81	1.37	6.1	19.14
Serpula narconensis	0.75	1.7	0.97	5.74	24.88
Dentalium majorinum	0.75	1.36	1.06	4.6	29.48
Ophioperla koehleri	0.75	1.36	1.06	4.6	34.09
Amphiura algida	0.67	1.27	0.82	4.3	38.39
Ceramaster patagonicus	0.67	1.25	0.81	4.21	42.61
stalked ascidia	0.67	1.16	0.82	3.94	46.54
Trilochites biformatus	0.67	1.15	0.82	3.88	50.42
Group 1000 (Average similarity: 16.84)					
Dentalium majorinum	0.78	2.12	1.12	12.58	12.58
Nematocarcinus lanceopes	0.67	1.35	0.83	8.04	20.62
Ophiolimna antarctica	0.67	1.35	0.83	8.04	28.66
Flabellidae	0.56	0.91	0.61	5.43	34.09
Elpidia glacialis	0.44	0.77	0.41	4.6	38.69
Actinernidae	0.44	0.61	0.43	3.64	42.33
Trilochites biformatus	0.44	0.61	0.43	3.64	45.97
Ophiocten dubium	0.44	0.55	0.44	3.27	49.24
Bathyarca pelseneeri	0.44	0.54	0.44	3.22	52.46
Group 1500 (Average similarity: 17.05)					
Dentalium majorinum	0.67	3.1	0.75	18.18	18.18
Actinernidae	0.67	2.95	0.74	17.31	35.49
Nemertea	0.5	1.65	0.46	9.65	45.14
Elpidia glacialis	0.5	1.21	0.48	7.11	52.25

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Table 5

One-ways SIMPER analysis for factor "geographic location" for 1,000 and 1,500 m stations.

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Group PIB troughs (Average similarity: 20.76)					
V50	0.8	3.35	1.05	16.11	16.11
V276	0.7	2.48	0.85	11.93	28.04
V3	0.6	1.82	0.59	8.79	36.83
V67	0.5	1.72	0.49	8.3	45.14
V9	0.4	1.48	0.34	7.14	52.27
Group continental slope (Average similarity: 38.36)					
V94	1	4.1	9.52	10.7	10.7
V112	1	4.1	9.52	10.7	21.4
V211	1	4.1	9.52	10.7	32.1
V216	1	4.1	9.52	10.7	42.8
V239	1	4.1	9.52	10.7	53.5

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Figure legends

Figure 1

Locations of the Agassiz trawl stations sampled during BIOPEARLII. Abbreviations: ASE – Amundsen Sea Embankment, BS – Bellingshausen Sea, MBS – Marie Byrd Seamount, PIB – Pine Island Bay

Figure 2

Species richness per station, sorted by increasing depth. A) Individual trawls including BIO1 in southern Bellingshausen Sea, B) Pooled trawls per station in the Amundsen Sea

Figure 3

Sampled and predicted species richness in the Amundsen Sea. ▲- Observed number of species, ☐ Chao 1, ■Chao 2, ○ Jacknife 1, ● Jacknife 2

Figure 4

Abundance patterns in AS benthos including BIO1 in southern Bellingshausen Sea. A) Relative abundance, B) Macro- and megabenthic abundance per 1,000 m^2

Figure 5

Amundsen Sea benthic assemblage structure. Jaccard similarity based on absence/presence. Water depth: ● 500 m, ■ 1,000 m, ▲1,500 m, ○ 2000 m, ● 3000 m

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Highlights

- First assessment of Amundsen Sea benthic macro- and megafauna
- Species richness comprises 270 species of 32 higher taxonomic groups
- Overall species richness lower compared to that in Weddell or Ross Seas
- Shelf basin fauna linked with continental slope by Circumpolar Deep Water intrusion

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Figure 1

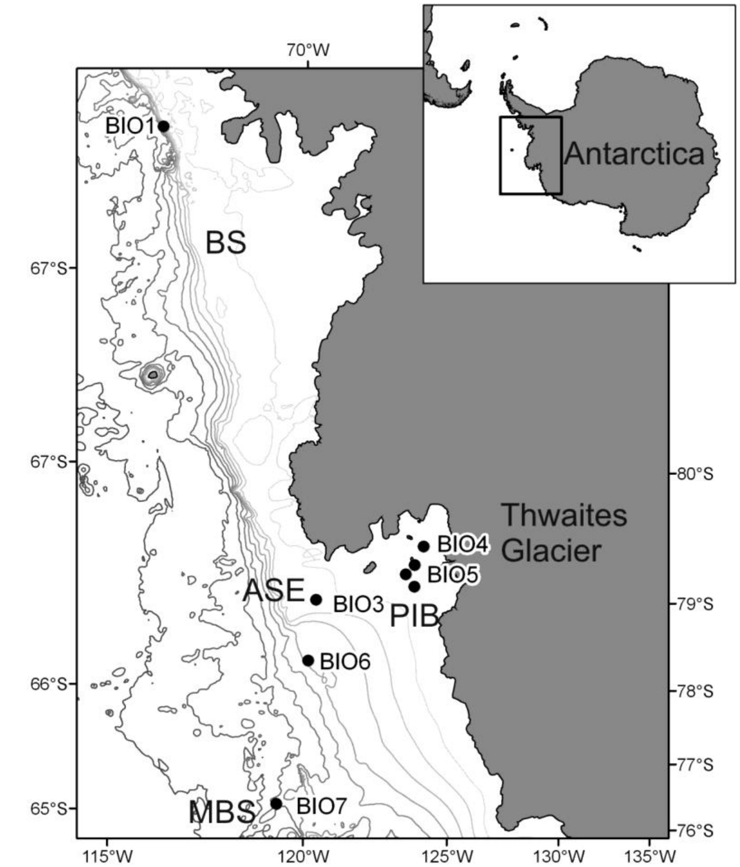

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Figure 2

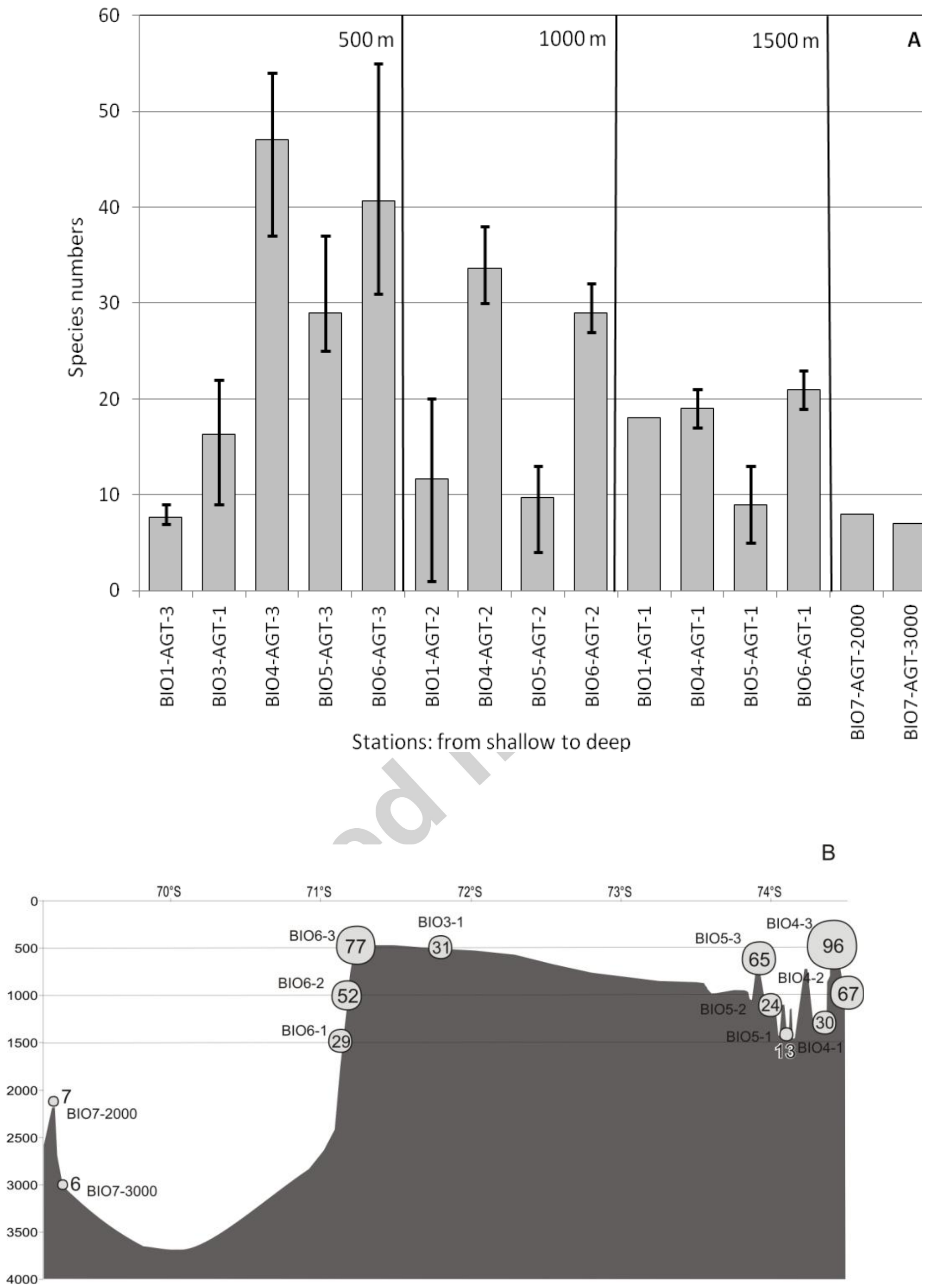

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Figure 3

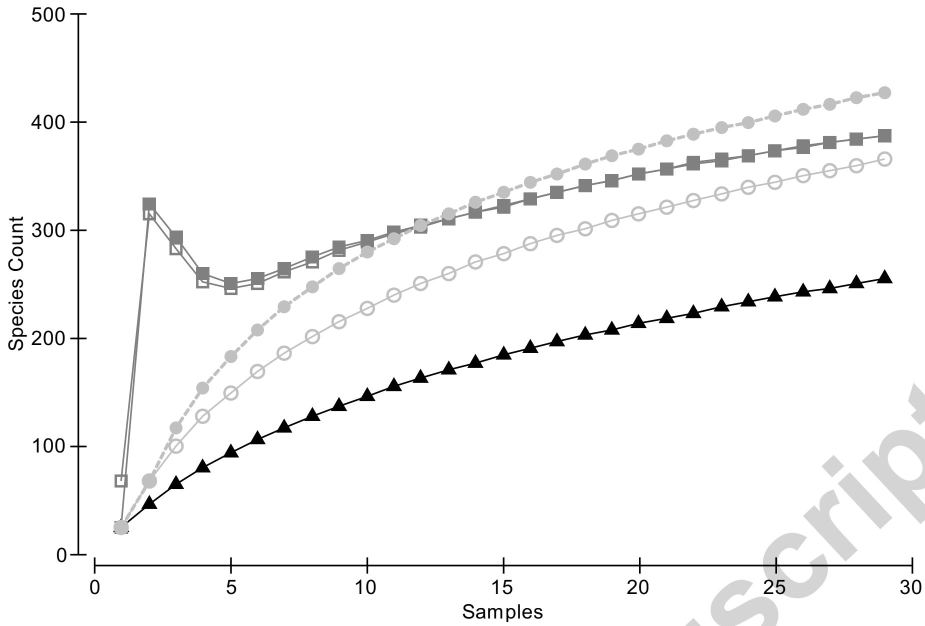

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Figure

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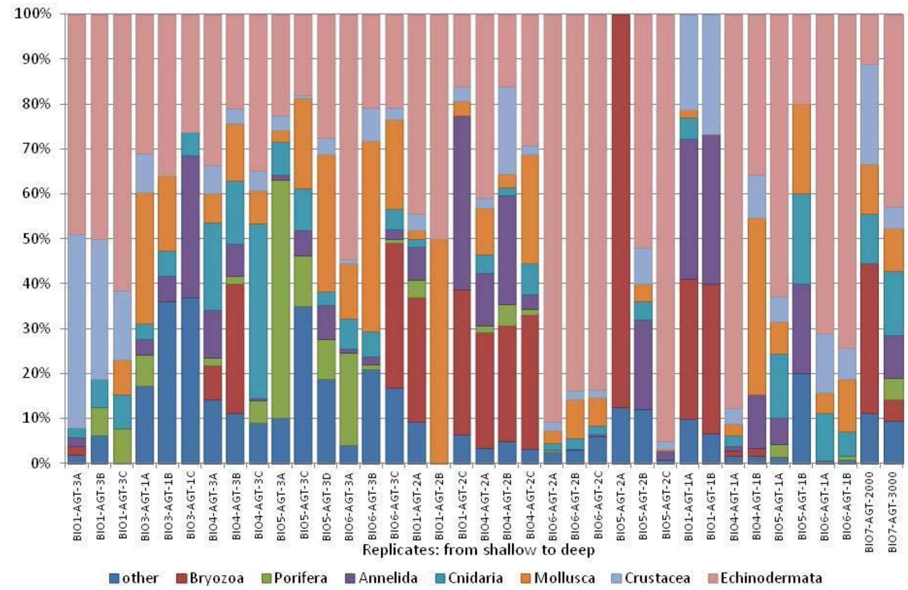
Figure 4

A)



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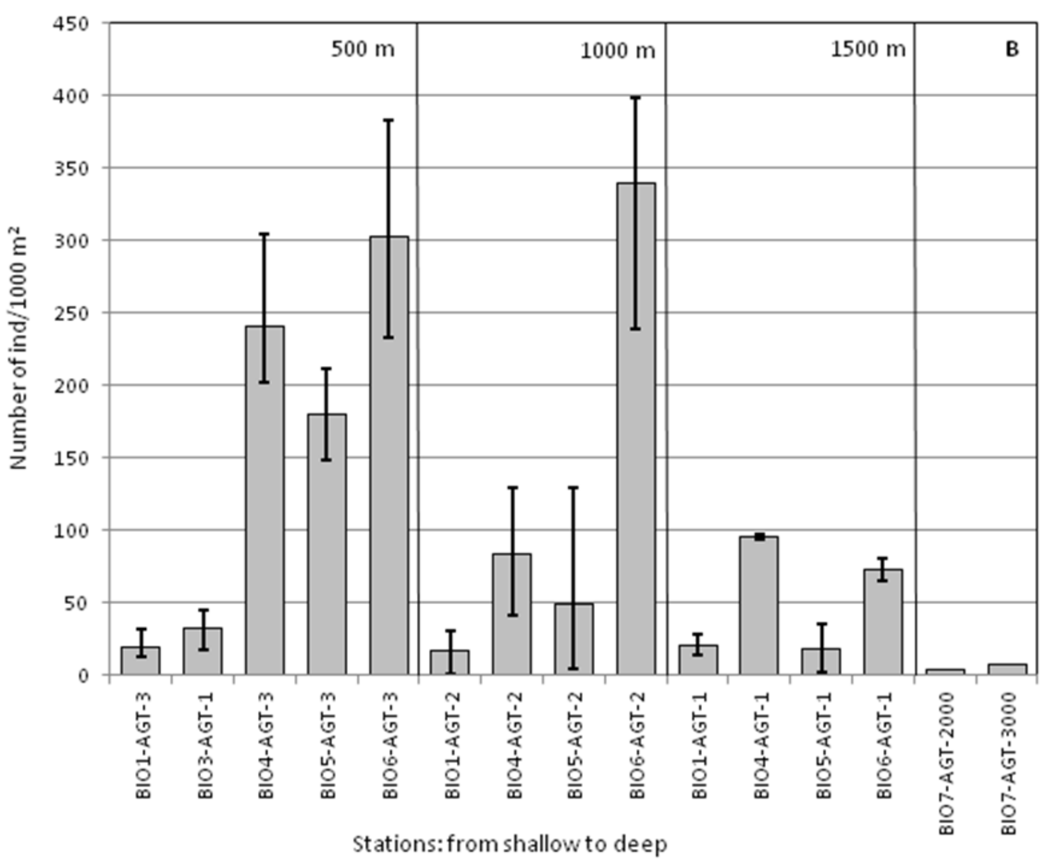

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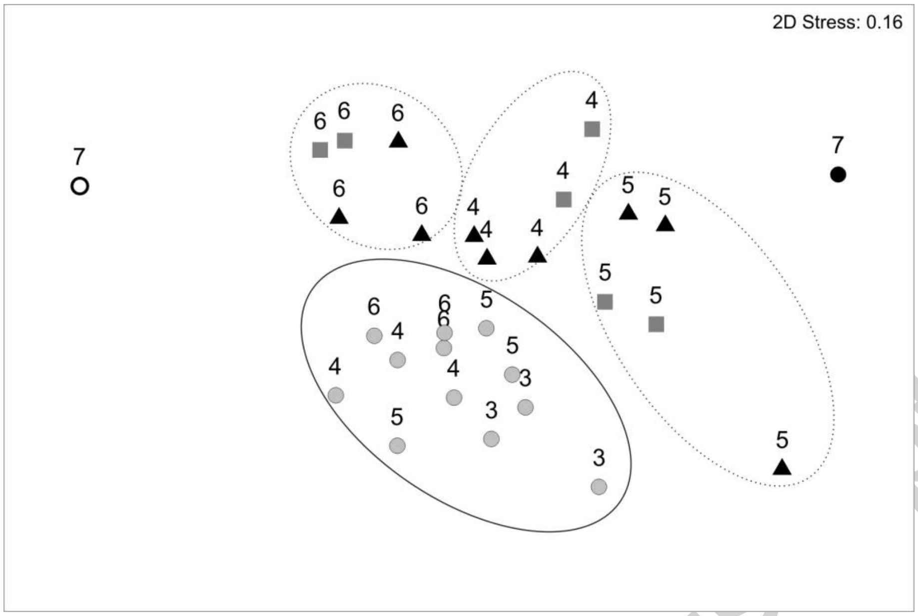
Figure 5



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