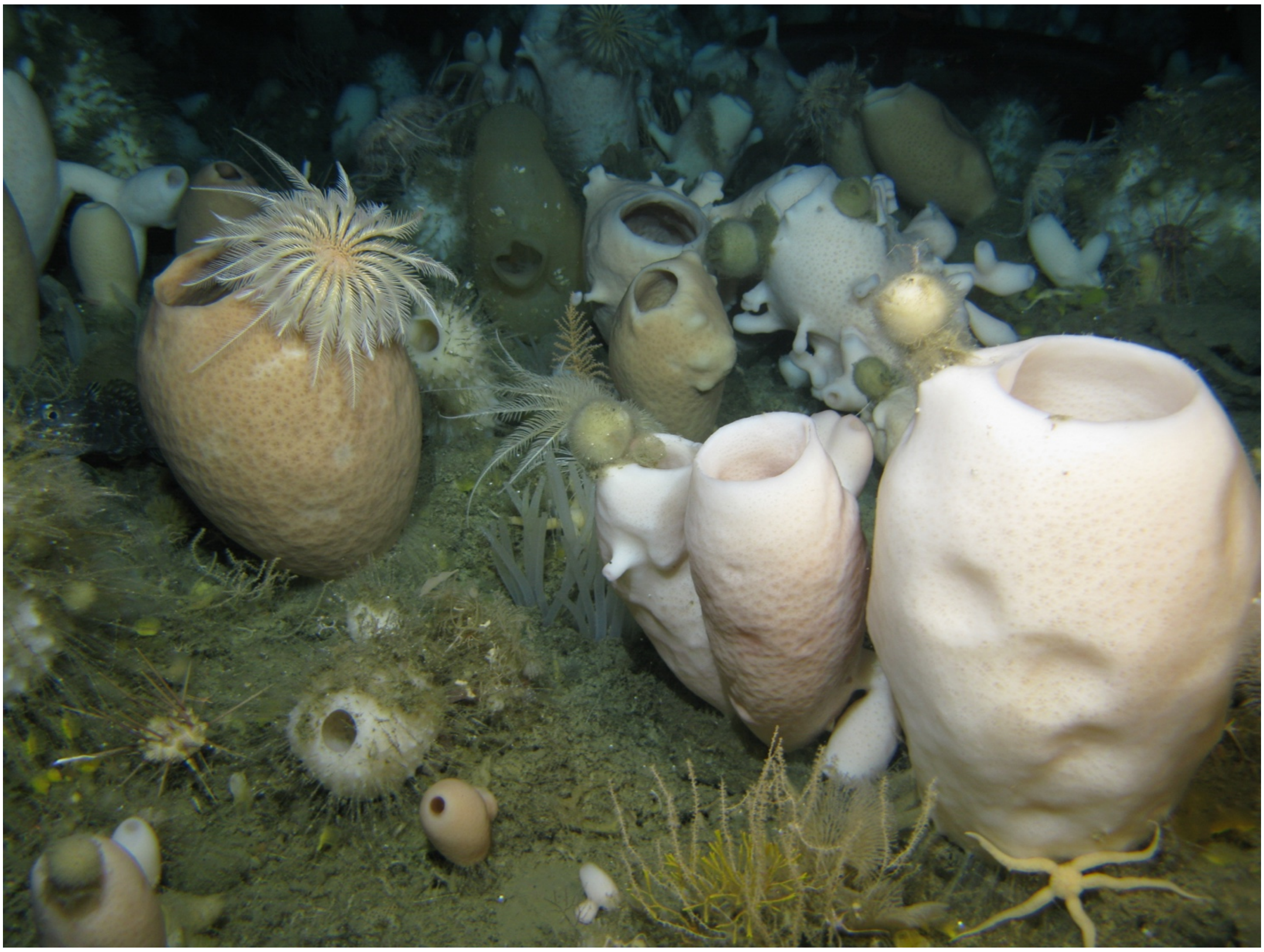
Distribution patterns and abundance of Antarctic pristine benthic communities

Stefano Ambroso



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Barcelona 2020 **PhD Thesis**

Distribution patterns and abundance of Antarctic pristine benthic communities

Patrones de distribución y abundancia de comunidades bentonicas pristinas del Antártida

Stefano Ambroso

Tesis presentada para la obtenciòn del tìtulo de Doctor
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Programa de Doctorado de Ciencias del Mar 2020

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"Distribution patterns and abundance of Antarctic pristine benthic communities"
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“Un hombre borracho y solo
Si cae no se levanta
Y si en el cielo ve una estrella
Es estrella de soledad

Dos hombres borrachos y unidos
Si caen juntos se levantan
Y si en el cielo ven una estrella
Es estrella de unidad”

Nicola Cicolin

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Summary

Knowledge of the abundance, distribution patterns, and population ecology of Antarctic benthic biodiversity have increased considerably during the last decades. Antarctic marine benthic biodiversity has been sampled primarily in areas close to research stations and mainly at shallow depths since more than 100 years using a range of sampling methods, including benthic sleds or trawls and grabs each of which targets a particular community or habitat. Recent technological advances and increased availability of remotely operated vehicles (ROVs), manned submersibles, and video equipped towed gears have significantly increased accessibility to mid and outer continental shelves, continental slopes, submarine canyons and seamounts, thus allowing the direct observation and quantitative study of megabenthic assemblages without any impact on the benthic community.

Due to the high cost and logistics of these benthic sampling, particularly in Antarctica, studies are often limited to only one biological sampling method. Results of biodiversity studies are used for a range of purposes, including taxonomy, trophic ecology, growth rates, reproductive ecology, environmental impact assessments, and predictive modelling, all of which underpin appropriate marine resource management. However, the generality of marine biodiversity patterns identified among different sampling methods is unknown. This is one of the reasons why more comparative studies are necessary to better understand the ecosystem patterns and processes in Antarctic regions in a context of climate change scenario.

Major regions of the Antarctic shelf appear to be undergoing rapid climate change, such as warming on the Antarctic Peninsula in the past few decades. Such climate change will affect benthic ecosystems through changes in

benthic-pelagic coupling. For this porpoise this thesis pretends to generally understand the distribution and the ecological paper that benthic organisms have on the benthic ecosystem of the Antarctic continental shelf. This thesis includes for chapters

In the first chapter we compared the performance of two sampling gears by assessing quantitative data on the continental shelf of three oceanographically very distinct regions in Antarctic Peninsula. In the second chapter we investigate ophiuroid assemblages in terms of the distribution and diversity patterns at three different environmental regimes and depths in the Antarctic Peninsula. In the third chapter we assessed the health status of Antarctic gorgonian assemblages in a pristine and remote area in the southernmost part of the Weddell Sea continental shelf. Finally, in the fourth chapter we tried to understand the way in which a gorgonian population affects the diversity of the surrounding megafaunal species, by characterizing gorgonian assemblages dwelling on two very contrasting continental shelves.

Resumen

El conocimiento de la abundancia, los patrones de distribución y la ecología de población de la biodiversidad bentónica antártica ha aumentado considerablemente durante las últimas décadas. La biodiversidad bentónica marina antártica se ha muestreado principalmente en áreas cercanas a las estaciones de investigación y principalmente a poca profundidad desde hace más de 100 años utilizando una variedad de métodos de muestreo, incluidos trineos o redes de arrastre bentónicos, cada uno de los cuales se dirige a una comunidad o hábitat en particular. Los recientes avances tecnológicos y una mayor disponibilidad de vehículos operados a distancia (ROV), sumergibles tripulados y aparatos de muestreo equipados con videocámara han aumentado significativamente la accesibilidad a las plataformas continentales, taludes continentales, cañones submarinos y montañas submarinas, lo que permite la observación directa y el estudio cuantitativo de comunidades megabentónicas sin ningún impacto en la comunidad misma.

Debido al alto coste y la compleja logística de estos muestreos, particularmente en la Antártida, los estudios que se generan a menudo se limitan a un solo método de muestreo biológico. Los resultados de los estudios de biodiversidad se utilizan para una variedad de propósitos, que incluyen taxonomía, ecología trófica, tasas de crecimiento, ecología reproductiva, evaluaciones de impacto ambiental y modelos predictivos, todos los cuales sustentan la gestión adecuada de los recursos marinos. Sin embargo, se desconoce la generalidad de los patrones de biodiversidad marina que se pueden identificar entre los diferentes métodos de muestreo.

Esta es una de las razones por las que se necesitan más estudios comparativos para comprender mejor los patrones y procesos de los

ecosistemas en las regiones antárticas en un contexto de escenario de cambio climático.

Las principales regiones de la plataforma antártica parecen estar experimentando un cambio climático rápido, como el calentamiento en la Península Antártica en las últimas décadas. Dicho cambio climático afectará a los ecosistemas bentónicos a través de cambios en el acoplamiento bento-pelágico. Para estos motivos esta tesis tiene como objetivo general comprender la distribución y el papel ecológico que tienen los organismos bentónicos sobre el ecosistema bentónico de la plataforma continental antártica. Esta tesis incluye cuatro capítulos

En el primer capítulo se compara el rendimiento de dos artes de muestreo mediante la evaluación de datos cuantitativos en la plataforma continental de tres regiones oceanográficamente muy distintas en la Península Antártica. En el segundo capítulo se investigan las asociaciones de ofiuras en términos de patrones de distribución y diversidad en tres regímenes ambientales y profundidades diferentes en la Península Antártica. En el tercer capítulo se evalúa el estado de salud de las poblaciones de gorgonias antárticas en un área prístina y remota en la parte más meridional de la plataforma continental del mar de Weddell. Finalmente, en el cuarto capítulo se trata de entender la forma en que una población de gorgonias afecta la diversidad de las especies de megafauna asociadas, caracterizando conjuntamente dos poblaciones de gorgonias que habitan en dos plataformas continentales muy diferentes.

General Introduction

Antarctic expeditions

In the late nineteenth century, expeditions such al Challenger, Belgica, and the Discovery were among the first expeditions with scientific purposes, which explored the ocean floor and brought new insights into descriptive oceanography and distribution of marine benthic fauna. During subsequent years, great number of expeditions were carried out in Antarctica and all of them greatly contributed to the knowledge of the Antarctic natural history. Recent advances in technology, such as scuba diving, underwater video footage, ice-capable research vessels, and remotely operated vehicles, have not only increased the rate of new species discovery (Griffiths 2010) but also how they were spatially distributed (Segelken-Voigt et al. 2016, Ambroso et al. 2017, Pineda-Metz et al. 2019). Today, Antarctica is home to an exceptionally rich, abundant and highly endemic biodiversity (Kükenthal 1924, Arntz et al. 1994, Clarke and Johnston 2003, Brandt et al. 2007), especially in areas of the continental shelf and around the Sub-Antarctic islands, which are considered to be one biodiversity "hot spots" in the world.

Antarctic biogeography

The biogeography of Antarctic benthos has been originally classified into three subregions defined as South Georgia, West Antarctica, and East Antarctica (Ekman 1953). More than a decade later, Hedgpeth (1969) proposed his biogeographical zones: the Antarctic and sub-Antarctic, which is still the base of much of modern Antarctic benthic biogeography. In the last three decades there has been a proliferation of work examining Southern Ocean biogeography referencing previous studies as the definitive patterns in Antarctic biogeography. Arnaud (1974), De Broyer & Jazdzewski (1996), Barnes & De Grave (2000), Rodriguez et al. (2007) among others define their biogeographical regions or categories based upon those of Hedgpeth (1969). Unlike the idea proposed by Hedgpeth (1969) based on a small proportion of number species collected, Griffiths (2010) show regions to differ depending upon the class of animals being considered especially considering the benthic communities inhabiting the Antarctic continental shelf. Although many areas of the Antarctic continental shelf remain unexplored, thanks to the advance in technology, the benthic marine fauna of Antarctica is comparatively well known.

Antarctic continental shelf biodiversity

The Antarctic continental shelf covers more than 4.6 million km2 and compared with the rest of the world's ocean shelfs is relatively narrow, varying in width from 15 to 240 km, although several glacial embayments (e.g., Weddell Sea) have shelf widths of up to 1000 km (Post et al. 2014). The shelf is unusually deep, ranging from 400 to 800 m deep (average 450 m) with troughs to over 1000 m because of scouring from ice shelves at previous glacial maxima and depression by the enormous mass of continental ice (Clarke and Johnston 2003). Antarctic benthic diversity, as mentioned before, is generally considered rich and diverse (Arntz et al., 1994) with species endemism rates of around 50% (Griffiths et al. 2009). More than 8,800 benthic species have been described for Southern Ocean shelves (Griffiths 2010), most of which can be found in the taxonomic repository Register of Antarctic Marine Species (RAMS). Based on data from the Weddell Sea the total number of macrozoobenthic species estimated for the entire Antarctic shelf ranged between 11000 and 17000 species, presenting an intermediate species richness when compared to other selected tropical, temperate or Arctic habitats (Gutt et al. 2004). Several ecological analyses of Antarctic assemblages described the general characteristics of Antarctic benthos: patchy distribution, high biodiversity and biomass, dominance of sessile suspension feeders, gigantism, adaptation to low temperature, low metabolic activity, slow growth rates and late maturity age (e.g. Gutt 1991, Gutt and Piepenburg 1991, Arntz et al. 1994, Orejas et al. 2001, Thatje et al. 2005a, Rogers 2012, Peck et al. 2014). The patchiness f the benthic organisms seems to be mainly affected by variation in sediment type and benthic food supply, which depends on primary production, sedimentation, hydrographic factors and seasonal ice cover (Picken 1984). Thanks to the resuspension due to tidal currents and the nutrition's quality of the sediment, there are almost constant benthic trophic conditions throughout the whole year. These events help to explain the high biomass of benthic communities around Antarctica even when food intake to the euphotic zone is scarce as the ocean's surface is covered by ice during the winter months.

Environmental conditions / bentho pelagic coupling

The benthic fauna of the Antarctic continental shelf resides in a cold, well oxygenated, and oceanographically constant environment, at least since the last glacial maxima. Sediments are generally of glacial origin (from silts to large boulders) and poorly sorted but include material of biogenic origin, ice rafted debris, and sediment carried by glacial meltwater (Clarke, 1996a; 1996b, Dayton, 1990). As in most oceans, primary productivity in the Southern Ocean mainly depends on light. But in these latitudes, primary productivity is very low during the austral winter and the highest occurs during spring, reaching values of up to 0.1 mg Chl/l (Turner et al. 2009). This fact is due to the marked seasonal variation in sunlight, although the water temperature remains fairly constant throughout the year. In early spring, phytoplankton coming from the melting season is not immediately consumed by zooplankton in areas where currents are weak. This phytoplankton settles to the bottom of the continental shelf and forms the so-called "food banks" or "green carpet", thus creating a potential food for benthic organisms (Gutt et al. 1998; Turner et al. 2009).

Sampling methods

The fauna of Antarctic continental shelf has been relatively well studied taxonomically; however, most studies have been conducted in areas close to research stations and mainly at depths shallower than 100 m, which are depths that are heavily affected by scouring produced by icebergs. In addition, trawls, sledges, and dredges were historically the most common methods of sampling the shelf benthic marine communities of Antarctica. While these methods are excellent for species identification of sessile and slow-moving benthic organisms, they are not as efficient at capturing mobile species, are destructive, and cannot describe species behavior and interactions present in the ecosystem. Advances in underwater image technology (e.g., photographic and video imagery, SCUBA, remotely operated vehicles, autonomous underwater vehicles) have increased the knowledge about the demographic processes structure and spatial distribution patterns of the Antarctic benthic megafauna on the Antarctic continental shelf (Teixido et al. 2006, Segelken-Voigt et al. 2016, Ambroso et al. 2017, Piazza et al. 2019, Pineda-Metz et al. 2019, Piazza et al. 2020).

All these studies helped to understand the important role that benthic communities have on the benthic ecosystem and provide basic information on their dynamics, as well as to facilitate their management and conservation in a climate change scenario (Gili et al. 2001, Gili et al. 2006).

Climate change

The Antarctic Peninsula (AP) and the Eastern Weddell Sea are two of the most rapidly changing ecosystems on the planet. The multiple components of climate change are anticipated to affect all levels of biodiversity, from organism to biome (reviewed in Parmesan 2006). The Antarctic Peninsula (AP) region is distinctive among Antarctic regions in its response to climate change, with strong decreases in sea ice (Turner et al. 2005), rapid winter warming (+7Cº air temperature since 1950) (Turner et al. 2005), ocean warming (+1Cº sea surface temperature since the second half of the twentieth century) (Meredith and King 2005), and retreat of maritime glaciers and ice shelves (Cook et al. 2005; Domack et al. 2005). Recent climatic trends have resulted in significant changes in Antarctic marine ecosystems, such as decrease in phytoplankton biomass (Stammerjohn et al. 2008; Montes-Hugo et al. 2009), loss of sea-ice habitat for juvenile euphausiid species (Fraser and Hofmann 2003), increase in rates of physiological functions with impacts on growth or feeding requirements (Peck et al. 2006), modification of species geographic distribution and potential invasion processes (Thatje et al. 2005b; Walther et al. 2009), and alteration of benthic assemblages (Smith et al. 2008). Thus, the warming climate threatens to change the composition and function of Antarctic marine communities in ways that are complex and not entirely predictable (Clarke et al. 2007; Walther et al. 2002).

Objectives of the thesis

The major aim of the present Ph.D. Thesis was to assess the status of Antarctic benthic communities in the Weddell Sea continental shelf and in the Antarctic Peninsula. Specifically, this thesis aims to (1) compare the performance of two sampling gears by assessing quantitative data on the continental shelf of three oceanographically very distinct regions in Antarctic Peninsula; (2) investigate ophiuroid assemblages in terms of the distribution and diversity patterns at three different environmental regimes and depths in the Antarctic Peninsula; (3) to assess the health status of Antarctic gorgonian assemblages in a pristine and remote area in the southernmost part of the Weddell Sea continental shelf and finally (4) understand the way in which a gorgonian population affects the diversity of the surrounding megafaunal species, by characterizing gorgonian assemblages dwelling on two very contrasting continental shelves.

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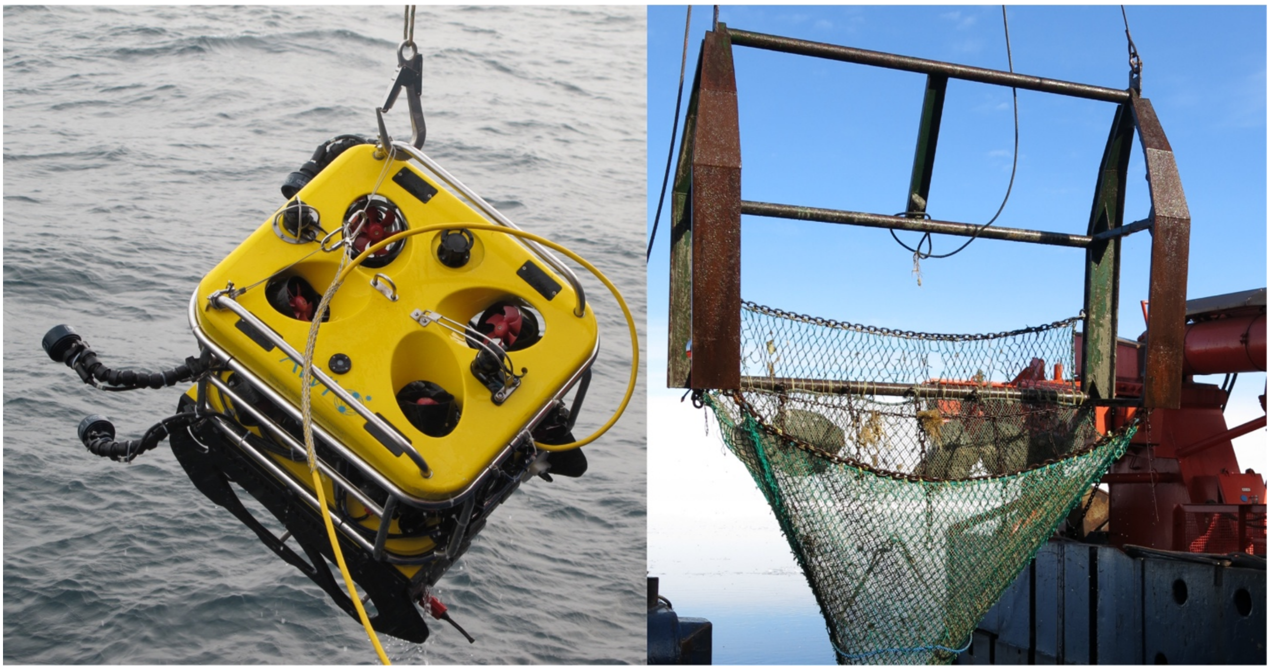
Chapter 1

Comparison of sampling methods to assess marine benthic communities: visual vs destructive methods.



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Introduction

During the last decades, great efforts have been made to study the diversity and the degree of heterogeneity of Antarctic benthic communities (Voß 1988; Gutt and Starmans 1998; Gutt 2000; Teixidó et al. 2002). These studies have helped to corroborate that the Antarctic region has higher diversity levels than expected (Clarke and Johnston 2003; Clarke 2008) and this is especially true for the Antarctic Peninsula (AP), which is considered the region with the highest environmental heterogeneity and a "hot spot" of benthic biodiversity in the Southern Ocean (Walther et al. 2002). Moreover, AP region is distinctive among Antarctic regions in its response to climate change: ocean warming (+1ºC sea surface temperature since the second half of the twentieth century) (Convey and Peck 2019), rapid winter warming (+7ºC air temperature since 1950) (Turner and Comiso 2017), with strong decreases in sea ice (Cook et al. 2016), and retreat of maritime glaciers and ice shelves (Cook et al. 2005).

Numerous investigations on macrobenthic communities have recently been carried out at different sites in AP using both visual (Fillinger et al. 2013; Segelken-Voigt et al. 2016; Gutt et al. 2019) and destructive methods (Piepenburg et al. 2002; Gutt et al. 2016) covering a wide latitudinal range. The use of different sampling techniques, such as video or photographic approaches and trawling, is an important question for benthic sampling design, since different methods may lead to variations in species composition. However, direct comparisons between different gears in Antarctica remain understudied. Two comparative studies off King George Island (Piepenburg et al. 2002) and in the southern Weddell Sea (Pineda-Metz and Gerdes 2017) were carried out using a combination of multibox corer and a still camera system to analyze the spatial distribution of infaunal and epifaunal benthic' assemblages. These studies showed contrasting results: Piepenburg et al. (2002) documented large differences in abundance and composition between quantitative data derived from different sampling methods while Pineda-Metz and Gerdes (2017) demonstrate similar and comparable spatial distribution patterns in the benthic communities sampled by different methods.

On the one hand, small bottom beam trawls, such as Agassiz trawls (AGT), are designed to sample sessile benthic and vagile species (Tecchio et al. 2011). Destructive techniques have an impact on species and habitats, which may not be desirable in the context of monitoring conservation strategies and are not recommended as a standard for quantitative benthos assessments (Rees and Service, 1993). On the other hand, imaging observation systems such as Remotely Operated Vehicle (ROV) or Ocean Floor Observation System (OFOS) have been extensively used to address different questions related to Antarctic marine benthic ecology such as the assessment of densities and distribution patterns of benthic organisms (Teixido et al. 2006; Segelken-Voigt et al. 2016; Ambroso et al. 2017), the description of benthic communities by means 3D reconstructions (Fillinger and Funke 2012; Piazza et al. 2019), the study of large scale area faunal composition (Gutt et al. 2019), and long-term benthic monitoring (Pineda-Metz et al. 2019; Piazza et al. 2020).

In the present study, we compare the performance of two sampling gears by assessing quantitative data obtained by Agassiz trawls (AGT) and seabed images collected by the Ocean Floor Observation System (OFOS) on the continental shelf of three oceanographically very distinct regions: the Weddell Sea, the Bransfield Strait, and the Drake Passage to provide new quantitative data on the combination of different sampling methods on Antarctic megabethos.

Materials and methods

Sampling area

Fieldwork was performed as a part of the multidisciplinary ANT XXIX/3 expedition on board the R/V Polarstern from January 22 to March 22, 2013 (Gutt 2013). The study area included the northwestern Weddell Sea, east of the tip of the AP, the Bransfield Strait, and the Drake Passage, west of the South Shetland Islands with a total extension of approximately 39,000 km^2 (Fig. 1).

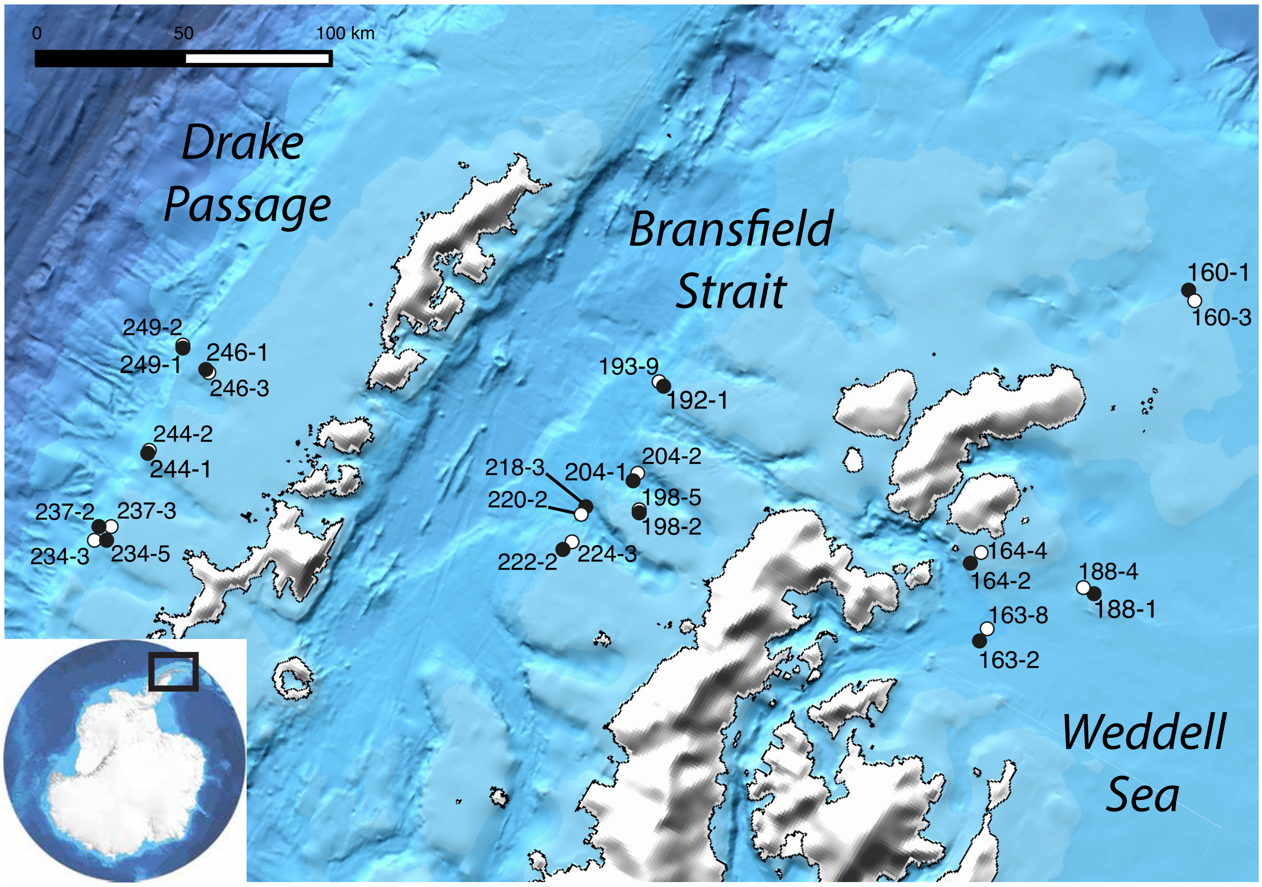

Fig. 1 Map of the study area showing the 14 stations sampled in the three regions and by different gears. Black spots are AGT stations and white spots are OFOS stations.

The study area was sampled with two different gears: the Ocean Floor Observation System (OFOS) and immediately afterward by means the Agassiz trawl (AGT). A total of 28 OFOS and 25 AGT stations were initially sampled. However, we restricted our statistical analyses to the subset of 14 stations grouped in two depth categories: shallow (from 100 to 350 m) and deep (from 400 to 600 m).

AGT sampling

Samples were taken with an AGT with 3.5-m-wide opening and 10-mm mesh size, which was towed on the seafloor for 10 min at 1 knot. From the total catch of each station, a 50-l subsample was randomly collected from the entire catch to be as representative as possible. We followed a standardized protocol to compare semiquantitative data which resulted in a good representation of benthic assemblages across the three regions. On deck, the subsamples were sieved through three mesh sizes (10, 5, and 1 mm). After the macro- and megabenthic fauna were sorted, the organisms were identified to species level whenever possible and, for this study, classified into 18 major taxonomic groups at a class level. Vagile fauna like the cephalopods, fishes and decapods, and organisms that were too small (< 1cm) were disregarded.

OFOS sampling

Seabed images were taken using the (OFOS), see Gutt (2013) for more information. All images, including metadata, are available in the data repository PANGAEA (www.pangaea.de; see DOIs for photographs, ranging from 10.1594/PANGAEA.818400 to 10.1594/PANGAEA.818515).

The setup and mode of deployment of the OFOS was the same as that described by Segelken-Voigt et al. (2015). Information on the exact position of every image was recorded by means of the Posidonia system used for the underwater navigation of the OFOS (see Segelken-Voigt et al. (2015) for more details on the Posidonia system). Three parallel lasers provided a reference scale of 50 cm used to calculate the photographed area in each image. Automatically, a seabed photograph was taken every 30 s to obtain a series of several hundred images along transects of up to 4 km length each. Following Pineda-Metz and Gerdes (2017) a randomly selected subset of 25 images was used for the description of the benthic community. The seabed area analyzed for each image was $1m^2$. In the laboratory, all the visible organisms were counted, identified to the lowest possible taxonomic level, then classified into the same taxonomic groups as for AGT data. Colonial specimens were counted as single individuals.

Statistical analyses and data visualization

To evaluate how stations and taxonomic groups are related to the major explanatory categorical factors of region and depth, we separately produced an ordination of each dataset by means of canonical correspondence analysis, which implicitly uses the chi-squared distance (Legendre 2018). For this analysis, abundance data was fourth-root transformed and significance of factors was assessed using marginal permutation tests with 999 permutations. Analyses were done with functions *cca* and *anova.cca* in the vegan *vxx* R package (Oksanen et al. 2019).

Bivariate relations for each taxonomic group by dataset (i.e. AGT vs. OFOS) were shown as scatterplots with Type II regression lines, which were fitted as standard major axis models using the *lmodel2* R package (Legendre 2018).

Finally, a joint ordination of AGT and OFOS datasets was produced by means of coinertia analysis (Dray et al. 2003), a symmetric joint ordination technique that attempts to find ordination axes that are orthogonal and maximize the covariance among ordination scores from the two confronted datasets. In our case, the coinertia analysis was based on a principal component analysis (PCA) on fourth-root transformed abundances using the Hellinger transformation (i.e. a PCA that implicitly used the Hellinger distance). The Hellinger transformation produces an ordination implicitly based on the Hellinger distance, which has been shown to have good statistical properties for ecological data (Legendre and Gallagher 2001). Coinertia analysis aims to reveal structures that are common to both datasets. It produces a joint ordination of sites from both datasets where the distances between sites from AGT and from OFOS (shown graphically as arrows from AGT to OFOS for each site) indicate the degree of agreement in the ordination of sites between datasets. In addition, coefficients for taxonomic groups from AGT and OFOS can be displayed as arrows and can be inspected to show agreements and discrepancies in the groups contributing to ordination in each dataset.

Coinertia analysis was performed using function coinertia in the *ade4* R package (Dray & Dufour 2007, Thioulouse et al. 2018). PCA analyses were done with function *dudi.pca* in the same package, based on data transformed using function *decostand* in the vegan package (Oksanen et al. 2019).

Results

A total of 4213 individuals were sampled with AGT and 10550 individuals with OFOS. Combining AGT and OFOS data, we found a total of 19 benthic taxonomic groups. The most dominant groups sampled with AGT were Polychaeta and Ophiuroidea, while Ophiuroidea and Ascidiacea were for OFOS (Fig. 2). Ophiuroidea was the most abundant group representing 45% of the individuals in OFOS and 19,1% in AGT.

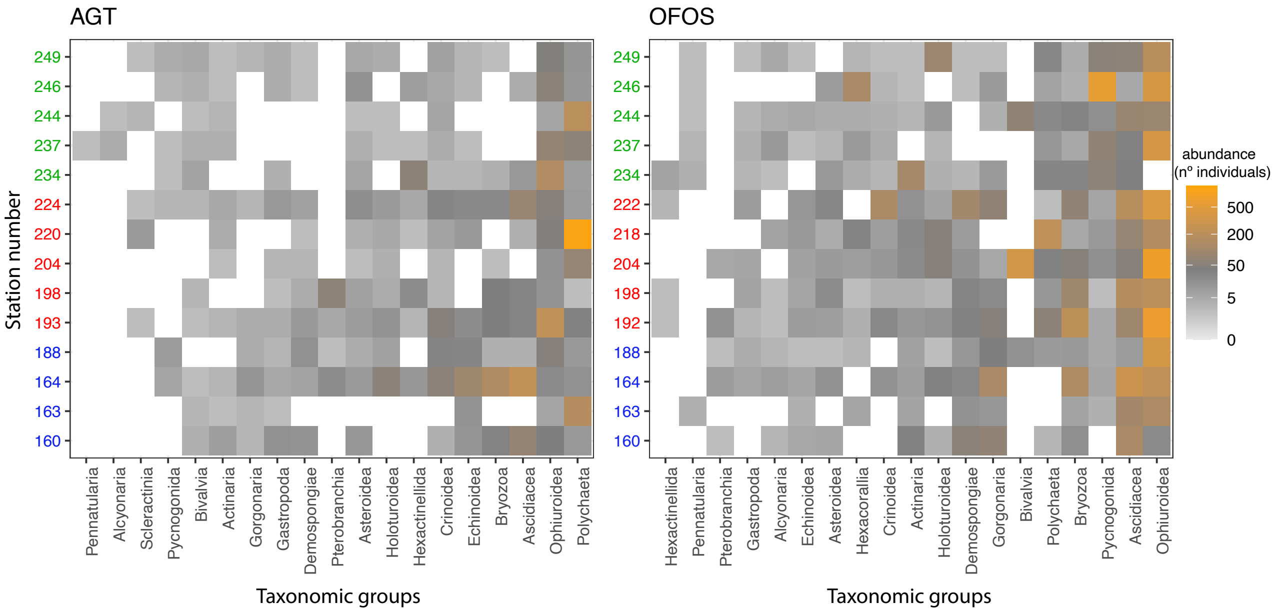

Fig. 2 Heatmap based on abundance data collected from AGT and OFOS. Abundance values shown were fourth-root transformed. Station numbers correspond to Bransfield Strait (red), Drake Passage (green) and Weddell Sea (blue).

The total inertia explained by the factors depth and region (33%) is the sum of the inertia explained by the two canonical axes (Fig. 3). Both factors were significat (permutation test, $p < 0.05$). In AGT, the depth clearly segregated shallow groups (Ascidiacea, Gatropoda and Hexactinellida) from those from the deep sites (Scleractinians, Polyplacophora and Gorgonians); while, in OFOS, the depth segregated shallow groups (Alcyonacea, Bivalvia and Holoturoidea) from those from the deeper sites (Hexactinellida, Asteroidea and Crinoidea). For both sampling methods, the factor region segregated Pennatulacea, Pycnogonida and Hexacorallia as the main groups of the Drake Passage and Pterobranquia, Demosponges and Echinodermata as the main groups of the Weddell Sea. On the other hand, Bransfield Strait was more heterogeneous for both methods (Fig. 3).

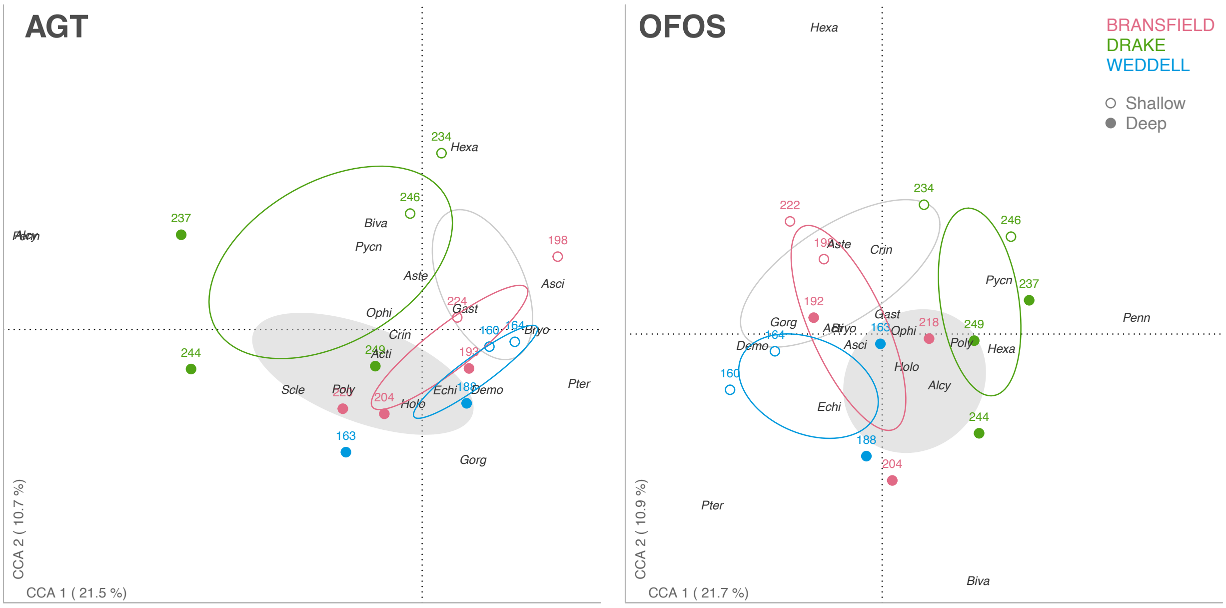

Fig. 3 Constrained correspondence analysis (CCA) of AGT and OFOS against regions and depth based on fourth root transformed abundances. Ellipses show one standard deviation of bivariate distribution of points around category centroids. Both factors were significant based on marginal permutation tests, $p < 0.05$.

According to the bivariate relations analysis, the abundance of almost all motile benthic groups sampled with OFOS did not show any statistically significant correlation with the abundance of motile taxa sampled with AGT (Spearman correlation, $p > 0.05$). In contrast, a positive and significant correlation ($p < 0.05$) was observed between the abundance of sessile groups sampled with both sampling methods. Only Bivalvia showed a negative correlation between two sampling methods (Fig. 4).

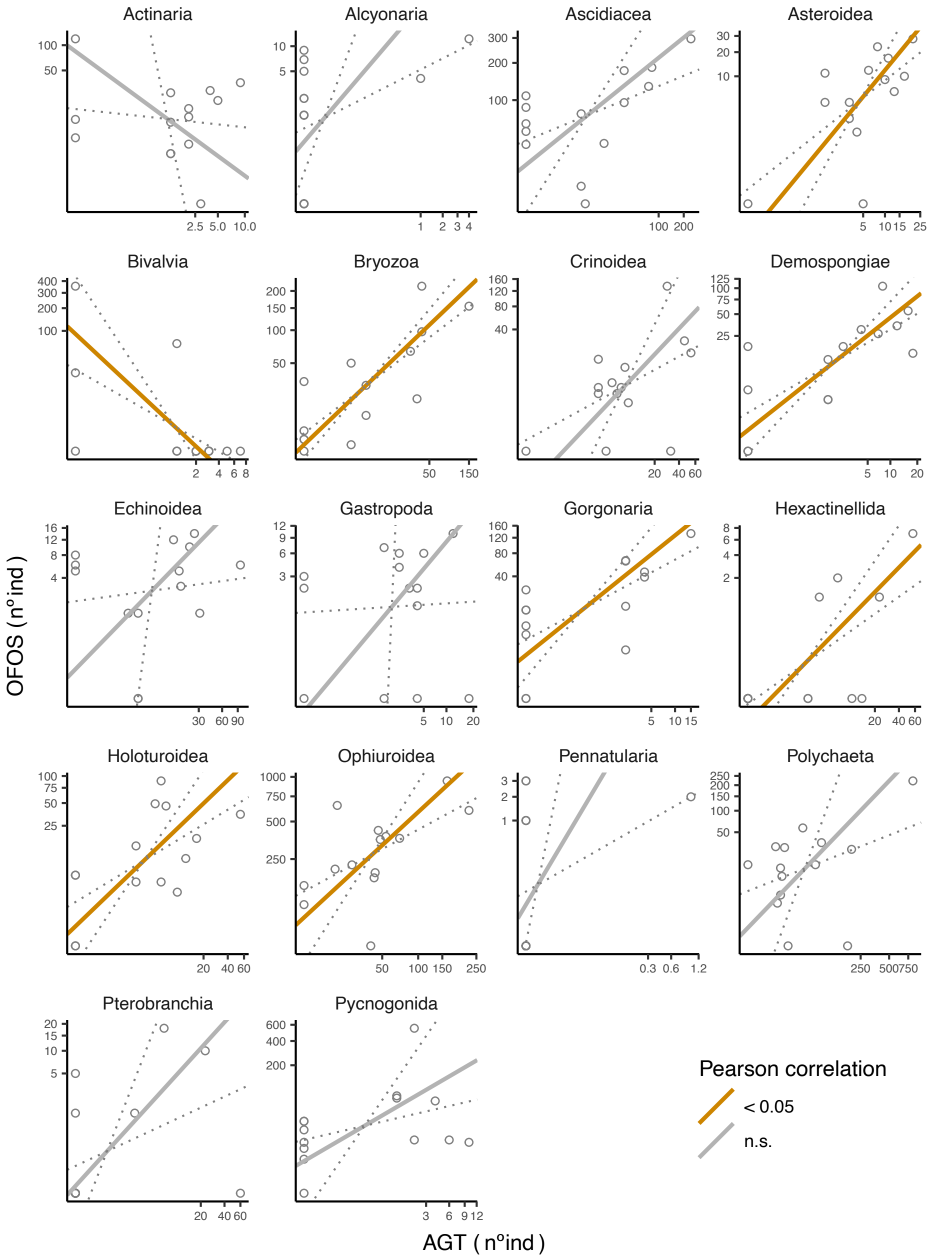

Fig. 4 Bivariate relations between AGT and OFOS for each taxonomic group. Scatterplots with Type II regression lines were fitted as standard major axis models. For reference, ordinary least squares regressions of y vs. x and x vs. y are shown as dashed lines. Orange-colored lines denote significant Spearman correlations.

Finally, the coinertia analysis showed a good separation between the 3 regions and high congruence in the ordination of sites between techniques. Only 4 out of the 16 stations sampled showed substantial discrepancies between AGT and OFOS. More importantly, a number of taxonomic groups presented similar weights on ordination axes, suggesting that the congruence in the ordination is, in fact, due to a congruence in the relative abundances of major groups. This can be seen, for example, in the coincidence in weights (seen as arrows in Fig. 5b and 5c) for Holoturia, Cinoidea and Asteroidea, for Bryozoa and Pterobranchia, and, to a lesser extent, for Ophiuroidea and Pennatulacea. Other groups, however, showed discrepancies between techniques in their weight on ordination axes. This is the case of Polychaeta, Ascidiacea, and Scleractinians.

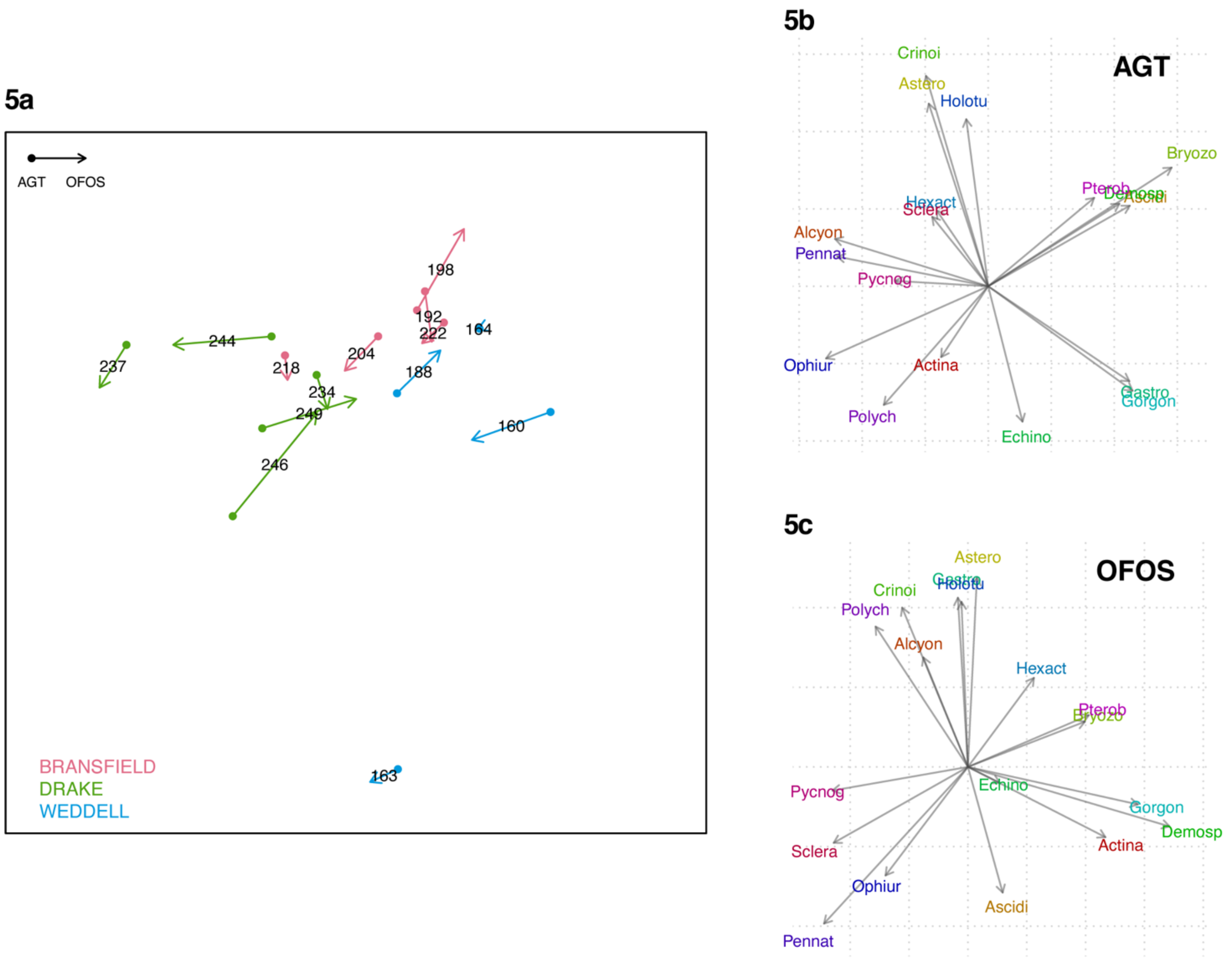

Fig. 5 Results from the analysis of coinertia between OFOS and AGT, based on PCA after fourth-root and subsequent Hellinger transformation of abundances. The main panel shows congruence in the ordination of sites, with shorter arrows between techniques for a given site indicating large congruence. The side panels show the weights of taxonomic groups on the coinertia axes (as arrows) for OFOS and AGT. Congruence is shown by groups with similar weights for both techniques (i.e., arrows pointing in similar directions).

Discussion

The present study contributes to increasing our understanding of how different sampling approaches characterize quantitatively Antarctic benthic communities. Our results expand upon previous research on Antarctic benthic communities by Gutt et al. (2016; 2019). In a higher taxonomic resolution, a previous study carried out in the same area using AGT data showed high among-station variability in biomass of 96 systematic groups (Gutt et al. 2016). The authors found large-scale patterns separating the three ecoregions and these patterns were correlated with two environmental factors: sea-ice and depth (Gutt et al. 2016). The factor habitat only poorly explained benthic composition and small-scale bottom topography did not explain such patterns at all. The large-scale factors, sea-ice and depth, might have caused large-scale differences in pelagic benthic coupling, whilst small-scale variability, also affecting larger scales, seemed to be predominantly driven by unknown physical drivers or biological interactions (Gutt et al. 2016). In the same area, mega-epibenthic communities and biota-environment relationships have been explored at multiple spatial scales by means of OFOS data indicating an increase in mega-epibenthic community complexity with increasing spatial scale. Moreover, strong relationships between biota and environmental drivers were found at scales of > 2 km. In contrast, few environmental variables contributed to explaining biotic structures at finer scales. These are likely rather determined by non-measured environmental variables, as well as biological traits and interactions that are assumed to be most effective at small spatial scales. (Gutt et al. 2019).

In this study, the extremely high abundance of all the taxa observed by OFOS with respect to the abundance estimated with AGT provides important insights into the efficiency of trawl gears in the study of benthic communities. Bottom-trawl surveys have been used since many decades to obtain abundance indices for benthos management (Arntz et al. 1994). Visual census methods using underwater vehicles such as ROVs, manned submersibles or still cameras are increasingly applied to achieve the same goal (Gutt and Piepenburg 2003). A wide range of factors can affect density estimations with both methods. In the case of trawling, these factors are related to gear configuration and to species ecology and biology (Piepenburg et al. 2002).

In Antarctica, comparative studies focused on abundance and distribution of benthic species using different sampling gears have provided relevant information. Piepenburg et al. (2002) documented enormous differences in abundance and composition between quantitative data derived from multibox corer samples and visual methods. These differences can be explained by the suitability of a gear for catching specific benthic components. Pineda-Metz and Gerdes (2017) demonstrate similar and comparable spatial distribution patterns in the benthic communities by both methods. They therefore highly recommend the use of both, multibox corer and visual methods in combination. Some studies have demonstrated that video observations still provide superior density estimates in deep-sea environments (Uzmann et al. 1977; Krieger and Siegler, 1996). Our results confirm this view, with higher abundance of all taxonomic groups in OFOS than in AGT except Bivalvia and Polychaeta. This is because these taxonomic groups, belonging to infauna, can withdraw into the sediment being poorly visible or not visible at all and consequently being under sampled with OFOS. Furthermore, high number of sessile taxonomic groups presented abundances similar between techniques. In contrast, almost all motile benthic taxonomics groups showed discrepancies between techniques.

Besides being considerably less invasive, OFOS surveys proved to be much more accurate for the quantitative study of benthic communities compared to trawl fishing nets. The abundance of many benthic taxa assessed with trawling is largely underestimated due to the scarce catch efficiency of the net, and to the patchy distribution that benthic organisms could have over the wide swept area. Although the trawl net is not the elective gear for fully quantitative sampling of benthic communities, it can represent a useful way to collect valuable information about the presence and distribution of benthic species, including the estimation of the biomass (Ambroso et al. 2016) or the identification of facies over large spatial scales (Arnaud et al. 2001).

Both methods can have pros and cons: trawling allows the direct measurement of total length, it is usually cheaper than visual census methods and it covers a wider area, but it is destructive and less efficient; visual census allows investigation of density and population structure at smaller spatial scales, but more efficiently. Trawling is still essential to taxonomists, while visual census can be used to monitor these species, once identified, in a non-destructive manner that would be consistent with protection measures.

Overall benthos catchability in trawls is low, mainly due to the small size and fragile nature of many species. Bryozoa, Octocorallia and Porifera that pass into the net are often broken into pieces which can give a biased account of their abundance and biomass. Benthos catchability is also understandably low in other destructive methods like box cores due to the limited area sampled by a single core (Pineda-Metz and Gerdes 2017). Box cores also collected more infauna taxa than the other collection methods, particularly small encrusting species which were not collected by trawls and were difficult to collect by visual census.

Management decisions, such as designation of an area as a representative or pristine community, can be made as a result of biological data collected from only one sampling method, yet it is unknown how biodiversity patterns from a single method represent those from other methods (Flannery and Przeslawski 2015). Successful marine biodiversity surveys thus require both careful planning of gear type combinations and planned preliminary studies in order to ensure collected data represent accurate trends (Flannery and Przeslawski

2015). To obtain the most reliable results for biodiversity assessments a combination of gear types, one from each group (epifaunal, infaunal, imagery) is needed. A lack of multi gear studies precluded the determination of the optimal combination of gear types for particular regions or environments. Despite considering the benthic fractions in different resolution but with similar distribution patterns, non-destructive monitoring with visual techniques is extensively recommended for the proper study of Antarctic benthic communities and their consequent management.

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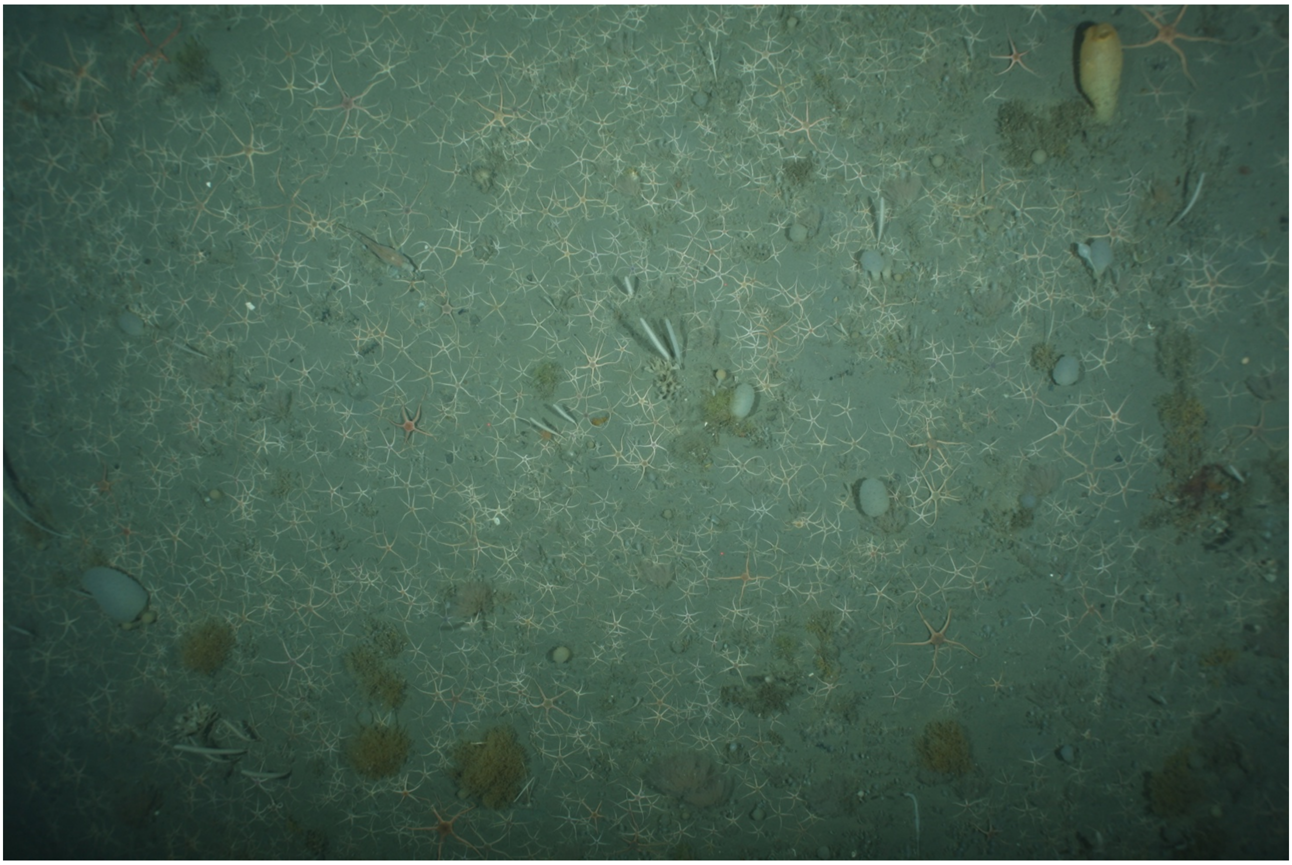
Chapter 2

Ophiuroid biodiversity patterns along the Antarctic Peninsula



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Introduction

The multiple components of climate change are anticipated to affect all levels of biodiversity, from organism to biome (reviewed in Parmesan 2006). The Antarctic Peninsula (AP) region is distinctive among Antarctic regions in its response to climate change, with strong decreases in sea ice (Turner et al. 2005), rapid winter warming (+7Cº air temperature since 1950) (Turner et al. 2005), ocean warming (+1Cº sea surface temperature since the second half of the twentieth century) (Meredith and King 2005), and retreat of maritime glaciers and ice shelves (Cook et al. 2005; Domack et al. 2005). Recent climatic trends have resulted in significant changes in Antarctic marine ecosystems, such as decrease in phytoplankton biomass (Stammerjohn et al. 2008; Montes-Hugo et al. 2009), loss of sea-ice habitat for juvenile euphausiid species (Fraser and Hofmann 2003), increase in rates of physiological functions with impacts on growth or feeding requirements (Peck et al. 2006), modification of species geographic distribution and potential invasion processes (Thatje et al. 2005; Walther et al. 2009), and alteration of benthic assemblages (Smith et al. 2008). Thus, the warming climate threatens to change the composition and function of Antarctic marine communities in ways that are complex and not entirely predictable (Clarke et al. 2007; Walther et al. 2002).

Ophiuroids are among the most important Antarctic benthic groups, in terms of abundance and ecological roles, from shallow sublittoral habitats to continental shelves and the deep sea (Fell 1961; Fell et al. 1969; Dell 1972; Dahm 1999; Piepenburg and Schmid 1996; Brandt et al. 2007; Moles et al. 2014). Moreover, there is a solid register in their systematics and biogeographic distributions with studies dating from the late nineteenth century (e.g., Studer 1876; Ludwig 1899) to recent reviews and biogeographic approaches (Martynov 2010; O'Hara et al. 2011; Martín-Ledo and López-González 2014).

Interestingly, the distribution of ophiuroids is mainly driven by temperature and depth, highlighting the importance of ecophysiology (e.g., stenothermality and stenobathymetry), reproduction mode, and life history traits (Fell et al. 1969; Hendler 1975; Hendler and Tran 2001; Sands et al. 2012; Martín-Ledo and López-González 2014). They are considered to play an important role in the transfer of energy between the water column and the seafloor because of their high biomass values and great abundance (Piepenburg and Juterzenka 1994; Piepenburg et al. 1997). Thus, given the accelerating pace of climate change in the AP and their sensitivity to temperature changes, we hypothesize that ophiuroids may exhibit different community responses with different biodiversity distribution patterns. From a community ecology and conservation perspective, the acquisition of data on species composition and assemblage structure over a variety of spatial scales is indispensable for understanding the variation of biodiversity at local and regional scales (Lourie and Vincent 2004). Moreover, these baseline datasets are valuable for assessing the changes associated with several threats and the outcome of management actions. Knowing and understanding the patterns of variability in benthic assemblages over a range of spatial, temporal, and bathymetric scales using standardized methods are crucial for the effective management and conservation of Antarctic marine habitats (Lockhart and Jones 2008; Kaiser et al. 2013).

During the Polarstern ANT XXIX/3 (PS81) expedition, three different regions at the tip of the AP, which are characterized by different environmental regimes mainly driven by seasonal sea-ice extent and permanent water mass circulation (Hofmann et al. 1996), were investigated: the northwestern Weddell Sea (polar conditions), the Bransfield Strait (transition conditions), and the northern boundary of the South Shetland Archipelago in the Drake Passage (oceanic conditions). Environmental conditions around the AP differ between the west and the east. The oceanic region north of the AP is characterized by two main converging water masses (the cold bottom water from the eastern AP shelf and the warm and salty waters of the circumpolar origin) and an interannual and seasonal sea-ice variability, both of which shape the local marine ecosystem (Björgo et al. 1997; Foldvik et al. 2004; Gutt et al. 2015a, b). The general idea was that differences in the quantity and quality of food to the benthos may result in different benthic community patterns. This assumption was based on the results of long-term studies of summer primary production (Trimborn et al. 2015), average summer sea-ice cover, and bottom water temperature (Clarke et al. 2009). Based on Agassiz trawl catches, the aim of this study was to investigate ophiuroid assemblages in terms of the distribution and diversity patterns at three different environmental regimes and depths. We quantified different community parameters in terms of the number of species, abundance, and biomass. Additionally, we assessed various components of species diversity (alpha, beta, and gamma diversity) for the three regions studied. The objective of this article is to contribute to the ecology of Antarctic benthos based on the most abundant and conspicuous ophiuroid species (around 99 % of all collected specimens). Parallel studies during the ANT XXIX/3 expedition used the same standardized sampling method and aimed to characterize major benthic megafaunal assemblages at a functional level (Gutt et al. 2015a, b).

Material and methods

Study area

Three study areas were sampled as a part of the multidisciplinary ANT XXIX/3 expedition on board the R/V Polarstern from January 22 to March 22, 2013 (Gutt 2013). These areas included the northwestern Weddell Sea (WED) east of the tip of the AP, the Bransfield Strait (BRA), and the Drake Passage (DRA) west of the South Shetland Islands (Fig. 1; Table 1).

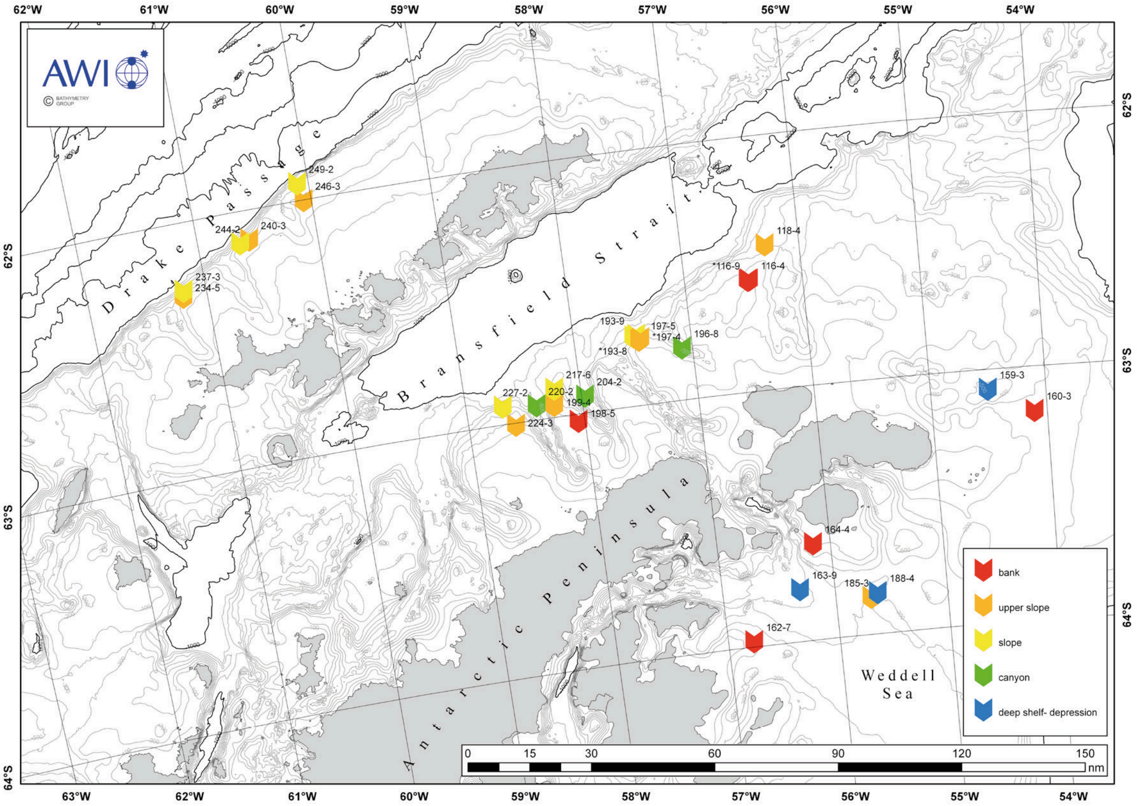

Fig. 1 Map of the study area showing the 18 stations sampled in the three regions and the different depths. The white patches on the map are the contours below 1000 m depth. The scale of the bathymetric contours is each 100 m

The study area extends for approximately 39,000 km2. Three core stations were performed in each area. At each core station, different habitats were selected when they were present: shallow bank (approximately 200 m), upper exposed slope (approximately 270 m), deeper slope (approximately 450 m), deep shelf depression (approximately 450 m), and canyon (approximately 500 m). A total of 25 Agassiz trawl (AGT) stations were initially sampled. However, because not all 5 of these habitats existed in the three regions, we restricted our statistical analyses to a subset of 18 stations, which were grouped in two depth categories: shallow (from 100 to 350 m) and deep (from 400 to 600 m). Thus, there were 3 shallow and 3 deep stations in each region.

Table 1. Station list of samples obtained from the Agassiz trawl. The subset of the 18 stations is marked in bold. Abbreviations are as following: Scenarios: Bank: B; Upper Slope: US; Deep shelf depression: DS; Canyon: C; Slope: S; Areas: Weddell Sea: WED; Bransfield Strait BRA; Drake Pasage: DRA; Proportion Subsample (50 liter) of total catch (total volume): Prop Sub to total Catch; Proportion of ophiuroid biomass (kg) of total benthos biomass of the subsample.

Station	Position Latitude Longitude	Depth (m)	Scenarios	Area	Prop Sub to total Catch	Prop Ophiuroids to benthos
116-4	S 62º 33.80' W 56º 27.31'	248	B	BRA	1	0.05
118-4	S 62º 26.53' W 56º 17.34'	445	US	BRA	0.25	0.27
159-3	S 63º 04.77' W 54º 29.29'	490	DS	WED	0.1	0.01
160-3	S 63º 10.32' W 54º 07.19'	227	B	WED	0.1	0.004
162-7	S 63º 58.60' W 56º 46.24'	217	B	WED	0.04	0.01
163-9	S 63º 48.30' W 56º 18.52'	553	DS	WED	0.07	0.01
164-4	S 63º 37.33' W 56º 08.64'	101	B	WED	0.05	0.01
185-3	S 63º 51.04' W 55º 40.68'	375	US	WED	0.33	0.02
188-4	S 63º 49.90' W 55º 37.09'	430	DS	WED	1	0.04
193-9	S 62º 43.32' W 57º 26.70'	410	S	BRA	0.33	0.04
196-8	S 62º 48.17' W 57º 04.53'	568	C	BRA	0.1	0.04
197-5	S 62º 44.49' W 57º 26.40'	293	US	BRA	0.07	0.09
198-5	S 63º 01.63' W 58º 02.80'	171	B	BRA	0.07	0.01
199-4	S 62º 57.08' W 58º 13.95'	301	US	BRA	0.04	0.05
204-2	S 62º 56.02' W 57º 56.84'	772	C	BRA	0.02	0.16
217-6	S 62º 53.49' W 58º 12.09'	408	S	BRA	0.1	0.04
220-2	S 62º 56.57' W 58º 22.51'	774	C	BRA	0.05	0.14
224-3	S 63º 00.48' W 58º 35.12'	269	US	BRA	0.07	0.25
227-2	S 62º 56.11' W 58º 40.32'	532	S	BRA	0.1	0.06
234-5	S 62º 17.40' W 61º 11.58'	246	US	DRA	0.1	0.03
237-3	S 62º 16.15' W 61º 10.90'	386	S	DRA	0.5	0.06
240-3	S 62º 06.91' W 60º 33.75'	274	US	DRA	0.1	0.04
244-2	S 62º 07.71' W 60º 39.50'	474	S	DRA	0.1	0.03
246-3	S 61º 59.95' W 60º 03.87'	283	US	DRA	0.1	0.01
249-2	S 61º 55.81' W 60º 05.07'	425	S	DRA	0.33	0.01

Stantardized protocol

Samples were taken with an AGT with 3.5-m-wide opening and 10-mm mesh size, which was towed on the seafloor for 10 min at 1 knot. From the total catch of each station, a 50-l subsample was randomly collected from the entire catch to be as representative as possible. We followed this standardized protocol to compare semiquantitative data across all the stations. This protocol was applied during the ANT XXIX/3 expedition as a representative, adequate, and time- and cost-efficient method for community characterization and assessment. The aim was to evaluate the assemblage structure and its natural variability. Gutt et al. (2015a, b) showed that this standardized subsample protocol resulted in a good representation of benthic assemblages across the three regions and different depths studied. For more information about subsampling, see Gutt et al. (2015a, b). See Table 1 for details about the proportions of the subsample to total catch and ophiuroid biomass to the benthos biomass.

Benthos sampling and processing

On deck, the subsamples were sieved through three mesh sizes (10, 5, and 1 mm). After the macro- and megabenthic fauna were sorted, the organisms were identified to species level whenever possible. Ophiuroids from each trawl were first sorted to morphotype, and a picture was taken. Taxonomic determinations were based on the examination of external morphological characters and were compared to the original descriptions and taxonomic literature of this group from the Southern Ocean (e.g., Lyman 1875, 1882; Studer 1876; Koehler 1901, 1908, 1912, 1922; Hertz 1927; Mortensen 1936; Bernasconi and D'Agostino 1977), and to the ophiuroid reference collection in the University of Seville (Spain). See Table 2 for taxonomic remarks on the identification of some species. In this study, *Ophioplinthus gelida* and *O. brevirima* were grouped together as well as *Ophiacantha vivipara* and *O. pentactis*. On board, all ophiuroid individuals were counted to calculate the number of individuals and weighed to estimate biomass (fresh weight).

Table 2. Remarks on the identification of some ophiuroid species

Species	Remarks
Ophionotus victoriae	Hunter & Halanych (2010) revealed an unexpected genetic structure along Antarctic Peninsula inconsistent with early life history data. The possibility of cryptic speciation is pointed out. According to the authors, further studies are needed to include material from additional Antarctic localities. Our sampling material mainly coincided geographically with the area named by the authors as "Northern Peninsula". The possible existence of these cryptic species, when demonstrated, could affect or not the number of species in our study area, but the ecological role of these possible closely related species will probably not affect the usefulness of our study.
Ophiacantha vivipara vs Ophiacantha pentactis	The original description of *O. pentactis* is 5 arms whereas O. vivipara is 5-8 (usually 6) arms. This was the main criterion used in this study. However, there exists a morphotype of *O. pentactis* with 6 arms that is easily confused with *O. vivipara*. Despite the often-used character of the number of arms in distinguishing *O. vivipara* and *O. pentactis*, the variability observed in the specimens (e.g. nº arms, nº oral papilae, shape of oral shield), as well as the variability discussed in the specialized literature blur the apparent clear differences once used to differentiate both forms previously considered subspecies. The size of the oral disc (larger in *O. pectantis*) is a continuous biometric character of doubtful utility when examining specimens of intermediate size. In this study, these two species were merged.
Ophioplinthus gelida vs Ophioplinthus breverima	They are morphologically very similar, both are often covered (and morphologically altered) by the sponge symbiont Iophon. In the case of these two species and despite the possible morphological alteration of plates by Iophon, the relative length of the genital slits is a useful character in distinguishing between these two species. The criterion adopted in this study was to merge also these two species.

Preliminary analyses: selection of ophiuroids for benthic assemblage characterization

We carried out preliminary analyses to verify the suitability of ophiuroids for the characterization of benthic assemblages. The criteria for selecting ophiuroids were based on the reliability of taxonomic identification (with exceptions) and sufficient number of individuals per station. As a first step, we applied a multivariate analytical procedure on abundance data of different groups of macroand megabenthic fauna: Porifera (Hexactinnellida, Demospongiae, Calcarea), Cnidaria (Hexacorallia and Octocorallia), Crustacea (Mysidacea, Amphipoda, Decapoda, Isopoda), Echinodermata (Echinoidea, Asteroidea, Crinoidea, Ophiuroidea), and Pisces. The preliminary identification of these taxa was carried out on board by specialists. However, further taxonomic identification was needed for a complete and definitive species list for all these groups. We compared the assemblage structure by using the abundance data of the preliminary identification of macro- and megabenthic taxy with the ophiuroids. The analysis revealed that the ophiuroid fauna displayed the same interregional variability as the combined macro- and megabenthic taxa mentioned above. Based on these preliminary analyses, we consider ophiuroids as a good model group to characterize the assemblages studied during the expedition.

Specimens that were in such a poor state that they could not be identified were not considered for further analyses. These specimens represented nearly 1 % of the collected individuals. In this work, we want to emphasize the usefulness and importance of the most common and abundant ophiuroids. Importantly, the species lists of this study should not be considered as the unique species living at the different widely considered ecoregions (other comprehensive works can be consulted as Martín-Ledo and López-González 2014), but they are the results of the comparative sampling program carried out during the ANT XXIX/3 cruise. The data used in this study are available as Electronic Supplementary Material 1 (doi:10.1007/s00300-016-1911-4).

Analysis of species diversity and assemblage structure

First, we performed a first group of analyses on species diversity for all 25 stations. The purpose of these analyses was to extract information on patterns that were relevant to species diversity and abundance from all sampled stations. We acknowledge the large discussion regarding species estimators (e.g., Colwell and Coddington 1994; Gotelli and Colwell 2001; O'Hara 2005; Magurran and McGill 2011), and our purpose was to select some of these estimators to quantify the overall faunal patterns of the stations sampled and not to review all of the methodological aspects. Furthermore, we recognize the methodological problems in measuring the number of species and individuals in a given area (for a review, see Gotelli and Colwell 2001). The following first analyses were performed: (1) cumulative rank dominance curves and (2) estimation of ‘‘true species richness’’ using the nonparametric estimators Chao2 (based on incidence data), Jacknife 2 (estimator for both even and uneven communities), and Chao1 (based on abundance data) (see Colwell and Coddington 1994; Gotelli and Colwell 2001). In addition, we also compiled the biogeographic and bathymetric distribution and computed the stenobathic–eurybathic index (S–E index) for the identified species. The S–E index ranges from close to 0 (narrow distribution) to 100 (wide distribution) (see Martín-Ledo and López-González (2014) for more information).

Second, we further investigated the diversity patterns and assemblage structure based on a subset of 18 AGT stations. We selected three stations per geographic area DRA, BRA, and WED and depths, shallow (from 100 to 350 m) and deep (from 400 to 600 m). We calculated various diversity measures: number of species, as well as the exponential Shannon index (ExpH’) and the reciprocal Simpson’s index (1/Simpson), following the suggestions of Jost et al. (2010) to estimate ‘‘effective number of species.’’ Spatial patterns of diversity measures were assessed by quantifying the alpha diversity (average number of species per catch), gamma diversity (the total number of species within a region), and beta diversity (the multivariate distance between group-centroids determined with the PERMDISP procedure, see below). To visualize the pattern of resemblance in the ophiuroid composition of 18 AGT catches, non-metric multidimensional scaling (nMDS) was performed on Bray–Curtis dissimilarities using square-root transformed ophiuroid abundance data. Furthermore, a similarity percentage procedure analysis (SIMPER, Clarke and Warwick 1994) was performed to identify the percentage contribution of taxa to average similarities and dissimilarities within and between regions.

Univariate diversity indices and multivariate assemblage structure were analyzed using a nonparametric analysis of variance, PERMANOVA (Anderson 2001a, b; Anderson et al. 2008), applied using Euclidean and Bray–Curtis distances for univariate and multivariate analyses, respectively. The analyses included two factors: area (fixed factor, 3 levels) and depth (fixed factor, 2 levels). Pair-wise comparisons for all combinations of area x depth were also performed using t tests and 9999 permutations of the raw data. PERMDISP is an approach that is used to compare the degree of sample dispersion of different groups based on a distance matrix. When PERMDISP is used on a Jaccard distance presence/absence matrix, it is directly interpretable as a test for similarity in beta diversity among groups (Anderson et al. 2011).

The above measurements and analyses were performed using the program Primer version 6 with the PERMANOVA + add-on package.

Results

A total of 3331 individuals were collected across the three regions and depths for the present study. A total of 17 species were identified, belonging to five ophiuroid families (Gorgonocephalidae, Ophiacanthidae, Amphiuridae, Ophiolepididae, and Ophiuridae; see Table 3 for a species list). Ophiuridae was the most important family in terms of abundance in BRA. It represented 74 % of the individuals in the shallow and 50 % of the individuals in the deep areas and 89 % of the biomass in the shallow and 71 % of the biomass in the deep areas. In WED, it represented 97 % of the individuals in the shallow and 95 % of the individuals in the deep areas and 74 % of the biomass in the shallow and 89 % of the biomass in the deep areas (Fig. 2). Ophiacanthidae was also abundant (33 % of individuals) in the BRA. Amphiuridae was the dominant family in DRA, in terms of both individuals (96–98 %) and biomass (89–96 %) across the two depths (Fig. 2).

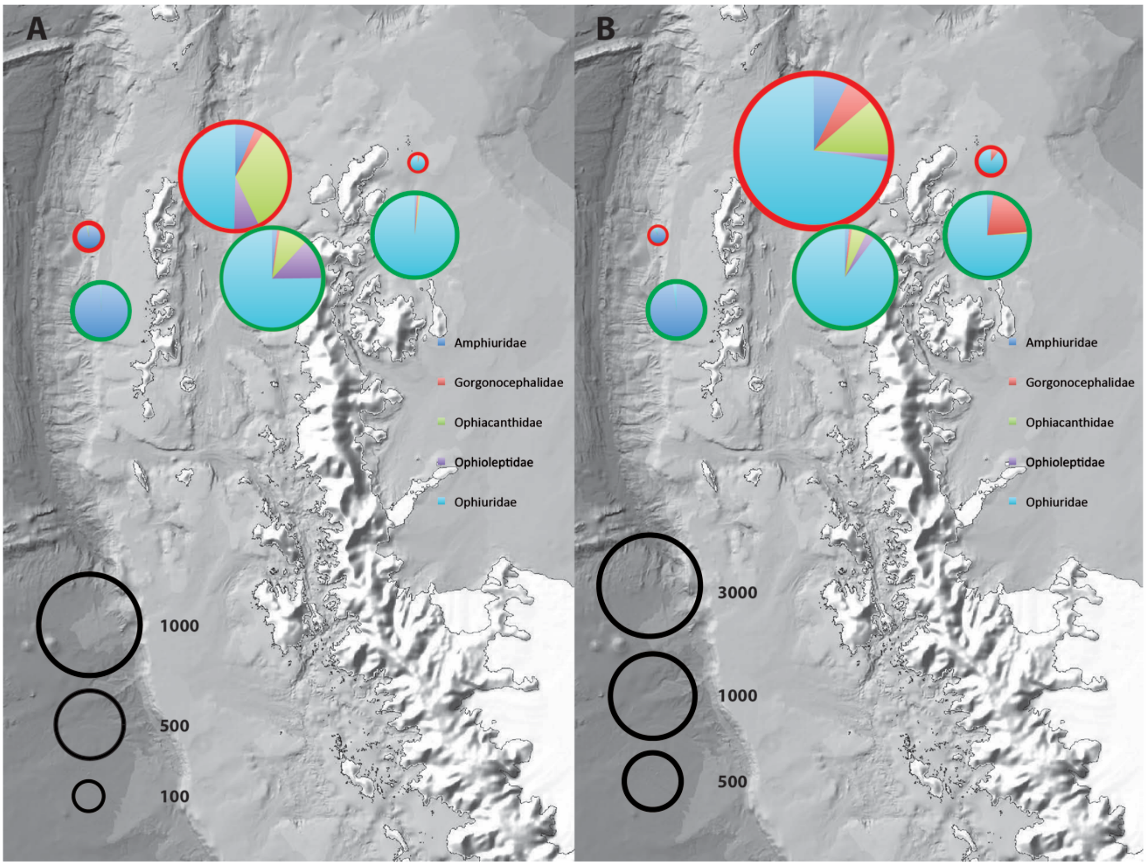

Fig. 2 **A** Number of individuals and **B** biomass based on the ophiuroid families sampled. A total of 3331 individuals were collected from the 25 AGT stations: Drake shallow n = 492; Drake deep n = 119; Bransfield shallow n = 999; Bransfield deep n = 1045; Weddell shallow n = 615; Weddell deep n = 61. Red = shallow stations; green = deep stations

Only *Ophioplinthus gelida/O. brevirima* was ubiquitously found in the three areas (DRA, BRA, and WED) and the two depth zones studied (shallow, deep) (Fig. 2; Table 3). *Amphioplus peregrinator* and *Amphiura joubini* were only absent in the WED-deep, whereas *Ophionotus victoriae* was only absent in the DRA-deep. Conversely, four species were only found in a single area and depth: *Ophiocten megaloplax* (BRA-shallow), *Ophioplinthus tumescens* (BRA-deep), *Ophiura (Ophiuroglypha) carinifera* (BRA-deep), and *Ophiura crassa* (BRA-deep). In general, all identified species have a circumantarctic distribution and a high stenobathic–eurybathic (S–E) index, with the exception of *Astrochlamis sol* with an S–E index of 36 % (Table 3). According to the sampled material, in the whole study area (DRA, BRA, and WED) the endemic component (Antarctic endemic (ANE) + Southern Ocean endemic (SOE)) was always more important than the wider geographic component (Southern Ocean and surrounding oceans (SOS)), (Table 3).

Table 3 List of the taxa identified in the 25 stations of the Antarctic Peninsula. +: present; -: absent. Distr Group, Distribution groups: A, Shared species between Drake Passage and Bransfield Strait; B, Shared species for all sampled localities; C: Exclusive species for Bransfield Strait; D: Shared species between Bransfield and Weddell Sea. Distribution: C: Circumantarctic; ANE: Antarctic endemic; SOE: Southern Ocean Endemic; SOS: Southern Ocean and surrounding oceans. S-E index: stenobathic–eurybathic index. S-E index ranges from close to 0 (narrow distribution) to 100 (wide distribution). For more information on the biogeographic and bathymetric information see Martín-Ledo and López-González (2014).

Taxon	Distr. Group	Drake Shallow	Drake Deep	Bransfield Shallow	Bransfield Deep	Weddell Shallow	Weddell Deep	Distribution	S-E index (%)
Ophioperla koehleri (Bell 1908)^{4}	A	+		+	+			C - SOE	93.52
Ophiacantha antarctica (Koehler 1901)^{2}			+	+	+			C - SOS	100
Amphioplus peregrinator (Koehler 1912)^{3}	B	+	+	+	+	+		C - SOE	99.70
Amphiura joubini (Koehler, 1912)^{3}		+	+	+	+	+		C - SOS	99.19
Ophioplinthus gelida-brevirima (Koehler 1901) (Mortensen 1936)^{4}		+	+	+	+	+	+	C – ANE, C – ANE	98.53, 86.87
Ophionotus victoriae (Bell 1902)^{4}		+		+	+	+	+	C - ANE	99.69
Ophiocten megaloplax (Koehler 1901)^{4}	C			+				C - ANE	87.64
Ophioceres incipiens (Koehler 1922)^{5}				+	+			C - SOE	100
Astrochlamys sol (Mortensen 1936)^{1}				+	+			C - ANE	36.67
Ophiura (*Ophiuroglypha*) *carinifera* (Koehler 1901)^{4}					+			C - SOS	98.65
Ophiura crassa (Mortensen 1936)^{4}					+			C - ANE	92.69
Ophioplinthus tumescens (Koehler 1922)^{4}					+			C - ANE	91.83
Astrohamma tuberculatum (Koehler 1923)^{1}	D			+	+		+	C - ANE	87.71
Astrotoma agassizii (Lyman 1875)^{1}					+	+	+	C - SOS	94.75
Ophiacantha vivipara-pentactis (Ljungman 1870) (Mortensen 1936)^{2}				+	+	+	+	C – SOE, C – SOE	100, 92.28
Ophiosteira antarctica (Bell 1902)^{4}				+	+		+	C - ANE	95.21
Ophiosparte gigas (Koehler 1922)^{4}					+	+		C - ANE	98.93

Families: 1: Gorgonocephalidae; 2: Ophiacanthidae; 3: Amphiuridae; 4: Ophiuridae; 5: Ophiolepididae.

Dominance

In general, the BRA stations showed low dominance (except for Stn 224-3, in which *Ophioplinthus gelida/O. brevirima* represented the 87 % of individuals), whereas the DRA and WED stations exhibited higher levels of dominance (Fig. 3). The 159-3 and 163-9 deep stations in the WED showed only the presence of *Ophionotus victoriae*. Species from the 227-2 deep station in BRA exhibited dominance values ranging from 2.5 to 16 %.

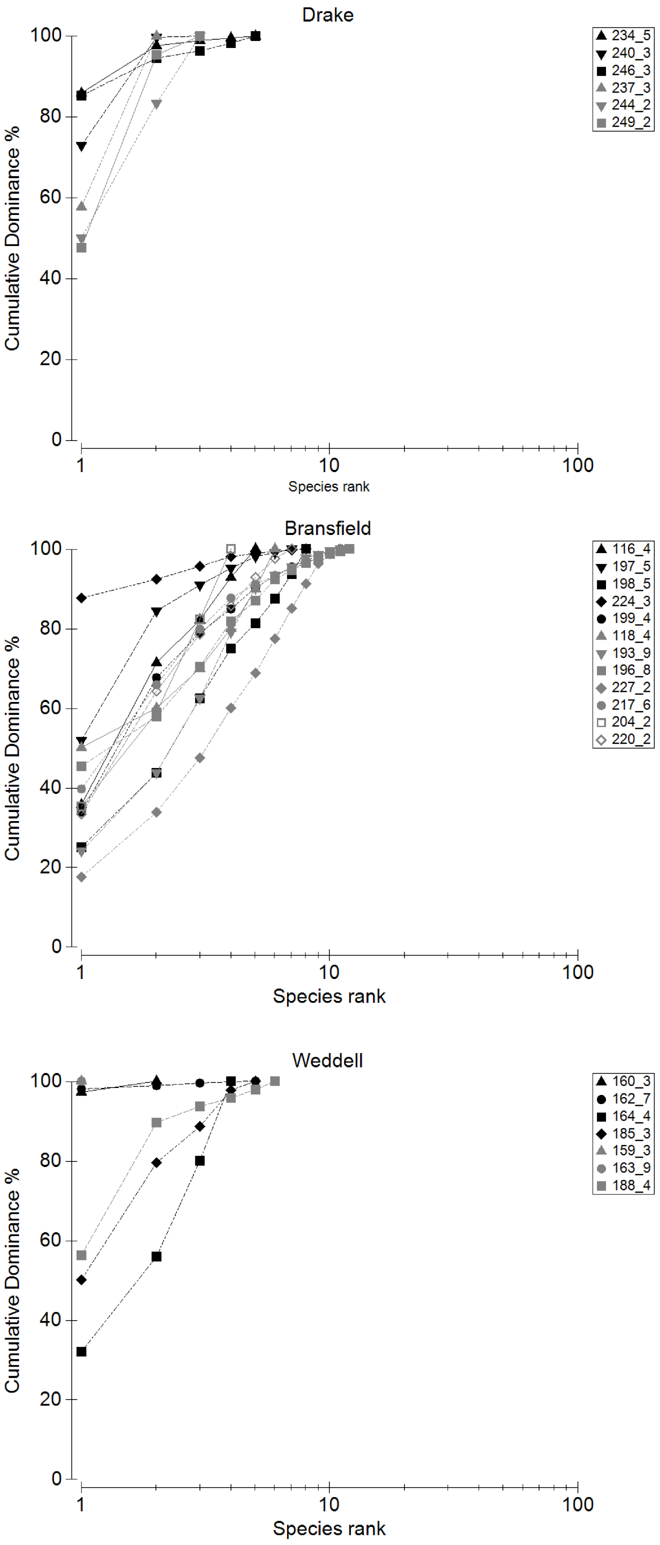

Fig. 3 Cumulative dominance plots in the three study areas. Black indicates shallow stations, whereas gray indicates deep stations. Note: Two deep stations in the Weddell Sea contained only 1 species

Species richness and diversity indices

Estimates of cumulative species richness showed little tendency to approach asymptotic values in all three regions (Fig. 4), indicating that all of the studied sites were undersampled and that uncertainty exists in these estimators.

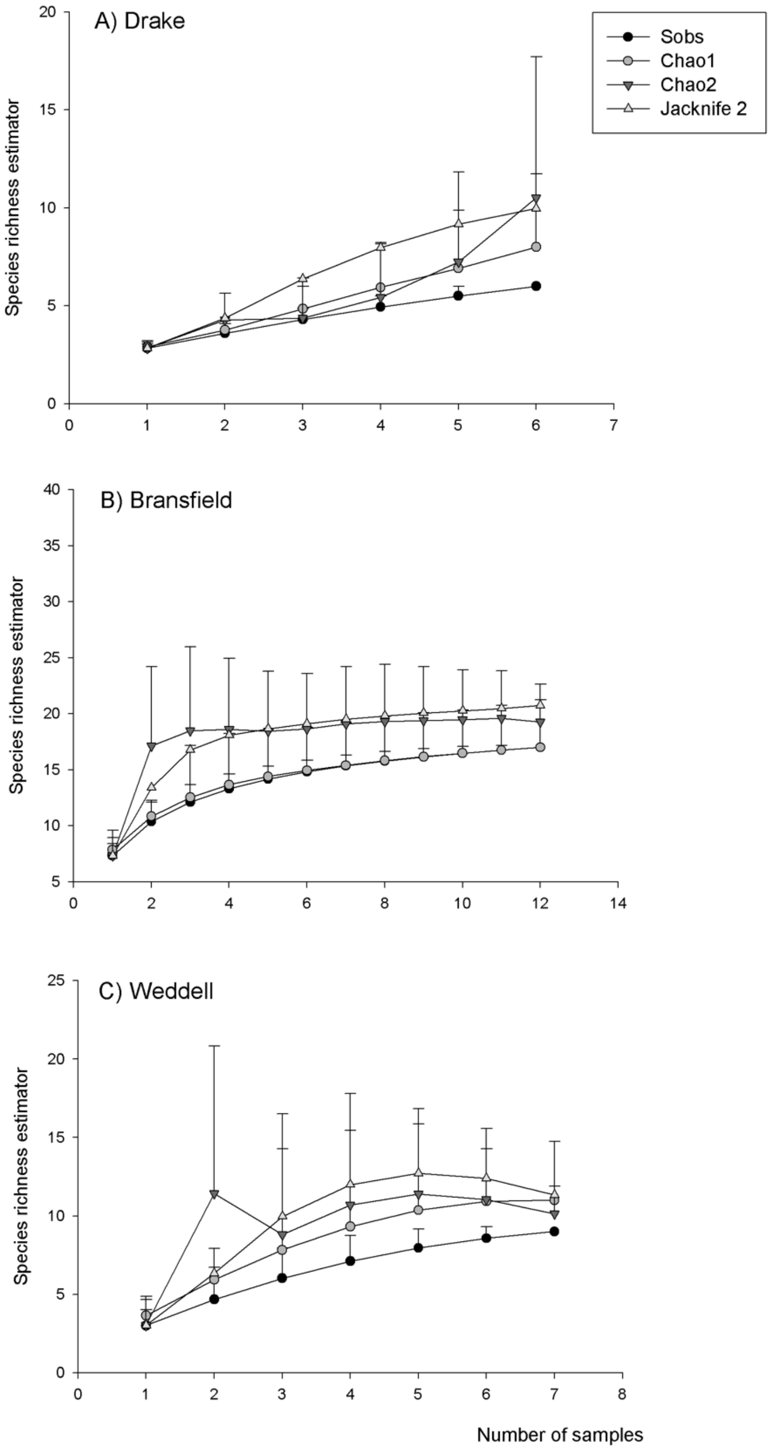

Fig. 4 Species accumulation curves. The estimators of species richness are as follows: Sobs, the total number of all species; Chao2, estimator of true richness; Chao1, estimator on individual-based abundance data; and Jack2, estimator for both even and uneven communities. The plotted values are mean ± SD

The total number of ophiuroid species observed was 17, whereas the Chao 2 estimator assessed values of 19 ± 3.2. Separate species accumulation curves for the DRA (6 observed species) and WED (9 observed species) regions did not stabilize, and BRA (17 observed species) slightly reached an asymptotic value. Interestingly, Chao1 provided a good estimation of true species richness at 17 ± 4.2 (Fig. 4).

From the 18 subset of stations, local species richness or alpha diversity showed significant differences among regions ($F_{2,12} = 11.2$, $p<0.001$), but not between depths ($F_{1,12} = 0.41$, $p>0.05$) (see ESM 2 for all the results and pairwise comparisons). BRA showed the highest alpha diversity values of 8 species ± 1, which differed significantly from 3 species ± 1 in WED and 3 species ± 1 in DRA (pair-wise tests $t_{BRA–WED} = 3.4$, $p<0.01$; $t_{BRA–DRA} = 5.1$, $p<0.001$, respectively) (Fig. 5).

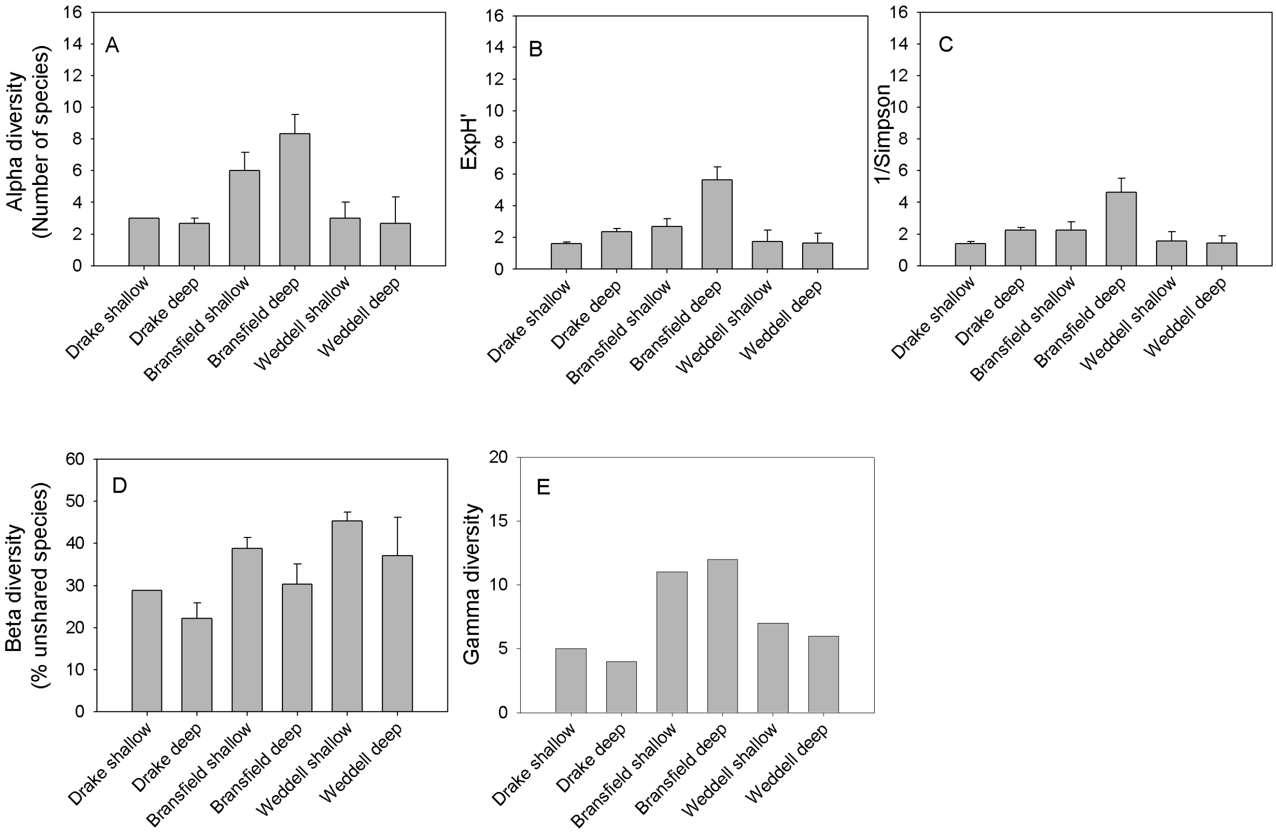

Fig. 5 Measures of **A** alpha diversity (number of species), **B** the exponential Shannon diversity index (ExpH’), **C** the reciprocal Simpson’s index (1/Simpson), **D** the beta diversity, and **E** the gamma diversity for the subset of 18 AGT stations

Similar results were found for values of ExpH' and 1/Simpson among the three regions and depths (Fig. 5). The data suggested highest diversity in terms of the ‘‘effective number of species’’ at BRA (ExpH' = 5 ± 1, 1/Simpson = 4 ± 1) and lower diversity in WED (ExpH' = 2 ± 0.4, 1/Simpson = 1.5 ± 0.3) and DRA (ExpH' = 2 ± 0.2, 1/Simpson = 2 ± 0.2) (Fig. 5). Beta diversity did not show a significant difference among the regions and depths (PERMDISP $F_{2,12} = 3.1$ $p>0.05$). DRA-deep stations were characterized by lower mean values (22.2 % ± 3.7) than WED-shallow stations (45.3 % ± 2.1). Regional species richness or gamma diversity ranged from 12 species in BRA-deep stations to 7 species in WED-shallow stations and 4 species in DRA-deep stations (Fig. 5).

Structural complexity/community assemblage

Overall, the pattern of resemblances in ophiuroid community structure among the regions reflected their relative geographic positions (Fig. 6). There was a significant resemblance difference from east to west ($F_{2,12} = 9.5$, $p<0.0001$), with a maximum resemblance distance between the DRA and WED stations. Considering the pair-wise comparisons, only BRA showed a significant difference compared to DRA and WED ($t_{BRA–WED} = 2.3$, $p<0.001$; $t_{BRA–DRA} = 3.4$, $p<0.001$). No significant differences were found between depth zones ($F_{1,12} = 0.9$, $p>0.05$).

The SIMPER analysis showed an average similarity in specific composition from 42 % in WED to 56 % in DRA (Table 4). The number of taxa contributing to 90 % of the similarity within each region ranged between 1 (WED) and 6 (BRA) (Table 4).

Species	Cum. Contribution%	% total ind
a) Similarity		
Group Drake (Aver. Sim=56%)		**n = 611 ind**
Amphioplus peregrinator	62.5	74.3%
Amphiura joubini	36.6	24.5%
Group Bransfield (Aver. Sim=45%)		**n= 1345 ind**
Ophioplinthus gelida-brevirima	50.6	57.1%
Ophionotus victoriae	66.5	4.3%
Ophioperla koehleri	77.1	6.7%
Ophioceres incipiens	83.3	12.8%
Ophiacantha antarctica	88.7	6.1%
Amphioplus peregrinator	92.4	1.7%
Group Weddell (Aver. Sim=42%)		**n= 651 ind**
Ophionotus victoriae	92.6	90.1%
b) Dissimilarity		
Groups Bransfield & Weddell (Aver. Diss=77%)		
Ophioplinthus gelida-brevirima	28.3	
Ophionotus victoriae	40.4	
Ophioperla koehleri	51.2	
Ophioceres incipiens	61.7	
Ophiacantha antarctica	69.1	
Amphioplus peregrinator	73.8	
Amphiura joubini	78.3	
Ophiosteira antarctica	82.6	
Ophioplinthus tumescens	86.6	
Astrotoma agassizii	90.8	
Groups Bransfield & Drake (Aver. Diss=85%)		
Ophioplinthus gelida-brevirima	26.5	
Amphioplus peregrinator	42.8	
Ophioceres incipiens	51.8	
Amphiura joubini	60.8	
Ophioperla koehleri	69.6	
Ophionotus victoriae	77.5	
Ophiacantha antarctica	83.6	
Ophiosteira antarctica	87.1	
Ophioplinthus tumescens	90.5	
Groups Weddell & Drake (Aver. Diss=95%)		
Amphioplus peregrinator	34.7	
Ophionotus victoriae	63.3	
Amphiura joubini	83.2	
Ophioplinthus gelida-brevirima	90.1	

Table 4 (a) Species that cumulatively contribute to 90 % of the average similarities within the regions (Aver. Sim). (b) Species that contribute cumulatively to 90 % of the average dissimilarities between the regions (Aver. Diss)

Certain taxa played determining roles in each region, such as *Amphioplus peregrinator* (similarity contribution of 62 %), *Ophioplinthus gelida/O. brevirima* (50 %), and *Ophionotus victoriae* (92 %) for DRA, BRA, and WED, respectively. Focusing on taxa dissimilarities, the most important taxa were *O. gelida/O. brevirima*, which contributed 28 % and 27 % of the average dissimilarity between BRA–WED and BRA–DRA, respectively. A. peregrinator contributed 35 % of the average dissimilarity between WED and DRA.

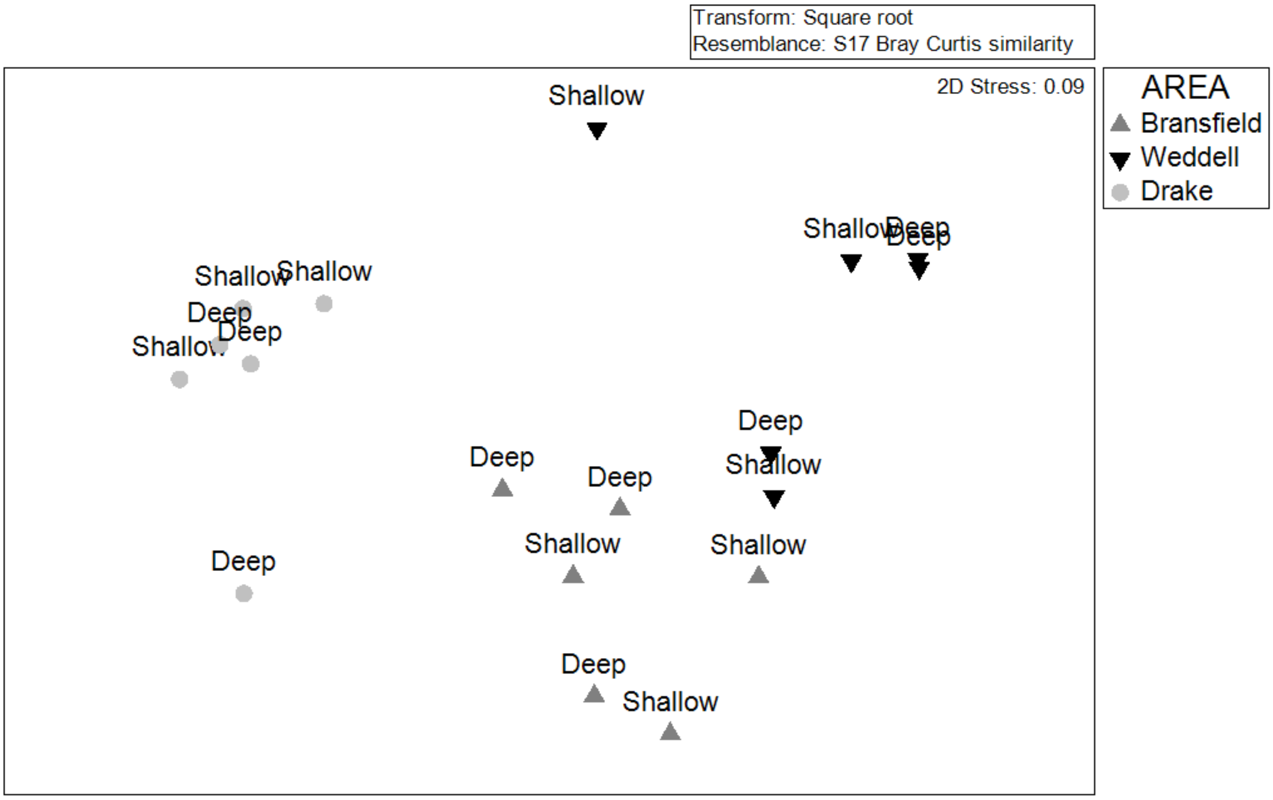

Fig. 6 Non-metric multidimensional scaling (nMDS) plot displaying the resemblance in the ophiuroid composition of 18 AGT catches in the three regions off the Peninsula Antarctica and two depths (shallow *100–350 m, and deep *400–600 m). Analysis performed on Bray–Curtis dissimilarities computed using square-root-transformed ophiuroid abundance data

Discussion

Importance of studies on species composition and biodiversity patterns in response to climate change in the Antarctic Peninsula

Studies that address the spatial and temporal patterns of species composition and biodiversity warrant special attention to identify the most key species and assemblages to discriminate environmental changes from the natural intra- or interannual variability. Such studies will facilitate sampling methods to rapidly detect Antarctica's rich biodiversity's responses to climate change and other anthropogenic stressor. Climate change is expected to become a major driving force regarding the extinctions of species and the loss of diversity and will likely include some degree of toleration, adaptation, and migration (Millenium Ecosystem Assessment 2005; Barnes and Peck 2008; Barnes et al. 2009). For benthic communities on the continental shelf of the AP, the challenge is even greater because the AP is a climate change hotspot, and declining or recovery trajectories are more difficult to detect because of the overall slow pace of change among Antarctic benthic species (Arntz et al. 1994; Clarke et al. 2007). In this context, large-scale long-term biodiversity datasets are a basic resource that furnishes the essential tools to provide information that promotes sound ecological studies (Lockart and Jones 2008; Magurran et al. 2010; Griffiths 2010). With the use of a standardized biodiversity survey, the present study provides baseline information on ophiuroid assemblages in three distinct environmental regions and depths at the AP, highlighting different diversity patterns in the different Cabeza and Ramos (2003) reported similar values for the number of individuals (2571 specimens) and species (18 species) identified during the BENTART expedition in the northwest AP. Based on current estimates of Antarctic ophiuroid species (65 within the Antarctic Peninsula, Martín-Ledo and López-González 2014), this study contributed to characterize approximately 26 % of ophiuroids despite the relatively low number of benthic stations examined in relation to the extent of the AP region.

Methodological constraints

No estimators of species accumulation reached an asymptote (Fig. 4), indicating that species were still accumulating with increasing numbers of samples. This general undersampling is important to note and is of relevance for accurate predictions of ophiuroid species and megabenthos assemblage diversities in the study region. Non-asymptotic patterns have been reported for marine benthos (Ugland et al. 2003). Marine invertebrate assemblages can be typified by rarity and with many singletons and the dominance of only a few species (Sanderson 1996). This has been reported as a common problem when sampling a small region relative to the vast areas of the seafloor of the continental shelf (Ellingsen et al. 2001). This case is also true for assemblages characterized by small-scale patchiness and many sparsely distributed species (Colwell and Coddington 1994). We also acknowledge the need of further studies to estimate the representativeness and time and cost-efficiency of Antarctic benthic surveys in order to survey the assemblage structure and its variability. The high degree of patchiness of benthic communities in the AP has previously been described mainly as a result of iceberg scouring (see below for further discussion) (Barnes and Conlan 2007; Smale and Barnes 2008). Among the estimators of species accumulation applied in this study, the Chao1 estimator was the most precise for the ophiuroids in DRA and BRA (Fig. 4). This may be because of the higher sampling size of the dataset and because this estimator also considers the number of individuals. Chao1 showed ^S (estimated) values that were quite close to S (observed) with little variance. In addition, using a variety of diversity estimators such as cumulative dominance plots, species accumulative estimators, and different diversity indices may allow solid comparisons within the areas studied and some further generalizations.

Assemblage patterns

The present study found differences in terms of ophiuroid species diversity and community assemblages (Figs. 5, 6). The BRA stations had a higher number of species at the local and regional scales and greater evenness compared with WED and DRA (Fig. 5). Although these values were not statistically correlated with environmental data, we suggest that our data partially support the relationship between ophiuroid species diversity and productivity. In addition, our results showed the importance of geographic regions in determining differences in species composition and structure of ophiuroid assemblages (Fig. 6; Table 4). BRA appeared in an intermediate position close to WED and DRA, indicating biological affinities among these two areas. These three regions shared a common pool of species with moderate values of overall similarity (approximately 40–55 %, Table 4). The four taxa *Amphioplus peregrinator, Amphiura joubini, Ophioplinthus gelida/O. brevirima,* and *Ophionotus victoriae* were found in all the three regions. The Antarctic Peninsula constitutes a unique system for assessing the genetic flow of Antarctic species, where different environmental factors (e.g., geographic distance, depth, and water currents) influence population connectivity (Hoffman et al. 2010). Studies assessing gene flow of the brooding species *Astrotoma agassizii* revealed a genetic continuity across large distances along the Drake Passage continental shelf (Hunter and Halanych 2008). The authors indicated that geographic distance alone did not represent a barrier of dispersal, but rather suggested the combined effects of geographic distance, depth, and water currents to hinder gene flow among these populations. Based on the assemblage data (composition and structure), our results indicate a community structure among the different geographic regions studied.

Interestingly, BRA and WED shared 50 % of species, but this value decreased to 30 % between BRA and DRA. Finally, there was approximately 35 % of species that were present in the BRA region, indicating some degree of endemism. We may conclude that this overall pattern may be related to nestedness component of diversity, which occurs when the biotas of sites with smaller numbers of species are subsets of the biotas at richer sites reflecting a non-random process of species loss as a consequence of any factor that promotes the orderly disaggregation of assemblages (Baselga 2010). This finding is important for effective management and would require devoting conservation efforts to the richest sites (Balvanera et al. 2006). Therefore, the Bransfield region represents a key area in terms of diversity and connectivity in structuring the assemblages at the tip of AP. These marine ecosystems are characterized by the convergence of two water masses (the cold bottom water from the eastern AP shelf and the warm and salty waters of the circumpolar origin), an interannual and seasonal sea-ice variability, and a complex bottom topography (Björgo et al. 1997; Foldvik et al. 2004; Gutt et al. 2015a, b; Jerosch et al. 2015; Dorschel et al. in press). Moreover, disturbance events such as iceberg scouring can also contribute to the differences of ophiuroid assemblages over the three geographic regions studied. Within the depth gradient, we did not find any significant differences concerning diversity and structure of assemblages. The Antarctic continental shelf is considerably deeper than most shelf regions of the world mainly due to the extent and retreat of the shelf ice during glacial and interglacial periods (Anderson 1999). This process may help to explain why Antarctic invertebrates in general, and ophiuroids in particular, show a wide bathymetric distribution (Brey et al. 1996; Thatje et al. 2005).

The impacts of global climate change on Antarctic ophiuroids are likely to differ among species that live in deeper waters. On the continental shelf, the changes associated with global climate change include, for instance, the increase of iceberg scouring, changes in duration and extent of the sea ice, and increased sedimentation and freshening from glacial melt (Barnes and Peck 2008; Smale and Barnes 2008; Gutt et al. 2015a, b). These climate impacts would primarily affect the Antarctic shelf ecosystems and especially the phenology, geographic ranges, and behaviors of a wide range of organisms (Aronson et al. 2007). We know too little about the implications of such ecological and physiological changes on the population dynamics of ophiuroid species. For this reason, more detailed investigations, especially involving the spatial distribution patterns, reproductive modes, and feeding types of benthic invertebrates, may help improve our understanding of the ecological responses of Antarctic benthos to climate change.

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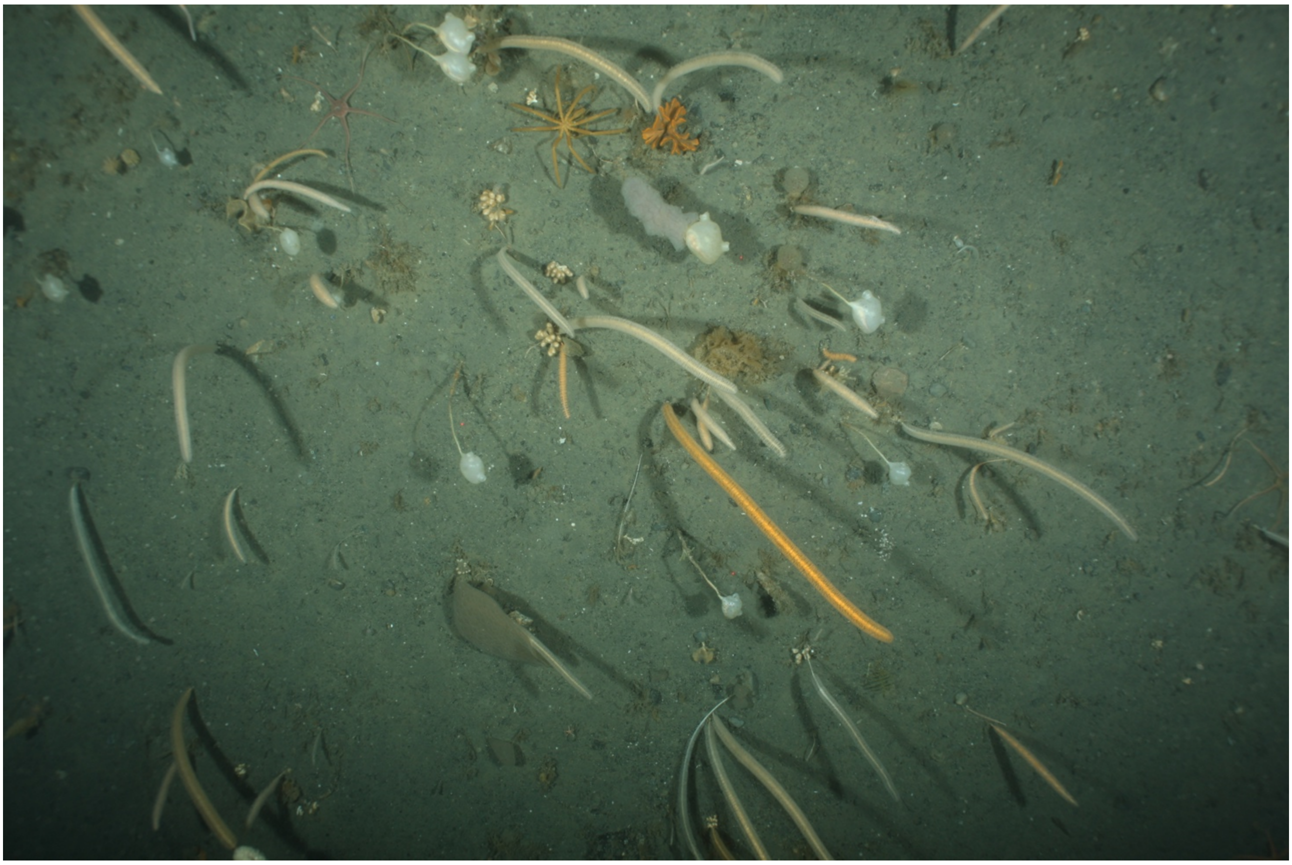
Chapter 3

Pristine populations of habitat-forming gorgonian species on the Antarctic continental shelf



Ambroso, S., Salazar, J., Zapata-Guardiola, R., Federwisch, L., Richter, C., Gili, J. M., & Teixidó, N. (2017). Pristine populations of habitat-forming gorgonian species on the Antarctic continental shelf. Scientific reports, 7(1), 1-11.

Introduction

The current state of the oceans is very different from what it was in the past (Jackson 1997; Halpern et al. 2012). Actually, most marine ecosystems are affected by climate change (e.g. ocean warming, acidification, sea level rise) (Blunier & Brook 2001; Hoegh-Guldberg et al. 2007; Halpern et al. 2008) and other multiple human-derived threats (e.g. overfishing, pollution, habitat destruction) (Jackson et al. 2001; Worm et al. 2006; Estes et al. 2011) which threaten marine global biodiversity and modify oceanic environments (Halpern et al. 2008) to the point of being considered "unnatural oceans" (Jackson & Sala 2001) nearly devoid of "pristine" areas (Cressey 2012). Such pristine areas are minimally affected by major human threats, thus providing a unique opportunity to better understand how marine ecosystems are structured and behave (Sandin et al. 2008; Knowlton & Jackson 2008). They are also essential to study the effects of climate change on benthic communities (Levin & Dayton 2009), particularly on the Antarctic continental shelf where one can find still relatively undisturbed environments (Clarke & Harris 2003; Smetacek & Nicol 2005). The potential impact of trawling activity has become also a major concern due to its extensive damage to continental shelves and deep cold-water coral reefs (Hall-Spencer et al. 2002; Althaus et al. 2009). Although there is evidence of fishing activity as by-catch from longline fisheries in South Georgia (Taylor 2011) and in the Ross Sea (Parker & Bowden 2010), most of the Antarctic continental shelf has been little influenced by industrial fishing (Ainley & Pauly 2014). The lack of terrigenous sediments (Anderson 1999), the relative constancy of its physical conditions (Hedgpeth 1977; Picken 1985) and the relative absence of human-derived threats (Halpern et al. 2008), make the Antarctic continental shelf a highly favourable environment for the development of high-density benthic megafauna communities.

In the last few decades, studies carried out on the continental shelf of the NE Weddell Sea have generated key insights on the diversity (Voß 1988; Gutt & Starmans 1998), the degree of heterogeneity (Gutt 2000; Teixidó et al. 2002), and the impact of iceberg scouring (Gutt & Starmans 2001; Gutt & Piepenburg 2003; Teixidó et al. 2007). Iceberg scouring constitutes one of the major natural disturbances for high-Antarctic shelf fauna and it is increasingly apparent that iceberg scouring events may be altered by iceberg calving associated with regional atmospheric warming (Scambos et al. 2000; Barnes et al. 2014). The estimated rate of disturbance of the Antarctic continental shelf by grounding icebergs is approximately 5% (Gutt 2000), although still considerably less than the 53% attributable to trawling in other continental shelves (Mc Allister 1995). Gorgonians are among the main structural species of many benthic communities across all latitudes and depths, from shallow sublittoral habitats to continental shelves and deep seas (Gili et al. 1989; Jones et al. 1994; Ballesteros 2006). Hence, the Commission for the Conservation of Marine Living Resources (CCAMLR) has recognized gorgonians as a Vulnerable Marine Ecosystems (VME) indicator taxa (Jones & Lockart 2011). These organisms contribute to the structure of benthic communities adding 3-dimensional complexity to the habitat (Jones et al. 1997; Orejas et al. 2000). During the last decade, knowledge about diversity, distribution, ecology and state of conservation of deep gorgonian populations on the continental shelf has significantly increased in the Mediterranean Sea (Salomidi et al. 2009, Grinyó et al. 2016), the Pacific Ocean (Matsumoto et al. 2007; Stone et al. 2014) and the Atlantic Ocean (Mortensen & Buhl-Mortensen 2004). In Antarctica, most of the studies of this group of organisms have focused on taxonomy (Zapata-Guardiola and López-González 2009, 2010), trophic ecology (Orejas et al. 2001, 2003), growth rates (Peck & Brockington 2013; Martínez-Dios et al. 2016) and reproductive ecology (Orejas et al. 2002, 2007). However, despite the high abundance of gorgonians in some locations of the Weddell Sea and their ecological role on Antarctic benthic communities (Starmans et al. 1999; Teixidó et al. 2007), there is still an important lack of knowledge on their ecological characteristics such as spatial distribution, abundance and demographic processes.

Non-destructive sampling techniques like video-equipped towed gears, Remotely Operated Vehicles (ROVs) or manned submersibles are commonly used to study coastal areas (Gori et al. 2011a), reference deep reefs of cold-water corals (Orejas et al. 2009), seamounts (Bo et al. 2009), and mesophotic areas (Rooney et al. 2010) to assess biodiversity patterns, characterize communities, evaluate spatial and temporal changes, and assess benthic ecosystem health status (Gutt 2007; Ludvigsen et al. 2007). Although the majority of studies on Antarctic benthos have been carried out using semi-quantitative techniques like Agassiz and bottom trawls (Thurston et al. 1994; Arnaud et al. 1998), non-destructive image methodology has also been commonly used in the high Antarctic to provide quantitative information on the distributional patterns of benthic megafauna communities over large spatial and bathymetrical domains (e.g. Gerdes et al. 1992; Piepenburg et al. 1997; Gutt & Starmans 1998; Starmans et al. 1999; Teixidó et al. 2006; Gutt 2007).

Knowledge of demographic processes and spatial distribution patterns is a prerequisite to understand their role on benthic communities and provide basic information on their underlying dynamics and resilience, as well as to facilitate their management and conservation (Jones et al. 1994; Gili & Coma 1998; Fortin & Dale 2005). The major aim of the present study was to assess the health status of Antarctic gorgonian assemblages in a pristine and remote area in the southernmost part of the Weddell Sea continental shelf. Specifically, (1) we characterized the diversity and the abundance of Antarctic gorgonians; (2) explored their distribution patterns, and (3) assessed their population size structure. This study attempts to be a benchmark for the investigation of continental shelf habitats modified by anthropogenic pressure and to contribute to the general knowledge of pristine areas with habitat-forming species.

Material and methods

Study area

The study area was sampled as a part of the multidisciplinary PS89 (ANT XXIX/9) expedition on board the R/V *Polarstern* from December 19, 2013, to March 5, 2014 (Knust & Schröder 2014). It is located in front of the Filchner Ronne Ice Shelf in the southernmost part of the Weddell Sea; a region poorly investigated due to the heavy sea ice conditions (Knust & Schröder 2014). The small amount of data available from this area has made it an area of special relevance to better understand oceanographic conditions and to gain new insights into biodiversity patterns in this remote and pristine region (Vaughan et al. 2003). The study area was divided into a south and a north section due to Brunt Ice Shelf, which may produce different oceanographic conditions (Knust & Schröder 2014).

ROV sampling procedure

In order to study the composition and distribution of gorgonians, an inspection-class ROV (Remotely Operated Vehicle, Ocean Modules V8 Sii) was deployed at six stations in the area of the Filchner Trench (Supplementary Table S5). Three random stations (stn. 41, stn. 81, stn. 86) were recorded in the southern part of the continental shelf and three random stations (stn. 128, stn. 136, stn. 170) in its northern part close to the shelf break. The ROV was equipped with a High Definition (HD) video camera (Kongsberg oe14-502) looking forward in an angle of 40-45° and two parallel lasers providing a reference scale of 4 cm on the video (see Knust and Shröder 2014 for more details on the ROV procedure). The ROV video material is available from the data publisher PANGEA at www.pangea.de (see Table S5 for DOIs).

Species identification

In order to confirm the taxonomic identification of the species observed in the videos, colonies of gorgonians were collected with an Agassiz Trawl (AGT) after the ROV deployments. Colonies were fixed and preserved in 10% formalin until analysed in the laboratory (see Supplementary Table S6 for taxonomic remarks on the identification of some groups of species). We identified 7 gorgonian species belonging to the family *Primnoidae* (*Ainigmaptilon* sp.*, Dasystenella acanthina, Fannyella rossii, Fannyella spinosa, Thouarella* sp.1*, Thouarella* sp.2*, and Thouarella variabilis*) an unbranched morphogroup (flagelliform colonies with polyps distributed in whorls along the main stem of the colony), which included specimens of the genera *Onogorgia, Armadillogorgia, Primnoella* and *Arntzia*, and a bamboo coral group of the Family Isididae, (Supplementary Figures S1 and S2).

Video analysis

Quantitative video analysis was performed using the software SONY XDCAM Viewer. Every gorgonian observed within a width of 0.3 m (based on the laser beams) along each video transect was identified with a distance from the beginning of the transect according to the ROV's ultra-short baseline (USBL) position data.

Spatial distribution and size structure

We examined the species composition and quantified the frequency as the relative proportion of each species present for each sampling unit of the transect and the abundance as the total number of colonies across all the transects (see below). The most abundant species of gorgonians were used to compare their abundance, spatial distribution and size class in both the north and south areas. These results were displayed in density plots, obtained by transforming each transect into a string of contiguous quadrats of 1 m^2 (0.3 × 3.33 m) and counting the number of colonies of each species only inside each quadrat. A total of 1836 useful sampling units were obtained from the 6 transects.

The significance of the deviation from a random distribution was analysed with the one-dimensional version of Ripley's K-function second-order spatial statistic. (Ripley 1976; Haase et al. 1996; Fortin & Dale 2005). When the sample statistic is found within the bounds of the confidence interval at any point, it indicates complete spatial randomness; a significant positive deviation of the sample statistic indicates over-dispersion of the colonies, whereas a significant negative deviation indicates a clumped distribution (Fortin & Dale 2005).

To study population size structure, the maximum height of each observed gorgonian colony was measured using the Macnification 2.0.1 software on still images extracted from recorded footage (Schols & Lorson 2008). The distance between the two laser beams was used to calibrate extracted images and measurements were performed on still images in which the laser beams were in the same plane as the colony base to reduce the error due to the perspective (Gori et al. 2011a).

Based on previous studies, colony size class was defined for each 10 cm (Gori et al. 2011a, Linares et al. 2008). We considered as young colonies the smallest colonies that could be distinguished using the video analysis (2–5 cm in height) (Gori et al. 2011b). Size structure was also analysed in terms of descriptive statistics using distribution parameters such as skewness and kurtosis. Skewness is a measure of the symmetry of a distribution using its mean, reflecting the proportion of small versus large colonies in a gorgonian population; if skewness is significant the distribution is asymmetric. Kurtosis is a measure of the peakedness of a distribution near its central mode. A significant kurtosis value indicates longer tails than would be expected for a normal distribution, and therefore a particular colony size prevails in the population. Only transects with more than 40 colonies were studied for population size structure in order to generate meaningful skewness and kurtosis estimates.

Population size structure and density data from other areas of the continental shelf.

To compare our data with that of other gorgonian populations dwelling on the continental shelf of other seas, we compiled data on maximum abundance, mean density and maximum height from previous studies using ROV observations. Overall, we compiled population structure data for 36 taxa and 12 different study areas (Supplementary Table S4).

Assemblage structure.

A non-metric multi-dimensional scaling (nMDS) ordination analysis was performed based on the Bray–Curtis similarity measure using square-root-transformed abundance data. For visualization purposes, data are presented for each 200 m length. Furthermore, a similarity percentage procedure analysis, SIMPER, was performed to identify the relative contribution of each species to average similarities between areas. A non-parametric analysis of variance, PERMANOVA, was applied using Bray-Curtis distance for the multivariate analyses. Statistical analyses were computed using the program Primer v6 with the PERMANOVA + add-on package.

Results

Abundance of gorgonian populations

A total of 3140 colonies (1402 in the north and 1738 in the south), comprising seven gorgonian species (*Ainigmaptilon* sp., *Dasystenella acanthina, Fannyella rossii, Fannyella spinosa, Thouarella* sp.1, *Thouarella* sp.2, and *Thouarella variabilis*), an unbranched morphogroup (which included specimens from the genus *Onogorgia, Armadillogorgia, Primnoella* and *Arntzia*) and the family Isididae, were counted along six transects (Supplementary Table S1), occurring with a frequency of 64.4% in 1836 sampling units of 1 m^2. Based on our count data, we estimated more than 46000 and more than 97000 colonies for the north and the south region, respectively. Overall, *Thouarella* sp.1 was the most abundant (n = 597 total colonies across all transects) and the second most frequent species representing 19% of observed colonies present in 20% of the sampling units. *Thouarella* sp.2 was the second most abundant (n = 572), but the most frequent (20%) species. The family Isididae (n = 535, 17.8%), *Fannyella rossii* (n = 474, 17.5%) and *Thouarella variabilis* (n = 438, 15.4%) were the third, fourth and fifth most abundant and frequent species, respectively. The unbranched group (n = 280) was more abundant than *Dasystenella acanthina* (n = 189), but less frequent (5.4% and 7.5%, respectively).

The other species accounted for less than 2% of the observed colonies, occurring in less than 3% of the sampling units. Generally, abundance of the gorgonians differed between the two study sections, being lower in the northern part. Only Isididae (n = 277) and *Dasystenella acanthina* (n = 87) abundance showed high values in the northern stations (Fig. 1).

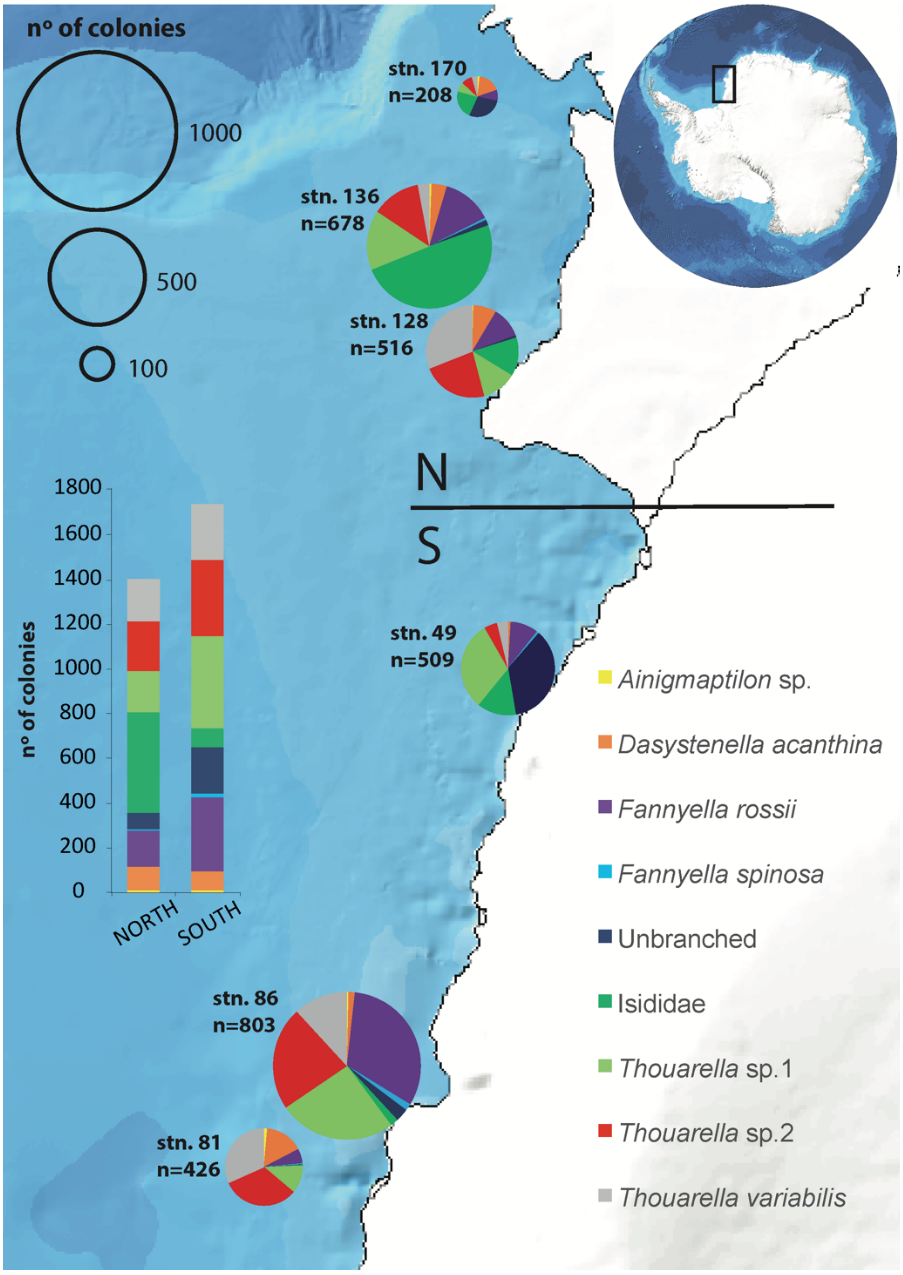


Fig. 1 Composition, distribution and abundance of gorgonian species. The pie charts display the percentage of gorgonians taxon at each station (n = number of colonies per station). The size of the pie charts represents the abundance of the gorgonians. The histogram shows the abundance of gorgonian species per region.

Spatial distribution

Ripley's K analysis revealed a significantly clumped distribution of the family Isididae, *Thouarella* sp.1 and *Thouarella* sp.2 colonies at all scales (from 1 m^2 to whole transect). *Thouarella variabilis* showed a clumped distribution in the north, but a random distribution in the south. An opposite result for spatial distribution was found for *Dasystenella acanthina, Fannyella rossii* and Unbranched (Fig. 2).

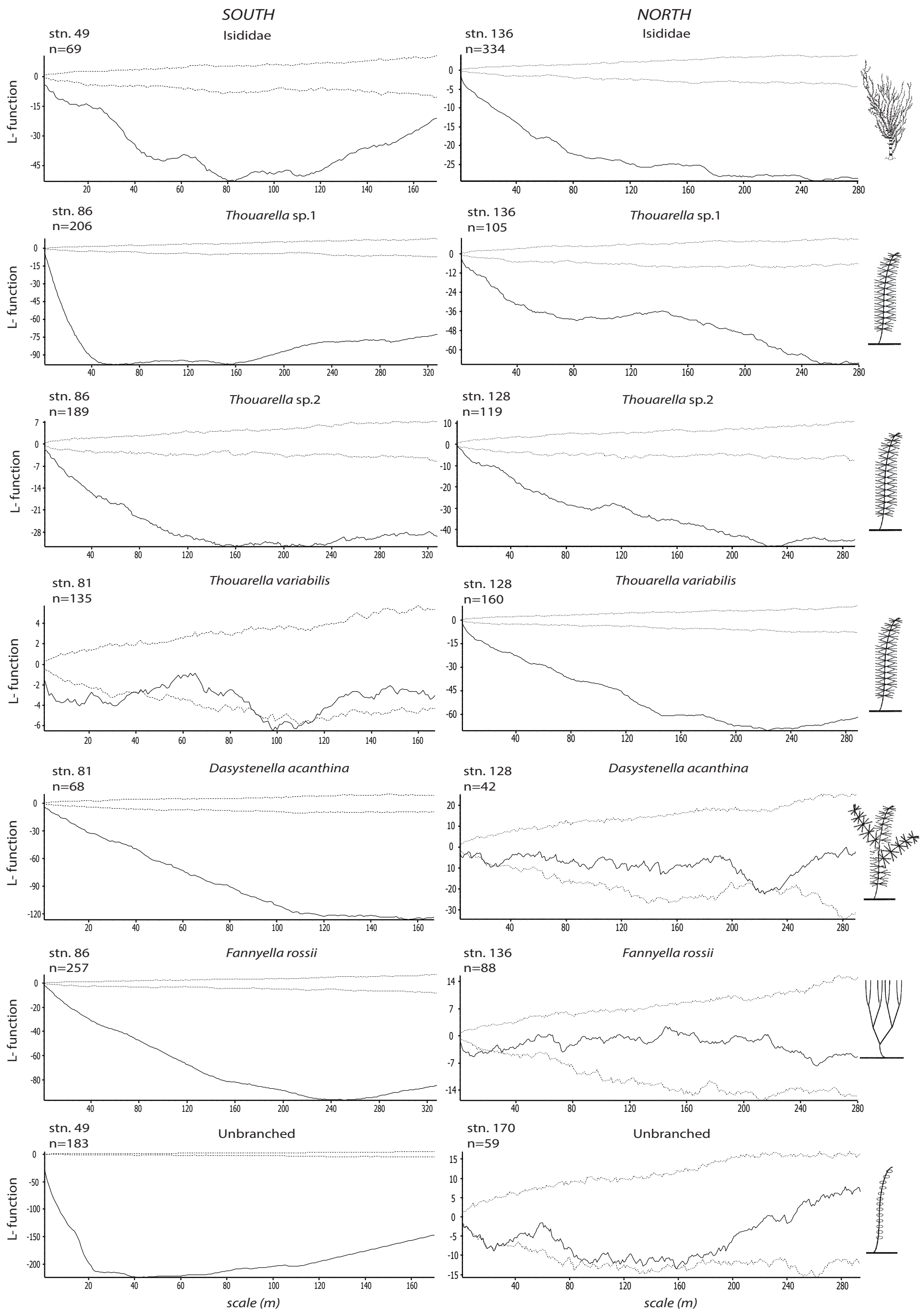


Fig. 2. L-function (Ripley’s K) for the most abundant species. Values below 95% confidence interval (dotted lines) indicate a statistically significant clumped distribution of colonies; values within the confidence interval indicate a random distribution; values over the confidence interval indicate a statistically significant over-dispersed distribution (n = number of colonies).

Gorgonian abundances varied markedly among the various stations ($F_{5,1179}$=53.3, $p<0.001$) (Fig. 3). In stn. 49, the Unbranched morphogroup was the group of gorgonians with the highest abundance (47 col/m^2) and mean density of 7.3±11.5 col/m^2 while the least abundant species were *Fannyella spinosa* and *Ainigmaptillon* sp., with highest abundance of 20 and 19 col/m^2, and mean density of 1.3±0.6 and 1.2±0.4 col/m^2 respectively (Fig. 3).

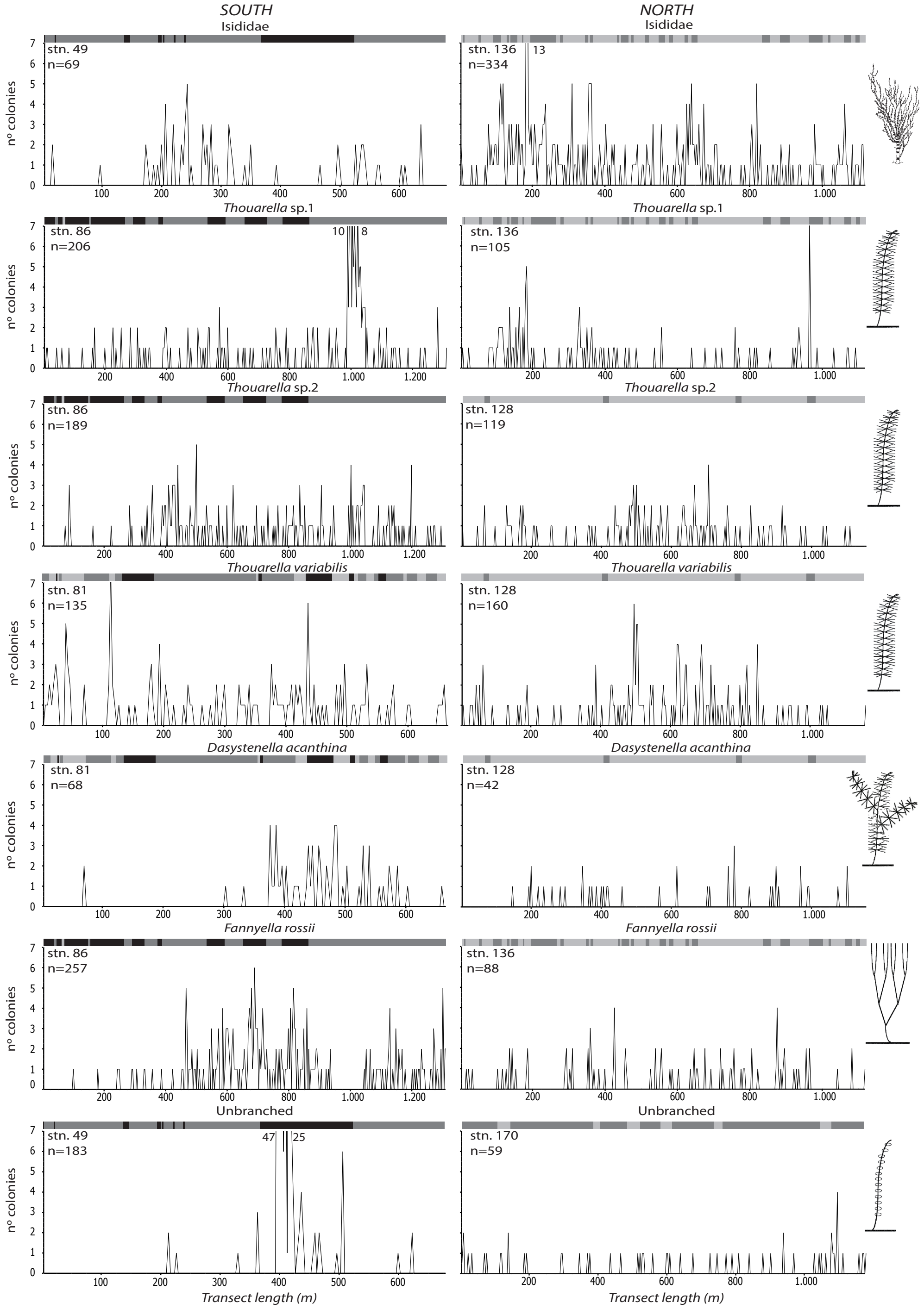


Fig. 3 Density plots. Densities of the most abundant species are plotted along the transects (n = number of colonies). Substrate type is indicated as black (coarse sediment), dark grey (intermediate sediment) and light grey (fine sediment).

Population size structure

The size frequency distributions of the 7 species populations, were unimodal (Fig. 4).

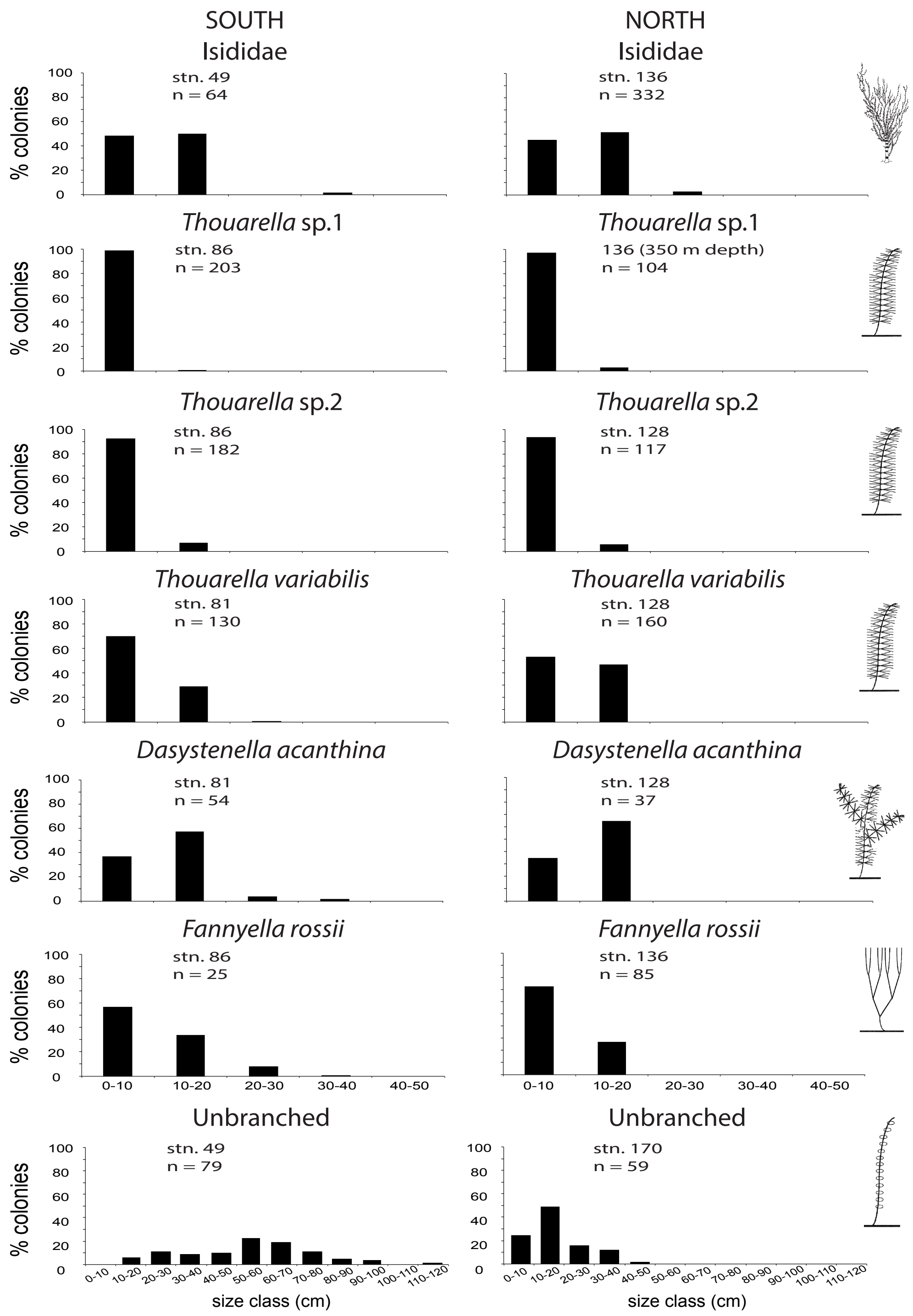


Fig. 4 Size-frequency distribution of gorgonian populations (n = number of colonies).

Most of the gorgonian populations were positively skewed, indicating an asymmetrical distribution of size frequency and a high proportion of small colonies (0–10 cm) (Fig. 4 and Supplementary Table S2). In contrast, the two populations of the Unbranched morphogroup were not skewed, being dominated by medium-sized colonies (10–20 cm in the south and 50–60 cm in the north) (Fig. 4 and Supplementary Table S2). Most of the northern populations showed no significant kurtosis while in the south all the gorgonian populations, except Unbranched, showed significant kurtosis (Supplementary Table S2). Finally, in both studied areas, all gorgonian populations displayed the same size class distributions (Fig. 4).

Population structure

The structure of gorgonian population gradually differed in both sections, with significant differences between north and south ($F_{1,1183}$=65.06, p<0.001) (Fig. 5).

The SIMPER analysis showed an average similarity in species composition which ranged from 17.89% to 31.68% (Supplementary Table S3). The number of species contributing up to 90% of the similarity was the same in the two sections (Supplementary Table S3). *Thouarella* sp.1 contributed most (25.14%) to the similarity in the northern transects, while the family Isididae was especially relevant in the southern transects (22.43% of contribution). Focusing on taxa dissimilarities, the family Isididae was the most important contributing with 17% of the average dissimilarity between north and south.

Discussion

This study focused on previously unknown extensive gorgonian assemblages in the southeastern Weddell Sea. Our results indicate that this region is a hotspot for gorgonian diversity in terms of both number of species and their abundance. The diversity of the studied gorgonian assemblages was similar to those reported on subtropical (Opresko 1973), Mediterranean shelf (Grinyó et al. 2016) and Antarctic coastal areas (Raguá-Gil et al. 2004). Seven different species, a gorgonian morphogroup and a gorgonian family Isididae were observed to dwell between 250 and 350 m depth within the study area (Fig. 1), in agreement with previous findings in coastal areas of the Antarctic Peninsula (Raguá-Gil et al. 2004). On the other hand, gorgonian density observed in these multi-specific assemblages clearly exceed (by ten-fold; 47 colonies/m^2) those reported for other Antarctic and Arctic shelf areas (Orejas et al. 2002; Stone 2006; Clark & Bowden 2015) (Supplementary Table S4). These high density values were similar to those found in temperate (Grigg 1977; Cúrdia et al. 2013) and tropical (Lasker & Coffroth 1983; Yoshioka & Yoshioka 1989) coastal assemblages (Supplementary table S4). Despite extreme environmental conditions and the general theory that species richness decreases with increasing latitude, it is also generally accepted that this theory is not strictly true and varies with species in the Southern Ocean (Arntz et al. 1994; Griffiths 2010). In addition, benthic biomass in some Antarctic areas is larger than in temperate and subtropical areas (Brey & Clarke 1993). Such dense three-dimensional communities cover large sections of the Antarctic continental shelf as well as the Mediterranean Sea (Grinyó et al. 2016) and deep undisturbed North Atlantic coral banks (Mortensen & Buhl-Mortensen 2004). *Fannyella rossii* and the three species of genus *Thouarella* showed high abundances in each video transect (Supplementary Table S1). This highlights the unique abundance of these Antarctic gorgonians species (Zapata-Guardiola & López-González 2009). Of additional note is their high abundance, with maximum values of 6 ind/m^2 for *Fannyella rossii* and 10 ind/m^2 for *Thouarella* sp.1 in the southern section (Supplementary Table S1).

All populations in this study were represented by many small colonies with a positively skewed colony size distribution (Fig. 4). The size structure of a population results from the action of biotic and abiotic factors and from the type, intensity, and frequency of disturbance to which individuals are exposed (Gilmour 2004; Gori et al. 2011b). Positively skewed size frequency distribution implies that a population is in a healthy state and growing, since it includes an abundance of juveniles (Meesters et al. 2001; Linares et al. 2008). On the contrary, a negative skewness indicates a lack of recent recruitment and therefore it implies a risk of population decline (Bak & Meesters 1998; Meesters et al. 2001). Population size structure of all *Thouarella* and *Fannyella* species was mostly asymmetrical with many small colonies (Fig. 4), suggesting high recruitment rates (Linares et al. 2008). The size structure also reflects the growth and the development of each individual within the population, as well as past recruitment and mass mortality events. Unfortunately, due to their inaccessibility, only a few studies of gorgonian population size structure have been done on continental shelves (Grinyó et al. 2016). Unbranched individuals seem to grow slowly and older without being replaced (low recruitment) with few small colonies (sexual juveniles) and dominance of large-sized individuals (Grinyó et al. 2016).

As a rule of thumb, because of their slow growth rate (Coma et al. 1998; Sherwood & Edinger 2009) and reproduction type, gorgonians are especially vulnerable to iceberg scouring (Gutt et al. 1996; Teixidó et al. 2004), making their recovery very slow (Althaus et al. 2009). All gorgonian species described in this study reproduce by internal brooding. This means that the settlement of the larvae occurs at short distances from the parents (Kahng et al. 2011) explaining the patchy distribution along all video transects. Some gorgonian species such as *Ainigmaptillon antarcticum* and *Primnoisis antarctica*, which are internal brooders, are also pioneer taxa appearing during the first stage of recolonization after iceberg scouring events with patchy distribution (Gutt et al. 1996; Teixidó et al. 2004).

The high diversity and abundance of deep gorgonian assemblages on the Antarctic continental shelf, and the vast area covered by high densities of genus *Thouarella* are probably related to the low iceberg scouring pressure and oceanographic-ice conditions. Constant hydrodynamic conditions that increase particle suspension in the near-bottom water layers may also imply enhanced food availability for gorgonians on the continental shelf (Thiem et al.

2006). Strong currents are advantageous to the establishment of this group of organisms supplying them with food and continuously keeping them completely clear of sediment (Genin et al. 1986; Rogers 1994). Moreover, based on our findings of high abundance and large sizes in the southern region of our study area, we hypothesize that it is little affected by iceberg scouring, thereby favouring the establishment of well-developed pristine gorgonian populations.

Reduced abundance of long-lived and habitat-forming species from the deep sea and continental shelves in shallow sublittoral habitats have attracted particular attention, given their disproportionate importance to ecosystem structure and function, and the social value of marine habitats (Althaus et al. 2009). Yet, factors responsible for such decline are mainly overexploitation and habitat destruction by bottom trawling and bycatch fishing (Mortensen et al. 2008). Evidence of fishing activities with *Thouarella* spp. as by-catch has been reported in South Georgia (Taylor 2011). Moreover, specimens from the genus *Primnoa* and the family Isididae from longline fisheries were found in the Ross Sea (Parker and Bowden 2010). To our knowledge, our results are the first to show pristine populations of gorgonians with the highest abundance and largest size ever recorded on the Antarctic continental shelf. These populations are far more mature and better preserved than any other known population in Antarctica. Clearly, more research is needed to determine the locations of such refuges and to devise strategies to protect such gorgonian populations as well as the many other species interacting with them. The study of these pristine gorgonian populations may also provide proxy knowledge on how other continental shelf and upper slope communities may have thrived in the decades before bottom trawling fishing ensued.

Supplementary Information

Supplementary Table S1 – Gorgonian presence and spatial distribution in the northern subarea. Occurrence (frequency of occurrence in the set of sampling units) is given for each transect and species; abundance (number of colonies) and maximum density of each species is given per each transect.

Supplementary Table S2 – Size structure characteristics of the studied gorgonians species: colony height, skewness and kurtosis. Asterisks indicate the degree of significance.

Supplementary Table S3 – SIMPER analysis: (a) Species that cumulatively contribute to 90% of the average similarities within the regions (Aver. Sim), (b) Species that contribute cumulatively to 90% of the average dissimilarities between the regions (Aver. Diss).

Supplementary Table S4 – Summary of gorgonian data reported from previous ROV observations from different continental shelfs. Data shows maximum abundance, mean density and maximum height.

Supplementary Table S5 – ROV deployment during ANT XXIX/9.

Supplementary Table S6 – Remarks on the identification of gorgonian species.

Supplementary Figure S1 – Studied species images from ROV. a) Isididae, b) *Thouarella variabilis*, c) *Thouarella* sp.1, d) *Thouarella* sp.2, e) *Dasystenella acanthina*, f) *Fannyella rossii*, g) *Fannyella spinosa*, h) Unbranched, i) *Ainigmaptilon* sp. Scale Bar: 4 cm.

Supplementary Figure S2 – Images of studied species collected with AGT. a) Isididae, b) *Thouarella variabilis*, c) *Thouarella* sp.1, d) *Thouarella* sp.2, e) *Dasystenella acanthina*, f) *Fannyella rossii*, g) *Fannyella spinosa*, h) Unbranched, i) *Ainigmaptilon* sp. Scale Bar: 4 cm.

Supplementary Table S1

Station	Sampling Units			Species	Sampling units per species		Colonies		Mean density ± SD	Max density
	Number	with gorgonians	(%)		Number	(%)	Number	(%)	(colonies · m^{-2})	(colonies · m^{-2})
128	348	234	(67.2)	*Ainigmaptilon sp.*	2	(0.6)	2	(0.4)	1 ± 0	1
				Dasystenella acanthina	33	(9.5)	42	(8.1)	1.3 ± 0.5	3
				Fannyella rossii	50	(14.4)	56	(10.9)	1.1 ± 0.4	3
				Thouarella sp.1	50	(14.4)	63	(12.2)	1.3 ± 0.5	3
				Thouarella sp.2	91	(26.1)	119	(23.1)	1.3 ± 0.6	4
				Thouarella variabilis	102	(29.3)	160	(31.0)	1.3 ± 1.0	6
				Unbranched	4	(1.1)	4	(0.8)	1 ± 0	1
				Isididae	54	(15.5)	70	(13.6)	1.3 ± 0.6	4
136	336	249	(74.1)	*Ainigmaptilon sp.*	4	(1.2)	4	(0.6)	1 ± 0	1
				Dasystenella acanthina	23	(6.8)	27	(4.0)	1.2 ± 0.4	2
				Fannyella rossii	62	(18.5)	88	(13.0)	1.4 ± 0.7	4
				Fannyella spinosa	3	(0.9)	4	(0.6)	1.3 ± 0.6	2
				Thouarella sp.1	74	(22.0)	105	(15.5)	1.4 ± 1.0	7
				Thouarella sp.2	65	(19.3)	86	(12.7)	1.3 ± 0.6	4
				Thouarella variabilis	14	(4.2)	20	(2.9)	1.4 ± 0.7	3
				Unbranched	10	(3.0)	10	(1.5)	1 ± 0	1
				Isididae	181	(53.9)	334	(49.3)	1.8 ± 1.5	13
170	354	147	(41.5)	*Ainigmaptilon sp.*	4	(1.1)	4	(1.9)	1 ± 0	1
				Dasystenella acanthina	31	(8.8)	37	(17.8)	1.2 ± 0.5	3
				Fannyella rossii	17	(4.8)	18	(8.7)	1.1 ± 0.2	2
				Thouarella sp.1	15	(4.2)	16	(7.7)	1.1 ± 0.3	2
				Thouarella sp.2	18	(5.1)	18	(8.7)	1 ± 0	1
				Thouarella variabilis	9	(2.5)	9	(4.3)	1 ± 0	1
				Unbranched	52	(14.7)	59	(28.4)	1.1 ± 0.5	4
				Isididae	42	(11.9)	47	(22.6)	1.1 ± 0.3	2
49	204	138	(67.7)	*Ainigmaptilon sp.*	1	(0.5)	1	(0.2)	1 ± 0	1
				Dasystenella acanthina	4	(2.0)	4	(0.8)	1 ± 0	1
				Fannyella rossii	30	(14.7)	49	(9.6)	1.6 ± 0.9	4
				Fannyella spinosa	3	(1.5)	4	(0.8)	1.3 ± 0.6	2
				Thouarella sp.1	88	(43.1)	157	(30.8)	1.8 ± 1.3	7
				Thouarella sp.2	18	(8.8)	23	(4.5)	1.3 ± 0.5	2
				Thouarella variabilis	7	(3.4)	19	(3.7)	2.7 ± 1.8	5
				Unbranched	25	(12.3)	183	(36.0)	7.3 ± 11.5	47
				Isididae	39	(19.1)	69	(13.6)	1.8 ± 1	5
81	200	139	(69.5)	*Ainigmaptilon sp.*	5	(2.5)	6	(1.4)	1.2 ± 0.4	2
				Dasystenella acanthina	37	(18.5)	68	(16.0)	1.8 ± 1	4
				Fannyella rossii	15	(7.5)	26	(6.1)	1.7 ± 1.1	4
				Fannyella spinosa	2	(1.0)	2	(0.5)	1 ± 0	1
				Thouarella sp.1	35	(17.5)	50	(11.7)	1.4 ± 0.7	4
				Thouarella sp.2	72	(36.0)	137	(32.2)	1.9 ± 1.1	5
				Thouarella variabilis	81	(40.5)	135	(31.7)	1.7 ± 1.2	8
				Unbranched	1	(0.5)	1	(0.2)	1 ± 0	1
				Isididae	1	(0.5)	1	(0.2)	1 ± 0	1
86	394	276	(70.1)	*Ainigmaptilon sp.*	3	(0.8)	3	(0.4)	1 ± 0	1
				Dasystenella acanthina	11	(2.8)	11	(1.4)	1 ± 0	1
				Fannyella rossii	150	(38.1)	257	(31.7)	1.7 ± 1	6
				Fannyella spinosa	12	(3.0)	12	(1.5)	1 ± 0	1
				Thouarella sp.1	107	(27.2)	206	(25.4)	1.9 ± 1.7	10
				Thouarella sp.2	126	(32.0)	189	(23.3)	1.5 ± 0.8	5
				Thouarella variabilis	70	(17.8)	95	(11.7)	1.4 ± 0.9	7
				Unbranched	17	(4.3)	23	(2.8)	1.4 ± 1.2	6
				Isididae	11	(2.8)	14	(1.7)	1.3 ± 0.5	2

Supplementary Table S2

			Height (cm)			Skewness			Kurtosis		
	stn.	n	Media	SD	Max	Skew	P-value	Sig.	Kurt	P-value	Sig.
Isididae	**49**	**64**	**10.61**	**4.1**	**30.5**	**1.929**	**<0.001**	*******	**9.806**	**<0.001**	*******
	128	70	7.4	1.8	12.5	0.324	0.2366		3.568	0.2089	
	136	**332**	**11.0**	**3.9**	**29.8**	**1.195**	**<0.001**	*******	**4.903**	**<0.001**	*******
	170	47	7.5	2.1	15.5	1.472	<0.001	***	6.090	0.0033	**
Thouarella sp. 1	49	135	9.9	3.5	19.3	0.347	0.09166		2.578	0.3059	
	81	50	5.3	1.7	10.8	0.857	0.01247	*	4.002	0.0989	
	86	**203**	**5.4**	**1.5**	**10.8**	**0.786**	**<0.001**	*******	**3.915**	**0.0250**	*****
	128	63	6.3	1.7	12.5	0.406	0.1611		3.753	0.1454	
	136	**104**	**5.9**	**1.8**	**14.0**	**1.144**	**<0.001**	*******	**5.958**	**<0.001**	*******
Thouarella sp. 2	81	127	8.0	3.0	17.7	1.007	<0.001	***	4.013	0.0397	*
	86	**182**	**6.3**	**2.3**	**15.5**	**1.428**	**<0.001**	*******	**5.892**	**<0.001**	*******
	128	**117**	**7.2**	**1.8**	**13.5**	**0.298**	**0.1722**		**3.260**	**0.3916**	
	136	83	7.1	2.5	17.2	1.383	<0.001	***	5.485	<0.001	***
Thouarella variabilis	**81**	**130**	**9.3**	**3.1**	**21.8**	**1.344**	**<0.001**	*******	**5.760**	**<0.001**	*******
	86	92	9.1	3.3	24.5	1.365	<0.001	***	6.642	<0.001	***
	128	**160**	**10.2**	**2.5**	**18.3**	**0.996**	**<0.001**	*******	**4.320**	**0.0093**	******
Dasystenella acanthina	**81**	**54**	**11.8**	**5.7**	**39.9**	**2.306**	**<0.001**	*******	**12.236**	**<0.001**	*******
	128	**37**	**11.8**	**3.4**	**19.4**	**0.511**	**0.1601**		**2.625**	**0.8733**	
	170	34	11.0	9.8	54.6	0.624	0.1019		2.366	0.5046	
Fannyella rossii	49	42	1.2	11.4	46.5	0.680	0.0557		2.452	0.5467	
	86	**251**	**10.7**	**6.1**	**39.9**	**1.389**	**<0.001**	*******	**4.106**	**<0.001**	*******
	128	56	9.8	3.0	20.1	1.132	<0.001	***	4.308	0.0506	
	136	**85**	**8.8**	**2.3**	**16.1**	**0.442**	**0.08439**		**3.182**	**0.4882**	
Unbranched	**49**	**79**	**54.6**	**21.8**	**111.9**	**0.016**	**0.948**		**2.580**	**0.5107**	
	170	**59**	**16.7**	**9.2**	**40.7**	**0.935**	**0.004157**	******	**3.104**	**0.5665**	

Supplementary Table S3

a) Similarity			
Species	Sim /SD	Contribution%	Cum. Contribution%
Group South (Aver. Sim=65%)			
Thouarella sp.1	3.7	25.1	25.1
Thouarella sp.2	2.6	22.6	47.7
Fannyella rossii	2.8	18	65.8
Thouarella variabilis	1,9	16.6	82.4
Isididae	0.9	4.8	87.2
Dasystenella acanthina	0.9	4.7	91.9
Group North (Aver. Sim=65%)			
Isididae	2.4	22.4	22.4
Thouarella sp.2	2.1	17	39.5
Dasystenella acanthina	2.9	15.6	55.1
Fannyella rossii	2.7	15.1	70.2
Thouarella sp.1	1.8	13.3	83.5
Thouarella variabilis	1.1	9.9	93.4
b) Dissimilarity			
Species	Diss /SD	Contribution%	Cum. Contribution%
Groups South & North (Aver. Diss=43%)			
Isididae	1.4	16.6	16.6
Thouarella sp.1	1.2	15.2	31.8
Thouarella variabilis	1.4	13.8	45.7
Thouarella sp.2	1.3	12.6	58.3
Fannyella rossii	1.1	11.9	70.2
Unbranched	0.7	10.8	81
Dasystenella acanthine	1.5	9	90
Fannyella spinosa	1.1	6.6	96.5

Supplementary Table S4

Species	Max density (ind./m²)	Mean density (ind./m²)	Maximum size (cm)	Study area	Depth (m)	Reference
Acanella arbuscula	4.7			Canada (Gully Canyon)	404-540	Mortensen and Buhl-Mortensen 2005
Acanthogorgia armata	1.99			Canada (Gully Canyon)	231-364	Mortensen and Buhl-Mortensen 2004
Acanthogorgia armata	0.5			Canada (Gully Canyon)	346-493	Mortensen and Buhl-Mortensen 2005
Acanthogorgia hirsuta		0.04 ± 0.2		Tirrenean Sea	200 - 250	Bo et al. 2013
Acanthogorgia hirsuta	5	1.0 ± 1.0		Western Mediterranean (Menorca channel)	100 - 180	Grinyó et al. 2016
Bebrice mollis	3	1.2 ± 0.3		Western Mediterranean (Menorca channel)	180 - 340	Grinyó et al. 2016
Callogorgia verticillata	2	0.4 ± 0.07		Tirrenian Sea	200 - 250	Bo et al. 2013
Callogorgia verticillata	5	1.0 ± 0.9	115.3	Western Mediterranean (Menorca channel)	100 - 180	Grinyó et al. 2016
Corallium lauuense		0.33 ± 0.63	20.3	Hawaii	350 - 500	Parrish 2007
Corallium secundum		0.56 ± 0.65	17.9	Hawaii	350 - 500	Parrish 2007
Eunicella cavolonii	24	2.9 ± 2.7	50.4	Western Mediterranean (Menorca channel)	100 - 180	Grinyó et al. 2016
Keratoisis ornata	0.54			Canada (Gully Canyon)	396-509	Mortensen and Buhl-Mortensen 2005
Keratoisisi sp.		0.05 ± 0.1		Bering Sea	466 - 533	Miller et al. 2012
Paragorgia arborea	0.49			Canada (Gully Canyon)	>235	Mortensen and Buhl-Mortensen 2004
Paragorgia arborea	0.6		180	Canada (Gully Canyon)	341 - 495	Mortensen and Buhl-Mortensen 2005
Paramuricea macrospina	9	1.5 ± 1.7	55.6	Western Mediterranean (Menorca channel)	100 - 180	Grinyó et al. 2016
Plumarella spp.		0.72 ±0.4		Bering Sea	237-356	Miller et al. 2012
Plumarella spp.	5.3	0.46		Bering Sea	300 - 349	Stone et al. 2006
Primnoa pacifica	15.3			Gulf of Alaska	69 - 306	Stone et al. 2014
Primnoa resedaeformis	5.3		86	Canada (Gully Canyon)	388 - 516	Mortensen and Buhl-Mortensen 2005
Radicipes gracilis	4.43			Canada (Gully Canyon)	404 - 535	Mortensen and Buhl-Mortensen 2005
Swiftia pacifica		0.08 ± 0.01		Bering Sea	351 - 530	Miller et al. 2012
Swiftia pallida	14	1.6 ± 2.8	17.4	Western Mediterranean (Menorca channel)	180 - 340	Grinyó et al. 2016
Viminella flagellum	60			Western Mediterranena (Italian Coast)	90-200	Angiolillo et al 2014
Viminella flagellum		0.08 ± 0.3		Tirrenean Sea	200 - 250	Bo et al. 2013
Viminella flagellum	26	3.2 ± 5.4	148.3	Western Mediterranean (Menorca channel)	180 - 360	Grinyó et al. 2016
Ainigmaptilon antarcticum	1.16	0.17 ± 0.31		Weddell Sea	142-363	Orejas et al. 2002

Ainigmaptilon antarcticum	0.7			Weddell Sea	100 - 283	Gutt et al. 2003
Ainigmaptilon sp.	2	1.2 ± 0.4	55.1	Weddell Sea	284 - 361	This study
Arntzia sp.	0,6			Weddell Sea	100 - 283	Gutt et al. 2003
Dasystenella acanthina	4	1.8 ± 1	54.6	Weddell Sea	284 – 361	This study
Fannyella rossii	6	1.7 ± 1	46.5	Weddell Sea	284 – 361	This study
Fannyella rossii			21	Ross Sea	324	Martinez-Dios et al. 2016
Fannyella spinosa	2	1.3 ± 0.6	19.3	Weddell Sea	284 – 361	This study
Isididae		0.03		Ross sea	341 - 555	Clark and Bowden 2015
Isididae	13	1.8 ± 1.5	30.5	Weddell Sea	284 – 361	This study
Primnoella antarctica	1.5			Weddell Sea	100 - 283	Gutt et al. 2003
Primnoidae		0.29		Ross sea	341 - 555	Clark and Bowden 2015
Primnoisis spp.	4,7			Weddell Sea	100 - 283	Gutt et al. 2003
Thouarella sp.		0.2		Ross sea	341 - 555	Clark and Bowden 2015
Thouarella sp. 1	10	1.9 ± 1.7	19.3	Weddell Sea	284 – 361	This study
Thouarella sp. 2	5	1.5 ± 0.8	17.7	Weddell Sea	284 – 361	This study
Thouarella variabilis	8	1.7 ± 1.2	24.5	Weddell Sea	284 - 361	This study
Thouarella/Dasystenella	0.7			Weddell Sea	100 - 283	Gutt et al. 2003
Unbranched	47	7.3 ± 11.5	111.9	Weddell Sea	284 – 361	This study

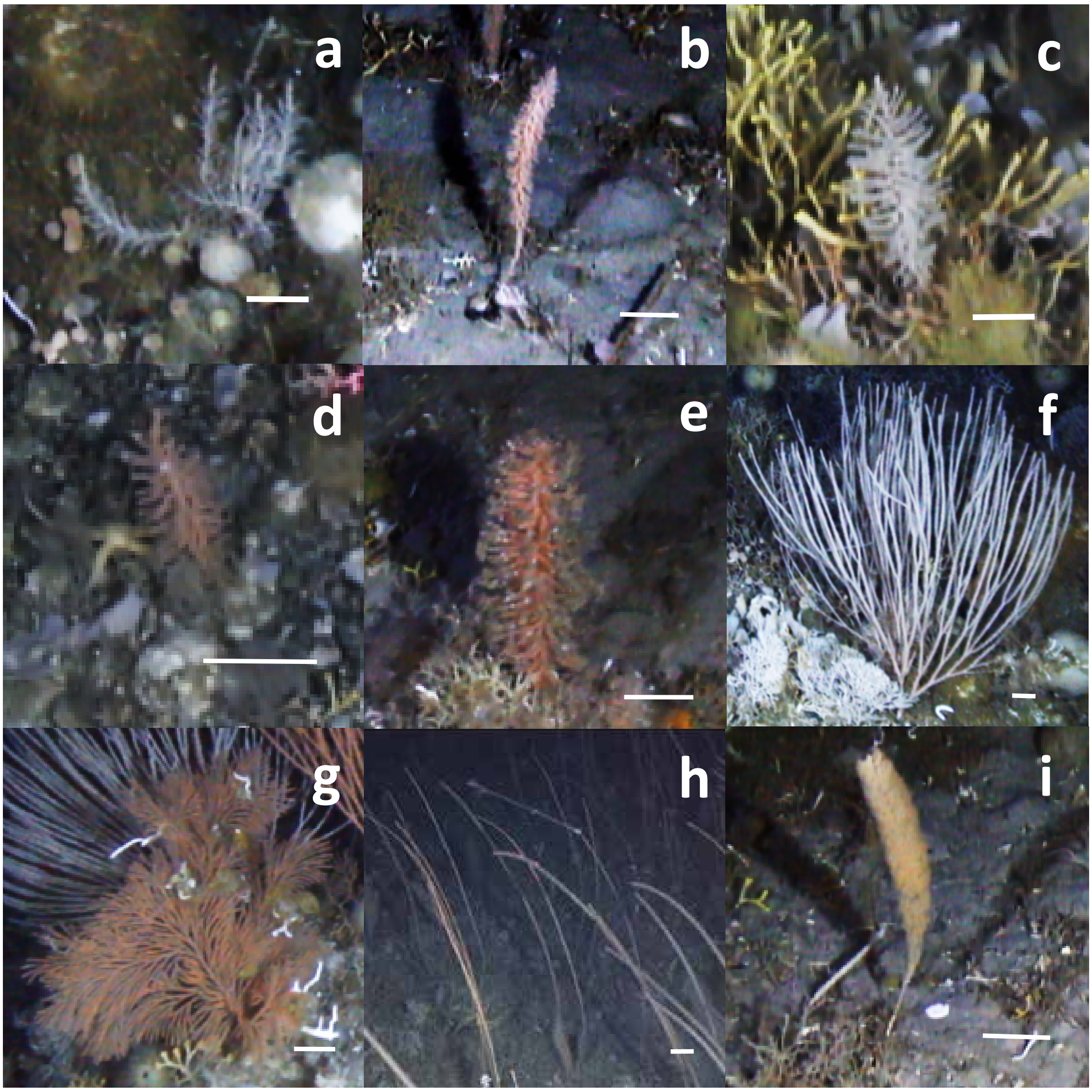
Supplementary Table S5

Station	Latitude	Longitude	Total length (m)	Depth (m)	Area N/S (North/South)
170	74º 53.89’	26º 38.10’	1175,77	295	N
136	75º 19.99’	27º 32.40’	1118,50	350	N
128	75º 29.99’	27º 27.17’	1156,00	292	N
49	76º 19.15’	29º 01.94’	678,90	251	S
86	76º 57.41’	32º 59.11’	1310,20	284	S
81	77º 04.82’	33º 39.02’	665,30	361	S

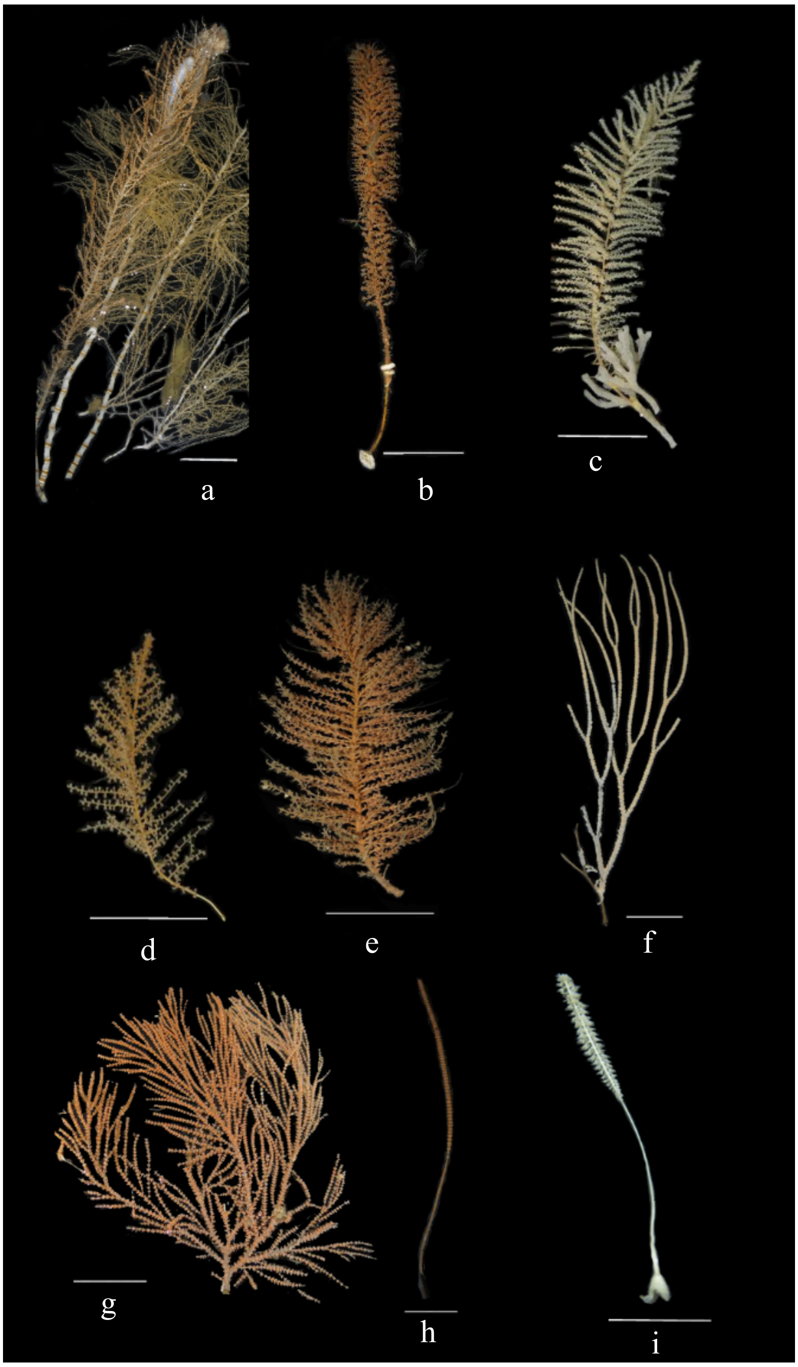
Supplementary Table S6

Morphotype	Species	Remarks
Unbranched morphogroup: Colonies are flagelliform; species included in this morphotype also have polyps distributed in whorls along the main stem of the colony.	*Onogorgia nodosa* (Molander, 1929)	Species allocated to several genera until Cairns and Bayer (2009) proposed the new genus Onogorgia[101]. This genus includes specimens with ascus body wall scales, a feature observable only under the microscope, making their identification rather difficult.
	Arntzia gracilis (Molander, 1929)	Originally described as *Primnoella gracilis*, this species was assigned to the new Antarctic genera *Arntzia*[102] due to significant differences with their closest genera, *Primnoella* and *Ainigmaptilon*. *Arntzia gracilis* is the only species included in the genera and it is easily recognizable. Its main features are the disposition of polyps in whorls which are fused basally, slender polyps with body sclerites aligned with the opercular ones, and, sometimes, not well-differentiated from body scales below, as they have a translucid appearance.
	Armadillogorgia Bayer, 1980	Two species are included in this genera *A. cyathella* Bayer, 1980 and *A. albertoi* Cerino and Lauretta, 2013. These authors conclude that specimens from this genus are not abundant; however, we cannot dismiss the possibility of having some specimens in our video footage, mainly because their general appearance can be confused with the other unbranched species. Upon closer inspection, their polyps lack opercular and marginal scales and have two perfect rows of more than forty sickle-like sclerites in the abaxial side.
	Primnoella Gray, 1858	Very controversial genus, for which different genera have been proposed since Bayer (1996)[103]. It differs from other unbranched species mainly in its sclerite properties such as disposition, size, ornamentations and their absence in the adaxial side, as well as the presence of non-fused polyps[104,105].
Grouped bamboo corals in the Family Isididae.		Family easily recognizable by their whitish, yellow-pale axis color and conspicuous white calcareous internodes alternating with dark proteinaceos nodes.

Supplementary Figure S1



Supplementary Figure S2



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Chapter 4

The role of gorgonian corals in shaping the diversity and composition of benthic communities

Corbera, G., Domínguez-Carrió, C., Ambroso, S., Grange, L., Corbera, J., Riera, JL., Gili, JM., The role of gorgonian corals in shaping the diversity and composition of benthic communities. Submitted

Introduction

Biodiversity plays an important role in maintaining and improving ecosystem functioning under constant conditions, thereby increasing ecosystem stability through time (Worm et al. 2006, Cadotte et al. 2012). High levels of biodiversity might be even more relevant in ecosystems that face greater environmental variability, since it provides an insurance against oscillations (Loreau et al. 2001). Habitats with a greater number of taxa may provide an ecological buffer to dramatic changes, owed to the differential response provided by each species to unexpected environmental variations (Allison 2004, Jactel et al. 2017). Similarly, increases in biodiversity have been reported to boost primary and secondary productivity, and hence the total biomass of the ecosystem (Cardinale et al. 2004, Balvanera et al. 2006). The enhancement of productivity observed in highly diverse communities is generally caused by the presence of more productive taxa (Fridley 2001) and a highly efficient consumption of resources owed to functional complementarity (Cardinale et al. 2006). Furthermore, the effective resources consumption witnessed in biodiverse habitats makes it more difficult for invasive species to thrive (Fargione and Tilman 2005). In this regard, several studies have demonstrated that highly diverse communities constitute a barrier to the settlement and growth of invader species (Levine 2000, Kennedy et al. 2002, Stachowicz et al. 2002).

In order to correctly manage ecosystems and to promote a more sustainable use of natural resources, it is important to understand the processes that underlie the maintenance of species richness and biological diversity. For instance, energy availability, expressed as temperature and net primary production (NPP), is a key environmental factor known to affect biodiversity (Wright et al. 1993, Allen et al. 2002). Habitats with higher temperature and net primary production generally host more species owed to greater speciation rates and food availability (Guégan et al. 1998, Allen et al. 2002). Similarly, habitat heterogeneity caused by structurally complex features (i.e. geological or biological), is also known to promote higher diversity through an increase in the number of ecological niches available (Mac Arthur and Wilson 1967, Bazzaz 1975, Tews et al. 2004, Vetter et al. 2010, De Leo et al. 2013). Geological structures such as valleys, ridges and submarine canyons are known to enhance spatial heterogeneity, at different scales, which in turn affects the number of species present in the area (Kubota et al. 2004, De Leo et al. 2013). In the same way, certain organisms are capable of creating three-dimensional structures that increase the spatial heterogeneity of the area at a local scale (Jones et al. 1994, Buhl-Mortensen et al. 2010). Through the creation of spatial heterogeneity, these organisms modify the habitat's biophysical conditions, and hence, promote the diversification of ecological niches in a given environment (Jones et al. 1994). Organisms that generate such structures are known as ecosystem engineers, since changes in the environmental conditions are mainly driven by the creation, modification or destruction of biotic and abiotic structures (Jones et al. 1994, 1997). Due to the modifications they cause in the physical environment, ecosystem engineers usually trigger changes in the species composition of the local assemblages (Crooks 2002). Depending on the engineer and the local conditions, this composition shift may either increase or decrease biodiversity (Crooks 2002, Freiwald et al. 2004).

In the case of autogenic ecosystem engineers, (i.e. those that change the environment via their own physical structures [sensu Jones et al. 1994]), increases in habitat complexity through structure addition may promote the creation of predator-free spaces (Borthagaray and Carranza 2007, Nagelkerken et al. 2008, Buhl-Mortensen et al. 2010, Gutiérrez et al. 2011). These newly formed areas are of upmost importance in ecological terms, since organisms can use them as spawning, nursery and settlement grounds (Beck et al. 2001, Gratwicke and Speight 2005). Mangroves and coral reefs can be considered examples of habitats formed by engineering species that are known to play an important role in the survival of juvenile fishes, crabs and shrimps (Gratwicke and Speight 2005, Nagelkerken et al. 2008, Corbera et al. 2019). Similarly, the habitat created by tropical trees and other autogenic engineers can be used as a settlement substratum by a rich group of organisms, such as orchids and bromeliads (Hundera et al. 2013). These organisms take advantage of either the hard substrate provided, or the different physical conditions experienced on top of the engineer structure (Jones et al. 1997, Gutt and Schickan 1998, Hundera et al. 2013). Biological structures can also cause indirect physical changes to the environment, which are mostly perceived as modifications in water hydrodynamics, soil composition or sediment fluxes, secondarily affecting organisms living at the site (Jones et al. 2007). In this sense, some engineers can increase sediment ventilation, nutrients and food availability (Vaughn and Hakenkamp 2001, Buhl-Mortensen et al. 2010, Gutiérrez et al. 2011) as well as provide shelter from the prevalence of unfavourable environmental factors such as non-optimal current speed or temperature (Dean et al. 1999, Hastings et al. 2007, Jones et al. 2010).

As a consequence of the outcomes stated, most autogenic ecosystem engineers have been observed to enhance biodiversity at the local scale (Dean et al. 1999, Freiwald et al. 2004, Idjadi and Edmunds 2006, Beazley et al. 2013, Hundera et al. 2013). Within these engineers, dense populations of certain marine benthic species, such as hard corals, sponges and mussels, have long been regarded to increase megafaunal, epifaunal and infaunal diversity (Gratwicke and Speight 2005, Borthagaray and Carranza 2007, Buhl-Mortensen et al. 2010, Beazley et al. 2013, Price et al. 2019).

One of the most important evolutionary responses of benthic sessile organisms is their tendency to develop patches where the spatial distribution of the organisms favours the capture of suspended particles, both by increasing the total contact surface area and by changing the hydrodynamic conditions between the colonies or individuals in the population. Empirical studies have shown that colonies of the same species generally do not merge or cover each other (Buss and Jackson 1981). Therefore, the formation of monospecific patches not only lowers competition (Best and Thorpe 1986) but also improves capture rates among the colonies of the species concerned. Experiments on alcyonarians (MacFadden 1986), actinians, and corals (Sebens et al. 1997) have shown that particle capture rates vary among colonies of different sizes within the population. This in turn gives rise to small-scale distribution patterns mainly determined by the optimum distance between colonies or individuals in order to maximise food intake (Eckman and Duggins 1993). For these meadow-forming organisms, the capture of suspended particles at higher flow rates is optimised in denser patches than in stands of more widely spaced colonies, while smaller colonies benefit from the fast flows found at the outer edges of those patches (Anthony 1997). Large assemblages of suspension feeders can deplete food sources under low flow conditions (Buss and Jackson 1981). However, because fast flow is generally the prevailing condition in these habitats, enhancement of feeding among neighbours occurs (Okamura 1988). Overall, populations of sessile species create a trophic habitat that not only favours their permanence but also generates new ecological niches for many other species that find food and protection from predators within the meadows that these organisms form (Jones et al. 1994, Buhl-Mortensen et al. 2010, Gutiérrez et al. 2011). However, only a few studies consider the ways gorgonians can affect the diversity of the surrounding benthic organisms, and instead they typically focus on meio- and macrofauna (Buhl-Mortensen and Mortensen 2005, Cerrano et al. 2010, Curdia et al. 2015). This lack of knowledge persists, regardless of the role octorals have in creating dense meadows of non-reef-forming corals that potentially promote physical and biological changes to the surrounding habitat (Bullimore et al. 2013). Although there is convincing evidence that suggests an increase in megafaunal diversity should occur with the presence of dense gorgonian assemblages, very little empirical data are available.

Jones et al. (1994) postulated that the effects of habitat modification depend on the density and activity of the engineering organism. Therefore, it would be expected that the biophysical effects of gorgonians should be positively correlated with their density, which in turn could be used as an indicator of the community environmental status. In this regard, the present study aims to understand the way in which a gorgonian population affects the diversity of the surrounding megafaunal species, by characterising gorgonian assemblages dwelling on two very contrasting continental shelves. Based on the ideas introduced by Jones et al. (1994), this study expects to find (1) an increase in the species richness and diversity of the surrounding fauna with increasing gorgonian density, (2) an increase in the species richness and diversity of the surrounding fauna with increasing gorgonian size and (3) a shift in the taxonomic composition of the associated community with increasing gorgonian density.

Materials and methods

Study area

Remotely Operated Vehicle (ROV) dives used in the present study were performed over the continental shelves of two very contrasting regions: the Gulf of Lion (NW Mediterranean Sea) and the Weddell Sea (Antarctica). The Mediterranean site corresponds to the narrow continental shelf in front of Cap de Creus, located in the southernmost part of the Gulf of Lion (Fig. 1a). The region is characterised by the presence of a submarine canyon, whose head is found just a few kilometres offshore. ROV dives were performed in a depth range of 95-110 m, where large shells and exposed bedrock are found mixed with fine-grained sediments. The waters of the Gulf of Lions receive important nutrient-rich freshwater and sediment inputs from the Rhone River, which stay enclosed inside the gulf due to the presence of the Northern Current, flowing southward along the slope (Arnau et al. 2004, Palanques et al. 2006).

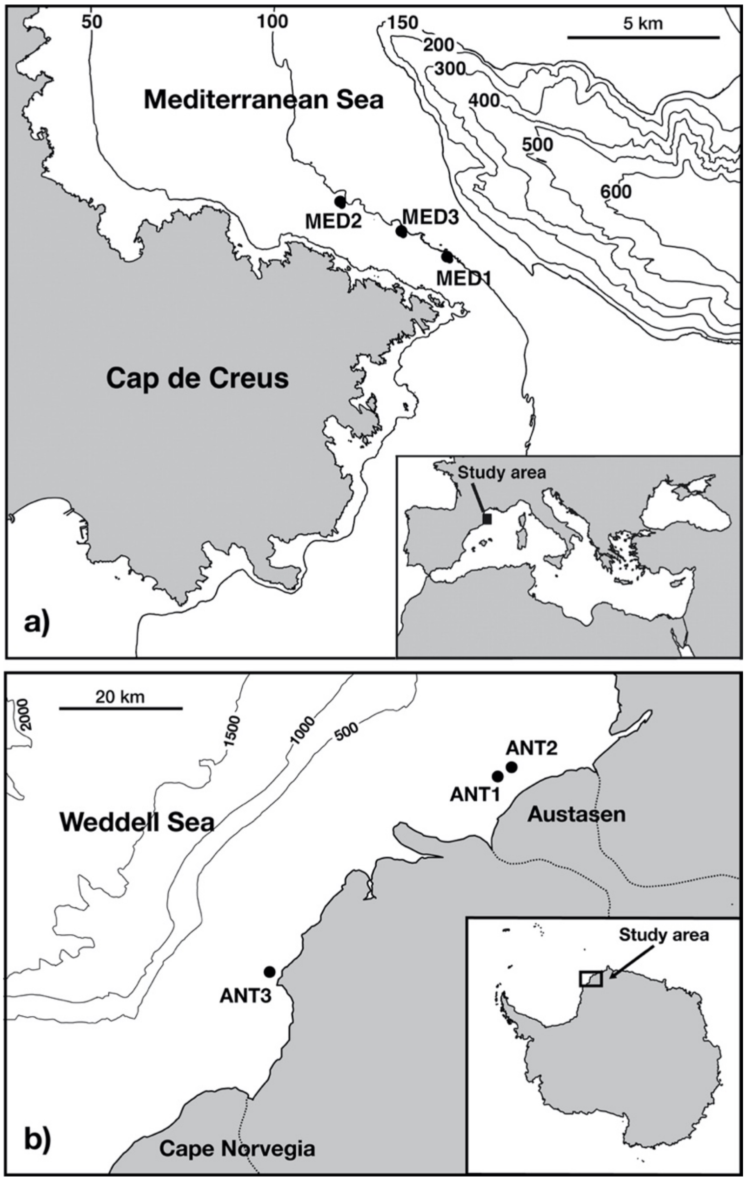

Fig. 1 Location of the ROV dives evaluated for this study on the continental shelves of (a) Cap de Creus, NW Mediterranean and (b) the Weddell sea, Antarctica. The exact coordinates of each dive are provided in Table 1

Table 1. Geographical position and depth range of each ROV dive performed in this study.

Dive	Location	Date	ROV	Geographical position		Depth (m)	
				Start	End	Min.	Max.
MED1	Mediterranean Sea	Jul ’12	Nemo ROV	42°20’10”N, 3°19’44”E	42°20’8”N, 3°19’32”E	95	97
MED2		Jul ‘12		42°21’36”N, 3°16’36”E	42°21’25”N, 3°16’37”E	96	101
MED3		Jul ‘12		42°20’48”N, 3°18’33”E	42°20’30”N, 3°18’26”E	95	111
ANT1	Weddell Sea	Mar ‘11	Sperre Sub-Fighter	70°54’35”S, 10°19’18”W	70°54’44”S, 10°19’19”W	210	212
ANT2		Mar ‘11		70°54’37”S, 10°22’2”W	70°54’36”S, 10°16’31”W	186	192
ANT3		Dec ‘03	Cherokee ROV	71°7’16”S, 11°26’54”W	71°7’19”S, 11º27’25”W	119	180

The cold northern winds that characterise the winter period are responsible for the formation of dense water masses that sink through the submarine canyon (Millot 1999, Canals et al. 2006, Palanques et al. 2006), transporting large quantities of sediment and organic matter from the shelf towards deeper regions (Palanques et al. 2006, Ulses et al. 2008).

The Antarctic study site is located in the Weddell Sea, between the Antarctic Peninsula and Cape Norvegia (Fig. 1b). An ice shelf permanently covers a large part of the southern region of this Sea, thus favouring a significant input of freshwater from nearby ice sheets (Beckmann et al. 1999). The Weddell Sea presents a crescent-shape continental shelf that gets narrower on the edges. Although the maximum depth of the continental shelf is 400-500 m east of Cape Norvegia, all ROV dives performed for this study were located in front of Austasen, at depths between 119 and 212 m, on areas covered by mixed soft substrata.

Study species

The benthic communities of both study areas are characterised by the presence of well-structured gorgonian populations. Besides the differences in species composition among areas, gorgonians constitute the dominant ecosystem engineers in both sites. The continental shelf of Cap de Creus exhibits dense patches of the octocoral *Eunicella cavolini* (von Koch 1887), which primarily develops in sub-outcropping and outcropping rocky areas in depths of 80-120 m (Dominguez-Carrió 2018). These shelf-dwelling *E. cavolini* colonies are characterised by their two-dimensional fan-shaped structure and their characteristic orange colour (Fig. 2a, b). There are only a few studies regarding the ecology and distribution of this gorgonian species, especially at shelf depths, but densities over 18 col·m^{-2} have been reported from the west coast of Corsica (Velimirov and Weinbauer 1992). It is usual to observe high percentages of colonies with heights of 10 cm or less in *E. cavolini* assemblages, sometimes representing an excess of 50% of the total population (Velimirov and Weinbauer 1992).

In contrast, one of the most abundant gorgonian species on the continental shelf of the Weddell Sea is *Thouarella variabilis* (Wright and Studer 1889), with densities reaching 7 col·m^{-2} (Ambroso et al. 2017). Colonies from this species are also orange in colour, but in contrast to *E. cavolini*, they are formed by a unique axis often with a few ramifications (Taylor et al. 2013). Small verticillate branches that bear polyps arise from the main axis and ramifications, giving *T. variabilis* a brush-like morphology (Fig. 2c, d). The size structure of this gorgonian species is still poorly constrained.

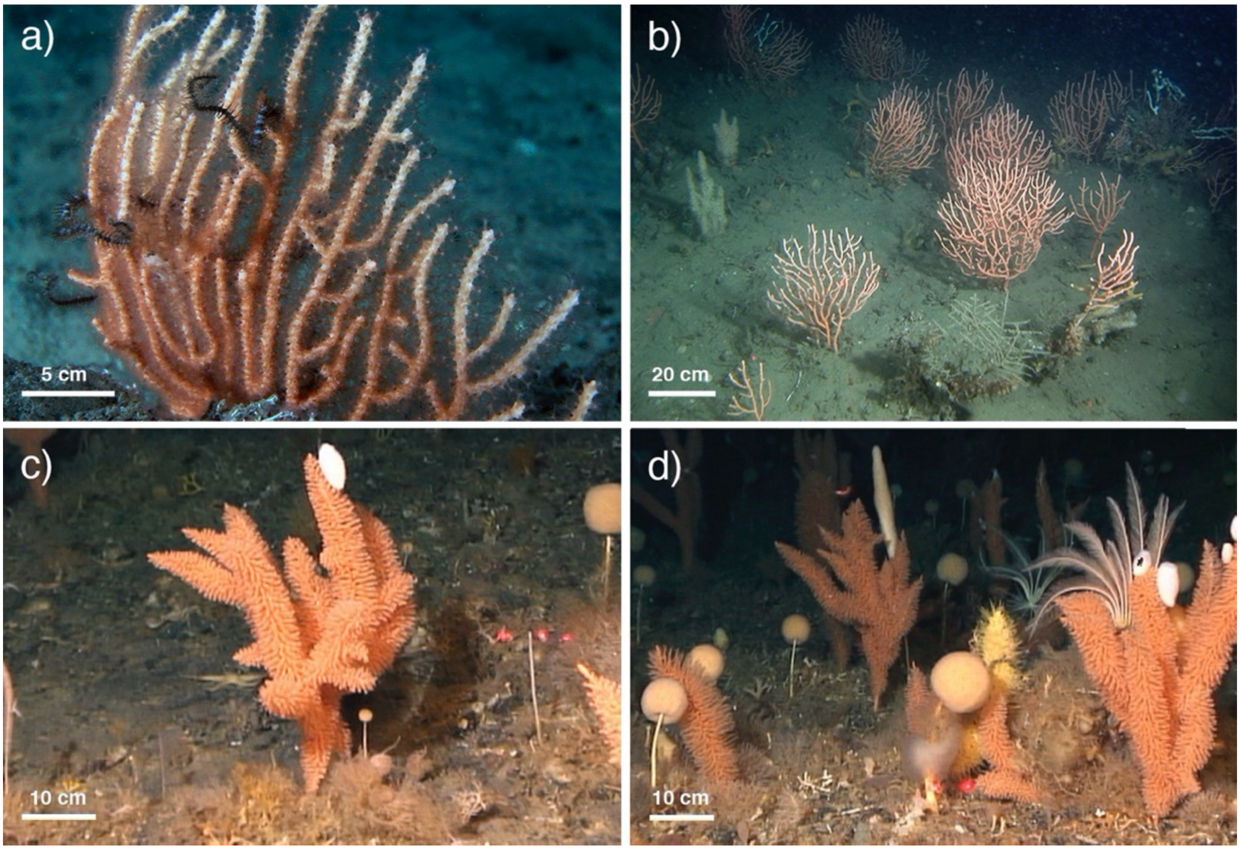

Fig. 2 Target gorgonian species, *Eunicella cavolini* and *Thouarella variabilis* which dominate the benthic assemblages in the study areas of the Mediterranean and Weddell Sea respectively

Data acquisition and image processing

Seafloor video images were recorded during three independent research expeditions. Footage from the Mediterranean Sea was obtained during the cruise Indemares 6 on board of the R/V “Garcia del Cid” in July 2012, as part of the Life+ Indemares project. Images were recorded by means of Nemo ROV, equipped with an HD video camera (1920×1080 pixels). Footage from Antarctica was obtained during two separate surveys on board of the R/V “Polarstern” in December 2003 (ANT-XXI/2) and in March 2011 (ANT-XXVII/3). For metadata and seabed videos of ANT-XXI/2, see https://doi.org/10.1594/PANGAEA.770359, for ANT-XXVII/3 see https://doi.pangaea.de/10.1594/PANGAEA.897581 and for cruise reports see Arntz and Brey (2005) and Knust et al. (2012). Images were recorded by means of an HD video camera (1920x1080 pixels) mounted on the ROV Cherokee and Sperre SubFighter 7500 DC, respectively. All ROVs were equipped with parallel laser beams that projected two laser points over the seafloor at a fixed width. Laser points were used to give spatial scale to the video footage, so the area to be analysed could be estimated and gorgonian height measured.

Three ROV dives from each geographical location were used in this study. Portions of 350 m long were selected matching the following criteria: (1) reduced number of bad visibility sequences, (2) distance between the ROV and the seabed kept as constant as possible and (3) laser beams visible at all times. Overall the total distance available for quantitative analyses was 2100 m. In order to avoid loss of video footage due to oscillations in ROV movement, a transect width of 30 cm was selected for all transects. Other ROV studies also use such transect width to evaluate the density of megabenthic species (e.g. Grinyó et al. 2016). The area analysed for each transect was, therefore, 105 m^2, adding up to 630 m^2 overall.

The location of each dive was estimated by means of a USBL transponder mounted on the ROVs, which gave an accurate geographic position every 3 to 20 seconds. After projecting the ROV positioning data using the open source Geographic Information System software Quantum GIS 2.2.0 (QGIS Development Team 2016), all outlier points were removed leaving a smooth geo-referenced transect. Outliers were identified as those points located away from the main path followed by the vehicle and for which, cruising speed would have had to be increased considerably to follow such trajectory. All video transects were divided into five sections in which ROV speed was calculated using the vehicle’s travelled distance and the time used to cover such distance. Following the formula shown in Corbera et al. (2019), the ROV velocities of each fragment were used to calculate the position of each observed organism along the dives.

Video analysis

Video images were edited using the software Final Cut Pro 7 (Apple Inc), removing those sections where the ROV was kept static due to sample collection or close-up image recording. Sequences displaying low quality footage due to inappropriate altitude of the ROV or sediment resuspension were also identified and removed. Removing non-valid footage left a total length of 1958 m of analysable sequences. All the benthic megafaunal invertebrates observed within a section of 30 cm across the path of the ROV were annotated and identified to the lowest possible taxonomic level. When the identification to species or genus level was not possible, the organisms were designated within higher taxonomic groups or defined as morphospecies (e.g. White encrusting sponge). Substratum type was also visually determined, following a simple classification scheme: soft or hard substrata.

Density and abundance of all megafaunal organisms were calculated by dividing each ROV transect into 2 m^2 sampling units (SU) of 6.66 m long fragments. This SU area was chosen in accordance to Weinberg (1978), who determined the minimum sampling area to work with invertebrate fauna in the Mediterranean Sea. Only those SU containing at least one organism were considered in the subsequent statistical analyses (294 SU in total, 156 corresponding to the Mediterranean and 138 to the Weddell Sea).

The height of each measurable gorgonian was estimated by means of still images acquired from the video footage when the parallel laser beams crossed the base of each colony. Stills were processed using the image software Macnification 2.0 (Orbicule, Inc.), in which the length of the gorgonians' principal axis was measured by following its path from the base to the tip of the colony. These measurements were then used to calculate the average gorgonian size in each SU. Overall, 1218 colonies of *E. cavolini* and 361 of *T. variabilis* were measured.

Statistical analyses

The density of each gorgonian species was plotted against their average size in all SU and the independence of both variables was tested using Pearson correlations and variance inflation factor (VIF) tests. Values obtained for both analyses were below the suggested threshold ($r<0.7$) ($VIF>0.1$), denoting a non-significant covariance between the two variables. Species richness and diversity of each SU (excluding the structural gorgonian species *E. cavolini* and *T. variabilis*) were calculated using the R package *vegan* 2.5-2 (Oksanen et al. 2018). Species richness was measured as the total number of species or morpho-species present in each SU, while alpha diversity was calculated using the exponential of Shannon index (exp*H'*), which consists on a linearization of the Shannon-Weiner diversity index. Jost et al. (2010) suggests exp*H'* as an alternative to the traditional Shannon-Wiener index, with the argument that such linearization considers the relative abundance of the species and at the same time it keeps constant the relevance of every new species added to the community.

Spearman rank correlations were used to assess the relationship between gorgonian density and megafaunal species richness and diversity. P-values were calculated using the algorithm AS89, present in the basic R environment (R Core Team 2018). Results were plotted displaying gorgonian density values per SU versus species richness and megafaunal diversity along transect length. A line indicating substrate type was added below the X-axis to visually evaluate the possible effects of the substratum type over such relationships. Spearman coefficient values (ρ), which indicate the degree of association between two variables and evidence whether a relationship is positive or negative, were added to each plot.

To examine the potential influence that density and average size of the gorgonians may have on the associated species richness and diversity, linear regression models were generated on pooled data using the Ordinary Least Squares (OLS) method with the function *lm* of the R environment (R Core Team 2018). In these regressions, average gorgonian size and log-transformed gorgonian density was correlated to megafaunal species richness (S) and diversity (exp*H'*). SU lacking gorgonians were not considered in the linear models that used size as independent variable. Regression lines were plotted only when a significant correlation was observed between the variables in the linear regression models (p-value < 0.05). Due to the absence of gorgonians in many SU, in the case of average gorgonian size, the individual transect regressions could not be performed and thus, only the overall regression lines of each region were plotted.

Potential differences in community composition of the associated fauna with increasing levels of gorgonian density were evaluated by means of a Principal

Coordinates Analysis (PCoA), performed using the *cmdscale* function from the R package *stats* (R core team 2018). For each region, the PCoA was computed over Bray-Curtis dissimilarity matrix on square-root transformed density data. Gorgonian density values were divided into three different levels (low, medium, high) in each region, using the Jenks natural breaks optimisation. To statistically assess changes in community composition with increasing degrees of gorgonian density, a unifactorial permutational ANOVA test and pairwise comparisons were performed using the *adonis* and *pairwise.adonis* functions from the R packages *vegan* 2.5-2 and *pairwiseAdonis* 0.3 (Oksanen et al. 2018, Martínez Arbizu 2019).

Results

General findings

Mediterranean Sea

A total of 7438 organisms, representing 74 different taxonomic groups, were identified in 156 SU from the Cap de Creus continental shelf. 66% of all organisms could be identified to species or genus level, 4% were included in broader taxonomic categories and 30% were considered as morphospecies. The most abundant species was the gorgonian *Eunicella cavolini*, which accounted for 34.8% of the total number of organisms. Other commonly observed species were the sponge *Suberites syringella*, (11.8%), the soft coral *Alcyonium palmatum* (10.6%) and the pennatulacean *Pteroides spinosum* (6.5%). Species richness shows a maximum of 22 species in a single SU of MED1 and an average value of 8.1 ± 4.9 species per SU. The average diversity (exp*H'*) value in this region is 5.9 ± 3.4, with a maximum of 18 observed in MED1. Considering all dives, *E. cavolini* had an average density per SU of 6.08 ± 5.86 col m^{-2}, with a maximum density of 32.5 col m^{-2}. Colonies of *E. cavolini* presented an average size of 7.04 ± 5 cm, with the tallest colony measuring just over 30 cm, and the smallest around 0.5 cm tall. Substrate was mainly composed of mixed medium sands and biogenic gravels, except for transect M1, which was characterised by the presence of several areas with coarse gravels and pebbles (56%) and sub-outcropping and outcropping rocks (44%).

Weddell Sea

A total of 6390 individuals belonging to 109 different taxa were identified in 159 SU. 41% of all organisms were identified to species or genus level, while 13% were included in higher taxonomic groups and 46% had to be classified as morpho-species. The most abundant species was the bryozoan *Melicerita obliqua* followed by the gorgonian *Thouarella variabilis* and the demosponge *Stylocordyla chupachups*, accounting for 19.4%, 15.4% and 5.9% of the total number of organisms, respectively. Species richness showed a maximum of 27 species in a single SU of ANT3 and an average value of 12.6 ± 5.8 species per SU. The average diversity (exp*H'*) value in this region was 8.5 ± 4.2, with a maximum of 18.6 observed in ANT3. Considering all dives, *T. variabilis* showed an average density of 4.39 ± 3.803 col m^{-2}, reaching a maximum value of 19 col m^{-2}. This gorgonian had an average size of 21.08 ± 8.54 cm, with some organisms reaching heights of up to 45 cm. The smallest colony recorded, measured 7.28 cm. The substrata in these transects was generally composed of sands and gravels with the sporadic occurrence of small pebbles.

Influence of gorgonian density on megafaunal diversity and community composition

According to the results of the Spearman rank correlations, gorgonian density had a significant (p-value < 0.01) and positive correlation with the associated species richness (Fig. 3). Although this correlation was significant in all 6 dives, its magnitude varied slightly in each dive. In the case of the Mediterranean region (Fig. 3a), the Spearman coefficient (ρ) showed a range of values between 0.38 and 0.59. In dive MED2, where ρ values where the lowest, some asynchrony between variables could be observed in the plot. However, most of the large density peaks correlated perfectly with those areas where the number of species was higher. A similar pattern was detected in the Antarctic dives, yet with even higher Spearman coefficient values than those witnessed in the Mediterranean. The ρ values in the polar region ranged from 0.48 to 0.91 (Fig. 3b). Furthermore, in the case of ANT3, every change in gorgonian density was perfectly mirrored by a corresponding variation in species richness, showing an almost total correlation between these two variables.

The exponential of Shannon diversity index (exp*H'*) showed a very similar pattern, with its correlation to gorgonian density being positive and significant in all 6 dives (p-value < 0.05).

In the Mediterranean region ρ values ranged from 0.26 to 0.61 (Fig. 3a), whereas Antarctic dives presented higher correlation values, ranging from 0.57 to 0.93 (Fig. 3b). Dives MED1 and MED3 had a lower fit of gorgonian density to exp*H'* than they had to species richness. In the case of Antarctic dives, they all presented higher Spearman coefficient values when assessing exp*H'* as dependent variable, instead of species richness (Fig. 3b).

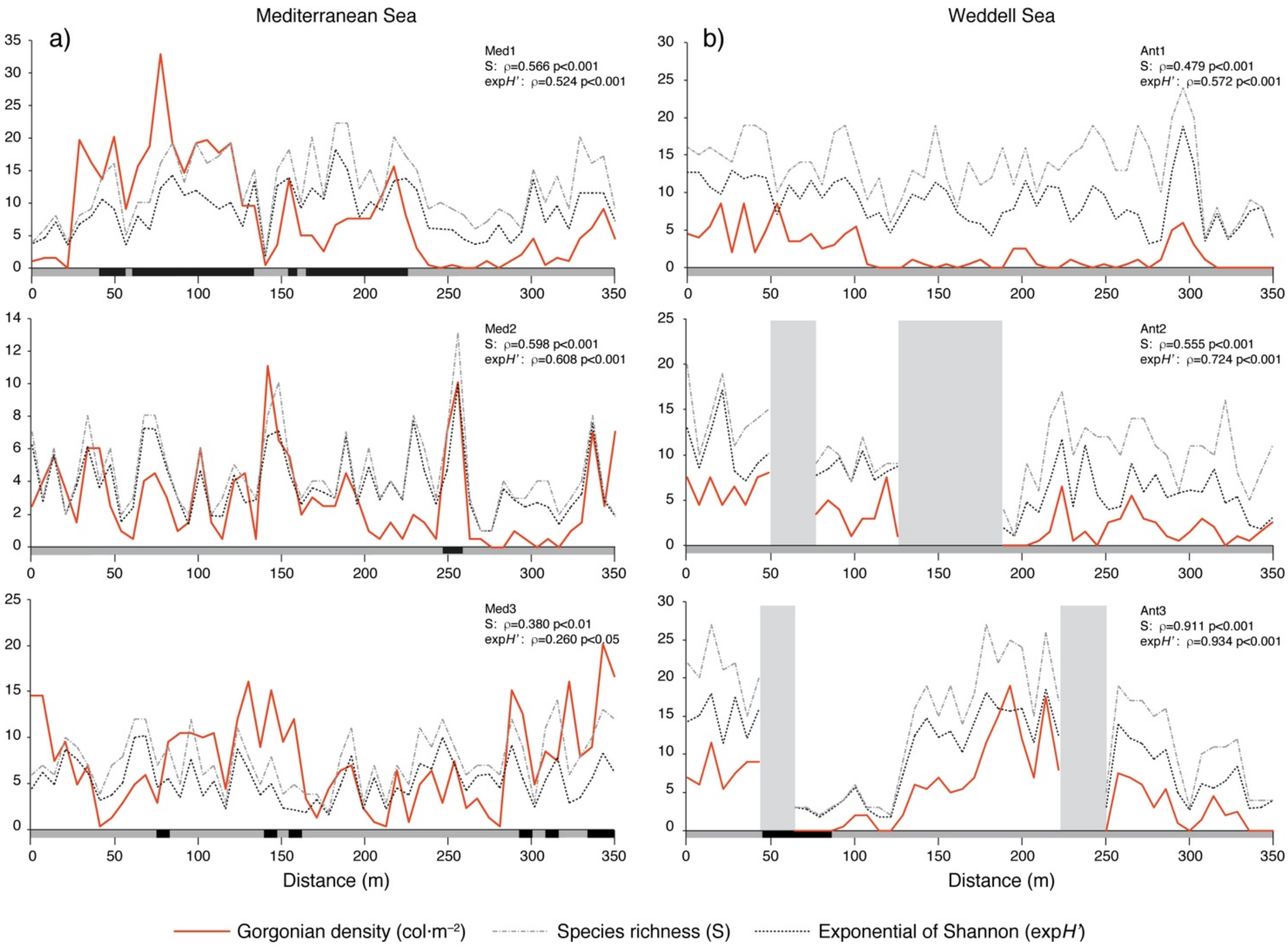

Fig. 3 Gorgonian density (col m^{-2}) correlation to species richness (S) and diversity (expH') along each ROV dive performed in the Mediterranean (a) and Weddell Sea (b). Substrate type is shown as a color band displayed at the bottom of each plot: soft substratum (grey) and hard substratum (black). Grey vertical bars indicate sections of the dives with low quality footage, not used in the analyses.

The higher proportion of hard substrata observed in the Mediterranean dives did not seem to affect the correlation between the studied variables. Although MED1 presented higher gorgonian densities on hard substrata, the peaks observed for species richness and megafaunal diversity still matched those of gorgonian density (Fig. 3a).

Results of the linear regression analyses showed that the relationship between gorgonian density and species richness in the Mediterranean region follows that of a linear model ($p < 0.01$; Table 2), with the number of species per sample increasing rapidly at low densities to stabilise at around 10-12 species per SU above 10 col m^{-2} thus, following a logarithmic curve (Fig. 4a).

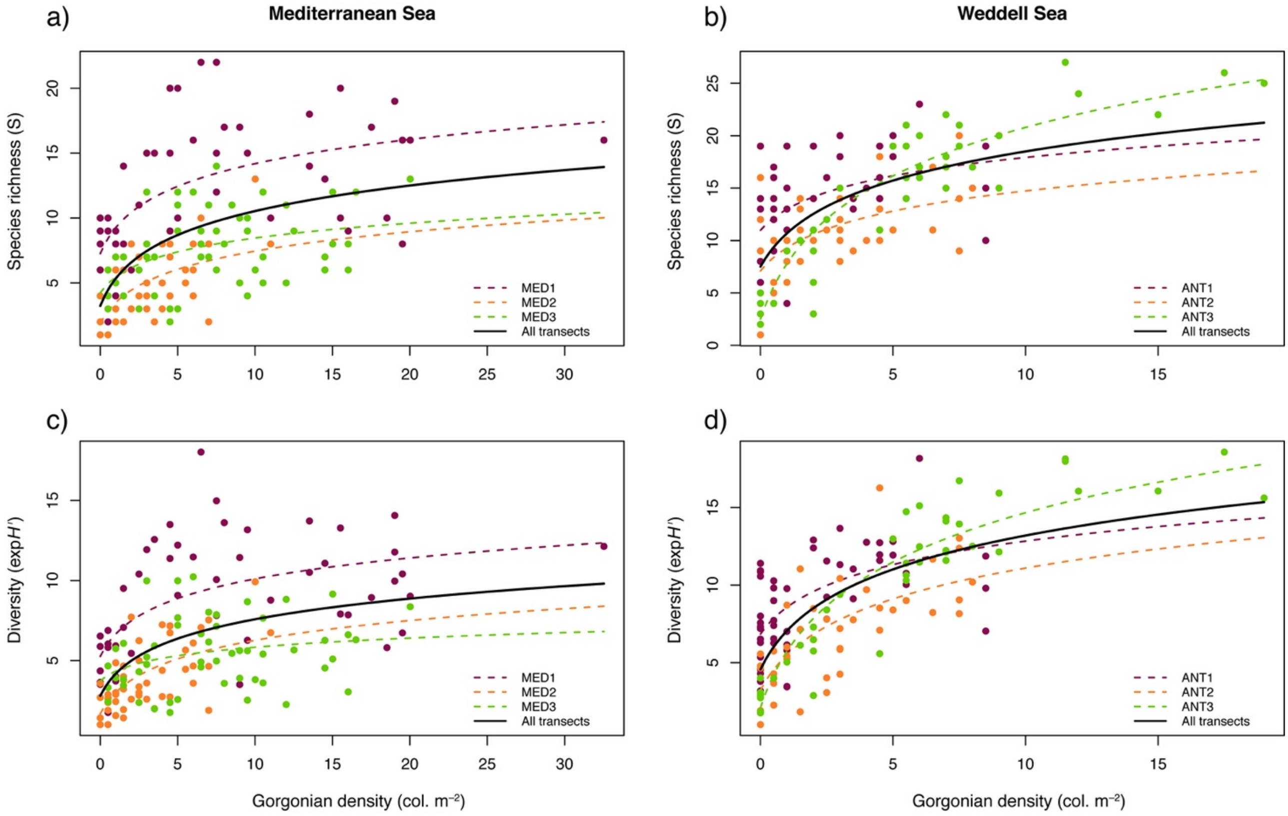

Fig. 4 Linear regression models based on log-transformed gorgonian density, species richness (S) and diversity (expH') for each dive and the entire study area in the Mediterranean (a, c) and Weddell Sea (b, d)

The Determination coefficient (R^2) values in the different dives varied from 0.153 to 0.402 and all together presented an overall R^2 of 0.301 (Table 2). In the Antarctic region a significant relationship between gorgonian density and species richness also occurred, following a similar trajectory to that of the Mediterranean, but with a higher slope and stabilising above 10 col m^{-2} with a maximum of 16-20 species per sample (Fig. 4b). Antarctic dives showed higher R^2 values, ranging from 0.221 to 0.882 and leading to an R^2 of 0.459 for the whole region (Table 2).

Table 2 Linear regression model results of gorgonian density and size against megafaunal species richness (S) and diversity (expH').

		res	d.f.	F	R^2	p-value
Density						
S	ANTall	4.253	136	117.1	0.4586	<0.0001
	ANT1	4.019	51	15.75	0.221	<0.001
	ANT2	3.159	38	19.16	0.3177	<0.0001
	ANT3	2.714	43	330.9	0.8823	<0.0001
	MEDall	4.087	154	67.73	0.301	<0.0001
	MED1	4.205	49	25.6	0.3289	<0.0001
	MED2	1.88	51	35.94	0.4019	<0.0001
	MED3	2.789	50	10.19	0.1526	<0.01
expH	ANTall	2.808	136	165.9	0.5462	<0.0001
	ANT1	2.557	51	29	0.35	<0.0001
	ANT2	2.418	38	34.81	0.4644	<0.0001
	ANT3	1.824	43	346.8	0.8871	<0.0001
	MEDall	2.933	154	56.42	0.2634	<0.0001
	MED1	3.053	49	23.7	0.3122	<0.0001
	MED2	1.543	51	36.45	0.4053	<0.0001
	MED3	2.185	50	4.11	0.0575	<0.05
Size						
S	ANTall	3.678	61	15.13	0.1856	<0.0001
	MEDall	5.612	92	3.86	0.0535	0.053
expH	ANTall	2.852	61	18.25	0.2177	<0.0001
	MEDall	3.871	92	2.47	0.0156	0.119

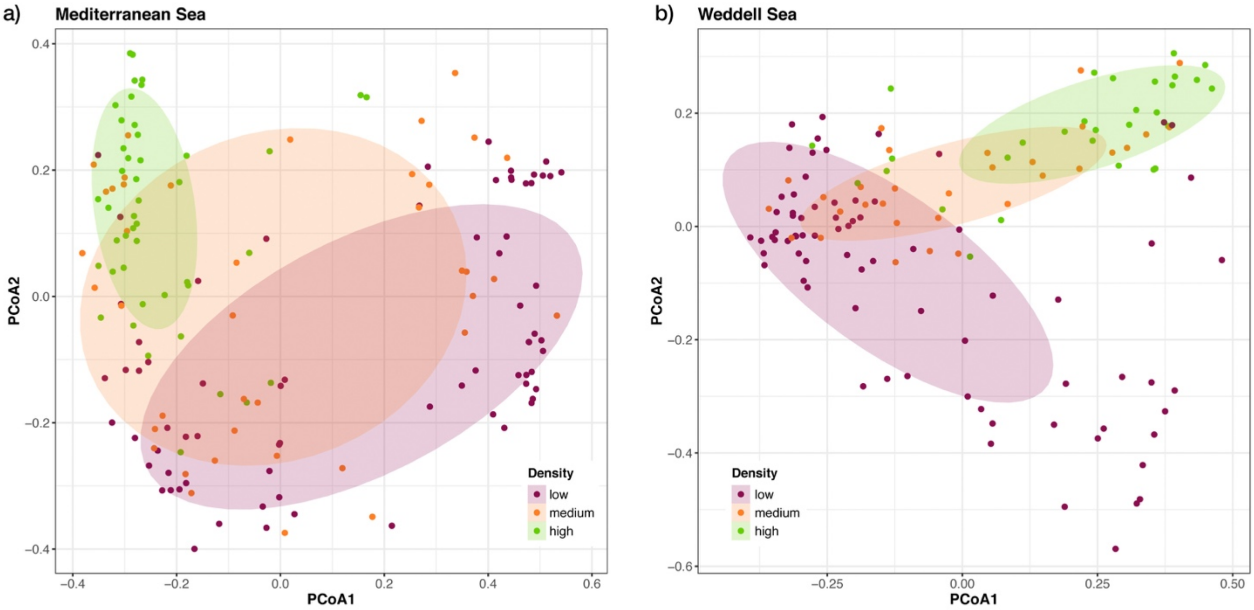

Fig. 5 Principal coordinates analysis (PCoA) plots of axes 1 and 2 performed on a Bray-Curtis dissimilarityvmatrix based on log-transformed density data of the taxa identified in the Mediterranean (a) and Weddell Sea (b) study areas. Colour coding of the sampling units (SU) indicate their gorgonian density level defined by the Jenks natural breaks optimisation

This exact situation was also observed for the exponential of Shannon diversity index. All linear models were statistically significant, showing a fast increase of diversity at low gorgonian densities and stabilising at ~10 col m^{-2} with maximum exp*H'* values of 7–10 in the Mediterranean and 13–15 in Antarctica ($p < 0.05$; Table 2 and Fig. 4c, d). The R^2 in the Mediterranean dives ranged between 0.057 and 0.405, displaying an R^2 of 0.263 for the whole region (Table 2). In contrast, the Weddell Sea models presented higher R^2 values, varying from 0.350 to 0.887 among the ROV dives and showing an R^2 of 0.546 for the entire region (Table 2).

The ordination of the Mediterranean and Antarctic SU in a reduced space through a PCoA is given in Figure 5. In both cases, the percentage of variance explained by the two first axes, was around 20-25%. Furthermore, the ordinations of both regions presented a significant shift (P-perm < 0.001) in the composition of the associated community as gorgonian density increased (PERMANOVA tests, Table 3), with pair-wise comparisons being also significant between all density levels (p-perm < 0.001).

Table 3 Permutational multivariate analysis of variance (PERMANOVA) based on square-root transformed density data of all the taxa identified in each region within the different gorgonian density levels, defined by the Jenks natural breaks optimisation.

	Df	Sum of Sqs	R^2	F	Pr(>F)
Mediterranean Sea					
Density	1	5.877	0.1113	19.3	0.001
Residual	154	46.892	0.8886		
Total	155	52.769	1.0000		
Weddell Sea					
Density	1	4.006	0.0829	12.294	0.001
Residuals	136	44.319	0.9171		
Total	137	48.325	1.0000		

Pairwise multilevel comparison	Df	Sums of Sqs	R^2	F	p-value	p-adj.
Mediterranean Sea						
low vs high	1	5.9619	0.1516	20.3754	0.001	0.003
low vs medium	1	1.0977	0.0297	3.3456	0.001	0.003
high vs medium	1	1.9993	0.0774	6.9698	0.001	0.003
Weddell Sea						
med vs high	1	1.2767	0.0687	4.3541	0.001	0.003
medium vs low	1	1.4625	0.0390	4.3084	0.001	0.003
high vs low	1	3.8548	0.1019	11.9143	0.001	0.003

Therefore, besides generally supporting a higher number of species, patches with high coral density also appeared to have a more stable community structure, as shown by the lower dissimilarity between SU (Fig. 5). In contrast, the degree of dispersion of those SU located in areas with low coral density was larger, indicating that their species composition displays a greater variability.

Effects of gorgonian size on megafaunal diversity

According to the OLS analysis, species richness and diversity did not show any statistically significant correlation with average gorgonian size in the Mediterranean region ($p > 0.05$; Table 2 and Fig. 6a, c). In contrast, a positive and significant correlation ($p < 0.001$) was observed in Antarctica between average gorgonian size and both variables evaluated (Fig. 6b, d), with a better fit in the case of diversity ($R^2 = 0.213$; Table 2). The highest number of species and diversity values per SU were found in areas with average coral heights between 23 and 30 cm.

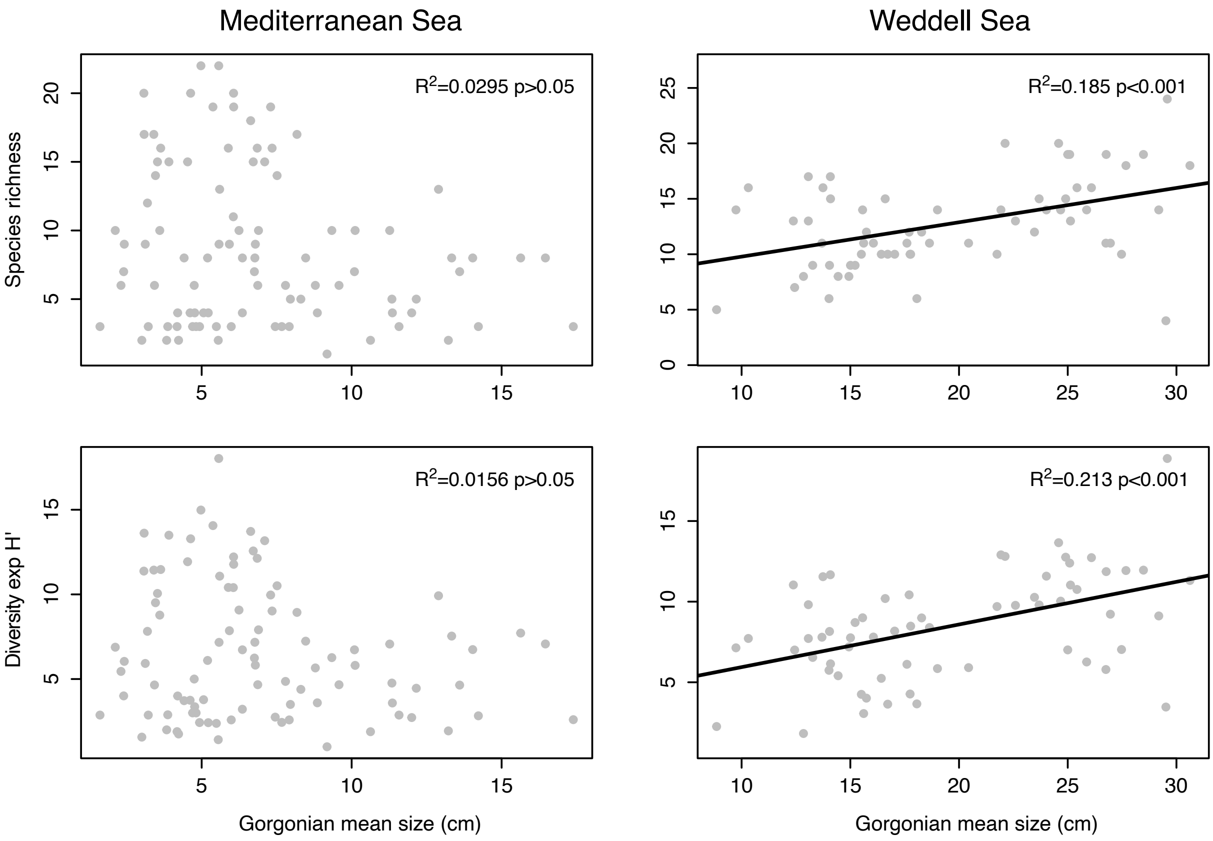

Fig. 6 Linear regression models based on average gorgonian size, species richness (S) and diversity (expH') in the Mediterranean (a, c) and Weddell Sea (b, d) study areas

Discussion

Influence of gorgonian density and size on the diversity and community composition of the associated benthic taxa

Organisms that create three-dimensional structures can be considered autogenic engineers and, in some cases, due to the positive changes that these organisms produce on the abiotic factors (e.g. lower current velocities, increases in sedimentation rates, protection from high temperatures, higher food availability), they can also act as foundation species (Jones et al. 1994, Dean et al. 1999 Gutiérrez et al. 2011). According to Jones et al. (1997), it must be assumed that the higher the density of these organisms, the stronger changes produced in the environment. Therefore, abundant engineering organisms would result in enhanced habitat heterogeneity, stress amelioration and more predator-free spaces, which ultimately would promote species richness and diversity.

In line with the theoretical development of the ecosystem engineer concept, results from the present study shows that species richness and biodiversity are positively correlated with gorgonian density in both the Mediterranean and the Weddell Sea. The pattern observed in these highly contrasting regions is very similar, even though they are dominated by two gorgonian species (*E. cavolini* and *T. variabilis*) with different branching morphologies. However, changes in the variance explained both by the Spearman rank correlations and the linear regression models did occur. In the case of the Weddell Sea, the models had a slightly better fit than in the Mediterranean (i.e. higher ρ and R^2 values). Such differences could be caused by the strong human pressure that has been exerted on Mediterranean benthic assemblages, as is the case of Cap de Creus where artisanal fishery has been developed for many decades (Gómez et al. 2006). In this area, some of the methods used are long-lines and trammel nets, which exert an effect on benthic organisms, especially gorgonians and corals due to their fragile structure (Fosså et al. 2002, Althaus et al. 2009, Sampaio et al. 2012, Pham et al. 2014). Warwick & Clarke (1993) observed that increasing levels of disturbance could cause higher variability in species diversity. Therefore, such fishing methods and their frequent use in the Mediterranean shelf areas might explain the lower R^2 values observed in this region.

A point in common regarding the influence of gorgonian density on diversity between the Mediterranean and Antarctic regions is that the logarithmic pattern that the linear model follows considering all dives, plateaus at ~10 col m^{-2} in both regions. Beyond this value, increases in gorgonian density do not suppose a significant change in species richness or diversity, which suggests that the diversity enhancing effect provided by the presence of these structuring organisms diminishes after reaching a certain density threshold. Furthermore, knowing the minimum gorgonian density that a coral garden needs to have in order to maximise the diversity of the associated community is fundamental for conservation, management and restoration purposes.

Besides the effects on diversity, increasing gorgonian density was also observed to promote changes in the taxonomic composition of the associated community, possibly since they allow for the settlement and growth of species that otherwise would be less abundant or even absent in such area. This situation occurs because, in the same way as other ecosystem engineers that act as foundation species, by regulating and stabilising ecosystem processes dense gorgonian meadows create locally stable conditions for other species (Dayton et al. 1972, Ellison et al. 2005).

It is important to highlight that gorgonian density is not the only factor that can benefit other taxa. Hard substrata, such as outcropping rocks, are also known to enhance species diversity through an increase in the heterogeneity of the region and space for larval settlement (MacArthur and Wilson 1967, Santín et al. 2018). The presence of this type of substratum could be the reason why the recorded values of species richness and diversity kept high in some parts of MED1, even though gorgonian density values were low. Overall, it could be perceived that diversity followed the trends of gorgonian density, with oscillations of both values in close synchrony, reaching higher peaks on hard substrata when compared to soft substrata (Fig. 3).

In the present study, gorgonian colony size has also been identified as a factor that can influence species richness and diversity. However, gorgonian density was observed to be more important at promoting higher diversities in both regions (i.e. better model fitting) and especially in the Mediterranean, where no correlation was observed when assessing the influence of gorgonian size. This could be caused by the limitations of the measurements used here (average gorgonian size per SU), since areas with high recruitment rates would show lower average sizes even if the overall structural complexity were high. Therefore, other measurements such summing the size of all the gorgonians in a SU might be a better approach to account for structural complexity. In fact, from Jones et al. (1994) and Curdia et al. (2015) view, it is very clear that areas combining high densities and large sizes would empower diversity in a more profound way. Nonetheless, although gorgonian size was observed to significantly affect species richness in the study performed by Curdia et al. (2015), the authors focused only on macrofaunal species, not megafauna. Therefore, gorgonian size may be a more relevant factor promoting species diversity, at a different scale than that analysed in this project.

Gorgonians as key organisms for ecosystem conservation and restoration

In most seas, gorgonians and other shelf-dwelling fauna are increasingly being affected by anthropogenic disturbances, such as bottom trawling and long-line fishing (De Groot 1984, Bavestrello et al. 1997, Reed et al. 2005, Queirós et al. 2006, Cupido et al. 2007). The former fishing method is known to be extremely destructive and its impacts on structural species are only comparable to forest clear-cutting (Watling and Norse 1998). Gorgonians are almost completely depleted after trawling events and any survivors may die from collapse due to the huge amount of resuspended sediment (Cortés and Risk 1985). In this study, high gorgonian densities were associated to elevated species richness and diversity and, therefore, mass mortalities of these octocorals could have devastating effects on local diversity (Coleman and Williams 2002). Furthermore, the destruction of their structures could also affect water-sediment processes such as the deposition of organic matter and erosion (Coleman and Williams 2002). Therefore, due to their critical ecosystem role (Buhl-Mortensen et al. 2010, Cerrano et al. 2010, Gutiérrez et al. 2011) and their implication for conservation biology, there is a need to protect gorgonians from such highly frequent fishing activities and further anthropogenic disturbances. Results from the present study also show that gorgonians are capable of increasing diversity even at very small scales, as observed in Figure 3. This fact could help towards improving management plans in marine protected areas, since small extensions of terrain dominated by gorgonian species could be exerting an important role on the diversity of the region. However, gorgonians are not the only ecosystem engineer species in need for protection. Deforestation of tropical trees due to wood demand and establishment of coffee plantations would have similar dramatic results, affecting epiphyte plants and faunal diversity (Cowlishaw 1999, Hundera et al. 2013). Although traditional conservation efforts have focused on the protection of charismatic taxa (Crain and Bertness 2006), the findings of the present study enhance the idea of protecting all species that are more critical to the ecosystem functioning. Gorgonians, like any other ecosystem engineer, would be particularly useful as umbrella species in conservation plans, as the protection of a single species could have a huge effect in the entire community (Crain and Bertness 2006, Roberge and Angelstam 2004).

Besides the need for conservation, ecosystem engineers that act as foundation species (Byers et al. 2006) could also be used to restore fragile ecosystems that have been altered by human activities and take them to a desired state. Most restoration efforts try to improve the damaged abiotic environment in order to facilitate the subsequent colonisation by many species (Byers et al. 2006). However, ecosystem engineers such as some vascular plants and benthic fauna are known to improve the abiotic environment by themselves (Jones et al. 1997, Dean et al. 1999, Buhl-Mortensen et al. 2010). Using these organisms in the first stages of restoration processes would accelerate the ecological succession reducing costs and efforts (Byers et al. 2006). In fact, Montseny et al. (2020) already carried out a cost-effective restoration of coral gardens in the Cap de Creus continental shelf, which coincides with the

Mediterranean region analysed in the present study. The authors used a technique that consists on attaching *E. cavolini* colonies, brought to the surface through by-catch of the artisanal fishermen in the area, to natural cobbles and gently throw these gorgonian transplants from a boat back to a water depth of 60 m. Although the methodological approach of Montseny et al. (2020) is easily reproducible due to the low economic budget needed, monitoring of these gorgonian patches should be performed in order to assess if they are dense enough to favour the settlement of new species through the modification of the biophysical conditions of the habitat at a small scale.

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ORIGINAL PAPER

Ophiuroid biodiversity patterns along the Antarctic Peninsula

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Abstract Benthic ecological surveys using standardized methods are crucial for assessing changes associated with several threats in the Southern Ocean. The acquisition of data on assemblage structure over a variety of spatial scales is important to understand the variation of biodiversity patterns. During the ANT XXIX/3 (PS81) expedition of RV Polarstern, three different regions at the tip of the Antarctic Peninsula were sampled: the northwestern Weddell Sea, the Bransfield Strait, and the northern boundary of the South Shetland Archipelago in the Drake Passage. The aim of this study was to characterize the distribution and biodiversity patterns of ophiuroid assemblages in these regions and depths. We quantified different community parameters in terms of the number of species, abundance, and biomass. Additionally, we calculated various components of species diversity (alpha, beta, and gamma diversity) over the three regions. Based on the benthic surveys, we collected 3331 individuals that were identified to species level (17 species). Overall, species diversity, as measured based on rarefaction, species richness and evenness estimators, was higher in the Bransfield Strait compared to the Weddell Sea and Drake Passage. Two deep stations in the Weddell Sea showed high dominance only of *Ophionotus victoriae*. Significant differences in the patterns of alpha diversity were found among the regions but not between depth zones, whereas beta diversity showed no differences. Regarding the resemblance among the ophiuroid assemblages of each region, there was a significant gradient from east to west with a maximum distance between the stations in the Drake Passage and the Weddell Sea. This study provides a baseline for detecting potential effects related to climate change, and it furnishes a basis for the implementation of monitoring schemes of Antarctic assemblages.

Keywords Benthos · Community · Climate change · Diversity · Distribution · Southern Ocean · Standardized protocol

Introduction

The multiple components of climate change are anticipated to affect all levels of biodiversity, from organism to biome (reviewed in Parmesan 2006). The Antarctic Peninsula (AP) region is distinctive among Antarctic regions in its response to climate change, with strong decreases in sea ice (Turner et al. 2005), rapid winter warming (+7 °C air temperature since 1950) (Turner et al. 2005), ocean warming (+1 °C sea surface temperature since the second

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half of the twentieth century) (Meredith and King 2005), and retreat of maritime glaciers and ice shelves (Cook et al. 2005; Domack et al. 2005). Recent climatic trends have resulted in significant changes in Antarctic marine ecosystems, such as decrease in phytoplankton biomass (Stammerjohn et al. 2008; Montes-Hugo et al. 2009), loss of sea-ice habitat for juvenile euphausiid species (Fraser and Hofmann 2003), increase in rates of physiological functions with impacts on growth or feeding requirements (Peck et al. 2006), modification of species geographic distribution and potential invasion processes (Thatje et al. 2005; Walther et al. 2009), and alteration of benthic assemblages (Smith et al. 2008). Thus, the warming climate threatens to change the composition and function of Antarctic marine communities in ways that are complex and not entirely predictable (Clarke et al. 2007; Walther et al. 2002).

Ophiuroids are among the most important Antarctic benthic groups, in terms of abundance and ecological roles, from shallow sublittoral habitats to continental shelves and the deep sea (Fell 1961; Fell et al. 1969; Dell 1972; Dahm 1999; Piepenburg and Schmid 1996; Brandt et al. 2007; Moles et al. 2014). Moreover, there is a solid register in their systematics and biogeographic distributions with studies dating from the late nineteenth century (e.g., Studer 1876; Ludwig 1899) to recent reviews and biogeographic approaches (Martynov 2010; O'Hara et al. 2011; Martín-Ledo and López-González 2014).

Interestingly, the distribution of ophiuroids is mainly driven by temperature and depth, highlighting the importance of ecophysiology (e.g., stenothermality and stenobathymetry), reproduction mode, and life history traits (Fell et al. 1969; Hendler 1975; Hendler and Tran 2001; Sands et al. 2012; Martín-Ledo and López-González 2014). They are considered to play an important role in the transfer of energy between the water column and the seafloor because of their high biomass values and great abundance (Piepenburg and Juterzenka 1994; Piepenburg et al. 1997). Thus, given the accelerating pace of climate change in the AP and their sensitivity to temperature changes, we hypothesize that ophiuroids may exhibit different community responses with different biodiversity distribution patterns. From a community ecology and conservation perspective, the acquisition of data on species composition and assemblage structure over a variety of spatial scales is indispensable for understanding the variation of biodiversity at local and regional scales (Lourie and Vincent 2004). Moreover, these baseline datasets are valuable for assessing the changes associated with several threats and the outcome of management actions. Knowing and understanding the patterns of variability in benthic assemblages over a range of spatial, temporal, and bathymetric scales using standardized methods are crucial for the effective management and conservation of Antarctic marine habitats (Lockhart and Jones 2008; Kaiser et al. 2013).

During the Polarstern ANT XXIX/3 (PS81) expedition, three different regions at the tip of the AP, which are characterized by different environmental regimes mainly driven by seasonal sea-ice extent and permanent water mass circulation (Hofmann et al. 1996), were investigated: the northwestern Weddell Sea (polar conditions), the Bransfield Strait (transition conditions), and the northern boundary of the South Shetland Archipelago in the Drake Passage (oceanic conditions). Environmental conditions around the AP differ between the west and the east. The oceanic region north of the AP is characterized by two main converging water masses (the cold bottom water from the eastern AP shelf and the warm and salty waters of the circumpolar origin) and an interannual and seasonal sea-ice variability, both of which shape the local marine ecosystem (Björgo et al. 1997; Foldvik et al. 2004; Gutt et al. 2015a, b). The general idea was that differences in the quantity and quality of food to the benthos may result in different benthic community patterns. This assumption was based on the results of long-term studies of summer primary production (Trimborn et al. 2015), average summer sea-ice cover, and bottom water temperature (Clarke et al. 2009). Based on Agassiz trawl catches, the aim of this study was to investigate ophiuroid assemblages in terms of the distribution and diversity patterns at three different environmental regimes and depths. We quantified different community parameters in terms of the number of species, abundance, and biomass. Additionally, we assessed various components of species diversity (alpha, beta, and gamma diversity) for the three regions studied. The objective of this article is to contribute to the ecology of Antarctic benthos based on the most abundant and conspicuous ophiuroid species (around 99 % of all collected specimens). Parallel studies during the ANT XXIX/3 expedition used the same standardized sampling method and aimed to characterize major benthic megafaunal assemblages at a functional level (Gutt et al. 2015a, b).

Materials and methods

Sampling area

Three study areas were sampled as a part of the multidisciplinary ANT XXIX/3 expedition on board the R/V Polarstern from January 22 to March 22, 2013 (Gutt 2013). These areas included the northwestern Weddell Sea (WED) east of the tip of the AP, the Bransfield Strait (BRA), and the Drake Passage (DRA) west of the South Shetland Islands (Fig. 1; Table 1). The study area extends for approximately 39,000 km^2. Three core stations were

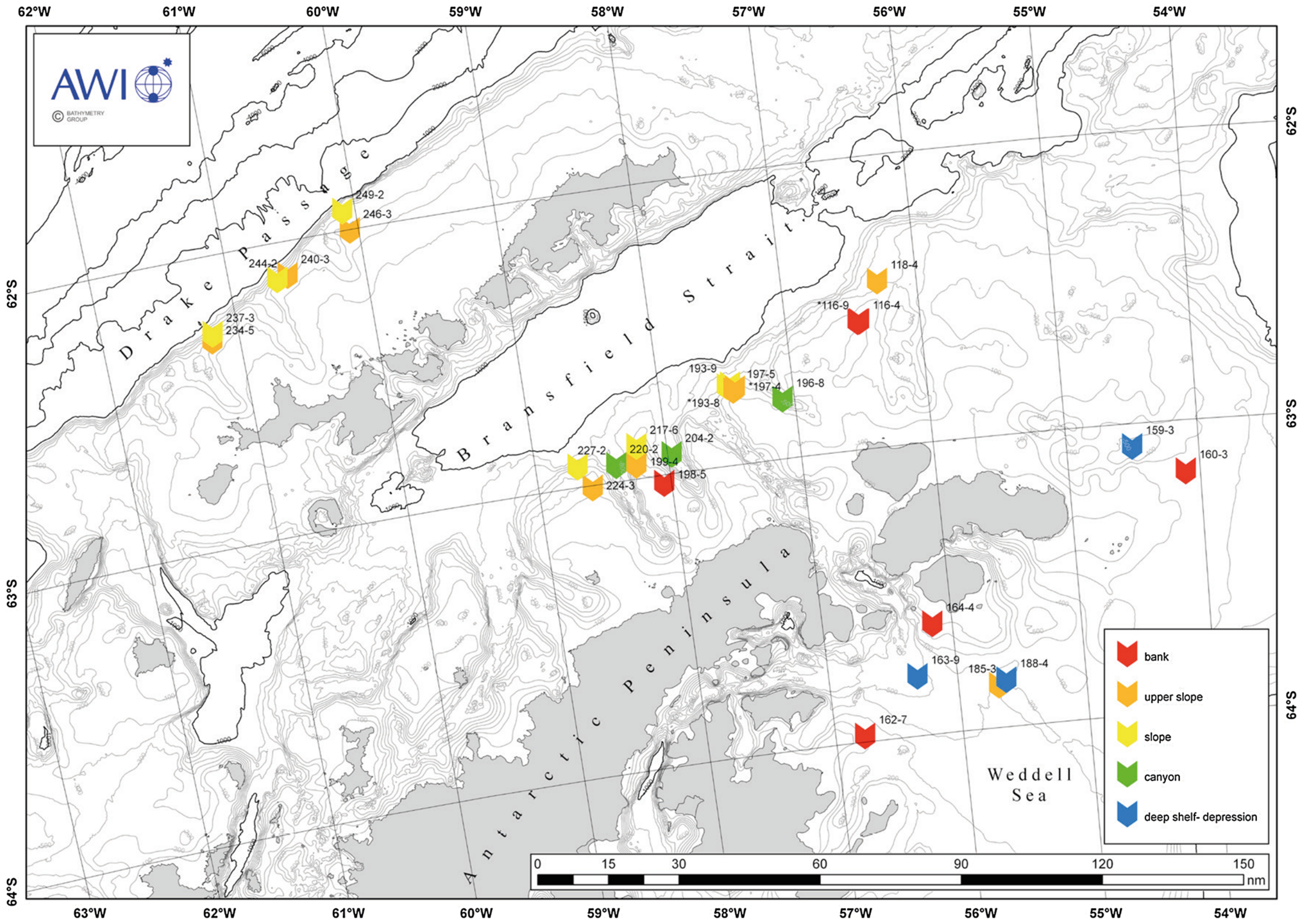

Fig. 1 Map of the study area showing the 18 stations sampled in the three regions and the different depths. The *white* patches on the map are the contours below 1000 m depth. The scale of the bathymetric contours is each 100 m

performed in each area. At each core station, different habitats were selected when they were present: shallow bank (approximately 200 m), upper exposed slope (approximately 270 m), deeper slope (approximately 450 m), deep shelf depression (approximately 450 m), and canyon (approximately 500 m). A total of 25 Agassiz trawl (AGT) stations were initially sampled. However, because not all 5 of these habitats existed in the three regions, we restricted our statistical analyses to a subset of 18 stations, which were grouped in two depth categories: shallow (from 100 to 350 m) and deep (from 400 to 600 m). Thus, there were 3 shallow and 3 deep stations in each region.

Standardized protocol

Samples were taken with an AGT with 3.5-m-wide opening and 10-mm mesh size, which was towed on the seafloor for 10 min at 1 knot. From the total catch of each station, a 50-l subsample was randomly collected from the entire catch to be as representative as possible. We followed this standardized protocol to compare semiquantitative data across all the stations. This protocol was applied during the ANT XXIX/3 expedition as a representative, adequate, and time- and cost-efficient method for community characterization and assessment. The aim was to evaluate the assemblage structure and its natural variability. Gutt et al. (2015a, b) showed that this standardized subsample protocol resulted in a good representation of benthic assemblages across the three regions and different depths studied. For more information about subsampling, see Gutt et al. (2015a, b). See Table 1 for details about the proportions of the subsample to total catch and ophiuroid biomass to the benthos biomass. For further metadata, see Dorschel et al. (in press).

Benthos sampling and processing

On deck, the subsamples were sieved through three mesh sizes (10, 5, and 1 mm). After the macro- and megabenthic fauna were sorted, the organisms were identified to species level whenever possible. Ophiuroids from each trawl were first sorted to morphotype, and a picture was taken.

Table 1 Station list of samples obtained from the Agassiz trawl

Station	Position latitude longitude	Depth (m)	Scenarios	Area	Prop Sub to total Catch	Prop Ophiuroids to benthos
116-4	**S 62°33.80′ W 56°27.31′**	**248**	**B**	**BRA**	**1**	**0.05**
118-4	**S 62°26.53′ W 56°17.34′**	**445**	**US**	**BRA**	**0.25**	**0.27**
159-3	**S 63°04.77′ W 54°29.29′**	**490**	**DS**	**WED**	**0.1**	**0.01**
160-3	**S 63°10.32′ W 54°07.19′**	**227**	**B**	**WED**	**0.1**	**0.004**
162-7	**S 63°58.60′ W 56°46.24′**	**217**	**B**	**WED**	**0.04**	**0.01**
163-9	**S 63°48.30′ W 56°18.52′**	**553**	**DS**	**WED**	**0.07**	**0.01**
164-4	S 63°37.33′ W 56°08.64′	101	B	WED	0.05	0.01
185-3	**S 63°51.04′ W 55°40.68′**	**375**	**US**	**WED**	**0.33**	**0.02**
188-4	**S 63°49.90′ W 55°37.09′**	**430**	**DS**	**WED**	**1**	**0.04**
193-9	**S 62°43.32′ W 57°26.70′**	**410**	**S**	**BRA**	**0.33**	**0.04**
196-8	S 62°48.17′ W 57°04.53′	568	C	BRA	**0.1**	0.04
197-5	**S 62°44.49′ W 57°26.40′**	**293**	**US**	**BRA**	**0.07**	**0.09**
198-5	S 63°01.63′ W 58°02.80′	171	B	BRA	0.07	0.01
199-4	S 62°57.08′ W 58°13.95′	301	US	BRA	**0.04**	0.05
204-2	S 62°56.02′ W 57°56.84′	772	C	BRA	**0.02**	0.16
217-6	S 62°53.49′ W 58°12.09′	408	S	BRA	**0.1**	0.04
220-2	S 62°56.57′ W 58°22.51′	774	C	BRA	**0.05**	0.14
224-3	**S 63°00.48′ W 58°35.12′**	**269**	**US**	**BRA**	**0.07**	**0.25**
227-2	**S 62°56.11′ W 58°40.32′**	**532**	**S**	**BRA**	**0.1**	**0.06**
234-5	**S 62°17.40′ W 61°11.58′**	**246**	**US**	**DRA**	**0.1**	**0.03**
237-3	**S 62°16.15′ W 61°10.90′**	**386**	**S**	**DRA**	**0.5**	**0.06**
240-3	**S 62°06.91′ W 60°33.75′**	**274**	**US**	**DRA**	**0.1**	**0.04**
244-2	**S 62°07.71′ W 60°39.50′**	**474**	**S**	**DRA**	**0.1**	**0.03**
246-3	**S 61°59.95′ W 60°03.87′**	**283**	**US**	**DRA**	**0.1**	**0.01**
249-2	**S 61°55.81′ W 60°05.07′**	**425**	**S**	**DRA**	**0.33**	**0.01**

The subset of the 18 stations is marked in bold

Scenarios: *B* bank; *US* upper slope; *DS* deep shelf depression; *C* canyon; *S* slope; Areas: *WED* Weddell Sea; *BRA* Bransfield Strait; *DRA* Drake Passage; *Prop Sub to total Catch* proportion subsample (50 l) of total catch (total volume); proportion of ophiuroid biomass (kg) of total benthos biomass of the subsample

Taxonomic determinations were based on the examination of external morphological characters and were compared to the original descriptions and taxonomic literature of this group from the Southern Ocean (e.g., Lyman 1875, 1882; Studer 1876; Koehler 1901, 1908, 1912, 1922; Hertz 1927; Mortensen 1936; Bernasconi and D'Agostino 1977), and to the ophiuroid reference collection in the University of Seville (Spain). See Table 2 for taxonomic remarks on the identification of some species. In this study, *Ophioplinthus gelida* and O. *brevirima* were grouped together as well as *Ophiacantha vivipara* and *O. pentactis*. On board, all ophiuroid individuals were counted to calculate the number of individuals and weighed to estimate biomass (fresh weight).

Preliminary analyses: selection of ophiuroids for benthic assemblage characterization

We carried out preliminary analyses to verify the suitability of ophiuroids for the characterization of benthic assemblages. The criteria for selecting ophiuroids were based on the reliability of taxonomic identification (with exceptions) and sufficient number of individuals per station. As a first step, we applied a multivariate analytical procedure on abundance data of different groups of macro- and megabenthic fauna: Porifera (Hexactinnellida, Demospongiae, Calcarea), Cnidaria (Hexacorallia and Octocorallia), Crustacea (Mysidacea, Amphipoda, Decapoda, Isopoda), Echinodermata (Echinoidea, Asteroidea, Crinoidea, Ophiuroidea), and Pisces. The preliminary identification of these taxa was carried out on board by specialists. However, further taxonomic identification was needed for a complete and definitive species list for all these groups. We compared the assemblage structure by using the abundance data of the preliminary identification of macro- and megabenthic taxy with the ophiuroids. The analysis revealed that the ophiuroid fauna displayed the same interregional variability as the combined macro- and megabenthic taxa mentioned above. Based on these preliminary analyses, we consider ophiuroids as a good model

Table 2 Remarks on the identification of some ophiuroid species

Species	Remarks
Ophionotus victoriae	Hunter and Halanych (2010) revealed an unexpected genetic structure along Antarctic Peninsula inconsistent with early life history data. The possibility of cryptic speciation is pointed out. According to the authors, further studies are needed to include material from additional Antarctic localities. Our sampling material mainly coincided geographically with the area named by the authors as "Northern Peninsula." The possible existence of these cryptic species, when demonstrated, could affect or not the number of species in our study area, but the ecological role of these possible closely related species will probably not affect the usefulness of our study
Ophiacantha vivipara versus *Ophiacantha pentactis*	The original description of *O. pentactis* is 5 arms, whereas *O. vivipara* is 5–8 (usually 6) arms. This was the main criterion used in this study. However, there exists a morphotype of *O. pentactis* with 6 arms that is easily confused with *O. vivipara*
	Despite the often used character of the number of arms in distinguishing *O. vivipara* and *O. pentactis*, the variability observed in the specimens (e.g., n° arms, n° oral papilae, shape of oral shield), and the variability discussed in the specialized literature blur the apparent clear differences once used to differentiate both forms of previously considered subspecies. The size of the oral disk (larger in *O. pentactis*) is a continuous biometric character of doubtful utility when examining specimens of intermediate size
	In this study, these two species were merged
Ophioplinthus gelida versus *Ophioplinthus brevirima*	They are morphologically very similar, both are often covered (and morphologically altered) by the sponge symbiont *Iophon*
	In the case of these two species and despite the possible morphological alteration of plates by *Iophon*, the relative length of the genital slits is a useful character in distinguishing between these two species
	The criterion adopted in this study was to merge also these two species

group to characterize the assemblages studied during the expedition.

Specimens that were in such a poor state that they could not be identified were not considered for further analyses. These specimens represented nearly 1 % of the collected individuals. In this work, we want to emphasize the usefulness and importance of the most common and abundant ophiuroids. Importantly, the species lists of this study should not be considered as the unique species living at the different widely considered ecoregions (other comprehensive works can be consulted as Martín-Ledo and López-González 2014), but they are the results of the comparative sampling program carried out during the ANT XXIX/3 cruise. The data used in this study are available as Electronic Supplementary Material 1 (ESM).

Analysis of species diversity and assemblage structure

First, we performed a first group of analyses on species diversity for all 25 stations. The purpose of these analyses was to extract information on patterns that were relevant to species diversity and abundance from all sampled stations. We acknowledge the large discussion regarding species estimators (e.g., Colwell and Coddington 1994; Gotelli and Colwell 2001; O'Hara 2005; Magurran and McGill 2011), and our purpose was to select some of these estimators to quantify the overall faunal patterns of the stations sampled and not to review all of the methodological aspects. Furthermore, we recognize the methodological problems in measuring the number of species and individuals in a given area (for a review, see Gotelli and Colwell 2001). The following first analyses were performed: (1) cumulative rank dominance curves and (2) estimation of "*true species richness*" using the nonparametric estimators Chao2 (based on incidence data), Jacknife 2 (estimator for both even and uneven communities), and Chao1 (based on abundance data) (see Colwell and Coddington 1994; Gotelli and Colwell 2001). In addition, we also compiled the biogeographic and bathymetric distribution and computed the stenobathic–eurybathic index (S–E index) for the identified species. The S–E index ranges from close to 0 (narrow distribution) to 100 (wide distribution) (see Martín-Ledo and López-González (2014) for more information).

Second, we further investigated the diversity patterns and assemblage structure based on a subset of 18 AGT stations. We selected three stations per geographic area DRA, BRA, and WED and depths, shallow (from 100 to 350 m) and deep (from 400 to 600 m). We calculated various diversity measures: number of species, as well as the exponential Shannon index (ExpH') and the reciprocal Simpson's index (1/Simpson), following the suggestions of Jost et al. (2010) to estimate "effective number of species." Spatial patterns of diversity measures were assessed by quantifying the alpha diversity (average number of species per catch), gamma diversity (the total number of species within a region), and beta diversity (the multivariate distance between group-centroids determined with the PERMDISP procedure, see below). To visualize the pattern of resemblance in the ophiuroid composition of 18 AGT catches, non-metric multidimensional scaling (nMDS) was performed on Bray–Curtis dissimilarities using square-root-transformed ophiuroid abundance data. Furthermore, a similarity percentage procedure analysis (SIMPER, Clarke and Warwick 1994) was performed to identify the percentage contribution of taxa to average similarities and dissimilarities within and between regions.

Univariate diversity indices and multivariate assemblage structure were analyzed using a nonparametric analysis of variance, PERMANOVA (Anderson 2001a, b; Anderson et al. 2008), applied using Euclidean and Bray–Curtis distances for univariate and multivariate analyses, respectively. The analyses included two factors: area (fixed factor, 3 levels) and depth (fixed factor, 2 levels). Pair-wise comparisons for all combinations of area x depth were also performed using *t* tests and 9999 permutations of the raw data. PERMDISP is an approach that is used to compare the degree of sample dispersion of different groups based on a distance matrix. When PERMDISP is used on a Jaccard distance presence/absence matrix, it is directly interpretable as a test for similarity in beta diversity among groups (Anderson et al. 2011).

The above measurements and analyses were performed using the program Primer version 6 with the PERMANOVA + add-on package.

Results

A total of 3331 individuals were collected across the three regions and depths for the present study. A total of 17 species were identified, belonging to five ophiuroid families (Gorgonocephalidae, Ophiacanthidae, Amphiuridae, Ophiolepididae, and Ophiuridae; see Table 3 for a species list). Ophiuridae was the most important family in terms of abundance in BRA. It represented 74 % of the individuals in the shallow and 50 % of the individuals in the deep areas and 89 % of the biomass in the shallow and 71 % of the biomass in the deep areas. In WED, it represented 97 % of the individuals in the shallow and 95 % of the individuals in the deep areas and 74 % of the biomass in the shallow and 89 % of the biomass in the deep areas (Fig. 2). Ophiacanthidae was also abundant (33 % of individuals) in the BRA. Amphiuridae was the dominant family in DRA, in terms of both individuals (96–98 %) and biomass (89–96 %) across the two depths (Fig. 2).

Only *Ophioplinthus gelida/O. brevirima* was ubiquitously found in the three areas (DRA, BRA, and WED) and the two depth zones studied (shallow, deep) (Fig. 2; Table 3). *Amphioplus peregrinator* and *Amphiura joubini* were only absent in the WED-deep, whereas *Ophionotus victoriae* was only absent in the DRA-deep. Conversely, four species were only found in a single area and depth: *Ophiocten megaloplax* (BRA-shallow), *Ophioplinthus tumescens* (BRA-deep), *Ophiura (Ophiuroglypha) carinifera* (BRA-deep), and *Ophiura crassa* (BRA-deep). In general, all identified species have a circumantarctic distribution and a high stenobathic–eurybathic (S–E) index, with the exception of *Astrochlamis sol* with an S–E index of 36 % (Table 3). According to the sampled material, in the whole study area (DRA, BRA, and WED) the endemic component (Antarctic endemic (ANE) + Southern Ocean endemic (SOE)) was always more important than the wider geographic component (Southern Ocean and surrounding oceans (SOS)), (Table 3).

Dominance

In general, the BRA stations showed low dominance (except for Stn 224-3, in which *Ophioplinthus gelida/O. brevirima* represented the 87 % of individuals), whereas the DRA and WED stations exhibited higher levels of dominance (Fig. 3). The 159-3 and 163-9 deep stations in the WED showed only the presence of *Ophionotus victoriae*. Species from the 227-2 deep station in BRA exhibited dominance values ranging from 2.5 to 16 %.

Species richness and diversity indices

Estimates of cumulative species richness showed little tendency to approach asymptotic values in all three regions (Fig. 4), indicating that all of the studied sites were undersampled and that uncertainty exists in these estimators. The total number of ophiuroid species observed was 17, whereas the Chao 2 estimator assessed values of 19 ± 3.2. Separate species accumulation curves for the DRA (6 observed species) and WED (9 observed species) regions did not stabilize, and BRA (17 observed species) slightly reached an asymptotic value. Interestingly, Chao1 provided a good estimation of true species richness at 17 ± 4.2 (Fig. 4).

From the 18 subset of stations, local species richness or alpha diversity showed significant differences among regions ($F_{2,12} = 11.2$, $p < 0.001$), but not between depths ($F_{1,12} = 0.41$, $p > 0.05$) (see ESM 2 for all the results and pair-wise comparisons). BRA showed the highest alpha diversity values of 8 species ± 1, which differed significantly from 3 species ± 1 in WED and 3 species ± 1 in

Table 3 List of the taxa identified in the 25 stations of the Antarctic Peninsula

Taxon	Distr. group	Drake shallow	Drake deep	Bransfield shallow	Bransfield deep	Weddell shallow	Weddell deep	Distribution	S–E index (%)
Ophioperla koehleri (Bell 1908)[d]	A	+		+	+			C—SOE	93.52
Ophiacantha antarctica (Koehler 1901)[b]			+	+	+			C—SOS	100
Amphioplus peregrinator (Koehler 1912)[c]		+	+	+	+	+		C—SOE	99.70
Amphiura joubini (Koehler 1912)[c]	B	+	+	+	+	+		C—SOS	99.19
Ophioplinthus gelida/O. brevirima (Koehler 1901) (Mortensen 1936)[d]		+	+	+	+	+	+	C—ANE, C—ANE	98.53, 86.87
Ophionotus victoriae (Bell 1902)[d]		+		+	+	+	+	C—ANE	99.69
Ophiocten megaloplax (Koehler 1901)[d]				+				C—ANE	87.64
Ophioceres incipiens (Koehler 1922)[e]				+	+			C—SOE	100
Astrochlamys sol (Mortensen 1936)[a]	C			+	+			C—ANE	36.67
Ophiura (*Ophiuroglypha*) *carinifera* (Koehler 1901)[d]					+			C—SOS	98.65
Ophiura crassa (Mortensen 1936)[d]					+			C—ANE	92.69
Ophioplinthus tumescens (Koehler 1922)[d]					+			C—ANE	91.83
Astrohamma tuberculatum (Koehler 1923)[a]				+	+		+	C—ANE	87.71
Astrotoma agassizii (Lyman 1875)[a]					+	+	+	C—SOS	94.75
Ophiacantha vivipara/O. pentactis (Ljungman 1870), (Mortensen 1936)[b]	D			+	+	+	+	C—SOE, C—SOE	100, 92.28
Ophiosteira antarctica (Bell 1902)[d]				+	+		+	C—ANE	95.21
Ophiosparte gigas (Koehler 1922)[d]					+	+		C—ANE	98.93

+, present; −, absent; Distr Group, distribution groups; A, shared species between Drake Passage and Bransfield Strait; B, shared species for all sampled localities; C, exclusive species for Bransfield Strait; D, shared species between Bransfield and Weddell Sea. Distribution: C, Circumantarctic; ANE, Antarctic endemic; SOE, Southern Ocean Endemic; SOS, Southern Ocean and surrounding oceans; S–E index, stenobathic–eurybathic index; S–E index ranges from close to 0 (narrow distribution) to 100 (wide distribution). For more information on the biogeographic and bathymetric information, see Martín-Ledo and López-González (2014)

Families: [a]Gorgonocephalidae; [b]Ophiacanthidae; [c]Amphiuridae; [d]Ophiuridae; [e]Ophiolepididae

DRA (pair-wise tests $t_{\text{BRA–WED}} = 3.4$, $p < 0.01$; $t_{\text{BRA–DRA}} = 5.1$, $p < 0.001$, respectively) (Fig. 5). Similar results were found for values of ExpH' and 1/Simpson among the three regions and depths (Fig. 5). The data suggested highest diversity in terms of the “effective number of species” at BRA (ExpH' = 5 ± 1, 1/Simpson = 4 ± 1) and lower diversity in WED (ExpH' = 2 ± 0.4, 1/Simpson = 1.5 ± 0.3) and DRA (ExpH' = 2 ± 0.2, 1/Simpson = 2 ± 0.2) (Fig. 5). Beta diversity did not show a significant difference among the regions and depths (PERMDISP $F_{2,12} = 3.1$ $p > 0.05$). DRA-deep stations were characterized by lower mean values (22.2 % ± 3.7) than WED-shallow stations (45.3 % ± 2.1). Regional species richness or gamma diversity ranged from 12 species in BRA-deep stations to 7 species in WED-shallow stations and 4 species in DRA-deep stations (Fig. 5).

Structural complexity/community assemblage

Overall, the pattern of resemblances in ophiuroid community structure among the regions reflected their relative geographic positions (Fig. 6). There was a significant resemblance difference from east to west ($F_{2,12} = 9.5$, $p < 0.0001$), with a maximum resemblance distance between the DRA and WED stations. Considering the pair-wise comparisons, only BRA showed a significant difference compared to DRA and WED ($t_{\text{BRA–WED}} = 2.3$, $p < 0.001$; $t_{\text{BRA–DRA}} = 3.4$, $p < 0.001$). No significant differences were found between depth zones ($F_{1,12} = 0.9$, $p > 0.05$).

The SIMPER analysis showed an average similarity in specific composition from 42 % in WED to 56 % in DRA (Table 4). The number of taxa contributing to 90 % of the similarity within each region ranged between 1 (WED) and

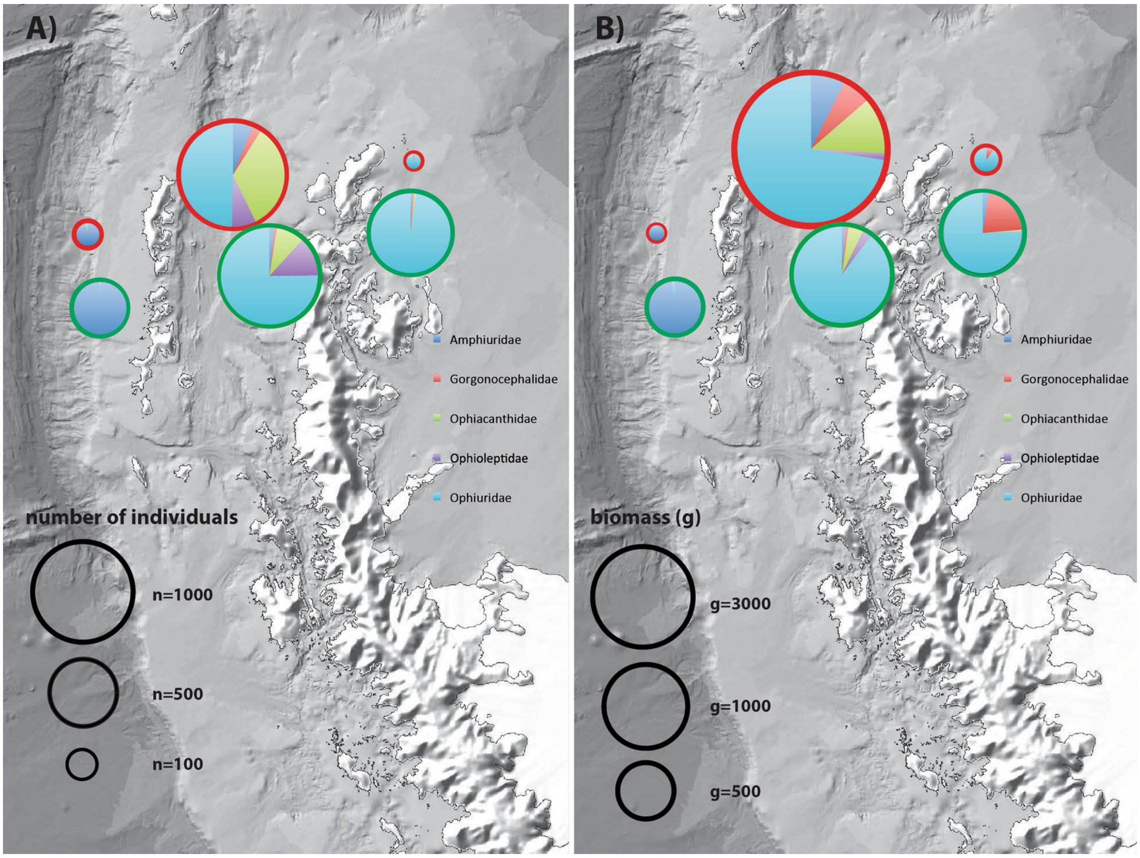

Fig. 2 **a** Number of individuals and **b** biomass based on the ophiuroid families sampled. A total of 3331 individuals were collected from the 25 AGT stations: Drake shallow $n = 492$; Drake deep $n = 119$; Bransfield shallow $n = 999$; Bransfield deep $n = 1045$; Weddell shallow $n = 615$; Weddell deep $n = 61$. *Red* = shallow stations; *green* = deep stations

6 (BRA) (Table 4). Certain taxa played determining roles in each region, such as *Amphioplus peregrinator* (similarity contribution of 62 %), *Ophioplinthus gelida/O. brevirima* (50 %), and *Ophionotus victoriae* (92 %) for DRA, BRA, and WED, respectively. Focusing on taxa dissimilarities, the most important taxa were *O. gelida/O. brevirima*, which contributed 28 % and 27 % of the average dissimilarity between BRA–WED and BRA–DRA, respectively. *A. peregrinator* contributed 35 % of the average dissimilarity between WED and DRA.

Discussion

Importance of studies on species composition and biodiversity patterns in response to climate change in the Antarctic Peninsula

Studies that address the spatial and temporal patterns of species composition and biodiversity warrant special attention to identify the most key species and assemblages to discriminate environmental changes from the natural intra- or interannual variability. Such studies will facilitate sampling methods to rapidly detect Antarctica's rich biodiversity's responses to climate change and other anthropogenic stressor. Climate change is expected to become a major driving force regarding the extinctions of species and the loss of diversity and will likely include some degree of toleration, adaptation, and migration (Millenium Ecosystem Assessment 2005; Barnes and Peck 2008; Barnes et al. 2009). For benthic communities on the continental shelf of the AP, the challenge is even greater because the AP is a climate change hotspot, and declining or recovery trajectories are more difficult to detect because of the overall slow pace of change among Antarctic benthic species (Arntz et al. 1994; Clarke et al. 2007). In this context, large-scale long-term biodiversity datasets are a basic resource that furnishes the essential tools to provide information that promotes sound ecological studies (Lockart and Jones 2008; Magurran et al. 2010; Griffiths 2010). With the use of a standardized biodiversity survey, the present study provides baseline information on ophiuroid assemblages in three distinct environmental regions and depths at the AP, highlighting different diversity patterns in the different

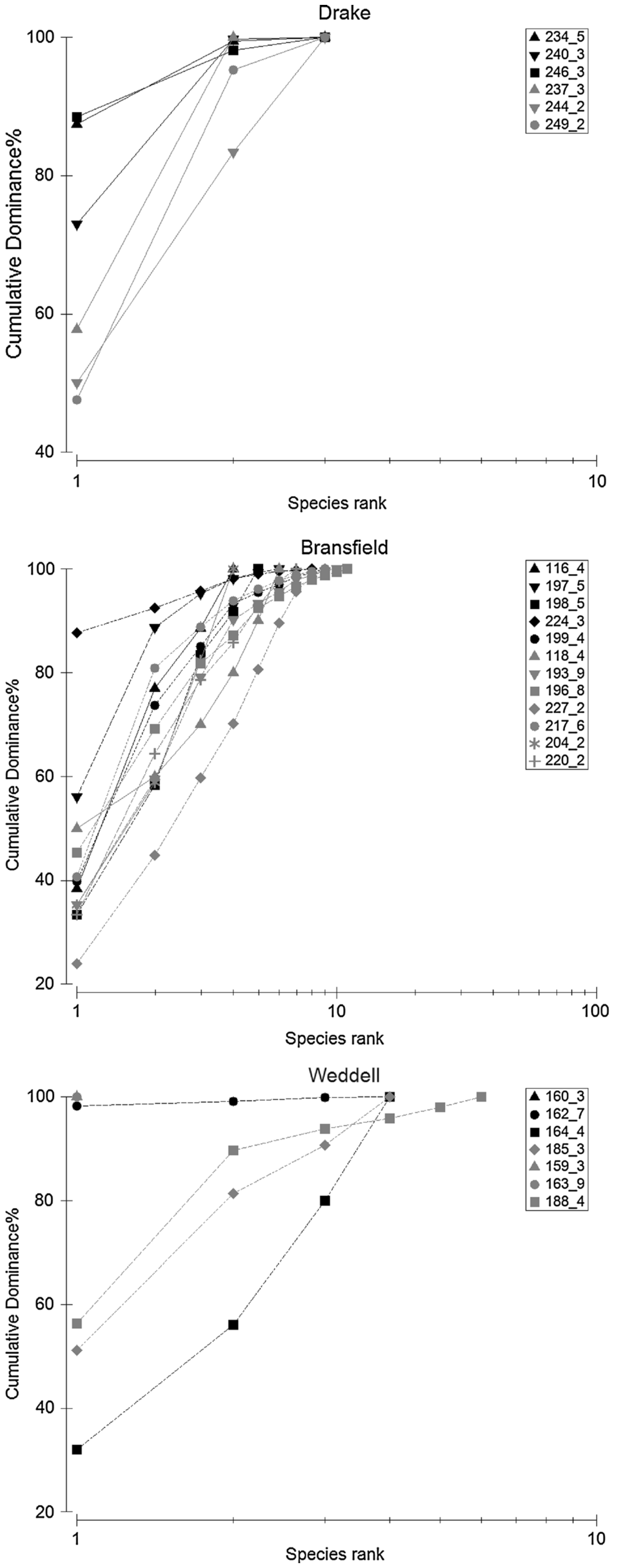

Fig. 3 Cumulative dominance plots in the three study areas. *Black* indicates shallow stations, whereas *gray* indicates deep stations. Note: Two deep stations in the Weddell Sea contained only 1 species

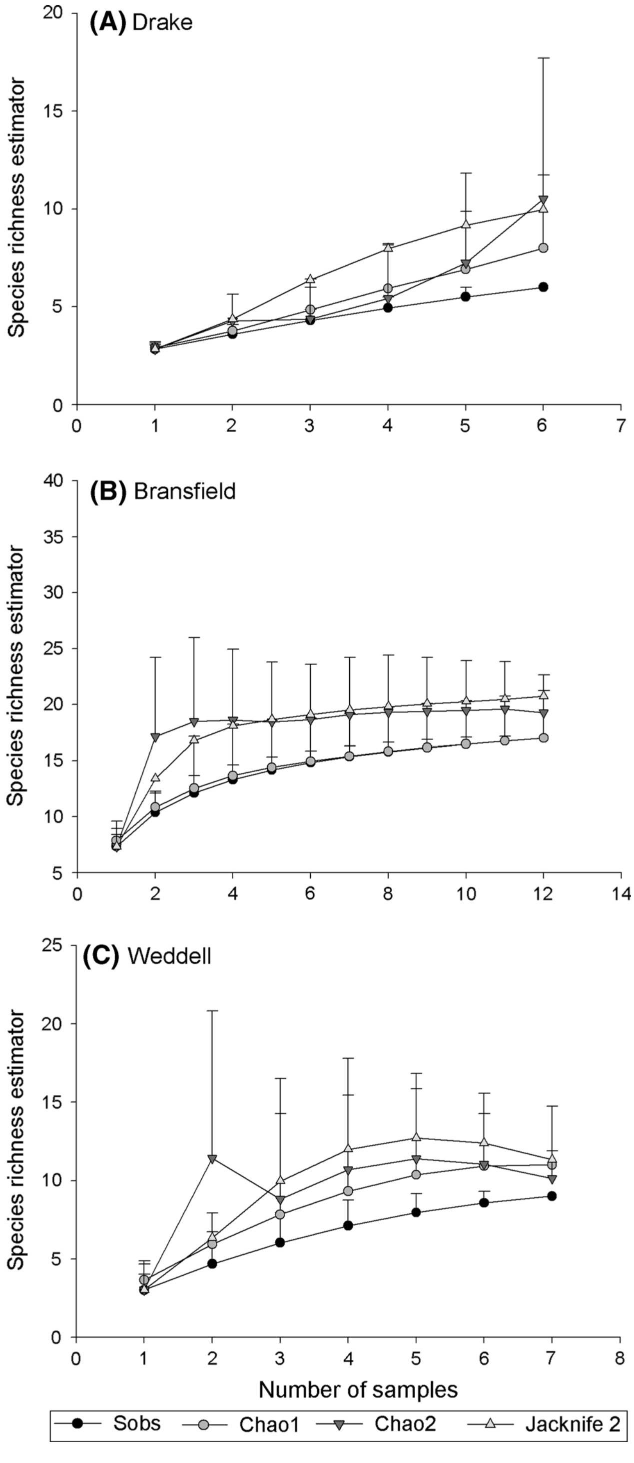

Fig. 4 Species accumulation curves. The estimators of species richness are as follows: Sobs, the total number of all species; Chao2, estimator of true richness; Chao1, estimator on individual-based abundance data; and Jack2, estimator for both even and uneven communities. The plotted values are mean ± SD

components of biodiversity over the study area and no significant changes between depths. Moreover, we identified 17 ophiuroid species from 3331 individuals. Manjón-

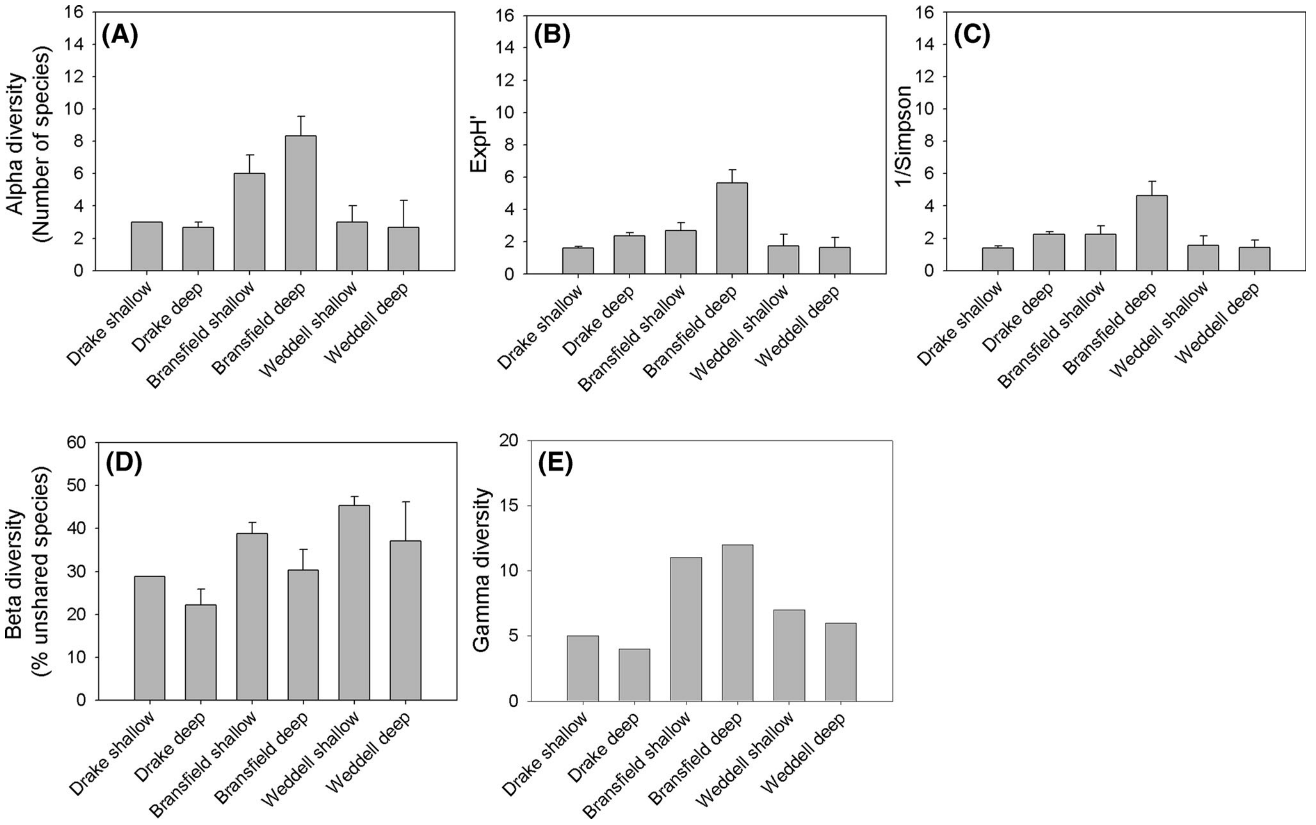

Fig. 5 Measures of **a** alpha diversity (number of species), **b** the exponential Shannon diversity index (ExpH'), **c** the reciprocal Simpson's index (1/Simpson), **d** the beta diversity, and **e** the gamma diversity for the subset of 18 AGT stations

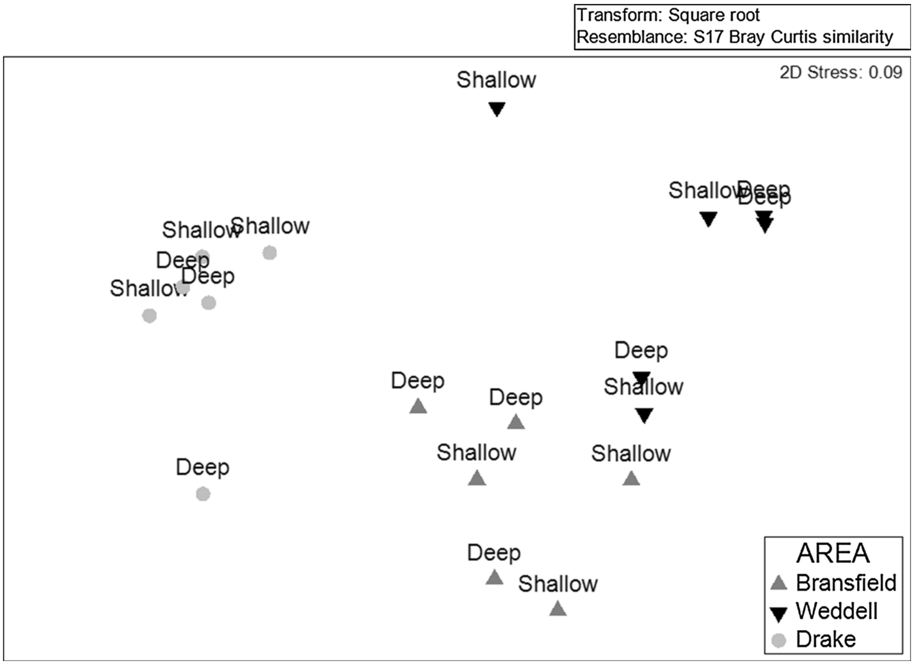

Fig. 6 Non-metric multidimensional scaling (nMDS) plot displaying the resemblance in the ophiuroid composition of 18 AGT catches in the three regions off the Peninsula Antarctica and two depths (shallow ~100–350 m, and deep ~400–600 m). Analysis performed on Bray–Curtis dissimilarities computed using square-root-transformed ophiuroid abundance data

Cabeza and Ramos (2003) reported similar values for the number of individuals (2571 specimens) and species (18 species) identified during the BENTART expedition in the northwest AP. Based on current estimates of Antarctic ophiuroid species (65 within the Antarctic Peninsula, Martín-Ledo and López-González 2014), this study

Table 4 (a) Species that cumulatively contribute to 90 % of the average similarities within the regions (Aver. Sim). (b) Species that contribute cumulatively to 90 % of the average dissimilarities between the regions (Aver. Diss)

Species	Cum. contribution %	% total ind
(a) Similarity		
Group Drake (Aver. Sim = 56 %)		*n* = 611 ind
Amphioplus peregrinator	62.5	74.3 %
Amphiura joubini	36.6	24.5 %
Group Bransfield (Aver. Sim = 45 %)		*n* = 1345 ind
Ophioplinthus gelida/O. brevirima	50.6	57.1 %
Ophionotus victoriae	66.5	4.3 %
Ophioperla koehleri	77.1	6.7 %
Ophioceres incipiens	83.3	12.8 %
Ophiacantha antarctica	88.7	6.1 %
Amphioplus peregrinator	92.4	1.7 %
Group Weddell (Aver. Sim = 42 %)		*n* = 651 ind
Ophionotus victoriae	92.6	90.1 %
(b) Dissimilarity		
Groups Bransfield and Weddell (Aver. Diss = 77 %)		
Ophioplinthus gelida/O. brevirima	28.3	
Ophionotus victoriae	40.4	
Ophioperla koehleri	51.2	
Ophioceres incipiens	61.7	
Ophiacantha antarctica	69.1	
Amphioplus peregrinator	73.8	
Amphiura joubini	78.3	
Ophiosteira antarctica	82.6	
Ophioplinthus tumescens	86.6	
Astrotoma agassizii	90.8	
Groups Bransfield and Drake (Aver. Diss = 85 %)		
Ophioplinthus gelida/O. brevirima	26.5	
Amphioplus peregrinator	42.8	
Ophioceres incipiens	51.8	
Amphiura joubini	60.8	
Ophioperla koehleri	69.6	
Ophionotus victoriae	77.5	
Ophiacantha antarctica	83.6	
Ophiosteira antarctica	87.1	
Ophioplinthus tumescens	90.5	
Groups Weddell and Drake (Aver. Diss = 95 %)		
Amphioplus peregrinator	34.7	
Ophionotus victoriae	63.3	
Amphiura joubini	83.2	
Ophioplinthus gelida/O. brevirima	90.1	

contributed to characterize approximately 26 % of ophiuroids despite the relatively low number of benthic stations examined in relation to the extent of the AP region.

Methodological constraints

No estimators of species accumulation reached an asymptote (Fig. 4), indicating that species were still accumulating with increasing numbers of samples. This general undersampling is important to note and is of relevance for accurate predictions of ophiuroid species and megabenthos assemblage diversities in the study region. Non-asymptotic patterns have been reported for marine benthos (Ugland et al. 2003). Marine invertebrate assemblages can be typified by rarity and with many singletons and the dominance of only a few species (Sanderson 1996). This has been reported as a common problem when sampling a small region relative to the vast areas of the seafloor of the continental shelf (Ellingsen et al. 2001). This case is also true for assemblages characterized by small-scale patchiness and many sparsely distributed species (Colwell and Coddington 1994). We also acknowledge the need of further studies to estimate the representativeness and time- and cost-efficiency of Antarctic benthic surveys in order to survey the assemblage structure and its variability. The high degree of patchiness of benthic communities in the AP has previously been described mainly as a result of iceberg scouring (see below for further discussion) (Barnes and Conlan 2007; Smale and Barnes 2008). Among the estimators of species accumulation applied in this study, the Chao1 estimator was the most precise for the ophiuroids in DRA and BRA (Fig. 4). This may be because of the higher sampling size of the dataset and because this estimator also considers the number of individuals. Chao1 showed $\hat{S}$ (estimated) values that were quite close to S (observed) with little variance. In addition, using a variety of diversity estimators such as cumulative dominance plots, species accumulative estimators, and different diversity indices may allow solid comparisons within the areas studied and some further generalizations.

Assemblage patterns

The present study found differences in terms of ophiuroid species diversity and community assemblages (Figs. 5, 6). The BRA stations had a higher number of species at the local and regional scales and greater evenness compared with WED and DRA (Fig. 5). Although these values were not statistically correlated with environmental data, we suggest that our data partially support the relationship between ophiuroid species diversity and productivity. In addition, our results showed the importance of geographic regions in determining differences in species composition and structure of ophiuroid assemblages (Fig. 6; Table 4). BRA appeared in an intermediate position close to WED and DRA, indicating biological affinities among these two areas. These three regions shared a common pool of species with moderate values of overall similarity (approximately 40–55 %, Table 4). The four taxa *Amphioplus peregrinator*, *Amphiura joubini*, *Ophioplinthus gelida/O. brevirima*, and *Ophionotus victoriae* were found in all the three regions. The Antarctic Peninsula constitutes a unique system for assessing the genetic flow of Antarctic species, where different environmental factors (e.g., geographic distance, depth, and water currents) influence population connectivity (Hoffman et al. 2010). Studies assessing gene flow of the brooding species *Astrotoma agassizii* revealed a genetic continuity across large distances along the Drake Passage continental shelf (Hunter and Halanych 2008). The authors indicated that geographic distance alone did not represent a barrier of dispersal, but rather suggested the combined effects of geographic distance, depth, and water currents to hinder gene flow among these populations. Based on the assemblage data (composition and structure), our results indicate a community structure among the different geographic regions studied.

Interestingly, BRA and WED shared 50 % of species, but this value decreased to 30 % between BRA and DRA. Finally, there was approximately 35 % of species that were present in the BRA region, indicating some degree of endemism. We may conclude that this overall pattern may be related to nestedness component of diversity, which occurs when the biotas of sites with smaller numbers of species are subsets of the biotas at richer sites reflecting a non-random process of species loss as a consequence of any factor that promotes the orderly disaggregation of assemblages (Baselga 2010). This finding is important for effective management and would require devoting conservation efforts to the richest sites (Balvanera et al. 2006). Therefore, the Bransfield region represents a key area in terms of diversity and connectivity in structuring the assemblages at the tip of AP. These marine ecosystems are characterized by the convergence of two water masses (the cold bottom water from the eastern AP shelf and the warm and salty waters of the circumpolar origin), an interannual and seasonal sea-ice variability, and a complex bottom topography (Björgo et al. 1997; Foldvik et al. 2004; Gutt et al. 2015a, b; Jerosch et al. 2015; Dorschel et al. in press). Moreover, disturbance events such as iceberg scouring can also contribute to the differences of ophiuroid assemblages over the three geographic regions studied. Within the depth gradient, we did not find any significant differences concerning diversity and structure of assemblages. The Antarctic continental shelf is considerably deeper than most shelf regions of the world mainly due to the extent and retreat of the shelf ice during glacial and interglacial periods (Anderson 1999). This process may help to explain why Antarctic invertebrates in general, and ophiuroids in particular, show a wide bathymetric distribution (Brey et al. 1996; Thatje et al. 2005).

The impacts of global climate change on Antarctic ophiuroids are likely to differ among species that live in deeper waters. On the continental shelf, the changes associated with global climate change include, for instance, the increase of iceberg scouring, changes in duration and extent of the sea ice, and increased sedimentation and freshening from glacial melt (Barnes and Peck 2008; Smale and Barnes 2008; Gutt et al. 2015a, b). These climate impacts would primarily affect the Antarctic shelf ecosystems and especially the phenology, geographic ranges, and behaviors of a wide range of organisms (Aronson et al. 2007). We know too little about the implications of such ecological and physiological changes on the population dynamics of ophiuroid species. For this reason, more detailed investigations, especially involving the spatial distribution patterns, reproductive modes, and feeding types of benthic invertebrates, may help improve our understanding of the ecological responses of Antarctic benthos to climate change.

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Pristine populations of habitat-forming gorgonian species on the Antarctic continental shelf

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Declines in the abundance of long-lived and habitat-forming species on continental shelves have attracted particular attention given their importance to ecosystem structure and function of marine habitats. The study of undisturbed habitats defined as "pristine areas" is essential in creating a frame of reference for natural habitats free of human interference. Gorgonian species are one of the key structure-forming taxa in benthic communities on the Antarctic continental shelf. Current knowledge of the diversity, distribution and demography of this group is relatively limited in Antarctica. To overcome this lack of information we present original data on pristine and remote populations of gorgonians from the Weddell Sea, some of which display the largest colony sizes ever recorded in Antarctica. We assessed the distribution patterns of seven gorgonian species, a morphogroup and a family in front of the Filchner Ronne Ice Shelf (Weddell Sea) by means of quantitative analysis of video transects. Analysis of these videos showed a total of 3140 colonies of gorgonians with the highest abundance in the southern section and a significantly clumped distribution. This study contributes to the general knowledge of pristine areas of the continental shelf and identifies the eastern Weddell Sea as a hotspot for habitat-forming species.

The current state of the oceans is very different from what it was in the past[1,2]. Actually, most marine ecosystems are affected by climate change (*e.g.* ocean warming, acidification, sea level rise)[3–5] and other multiple human-derived threats (*e.g.* overfishing, pollution, habitat destruction)[6–8] which threaten marine global biodiversity and modify oceanic environments[5] to the point of being considered "unnatural oceans"[9] nearly devoid of "pristine" areas[10]. Such pristine areas are minimally affected by major human threats, thus providing a unique opportunity to better understand how marine ecosystems are structured and behave[11,12]. They are also essential to study the effects of climate change on benthic communities[13], particularly on the Antarctic continental shelf where one can find still relatively undisturbed environments[14,15]. The potential impact of trawling activity has also become a major concern due to its extensive damage to continental shelves and deep cold-water coral reefs[16,17]. Although there is evidence of fishing activity as by-catch from longline fisheries in South Georgia[18] and in the Ross Sea[19], most of the Antarctic continental shelf has been little influenced by industrial fishing[20]. The lack of terrigenous sediments[21], the relative constancy of its physical conditions[22,23] and the relative absence of human-derived impacts[5], make the Antarctic continental shelf a highly favourable environment for the development of high-density benthic megafauna communities.

In the last few decades, studies carried out on the continental shelf of the northeastern Weddell Sea have generated key insights on the diversity[24,25], the degree of heterogeneity[26,27], and the impact of iceberg scouring[28–30]. Iceberg scouring constitutes one of the major natural disturbances for high-Antarctic shelf fauna and it is increasingly apparent that iceberg scouring events may be altered by iceberg calving associated with regional atmospheric warming[31,32]. The estimated rate of disturbance of the Antarctic continental shelf by grounding icebergs is approximately 5%[26], although still considerably less than the 53% attributable to trawling in other continental shelves[33].

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Gorgonians are among the main structural species of many benthic communities across all latitudes and depths, from shallow sublittoral habitats to continental shelves and deep seas[34–36]. Hence, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has recognized gorgonians as a Vulnerable Marine Ecosystems (VME) indicator taxon[37]. These organisms contribute to the structure of benthic communities adding three-dimensional complexity to the habitat[38,39]. During the last decade, knowledge about diversity, distribution, ecology and state of conservation of gorgonian populations on the continental shelf has significantly increased in the Mediterranean Sea[40,41], the Pacific Ocean[42,43] and the Atlantic Ocean[44]. In Antarctica, most of the studies of this group of organisms have focused on taxonomy[45,46], trophic ecology[47,48], growth rates[49,50] and reproductive ecology[51,52]. However, despite the high abundance of gorgonians in some locations of the Weddell Sea and their ecological role in Antarctic benthic communities[30,53], there is still an important lack of knowledge on their ecological characteristics such as spatial distribution, abundance and demographic processes[54].

Non-destructive sampling techniques like video-equipped towed gear, Remotely Operated Vehicles (ROVs) or manned submersibles are commonly used to study coastal areas[55], deep reefs of cold-water corals[56], seamounts[57], and mesophotic areas[58] to assess biodiversity patterns, characterize communities, evaluate spatial and temporal changes, and assess benthic ecosystem health status[59,60]. Although the majority of studies on Antarctic benthos have been carried out using semi-quantitative techniques like Agassiz and bottom trawls[61,62], non-destructive image methodology has also been commonly used in the high Antarctic to provide quantitative information on the distributional patterns of benthic megafauna communities over large spatial and bathymetrical domains[28,53,58,63–65].

Knowledge of demographic processes and spatial distribution patterns is a prerequisite to understand their role in benthic communities and provide basic information on their underlying dynamics and resilience, as well as to facilitate their management and conservation[66,67]. The major aim of the present study was to assess the health status of Antarctic gorgonian assemblages in a pristine and remote area in the southernmost part of the Weddell Sea continental shelf. Specifically, (1) we characterized the diversity and the abundance of gorgonians group; (2) explored their distribution patterns, and (3) assessed their population size structure. This study attempts to be a benchmark for the investigation of continental shelf habitats modified by anthropogenic pressure and to contribute to the general knowledge of pristine areas with habitat-forming species.

Results

Abundance of gorgonian populations. A total of 3140 colonies (1402 in the north and 1738 in the south), comprising seven gorgonian species (*Ainigmaptilon* sp., *Dasystenella acanthina*, *Fannyella rossii*, *Fannyella spinosa, Thouarella* sp.1, *Thouarella* sp.2, and *Thouarella variabilis*), an unbranched morphogroup (which included specimens from the genus *Onogorgia*, *Armadillogorgia*, *Primnoella* and *Arntzia*) and the family Isididae, were counted along six transects (Supplementary Table S1), occurring with a frequency of 64.4% in 1836 sampling units of 1 m^2. Based on our count data, we estimated more than 46000 and more than 97000 colonies for the north and the south region, respectively. Overall, *Thouarella* sp.1 was the most abundant (n = 597 total colonies across all transects) and the second most frequent species representing 19% of observed colonies present in 20% of the sampling units. *Thouarella* sp.2 was the second most abundant (n = 572), but the most frequent (20%) species. The family Isididae (n = 535, 17.8%), *Fannyella rossii* (n = 474, 17.5%) and *Thouarella variabilis* (n = 438, 15.4%) were the third, fourth and fifth most abundant and frequent species, respectively. The unbranched group (n = 280) was more abundant than *Dasystenella acanthina* (n = 189), but less frequent (5.4% and 7.5%, respectively). The other species accounted for less than 2% of the observed colonies, occurring in less than 3% of the sampling units. Generally, abundance of the gorgonians differed between the two study sections, being lower in the northern part. Only Isididae (n = 277) and *Dasystenella acanthina* (n = 87) abundance showed high values in the northern stations (Fig. 1).

Spatial distribution. Ripley's K analysis revealed a significantly clumped distribution of the family Isididae, *Thouarella* sp.1 and *Thouarella* sp.2 colonies at all scales (from 1 m^2 to whole transect). *Thouarella variabilis* showed a clumped distribution in the north, but a random distribution in the south. An opposite result for spatial distribution was found for *Dasystenella acanthina, Fannyella rossii* and Unbranched (Fig. 2). Gorgonian abundances varied markedly among the various stations ($F_{5,1179} = 53.3$, $p < 0.001$) (Fig. 3). In stn. 49, the Unbranched morphogroup was the group of gorgonians with the highest abundance (47 col/m^2) and mean density of 7.3 ± 11.5 col/m^2, while the least abundant species were *Fannyella spinosa* and *Ainigmaptillon* sp., with highest abundance of 20 and 19 col/m^2 and mean density of 1.3 ± 0.6 and 1.2 ± 0.4 col/m^2, respectively (Fig. 3).

Population size structure. The size-frequency distributions of the 7 species populations were unimodal (Fig. 4). Most of the gorgonian populations were positively skewed, indicating an asymmetrical distribution of size frequency and a high proportion of small colonies (0–10 cm) (Fig. 4 and Supplementary Table S2). In contrast, the two populations of the Unbranched morphogroup were not skewed, being dominated by medium-sized colonies (10–20 cm in the south and 50–60 cm in the north) (Fig. 4 and Supplementary Table S2). Most of the northern populations showed no significant kurtosis while in the south all the gorgonian populations, except Unbranched, showed significant kurtosis (Supplementary Table S2). Finally, in both studied areas, all gorgonian populations displayed the same size class distributions (Fig. 4).

Population structure. The structure of gorgonian populations gradually differed in both areas, with significant differences between north and south ($F_{1,1183} = 65.06$, $p < 0.001$) (Fig. 5).

The SIMPER analysis showed an average similarity in species composition which ranged from 17.89% to 31.68% (Supplementary Table S3). The number of species contributing up to 90% of the similarity was the same in the two sections (Supplementary Table S3). *Thouarella* sp.1 contributed most (25.14%) to the similarity in the

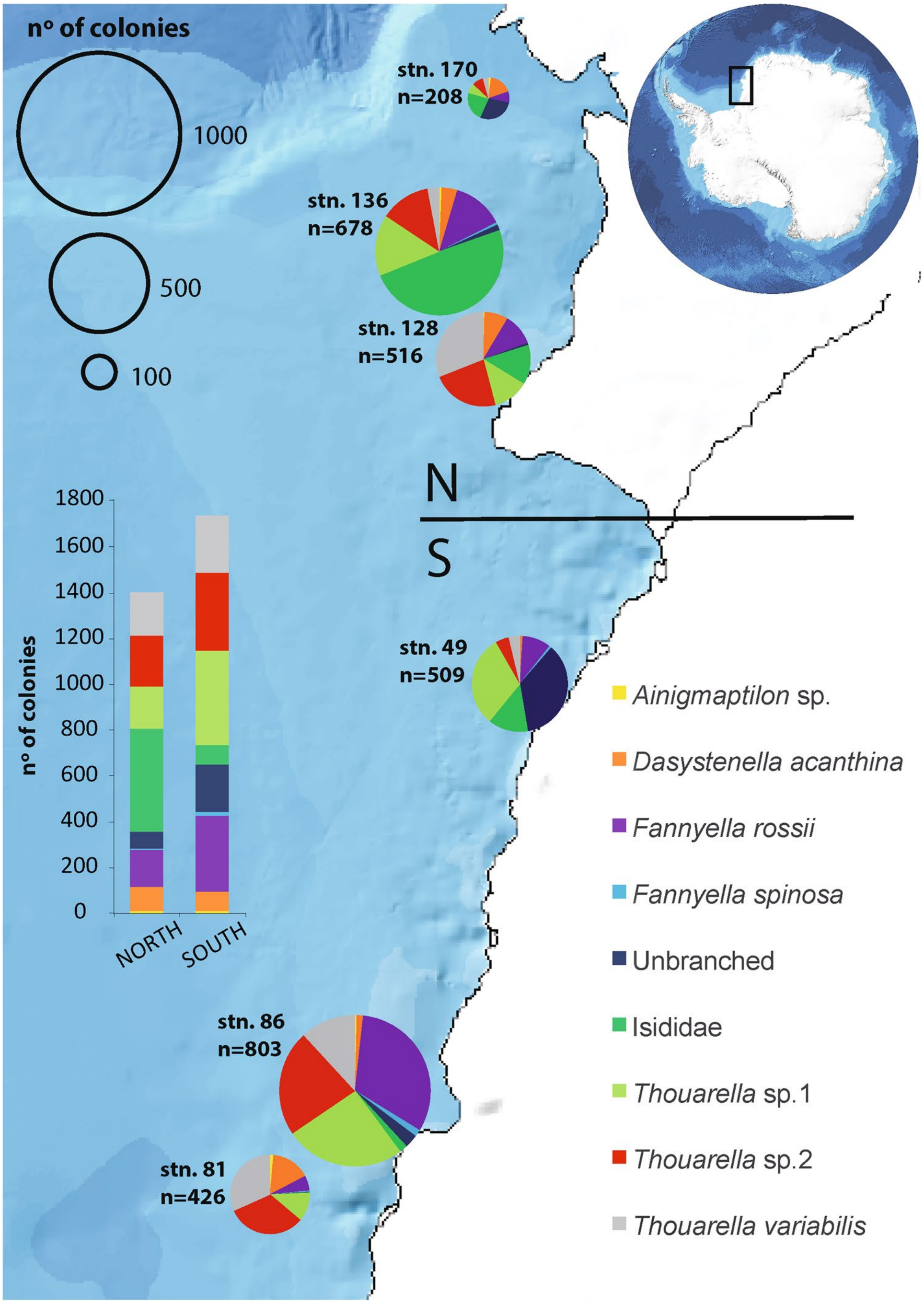

Figure 1. Composition, distribution and abundance of gorgonian species. The pie charts display the percentage of gorgonian taxa at each transect (n = number of colonies per transect). The size of the pie charts represents the abundance of the gorgonians. The histogram shows the abundance of gorgonian species per region (north: stations 128, 136, 170; south 49, 81, 86). Map of Antarctica was downloaded from http://www.ibcso.org/data.html[100]. The figure was generated with QGIS Version 2.12 http://www.qgis.org/it/site/.

northern transects, while the family Isididae was especially relevant in the southern transects (22.43% of contribution). Focusing on taxa dissimilarities, the family Isididae was the most important contributing with 17% of the average dissimilarity between north and south.

Discussion

This study focused on previously unknown extensive gorgonian assemblages in the southeastern Weddell Sea. Our results indicate that this region is a hotspot for gorgonian diversity in terms of both number of species and their abundance. The diversity of the studied gorgonian assemblages was similar to those reported on subtropical[68], Mediterranean shelf[41] and other Antarctic coastal areas[69]. Seven different species, a gorgonian morphogroup

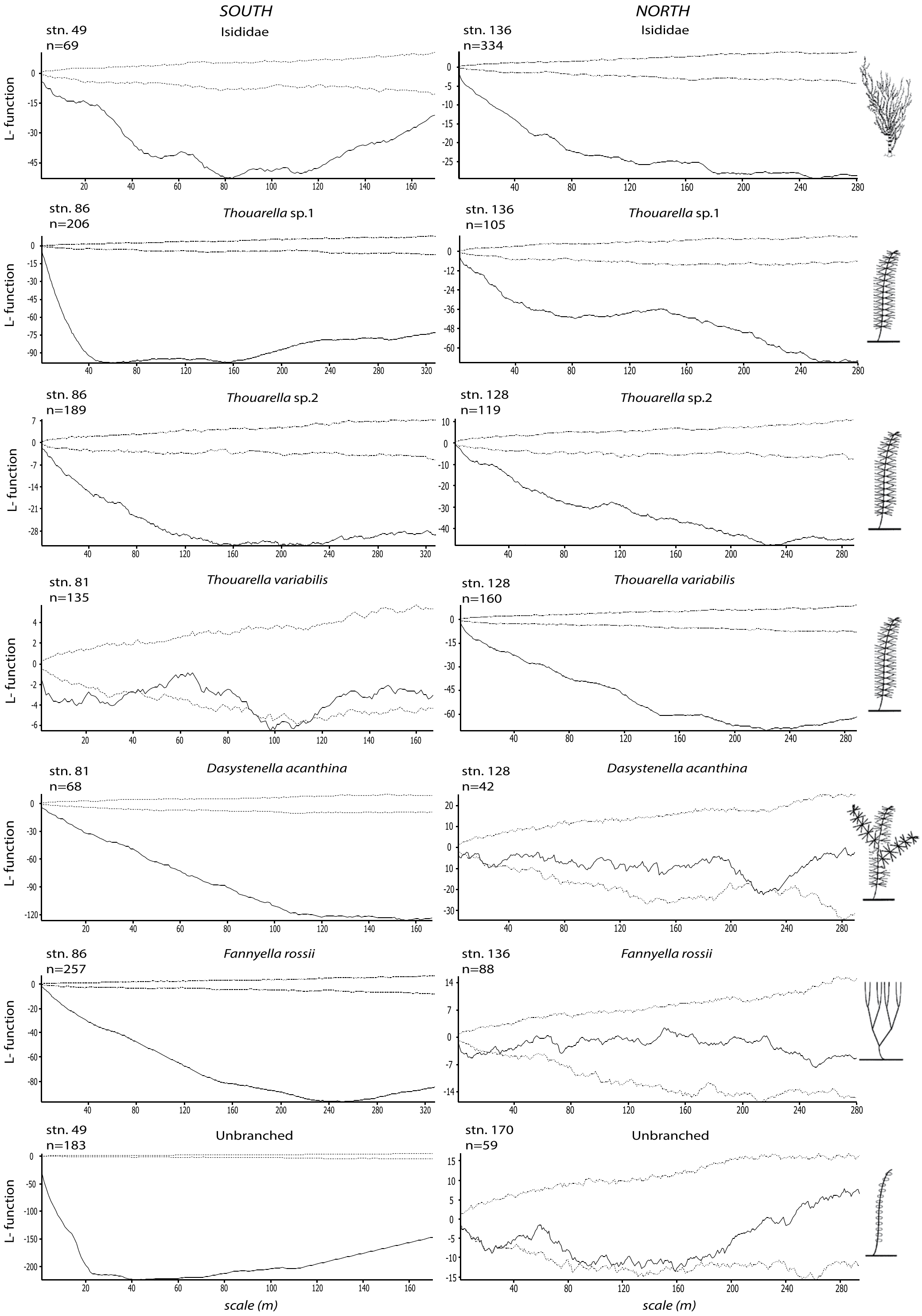

Figure 2. L-function (Ripley's K) for the most abundant species. Values below 95% confidence interval (dotted lines) indicate a statistically significant clumped distribution of colonies; values within the confidence interval indicate a random distribution; values above the confidence interval indicate a statistically significant over-dispersed distribution (n = number of colonies).

and a gorgonian family Isididae were observed to dwell between 250 and 350 m depth within the study area (Fig. 1), in agreement with previous findings in coastal areas of the Antarctic Peninsula[69]. On the other hand, gorgonian density observed in these multi-specific assemblages clearly exceeds (by ten-fold; 47 colonies/m^2) those reported for other Antarctic and Arctic shelf areas[70,71] (Supplementary Table S4). These high density values were similar to those found in temperate[72,73] and tropical[74,75] coastal assemblages (Supplementary Table S4). Despite extreme environmental conditions and the general theory that species richness decreases with increasing latitude,

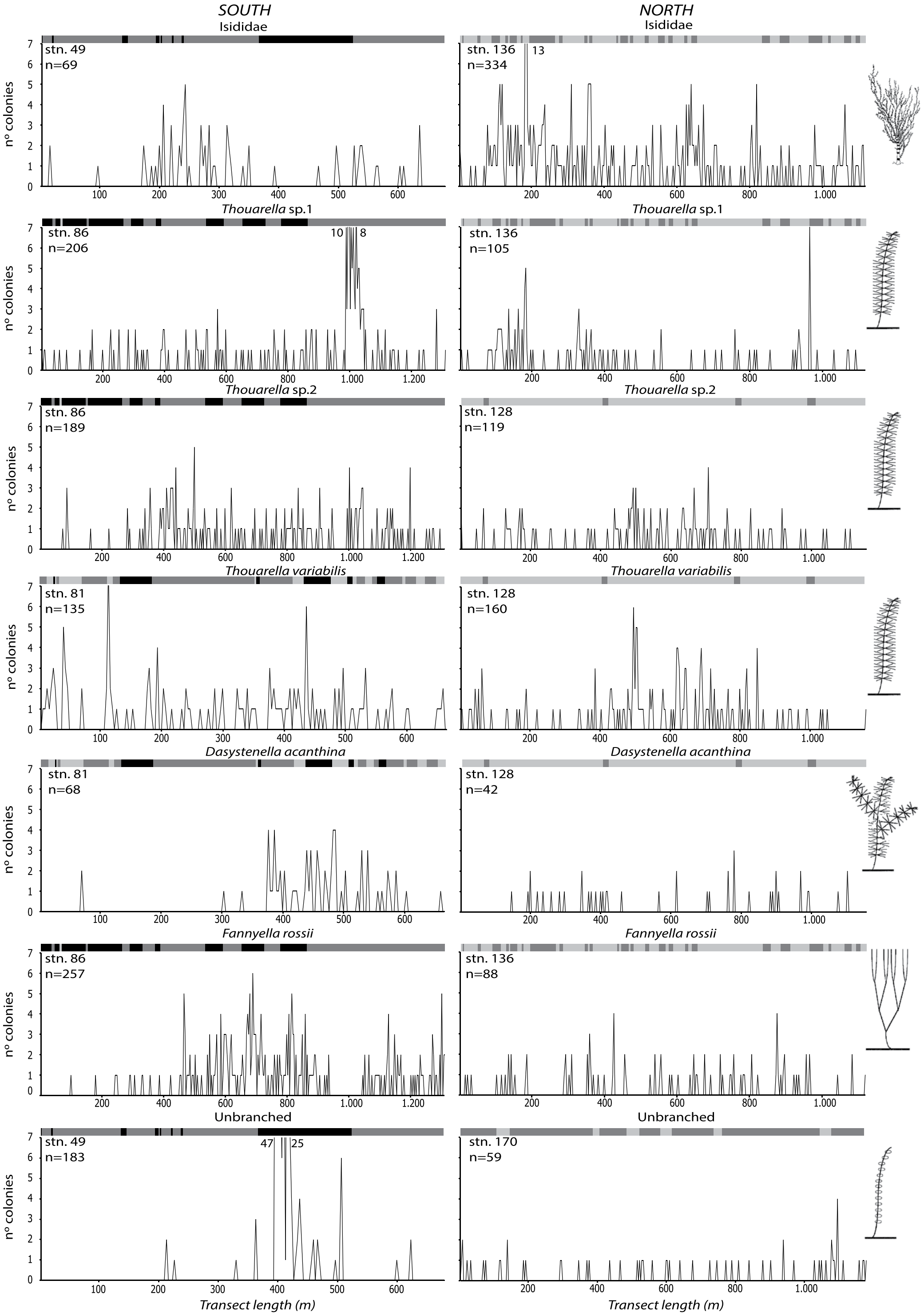

Figure 3. Density plots. Densities of the most abundant species are plotted at each station (n = number of colonies). Substrate type is indicated as black (coarse sediment), dark grey (intermediate sediment) and light grey (fine sediment).

it is also generally accepted that this theory is not strictly true and varies with species in the Southern Ocean[76,77]. In addition, benthic biomass in some Antarctic areas is larger than in temperate and subtropical areas[78]. Such dense three-dimensional communities cover large sections of the Antarctic continental shelf as well as the Mediterranean Sea[41] and deep undisturbed North Atlantic coral banks[44]. *Fannyella rossii* and the three species of genus *Thouarella* showed high abundances in each video transect (Supplementary Table S1). This highlights the unique abundance of these Antarctic gorgonian species[45]. Of additional note is their high density, with maximum

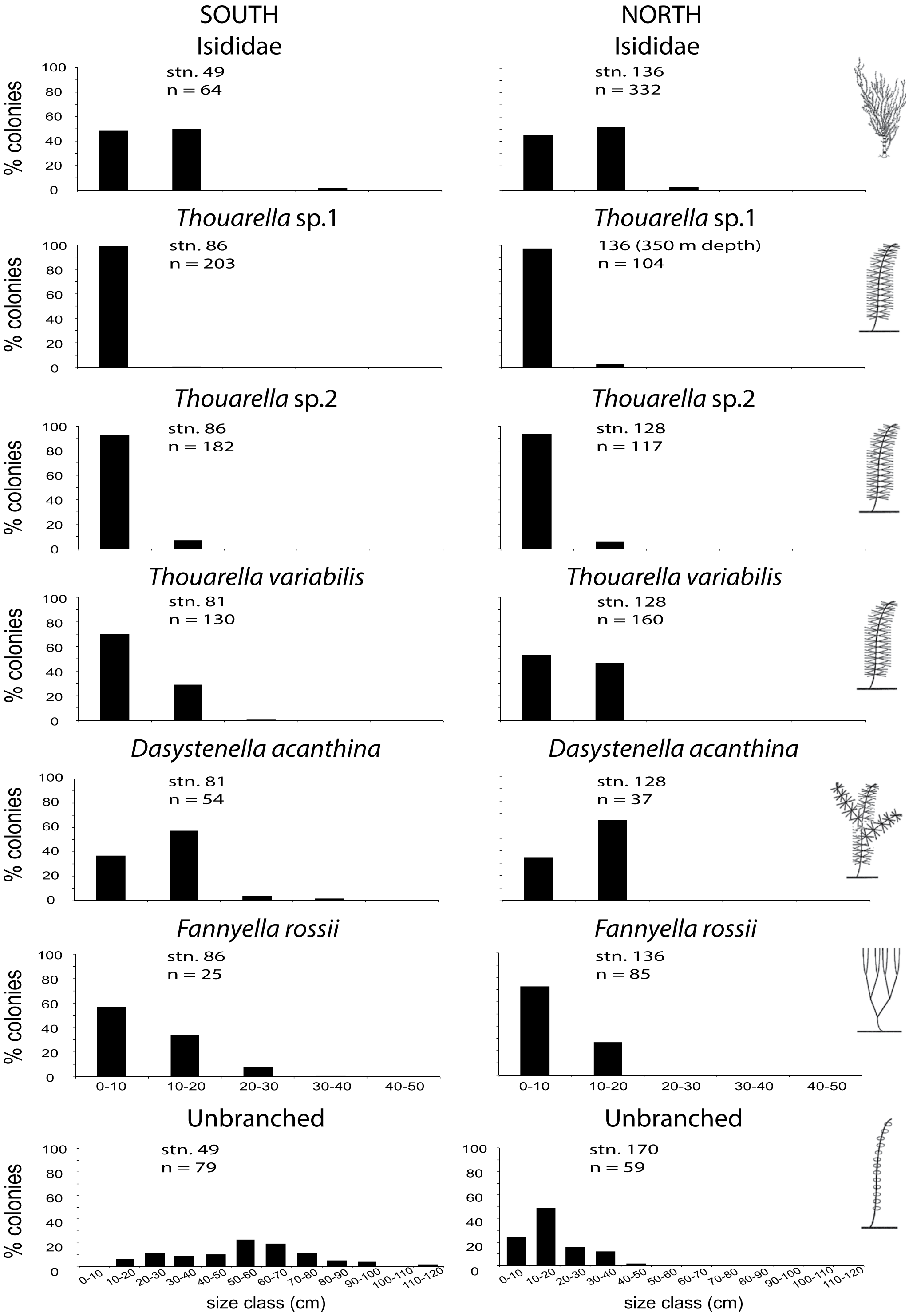

Figure 4. Size-frequency distribution of gorgonian populations (n = number of colonies).

values of 6 ind/m^2 for *Fannyella rossii* and 10 ind/m^2 for *Thouarella* sp.1 in the southern section (Supplementary Table S1).

All populations in this study were represented by many small colonies with a positively skewed colony size distribution (Fig. 4). The size structure of a population results from the action of biotic and abiotic factors and from the type, intensity, and frequency of disturbance to which individuals are exposed[79,80]. Positively skewed size frequency distribution implies that a population is in a healthy state and growing, since it includes an abundance of juveniles[81,82]. On the contrary, a negative skewness indicates a lack of recent recruitment and therefore it implies a risk of population decline[81,83]. Population size structure of all *Thouarella* and *Fannyella* species was mostly asymmetrical with many small colonies (Fig. 4), suggesting high recruitment rates[82]. The size structure also reflects the

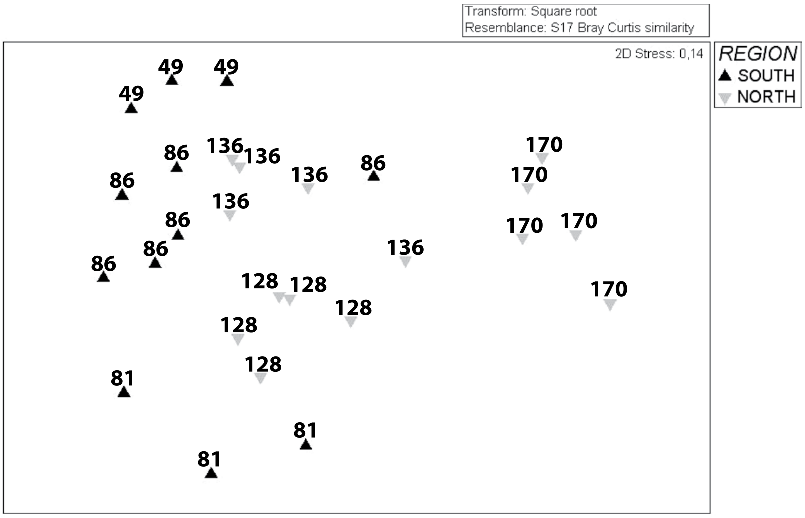

Figure 5. Non-metric multidimensional scaling (nMDS) ordination plot of abundance of gorgonian species in the south and north region of the SE Weddell Sea. Analysis performed on Bray-Curtis dissimilarities for abundance (colonies/m^2). Each point represents a subsample of 200 m length for each station.

growth and the development of each individual within the population, as well as past recruitment and mass mortality events. Unfortunately, due to their inaccessibility, only a few studies of gorgonian population size structure have been done on continental shelves[41]. Unbranched individuals seem to grow slowly and older without being replaced (low recruitment) with few small colonies (sexual juveniles) and dominance of large-sized individuals[41].

As a rule of thumb, because of their slow growth rate[84,85] and reproduction type, gorgonians are especially vulnerable to iceberg scouring[86,87], making their recovery very slow[17]. All gorgonian species described in this study reproduce by internal brooding. This means that the settlement of the larvae occurs at short distances from the parents[88] explaining the patchy distribution along all video transects. Some gorgonian species such as *Ainigmaptillon antarcticum* and *Primnoisis antarctica*, which are internal brooders, are also pioneer taxa appearing during the first stage of recolonization after iceberg scouring events with patchy distribution[86,87].

The high diversity and abundance of gorgonian assemblages on the Antarctic continental shelf, and the vast area covered by high densities of genus *Thouarella* are probably related to the low iceberg scouring pressure and oceanographic-ice conditions. Constant hydrodynamic conditions that increase particle suspension in the near-bottom water layers may also imply enhanced food availability for gorgonians on the continental shelf[89]. Strong currents are advantageous to the establishment of this group of organisms supplying them with food and continuously keeping them completely clear of sediment[90,91]. Moreover, based on our findings of high abundance and large sizes in the southern section of our study area, we hypothesize that it is little affected by iceberg scouring, thereby favouring the establishment of well-developed pristine gorgonian populations.

Reduced abundance of long-lived and habitat-forming species from the deep sea and continental shelves in shallow sublittoral habitats have attracted particular attention, given their disproportionate importance to ecosystem structure and function, and the social value of marine habitats[14]. Yet, factors responsible for such decline are mainly overexploitation and habitat destruction by bottom trawling and by-catch fishing[92]. Evidence of fishing activities with *Thouarella* spp. as by-catch has been reported in South Georgia[18]. Moreover, specimens from the genus *Primnoa* and the family Isididae from longline fisheries were found in the Ross Sea[19]. To our knowledge, our results are the first to show pristine populations of gorgonians with the highest abundance and largest size ever recorded on the Antarctic continental shelf. These populations are far more mature and better preserved than any other known population in Antarctica. Clearly, more research is needed to determine the locations of such refuges and to devise strategies to protect such gorgonian populations as well as the many other species interacting with them. The study of these pristine gorgonian populations may also provide basic knowledge on how other continental shelf and upper slope communities may have thrived in the decades before bottom trawling fishing ensued.

Methods

Study area.

The study area was sampled as part of the multidisciplinary PS82 (ANT XXIX/9) expedition on board R/V *Polarstern* from December 19, 2013, to March 5, 2014[93]. It is located in front of the Filchner Ronne Ice Shelf in the southernmost part of the Weddell Sea; a region poorly investigated due to the heavy sea ice conditions[93]. The small amount of data available from this area has made it an area of special relevance to better understand oceanographic conditions and to gain new insights into biodiversity patterns in this remote and pristine region[94]. The study area was divided into a south and a north section due to Brunt Ice Shelf, which may produce different oceanographic conditions[93].

ROV sampling procedure.

In order to study the composition and distribution of gorgonians, an inspection-class ROV (Remotely Operated Vehicle, Ocean Modules V8 Sii) was deployed at six stations in the area of the Filchner Trough (Supplementary Table S5). Three random stations (stn. 49, stn. 81, stn. 86) were recorded in the southern part of the continental shelf and three random stations (stn. 128, stn. 136, stn. 170) in its northern part closer to the shelf break. The ROV was equipped with a High Definition (HD) video camera (Kongsberg oe14–502) looking forward in an angle of 40–45° and two parallel lasers providing a reference scale of 4 cm on the video (see Knust and Schröder 2014[93] for more details on the ROV procedure). The ROV video material is available from the data publisher PANGEA at www.pangea.de (see Table S5 for DOIs).

Species identification. In order to confirm the taxonomic identification of the species observed in the videos, colonies of gorgonians were collected with an Agassiz Trawl (AGT) after the ROV deployments. Colonies were fixed and preserved in 10% formalin until analysed in the laboratory (see Supplementary Table S6 for taxonomic remarks on the identification of some groups of species). We identified 7 gorgonian species belonging to the family *Primnoidae* (*Ainigmaptilon* sp., *Dasystenella acanthina*, *Fannyella rossii*, *Fannyella spinosa, Thouarella* sp.1, *Thouarella* sp.2, *and Thouarella variabilis*), an unbranched morphogroup (flagelliform colonies with polyps distributed in whorls along the main stem of the colony), which included specimens of the genera *Onogorgia*, *Armadillogorgia*, *Primnoella* and *Arntzia*, and a bamboo coral group of the Family Isididae, (Supplementary Figures S1 and S2).

Video analysis. Quantitative video analysis was performed using the software SONY XDCAM Viewer. Every gorgonian observed within a width of 0.3 m (based on the laser beams) along each video transect was identified with a distance from the beginning of the transect according to the ROV's ultra-short baseline (USBL) position data.

Spatial distribution and size structure. We examined the species composition and quantified the frequency as the relative proportion of each species present for each sampling unit of the transect and the abundance as the total number of colonies across all the transects (see below). The most abundant species of gorgonians were used to compare their abundance, spatial distribution and size class in both the north and south areas. These results were displayed in density plots, obtained by transforming each transect into a string of contiguous quadrats of 1 m^2 (0.3×3.33 m) and counting the number of colonies of each species only inside each quadrat. A total of 1836 useful sampling units were obtained from the 6 transects.

The significance of the deviation from a random distribution was analysed with the one-dimensional version of Ripley's K-function second-order spatial statistic[95,96]. When the sample statistic is found within the bounds of the confidence interval at any point, it indicates complete spatial randomness; a significant positive deviation of the sample statistic indicates over-dispersion of the colonies, whereas a significant negative deviation indicates a clumped distribution[67].

To study population size structure, the maximum height of each observed gorgonian colony was measured using the Macnification 2.0.1 software on still images extracted from recorded footage[97]. The distance between the two laser beams was used to calibrate extracted images and measurements were performed on still images in which the laser beams were in the same plane as the colony base to reduce the error due to the perspective[55]. Based on previous studies, colony size class was defined for each 10 cm[55,82]. We considered as young colonies the smallest colonies that could be distinguished using the video analysis (2–5 cm in height)[80]. Size structure was also analysed in terms of descriptive statistics using distribution parameters such as skewness and kurtosis. Skewness is a measure of the symmetry of a distribution using its mean, reflecting the proportion of small versus large colonies in a gorgonian population; if skewness is significant the distribution is asymmetric. Kurtosis is a measure of the peakedness of a distribution near its central mode. A significant kurtosis value indicates longer tails than would be expected for a normal distribution, and therefore a particular colony size prevails in the population. Only transects with more than 40 colonies were studied for population size structure in order to generate meaningful skewness and kurtosis estimates.

Population size structure and density data from other areas of the continental shelf. To compare our data with that of other gorgonian populations dwelling on the continental shelf of other seas, we compiled data on maximum abundance, mean density and maximum height from previous studies using ROV observations. Overall, we compiled population structure data for 36 taxa and 12 different study areas (Supplementary Table S4).

Assemblage structure. A non-metric multi-dimensional scaling (nMDS) ordination analysis was performed based on the Bray–Curtis similarity measure using square-root-transformed abundance data. For visualization purposes, data are presented for each 200 m length. Furthermore, a similarity percentage procedure analysis, SIMPER[98], was performed to identify the relative contribution of each species to average similarities between areas. A non-parametric analysis of variance, PERMANOVA[99], was applied using Bray-Curtis distance for the multivariate analyses. Statistical analyses were computed using the program Primer v6 with the PERMANOVA + add-on package.

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Author Contributions

J.M.G. and N.T. conceived the research. R.Z.G. identified the species. L.F. and C.R. led the R.O.V. surveys and provided the video material, S.A. assisted in the surveys. J.S. and S.A. analysed the videos and treated the data. S.A. and N.T. wrote the manuscript. All authors revised the manuscript.

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Una selva animal bajo un desierto de hielo

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Una selva animal bajo un desierto de hielo

Los fondos marinos de la alta Antártida son los mejor conservados del planeta

Durante más de seis meses al año, los mares de Weddell y Ross, conocidos también como la alta Antártida, están recubiertos por una capa de hielo de más de un metro de espesor. En esta región, la temperatura de los fondos marinos, que alcanzan una profundidad de entre 50 y 500 metros, se ha mantenido estable durante cientos de miles de años. Allí se han descubierto comunidades marinas que presentan una de las más altas diversidades del planeta. Este excepcional paradigma de la diversidad biológica es aún hoy un aspecto que sorprende a los científicos y forma parte de una de las líneas de investigación más importantes del océano Antártico.

Comunidades dominadas por esponjas, gorgonias, ascidias y briozoos cubren por completo el lecho marino a lo largo de miles de kilómetros cuadrados. Tales formaciones han sido escasamente afectadas por las perturbaciones naturales desde hace millones de años y, debido a su inaccesibilidad, no han sufrido las consecuencias de las actividades humanas. Esas circunstancias han hecho de estos fondos los mejor conservados del planeta, lo que los convierte en un laboratorio ideal para conocer y entender la vida y los ecosistemas marinos en un ambiente inalterado.

Los organismos de los fondos presentan características fisiológicas y ecológicas que les permiten vivir en condiciones extremas de baja temperatura y escasez de luz. La vida que crece dentro del hielo superficial es una de las claves para explicar este fenómeno. Allí proliferan millones de microalgas con un elevado poder nutritivo y que caen al fondo cada verano cuando el hielo se funde. De esta manera, a las comunidades mejor preservadas del planeta no les ha faltado nunca el mejor alimento posible y han evolucionado lentamente para llegar a desarrollar una elevada biodiversidad, que se ha descubierto hace tan solo unos pocos años gracias a los trabajos realizados por nuestro grupo.

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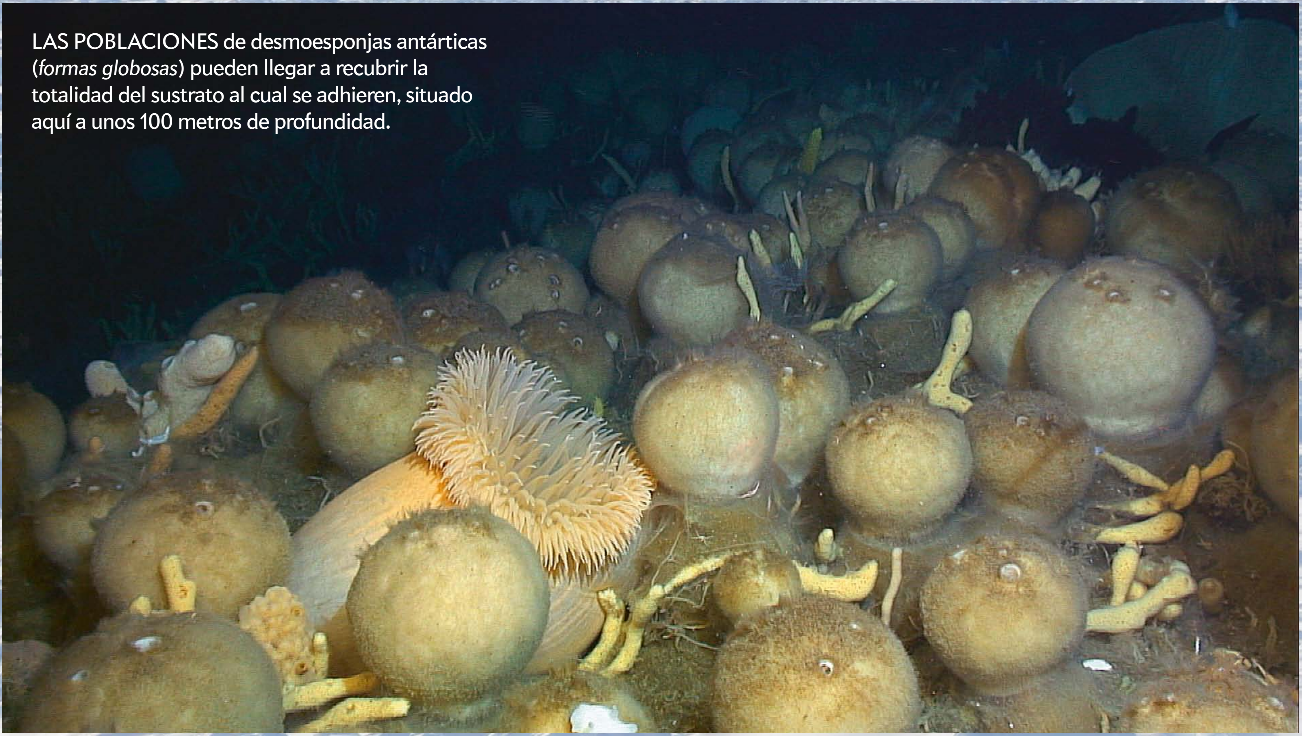
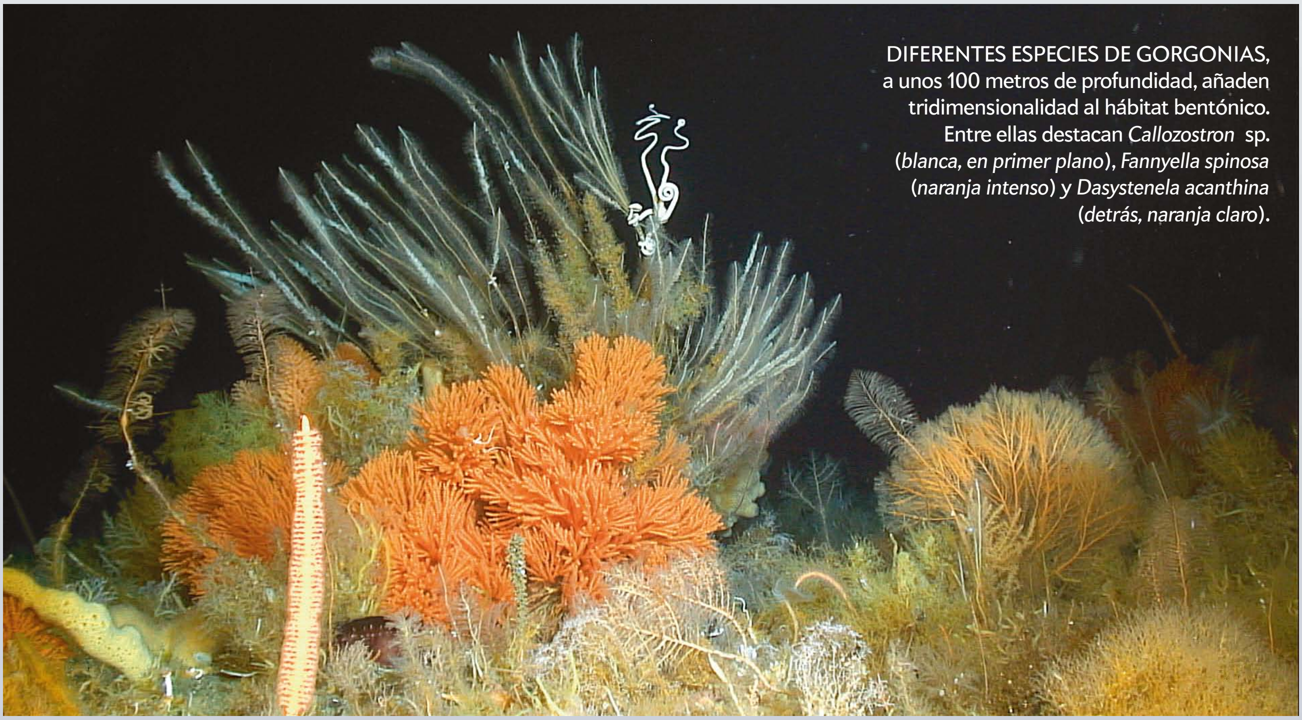


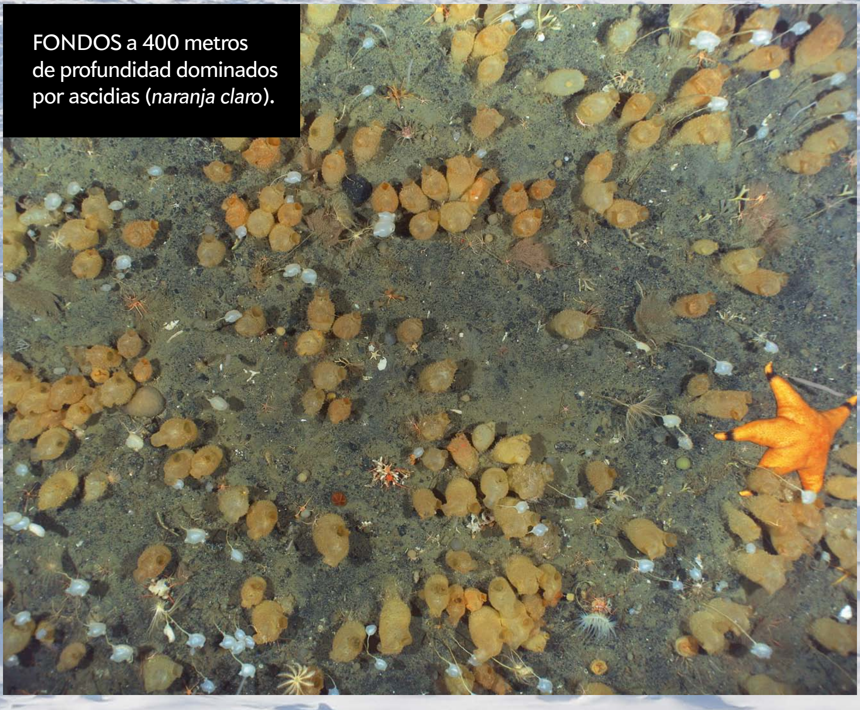
LAS POBLACIONES de desmoesponjas antárticas (*formas globosas*) pueden llegar a recubrir la totalidad del sustrato al cual se adhieren, situado aquí a unos 100 metros de profundidad.

THOMAS LÜNDALV (*desmosponjas y gorgonias*), INSTITUTO ALFRED WEGENER DE INVESTIGACIONES POLARES Y MARINAS (*ascidias*), STEFANO AMBROSO (*imagen de fondo*)



DIFERENTES ESPECIES DE GORGONIAS, a unos 100 metros de profundidad, añaden tridimensionalidad al hábitat bentónico. Entre ellas destacan *Callozostron* sp. (*blanca, en primer plano*), *Fannyella spinosa* (*naranja intenso*) y *Dasystenela acanthina* (*detrás, naranja claro*).

LA RIQUEZA NATURAL del fondo marino de la Antártida se debe a la fertilidad de los hielos, dentro de los cuales se encuentra una infinidad de microalgas que representan el primer eslabón de la cadena trófica antártica (*imagen de fondo*).



FONDOS a 400 metros de profundidad dominados por ascidias (*naranja claro*).

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LA VIDA EN CONDICIONES EXTREMAS

LA PARADOJA DE LA BIODIVERSIDAD MARINA ANTÁRTICA

Stefano Ambroso, Janire Salazar, Josep-Maria Gili y Rebeca Zapata Guardiola

El estudio de lugares prístinos es de gran importancia para conocer los océanos tal como eran sin el impacto del ser humano. Por efecto de las condiciones ambientales extremas, la lejanía de los otros continentes y por su profundidad, a causa del peso del hielo continental, la plataforma continental antártica ofrece una gran oportunidad para entender mejor cómo sería un ecosistema prístino. Además de una elevada biodiversidad, los organismos bentónicos antárticos presentan pautas de distribución espacial y demográfica diferentes de las comunidades de las plataformas continentales de otros mares y océanos del mundo. Eso hace que las comunidades bentónicas antárticas se parezcan más de lo que cabría pensar a aquellas comunidades del planeta con la más alta biodiversidad conocida.

Palabras clave: biodiversidad marina, conservación, Antártida, bentos, gorgonias.

Tras más de una centuria de explotación de los recursos marinos en todos los océanos del planeta Tierra y de considerarlos como el gran imbornal o cubo de basuras de la humanidad, quedan muy pocos sitios donde la huella del hombre no esté presente. Los efectos o las consecuencias de la contaminación, de los vertidos de todo tipo, de la extracción indiscriminada de recursos y, últimamente, del cambio climático son patentes y visibles en diferentes grados de afectación en todos los mares y océanos del mundo. Pero aún quedan algunos lugares donde, por la lejanía de la actividad humana, la vida marina permanece casi intacta o, cuando menos, sin los efectos producidos por el ser humano. Un claro ejemplo son las islas en medio del océano Pacífico o los grandes y extensos fondos abisales. Pero incluso a estos últimos, casi inaccesibles, han llegado hoy en día vertidos o elementos contaminantes arrastrados por las corrientes marinas. Mucho más complicada es la situación en la superficie de los océanos con las llamadas «islas de plástico».

El estudio de lugares realmente prístinos es de gran importancia para poder conocer cómo eran originalmente antes de que ya no quede ninguno. Uno de los motivos más importantes para conocer los océanos sin el impacto del ser humano es saber qué grado de degeneración o destrucción experimentan los fondos marinos. Es vital desarrollar medidas de restauración o recuperación más efectivas y adecuadas, de acuerdo a cómo deberían ser los fondos marinos, sin introducir cambios artificiales que, muy posiblemente, generen todavía más alteraciones en el medio.

> «EL ESTUDIO DE LUGARES REALMENTE PRÍSTINOS ES DE GRAN IMPORTANCIA PARA PODER CONOCER CÓMO ERAN ORIGINALMENTE ANTES DE QUE YA NO QUEDE NINGUNO»

¿POR QUÉ LA ANTÁRTIDA?

La investigación de los fondos marinos más prístinos del planeta Tierra nos llevó a estudiar la vida que se encuentra en las plataformas continentales de la alta Antártida, zonas más interiores de los grandes mares antárticos como son el mar de Weddell y el mar de Ross. Estas plataformas están cubiertas de hielo marino la mayor parte del año (Lange, Ackley, Wadhams, Dieckmann y Eicken, 1989). Esta capa de hielo llamada *banquisa*, de unos dos metros de espesor, se forma y se funde cada año desde hace más de 25 millones de años (Figura 1). La persistencia de la capa de hielo marino ha preservado estas áreas durante miles de años de las perturbaciones naturales y, también, de las posibles alteraciones que podría ocasionar la actividad humana. La banquisa se extiende más allá de la zona

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Figura 1. El estudio de las plataformas continentales de la alta Antártida nos puede proporcionar una referencia de un hábitat con poca influencia humana para conocer mejor el estado de los fondos marinos de todo el planeta. En la imagen, panorámica del mar de Weddell.

exterior de las plataformas del propio continente antártico, donde los glaciares van generando periódicamente nuevos icebergs que producen los principales impactos naturales sobre el fondo marino.

Los icebergs que se desprenden de los glaciares del continente antártico son la perturbación natural más importante, o casi la única, que afecta a los fondos marinos de las plataformas antárticas (Figura 2). Las masas de hielo flotante se arrastran durante días o semanas sobre el fondo, afectan a grandes distancias y crean un hábitat complejo formado por un mosaico de zonas perturbadas y no perturbadas. Estos fondos parcial o totalmente perturbados serán recolonizados por organismos de zonas próximas, lo cual dará inicio al proceso de sucesión. Los estadios iniciales de este proceso se caracterizan por una baja abundancia y diversidad, y por un bajo recubrimiento del sustrato. Los primeros colonizadores tienen, mayoritariamente, un crecimiento rápido y una complejidad estructural baja, mientras que los estadios finales de la sucesión presentan una elevada riqueza de especies y una biomasa excepcionalmente alta (Figura 3). Estas son situaciones que se dan en otros tipos de sucesión ecológica: la recuperación de un área forestal incendiada, los fondos dañados por la pesca de arrastre cuando se deja de pescar, etc. Aunque se calcula que tan solo un 5 % de los fondos de la alta Antártida han sido afectados por la acción de icebergs en el último milenio (Gutt, 2000), el impacto es muy alto, ya que las comunidades que son destruidas tienen millones de años de historia (Aronson y Blake, 2001). Cualquier fenómeno ambiental que pueda aumentar el régimen habitual de liberación de icebergs tendrá una repercusión capital sobre la vida de los fondos antárticos. En este aspecto, el fenómeno a tener más en cuenta es el incremento de temperaturas en todo el planeta a causa del calentamiento global.

En la campaña antártica ANTXXIX/9, llevada a cabo durante el 2013 y el 2014 a bordo del barco de investigación *Polarstern,* se pudo acceder a zonas habitualmente inaccesibles del sudeste del mar de Weddell, concretamente a la plataforma de hielo de Filchner-Ronne. Aprovechando este hecho casi excepcional, se estudiaron los fondos marinos de alrededor de 300 metros de profundidad (Ambroso et al., 2017). El estudio se hizo mediante la utilización de robots submarinos que permitieron obtener imágenes registradas a lo largo de un recorrido de unos 6 km de longitud. Se practicaron transectos con robot de lugares que nunca

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Figura 2. A la derecha, marca de arrastre hecha por un iceberg como el de la imagen de la izquierda. Esta es la perturbación natural más importante que afecta a los fondos marinos de las plataformas antárticas. Cualquier fenómeno ambiental, como el calentamiento global, que aumenta el régimen de liberación de icebergs, tendrá consecuencias importantes en la vida de los fondos antárticos.

antes se habían explorado y que se han conservado sin perturbaciones antropogénicas de ninguna clase. Las imágenes mostraban fondos marinos que se podían calificar de excepcionales por su riqueza biológica. En gran parte de la superficie del fondo marino explorado no había espacio que no estuviese ocupado por organismos sésiles (esponjas, cnidarios, briozoos, etc.) con una gran riqueza de fauna epibionte, además de peces y crustáceos. Aunque sabíamos por estudios previos (Gutt y Starmans, 1998) que en las plataformas continentales de la Antártida la biodiversidad bentónica, definida como la riqueza de especies que habitan en el fondo marino, es de las más elevadas de todos los océanos del planeta, nos sorprendió que en un lugar que durante años ha estado cubierto de hielo marino encontrásemos tanta o más diversidad de la que se conoce hoy en día en los fondos antárticos.

> «EL CONTINENTE ANTÁRTICO QUEDÓ PARCIALMENTE AISLADO DEL RESTO DEL PLANETA CUANDO SE FORMÓ LA CORRIENTE CIRCUMPOLAR ANTÁRTICA HACE UNOS 35 MILLONES DE AÑOS»

Este estudio ha demostrado que, además de una elevada biodiversidad, los organismos bentónicos antárticos presentan pautas de distribución espacial y demográfica diferentes de las comunidades de las plataformas continentales de otros mares y océanos del mundo que han estado afectadas en diferentes grados por las perturbaciones antropogénicas. En la Antártida, las poblaciones de especies sésiles como gorgonias, esponjas o briozoos, además de ser muy densas, presentan individuos o colonias de diferentes edades fruto de un largo proceso de colonización y crecimiento (Figura 4). Se puede intuir muy fácilmente una gran estabilidad ambiental y una baja mortalidad natural. Las pautas de distribución encontradas en este estudio son, pues, un referente para el resto de comunidades. Cuanto más se parezcan las pautas de distribución de organismos bentónicos de otros mares y océanos a las encontradas en los fondos antárticos, más podremos decir que se encuentran en un buen estado de conservación. Así, el estudio de los fondos antárticos nos permite demostrar la gran importancia de conocer la vida en lugares realmente prístinos para poder saber cómo eran los fondos de las plataformas marinas de los océanos del planeta antes de que la actividad del ser humano las alterase. Además, es muy difícil determinar cuándo o cómo se ha perturbado una comunidad bentónica y si lo que estamos observando es realmente prístino. Tener este referente antártico marca un paso importante para conocer mejor el estado de los fondos marinos de profundidad media en todo el mundo.

¿POR QUÉ EXISTE ESTA DIVERSIDAD TAN ELEVADA EN LOS FONDOS ANTÁRTICOS?

El continente antártico quedó parcialmente aislado del resto del planeta cuando se formó la corriente circumpolar antártica hace unos 35 millones de años. A partir de aquel momento, la circulación atmosférica cambió drásticamente, las temperaturas bajaron rápidamente y el continente se cubrió de hielo. Con esta cobertura de hielo, dejaron de llegar sedimentos finos arrastrados por las aguas fluviales y, a diferencia del resto de plataformas continentales de todo el mundo, las antárticas no se cubrieron de sedimentos. De esta manera, mientras que las llegadas masivas de sedimentos finos eliminaban gran parte de la fauna sésil de los fondos de plataforma de casi todo el mundo, las comunidades antárticas recibieron muy pocos sedimentos con una medida más gruesa, arrastrados por los glaciares. Por eso, la vida bentónica ha podido persistir millones de años (Gili et al., 2006). Así, la vida marina de la Antártida ha evolucionado ajena a la última gran extinción que hubo en los océanos y ha podido generar un gran número de especies que son endémicas del océano Antártico. De hecho, el nivel de endemismo de las especies antárticas es muy elevado: en algunos grupos como los peces es del 90 % y en otros es fácil que sea de más del 50 % (Arntz, Brey y Gallardo, 1994). El aislamiento ambiental y físico, además de una larga historia en solitario, son las explicaciones aceptadas de este fenómeno biogeográfico.

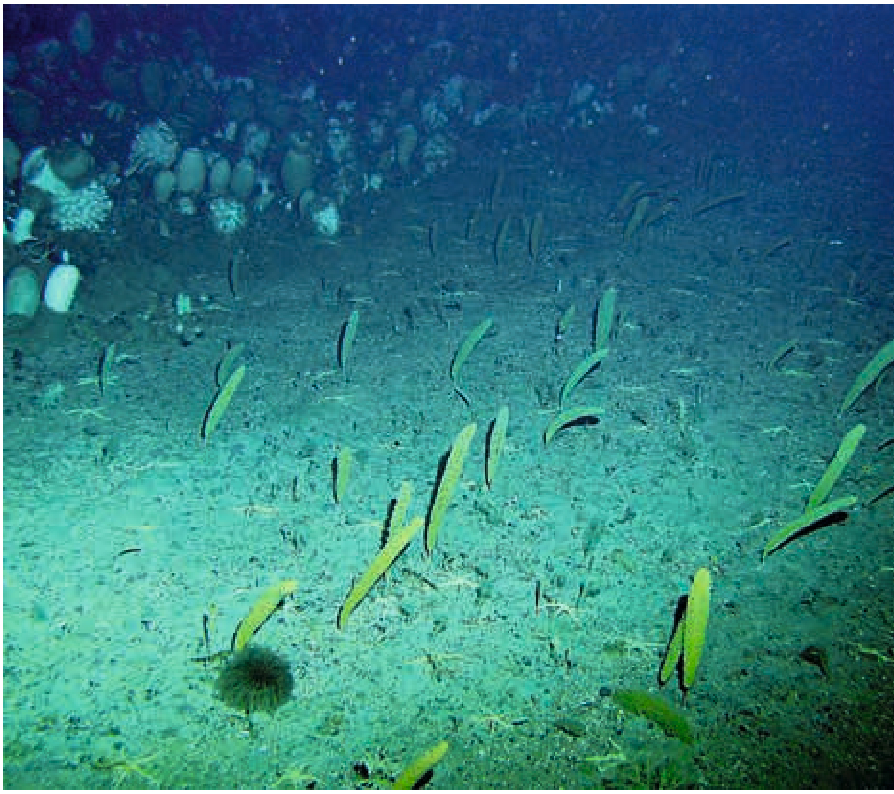
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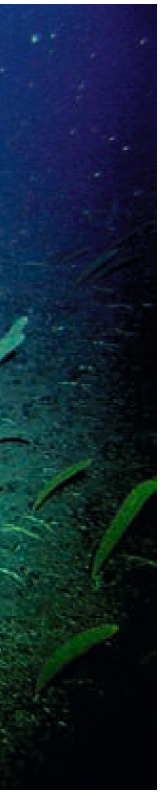
Figura 3. Mosaico de zonas perturbadas (en primer término), con una población de una gorgonia pionera (*Ainigmaptillon* sp.), y no perturbadas (en segundo término), con una comunidad caracterizada por una complejidad estructural mucho mayor.

La elevada biodiversidad de los fondos antárticos también se ha explicado por otros factores ambientales y biológicos (Figura 5). Entre los primeros, lo más importante es la estabilidad ambiental, con unas aguas que no varían su temperatura, entre 1 y –1° C, a lo largo de todo el año y a lo largo de miles de años. Entre los segundos, es destacable la baja cantidad de depredadores de las especies bentónicas que existen en la Antártida, ya que las bajas temperaturas han hecho que grandes depredadores como crustáceos decápodos o tiburones, entre otros, no puedan sobrevivir allí. Las aguas frías antárticas están también muy cargadas de nutrientes y eso permite elevadas tasas de producción primaria. Estas elevadas tasas de producción primaria son la razón principal de la elevada cantidad de vertebrados que se desarrollan en aguas antárticas.

Una de las preguntas más habituales hace referencia al origen de tanta diversidad en un lugar en que las condiciones ambientales son tan extremas. Las bajas temperaturas son otra vez uno de los factores clave. Desde hace millones de años, las plataformas antárticas se han cubierto de una capa de hielo marino en la superficie que se mantiene durante el largo invierno austral para fundirse los meses de verano. El hielo marino es uno de los ecosistemas más productivos del mundo (Thomas y Dieckmann, 2002). En su interior, gracias a la sal que queda atrapada durante el proceso de congelación, se favorece la formación de un sistema de millones de pequeños canales, donde se permite el desarrollo de un ecosistema muy singular. Un ecosistema dominado por microalgas (diatomeas y otros grupos de fitoplancton), rodeadas por una rica comunidad de bacterias y otros microorganismos. La fotosíntesis es una máquina que nunca se para. Las microalgas sirven de alimento a la comunidad de organismos de su alrededor, y estos, mediante los productos de excreción de su metabolismo, generan nutrientes esenciales para las algas; así, el ecosistema tiene una actividad constante a pesar de las bajas temperaturas. A causa del poco espacio que tienen las microalgas dentro del hielo, no se pueden multiplicar y por tanto, acumulan grandes cantidades de sustancias de reserva en su interior, sobre todo lípidos (muchos de los cuales del grupo omega-3), que además les sirven para mantener la impermeabilidad de las paredes celulares. Durante más de seis meses las microalgas convierten el hielo marino en un reservorio del mejor alimento que se puede generar en los océanos. Cuando llega la primavera austral, el hielo se funde y las microalgas que se liberan del hielo empiezan a crecer rápidamente hasta formar,



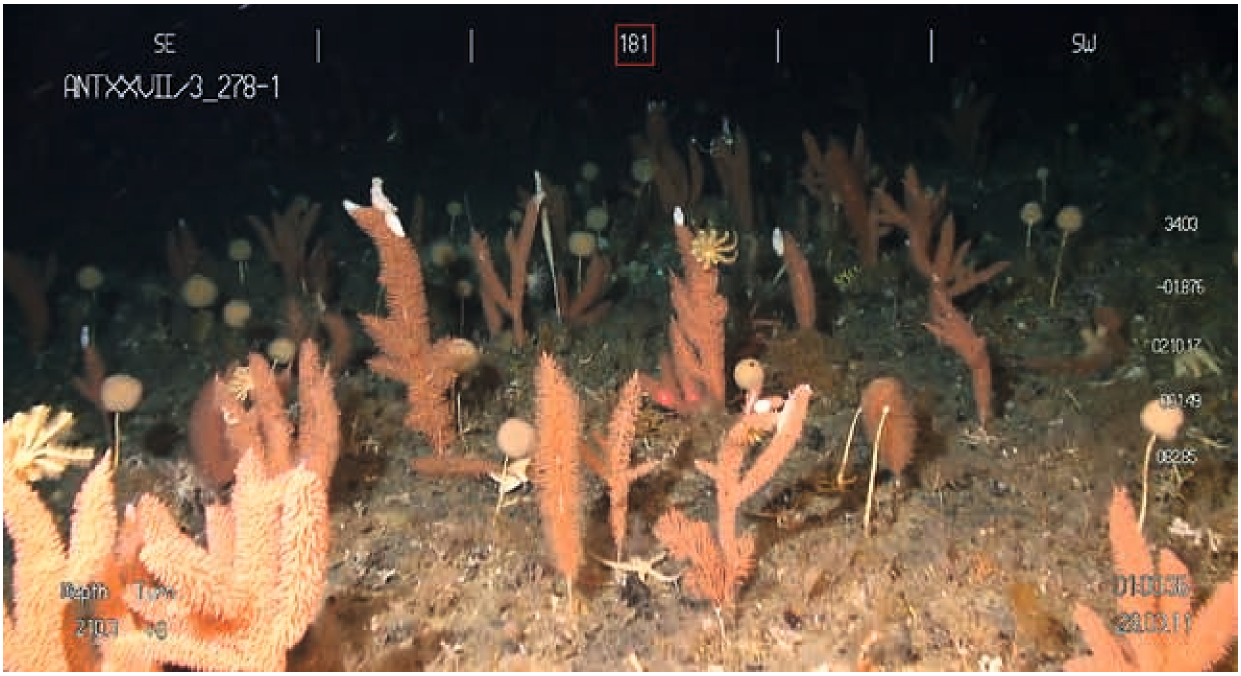


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Figura 4. Población muy densa de gorgonias, esponjas y briozoos, con individuos o colonias de diferentes medidas. En la Antártida las poblaciones de especies sésiles, además de una alta densidad, presentan individuos de diferentes edades fruto de un largo proceso de colonización y crecimiento.

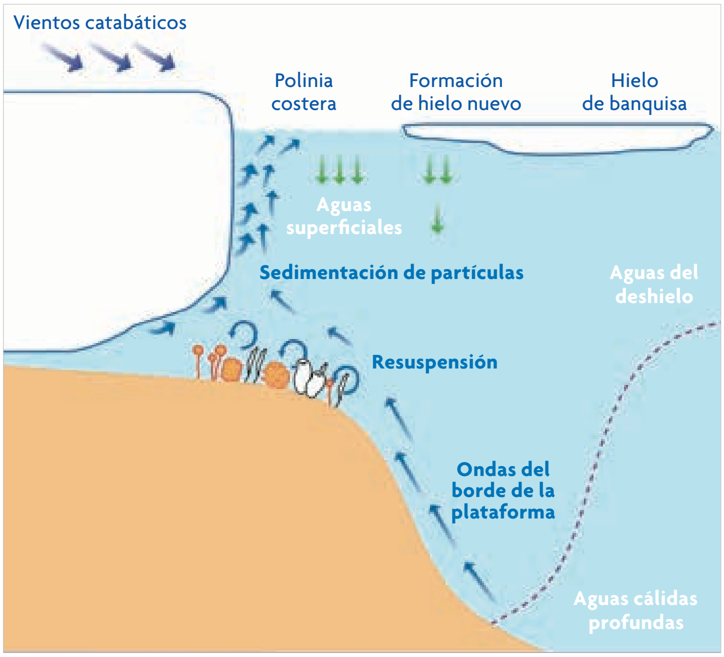
muchas veces, largas cadenas que caen rápidamente hacia el fondo marino.

Cada primavera, los fondos antárticos se ven fertilizados por millones de toneladas de un alimento de primera calidad y que, además, como la temperatura es muy baja, no se descompone (Figura 6). Este alimento que se acumula en los fondos marinos forma lo que se conoce como «alfombras verdes», que pueden alimentar durante meses la vida que se encuentra en el fondo de las plataformas antárticas. Pero las cadenas de microalgas que precipitan desde la superficie no son la única fuente de alimento de los organismos bentónicos. Cuando el hielo se funde, el krill, que con más de mil millones de toneladas es el invertebrado más abundante del océano Antártico, consume grandes cantidades del fitoplancton liberado del hielo marino. El krill se alimenta tan rápido que no puede digerir la mitad de lo que come, y lo excreta en forma de paquetes fecales (Arntz et al., 1994). Estos paquetes caen rápidamente al fondo y en su interior aún hay un gran número de microalgas frescas que se suman a las que ya han precipitado al fondo marino como fuente de alimento de los organismos sésiles. Así, la elevada biodiversidad de las comunidades bentónicas antárticas también se puede explicar gracias a que durante millones de años a estas comunidades no les ha faltado nunca un alimento rico y muy abundante que permanece fresco durante meses debido a las bajas temperaturas. Esta lluvia continua de alimento es una parte fundamental de la relación entre la producción planctónica y el sistema bentónico que se llama *acoplamiento bentopelágico*. La alta disponibilidad de alimento y su alta calidad va a la par con la baja demanda energética de muchas especies, lo que se ha comprobado con el bajo consumo de oxígeno debido a las bajas temperaturas. Por ejemplo, en moluscos bivalvos antárticos el consumo de oxígeno es de uno a dos órdenes de magnitud inferior al de las especies de mares templados.

«EN MOLUSCOS BIVALVOS ANTÁRTICOS, EL CONSUMO DE OXÍGENO ES DE UNO A DOS ÓRDENES DE MAGNITUD INFERIOR AL DE LAS ESPECIES DE MARES TEMPLADOS»

LAS COMUNIDADES BENTÓNICAS ANTÁRTICAS: BIODIVERSIDAD, ESTRUCTURA Y DINÁMICA

En estudios previos en los que se ha comparado la diversidad antártica con otras regiones del planeta, se ha podido evidenciar que algunos grupos de organismos como poliquetos, anfípodos o equinodermos, entre otros, presentan una complejidad estructural y diver-



Jordi Corbera. Figura modificada de Gili, Coma, Orejas, López-González y Zabala, 2001

Figura 5. Diagrama de los procesos ligados a la llegada de alimento a las comunidades bentónicas de la alta Antártida. Durante los meses de invierno, las microalgas crecen en los pequeños canales al interior de las placas de hielo y acumulan grandes cantidades de reserva de nutrientes en su interior. Cuando llega el deshielo en primavera, las microalgas se liberan del hielo y empiezan a crecer rápidamente, formando largas cadenas que caen al fondo marino. Las flechas en verde representan la caída de plancton del hielo marino al fondo, mientras que las flechas azules representan las corrientes de afloramiento.

sidad más alta en el océano Antártico que en otras regiones como Hawai o Gran Bretaña (Clarke, Aronson, Crame, Gili y Blake, 2004). Además, la abundancia de organismos es un aspecto que hay que resaltar de la Antártida: en términos de biomasa, se sabe que hay un orden de magnitud de diferencia entre el océano Ártico y el Antártico. Hay que destacar también un aspecto importante como es la gran longevidad de las especies que forman parte de las comunidades bentónicas antárticas, aunque hoy en día solo se conoce la edad aproximada de algunas gorgonias, esponjas, estrellas de mar, moluscos y crustáceos. Los lentos ritmos de crecimiento junto a los largos ciclos de vida de estos invertebrados antárticos les han permitido crear comunidades maduras y altamente estructuradas. En el caso de las gorgonias del género *Thouarella* se han podido estimar edades de entre 650 y 1.100 años. Estos ejemplares recogidos recientemente en la alta Antártida forman parte de la fauna actual y son el resultado de una larga y compleja historia evolutiva (Martinez-Dios, Domínguez-Carrió, Zapata-Guardiola y Gili, 2016).

Desde el punto de vista espacial, la comprensión de los procesos que inciden en la distribución, la abundancia y las interacciones de las especies es una de las principales líneas de investigación dentro de la ecología de los organismos antárticos. En este aspecto, la distribución agrupada que presentan la mayoría de las especies de gorgonias antárticas se vería relacionada con la presencia de una larva lecitotrófica, que favorecería el rápido asentamiento después de su liberación. Se ha observado en *Thouarella variabilis* la presencia simultánea de gametos de dos clases de medidas tanto en colonias macho como en colonias hembra, lo cual evidencia la presencia de diferentes generaciones al mismo tiempo, que hace posible una gametogénesis continua en que las larvas serían liberadas durante todo el año, y gracias a la continuada resuspensión de la materia orgánica depositada en el fondo marino durante la primavera antártica, se haría posible el éxito del asentamiento de las larvas. Estas especies también se ven afectadas por las relaciones epibentónicas (depredación, ruptura de las ramas por asentamiento), y por este motivo son las zonas más protegidas de las colonias las que presentan un mayor número de pólipos en fases reproductivas, mientras que los pólipos de la periferia están especializados en la alimentación.

> «EL HIELO MARINO ES UNO DE LOS ECOSISTEMAS MÁS PRODUCTIVOS DEL MUNDO. EN SU INTERIOR SE DESARROLLA UN ECOSISTEMA MUY SINGULAR»

Las relaciones epibentónicas que se establecen entre los organismos epibiontes y la fauna sésil son clave para la vida de los organismos. Esta estrategia permite evitar la competencia por el espacio y tener un mayor acceso a la columna de agua, lo cual aumenta la diversidad local. Esta estrategia hace que las comunidades bentónicas sean muy complejas y que tengan una estructura tridimensional, aspecto característico de comunidades formadas por suspensívoros bentónicos. Es muy frecuente ver que en las plataformas antárticas las comunidades bentónicas de fondos blandos están caracterizadas por una alta diversidad, biomasa y complejidad estructural. Este hecho también lo encontramos en algunas áreas de zonas tropicales o templadas, donde los arrecifes de coral o las comunidades de fondos rocosos tienen una elevada

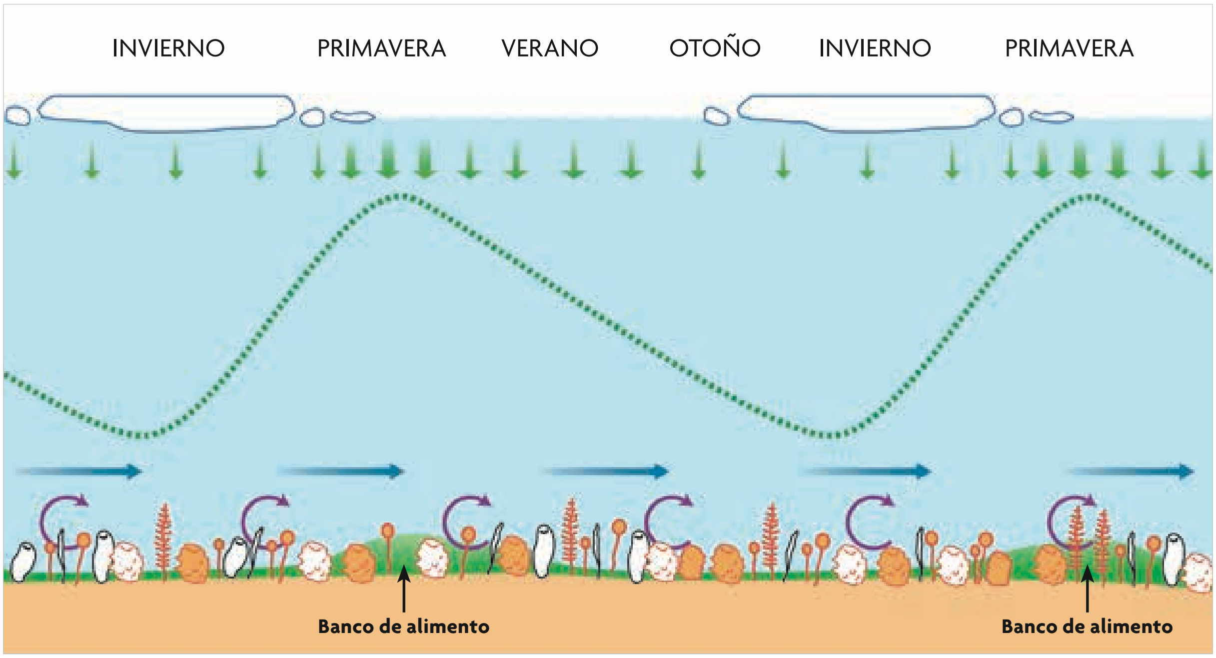


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Figura 6. Ciclo anual de fertilización de las comunidades bentónicas. Las flechas verdes representan el plancton que cae cada primavera del hielo marino al fondo. Este alimento se acumula en el fondo en forma de alfombra verde y puede alimentar durante meses la vida del fondo de las plataformas antárticas. Las flechas azules representan las corrientes de fondo y las moradas la resuspensión causada por estas corrientes.

densidad de organismos. Eso hace que las comunidades bentónicas antárticas se parezcan más de lo que se podría pensar a aquellas comunidades del planeta con la más alta biodiversidad conocida.

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