

Biological and physical characterization of the seabed surrounding Ascension Island from 100–1000 m

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*Recent studies have improved our understanding of nearshore marine ecosystems surrounding Ascension Island (central Atlantic Ocean), but little is known about Ascension's benthic environment beyond its shallow coastal waters. Here, we report the first detailed physical and biological examination of the seabed surrounding Ascension Island at 100–1000 m depth. Multibeam swath data were used to map fine scale bathymetry and derive seabed slope and rugosity indices for the entire area. Water temperature and salinity profiles were obtained from five Conductivity, Temperature, Depth (CTD) deployments, revealing a spatially consistent thermocline at 80 m depth. A camera lander (Shelf Underwater Camera System; SUCS) provided nearly 400 images from 21 sites (100 m transects) at depths of 110–1020 m, showing high variability in the structure of benthic habitats and biological communities. These surveys revealed a total of 95 faunal morphotypes (mean richness >14 per site), complemented by 213 voucher specimens constituting 60 morphotypes collected from seven targeted Agassiz trawl (AGT) deployments. While total faunal density (maximum >300 m⁻² at 480 m depth) increased with rugosity, characteristic shifts in multivariate assemblage structure were driven by depth and substratum type. Shallow assemblages (~100 m) were dominated by black coral (*Antipatharia* sp.) on rocky substrata, cup corals (*Caryophyllia* sp.) and sea urchins (*Cidaris* sp.) were abundant on fine sediment at intermediate depths (250–500 m), and shrimps (*Nematocarcinus* spp.) were common at greater depths (>500 m). Other ubiquitous taxa included serpulid and sabellid polychaetes and brittle stars (*Ophiocantha* sp.). Cold-water corals (*Lophelia* cf. *pertusa*), indicative of Vulnerable Marine Ecosystems (VMEs) and representing substantial benthic carbon accumulation, occurred in particularly dense aggregations at <350 m but were encountered as deep as 1020 m. In addition to enhancing marine biodiversity records at this locality, this study provides critical baseline data to support the future management of Ascension's marine environment.*

Keywords: Ascension Island, benthic shelf, marine biodiversity, tropical South Atlantic, Vulnerable Marine Ecosystems

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INTRODUCTION

Ascension Island is a relatively young (~1 my; Jicha *et al.*, 2013), South Atlantic Ocean island (07°57'S 14°22'W) ~80 km west of the mid-Atlantic ridge. It is extremely remote with its nearest neighbour St. Helena 1300 km to the south (Figure 1, inset). To date, most studies on the marine biodiversity surrounding the island have focussed on turtles (Weber *et al.*, 2014), seabirds (Bourne & Simmons, 2001) and shallow water coastal assemblages, typically located within depths less than 30 m (e.g. Price & John, 1980; Brewin *et al.*, 2016). The island's shallow marine biodiversity represents a unique assemblage of western and eastern

Atlantic biota (Floeter *et al.*, 2007; De Grave *et al.*, in press; Tsiamis *et al.*, 2017; Wirtz *et al.*, 2017). The inshore fish community is characterized as extremely abundant with low species richness and relatively high levels of endemism when compared with other Atlantic oceanic islands (Floeter *et al.*, 2007), probably due to its young age and isolation. In comparison, invertebrate richness and diversity still needs to be quantified but is inconspicuous owing to the abundance of fish (Brewin *et al.*, 2016).

Habitat diversity in the shallow sub-littoral is comparatively limited. Being a small oceanic island (97 km²) with no enclosed bays or sheltered lagoons, the entire coastline of Ascension is subject to large Atlantic swells. Many typical tropical coastal habitats often associated with high biological diversity such as mangroves, seagrass beds and coral reefs are absent, and the coast is dominated by volcanic rock, rhodolith (maerl) pebble and sand substrates. Coralline algal rhodolith beds, which form the only substantial biogenic

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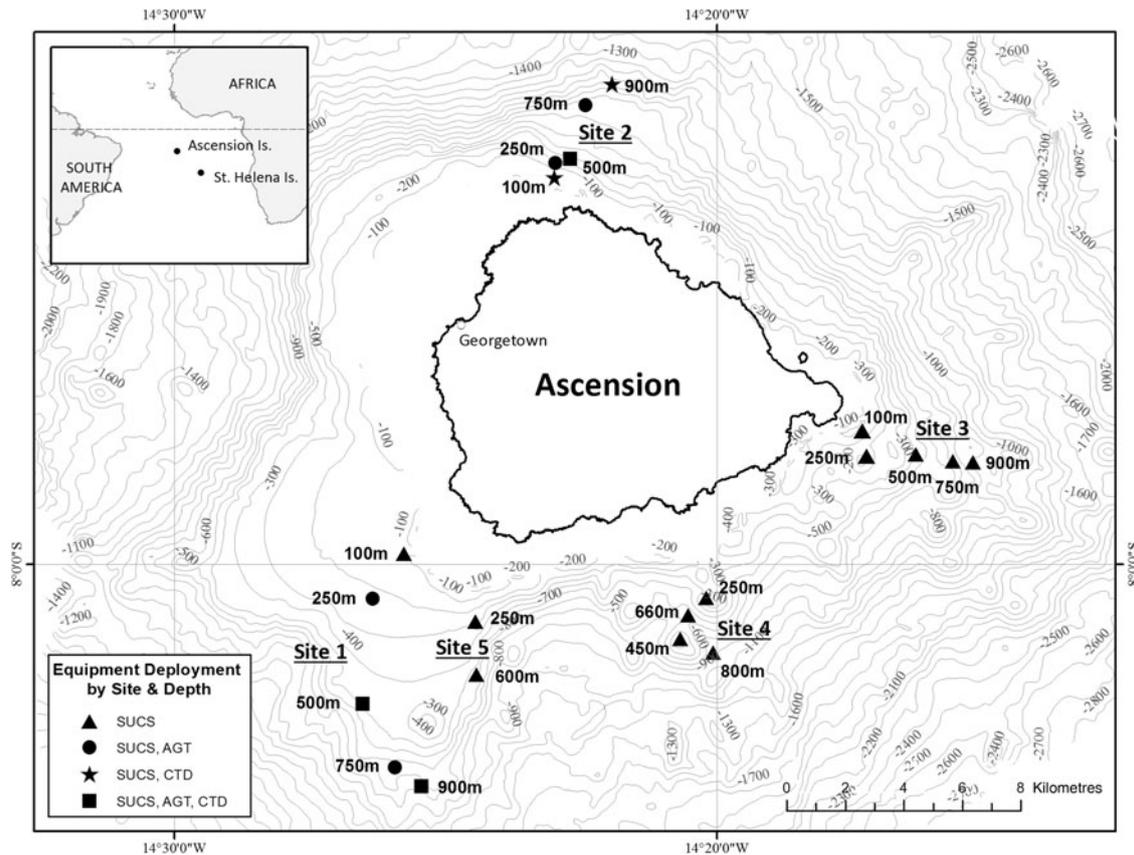


Fig. 1. Site locations showing equipment and depth. Inset: position of Ascension and St Helena Islands in the Atlantic Ocean.

three-dimensional habitat in shallow waters, are known to support a diverse infaunal community (Macaya *et al.*, 2015; Neill *et al.*, 2015; Torrano-Silva *et al.*, 2015) as well as being important in carbon cycling (Nelson, 2009; Cavalcanti *et al.*, 2014).

Although recent work has substantially advanced our understanding of Ascension's coastal marine environment (Darwin Initiative projects EIDCF012 and DPLUS021), data on benthic communities and habitats below a depth of 30 m are still remarkably rare. The marine biota of Ascension has been of interest to scientists since the 19th century, with famous expeditions such as 'Challenger' and 'Discovery' visiting the island in 1876 and 1925 respectively (Manning & Chace, 1990). These early scientific expeditions were among the only previously known attempts to systematically sample Ascension's deep-water benthos and although they contributed much to the identification of certain taxa, did little to improve our understanding of the ecology of the benthic marine environment. Given the narrow fringe of shallow, coastal water that is accessible to divers, much of Ascension's shelf ecosystem therefore remains largely undiscovered.

Knowledge of seafloor topography and habitats is similarly sparse. The UK Hydrographic Office navigational chart of the area is constructed from data collected between 1826 and 1984 and is focussed on areas surrounding the main anchorages. More complete coverage is provided by the General Bathymetric Chart of the Ocean (GEBCO), but resolution is coarse at 30 arc-seconds (~ 2 km) and not sufficiently detailed

for mapping variation in seabed topography at the scale typically of interest for ecological studies.

This study was developed as an objective of the Darwin Initiative-funded Ascension Island Marine Sustainability project (DPLUS021) aimed at addressing some of the key knowledge gaps relating to Ascension Island's deeper water ecosystem and was conducted aboard the Natural Environment Research Council research vessel the Royal Research Ship 'James Clark Ross' (hereafter JCR) during 14–18 October 2015. The study's main objectives were: (1) to map Ascension Island's shelf seabed bathymetry and characterize spatial variation in seafloor structure and topography; (2) to identify, quantify and compare benthic assemblages to fine scale seabed characteristics between 100 and 1000 m; and (3) to collect benthic specimens for identification from previously unsampled areas.

MATERIALS AND METHODS

The sampling protocol utilized during the Ascension Island cruise (cruise identifier JR864) was adapted from previous continental shelf biodiversity survey expeditions conducted aboard the JCR (e.g. JR262 and JR287; Barnes *et al.*, 2011, 2013) and incorporated four key aspects: (1) fine scale bathymetry (multibeam echosounder); (2) temperature and salinity profiles (Conductivity-Temperature-Depth [CTD]), (3) benthic habitats and faunal assemblages (Shelf

Underwater Camera System [SUCS]) and (4) biological specimen collection (Agassiz trawl [AGT]).

Fine scale bathymetry

A Kongsberg EM122 multibeam system was used, run through the Kongsberg SIS software. The system was run in external trigger mode with the ping rate calculated by the Kongsberg Synchronization Unit (K-Sync). The number of cells in the processing grid was set to 128 × 128 and the grid cell size was set to 50 m. Angular coverage mode was set to manual and beam spacing to high density equidistant. The maximum beam angle was varied from 50° to 75° depending on the sea state, water depth and bathymetry, often on the slope the uphill beam was extended much further than the downhill beam to try and maximize data capture.

In addition to water depth, several derived bathymetric datasets were also extracted from multibeam data to describe spatial variation in aspects of seabed structure and topography that may influence biological assemblages and species distributions. Derived datasets included slope, terrain ruggedness index (TRI) and topographic position index (TPI). Slope was calculated as a measure in degrees (°) of the inclination of the seabed using Landserf (version 2.3) multi-scale analysis. TRI is a measure of seabed rugosity calculated using SAGA

GIS (version 2.0) and is derived by comparing the 2-dimensional footprint area of the seabed versus the 3-dimensional area of the bathymetry dataset. A data point that differs in depth most from the mean depth of the surrounding cells will have the highest TRI. Topographic position index (TPI) is a local elevation index which measures the relative topographic position of each bathymetric point in relation to its neighbours. TPI is a useful tool in identifying landscape features and topographic boundaries at different spatial resolutions and provides an indication as to whether a site is located on a peak, in a valley or in a region of constant gradient. TPI was calculated using the Land Facet Corridor Tools extension for ArcGIS.

Data from derived bathymetric datasets were used to select five broad sampling site locations (Figure 1), representing as wide a range of bottom topography (or habitats) as possible over depths of 100 to 1000 m to deploy CTD, SUCS and AGT apparatus (Table 1).

Temperature and salinity profiles

A CTD unit was used to vertically profile the water column. The SBE9Plus unit held dual SBE3Plus temperature and SBE4 conductivity sensors and a Paroscientific pressure sensor. The CTD was raised as close to the surface as sea conditions allowed and then lowered to within 10 m of the seabed.

Table 1. Site locations, depths and unique identifiers for all deployments.

Event name	Latitude	Longitude	Depth (m)	SUCS photos
SUCS 1	S 08° 4' 7.068"	W 14° 25' 26.904"	880	20
SUCS 2	S 08° 3' 46.440"	W 14° 25' 56.208"	770	20
SUCS 3	S 08° 2' 35.232"	W 14° 26' 31.740"	500	20
SUCS 4	S 08° 0' 38.592"	W 14° 26' 21.012"	220	20
SUCS 5	S 07° 59' 47.832"	W 14° 25' 46.236"	110	20
AGT 1	S 08° 0' 31.104"	W 14° 26' 32.352"	210	
AGT 2	S 08° 2' 33.288"	W 14° 26' 34.368"	500	
AGT 3	S 08° 3' 47.520"	W 14° 26' 0.960"	770	
AGT 4	S 08° 3' 59.796"	W 14° 25' 34.680"	840	
CTD 1	S 08° 4' 13.512"	W 14° 25' 20.352"	880	
CTD 2	S 08° 2' 27.744"	W 14° 26' 40.596"	500	
CTD 3	S 07° 51' 5.400"	W 14° 21' 56.592"	960	
CTD 4	S 07° 52' 29.748"	W 14° 22' 41.448"	340	
CTD 5	S 07° 52' 49.620"	W 14° 23' 0.240"	120	
SUCS 6	S 07° 52' 49.476"	W 14° 23' 0.096"	120	20
SUCS 7	S 07° 52' 33.024"	W 14° 22' 59.088"	260	20
SUCS 8	S 07° 52' 28.704"	W 14° 22' 42.780"	340	20
SUCS 9	S 07° 51' 29.016"	W 14° 22' 25.464"	750	20
SUCS 10	S 07° 51' 8.784"	W 14° 22' 0.156"	890	20
AGT 5	S 07° 51' 29.880"	W 14° 22' 31.764"	750	
AGT 6	S 07° 52' 29.388"	W 14° 22' 48.108"	330	
AGT 7	S 07° 52' 33.600"	W 14° 22' 53.940"	230	
SUCS 11	S 07° 57' 31.032"	W 14° 17' 19.248"	110	20
SUCS 12	S 07° 57' 59.112"	W 14° 17' 15.000"	210	20
SUCS 13	S 07° 57' 57.744"	W 14° 16' 20.496"	500	20
SUCS 14	S 07° 58' 4.944"	W 14° 15' 39.420"	800	20
SUCS 15	S 07° 58' 6.060"	W 14° 15' 17.172"	1020	11
SUCS 16	S 08° 0' 37.404"	W 14° 20' 12.228"	280	20
SUCS 17	S 08° 0' 56.664"	W 14° 20' 31.776"	670	20
SUCS 18	S 08° 1' 22.944"	W 14° 20' 40.920"	480	20
SUCS 19	S 08° 1' 38.172"	W 14° 20' 4.452"	850	20
SUCS 20	S 08° 1' 3.828"	W 14° 24' 27.540"	280	20
SUCS 21 ^a	S 08° 2' 2.400"	W 14° 24' 25.884"	500	7

^aExcluded from analyses owing to small sample size.

CTD data was collected using software Seasave Win32 (Sea-Bird Electronics, Inc). A total of five CTD deployments were undertaken (Table 1), two from the south-west of Ascension at depths of 900 and 500 m, and three to the north of the island at depths of 900, 300 and 100 m (Figure 1). CTD deployments did not take place at other locations due to time constraints.

Benthic habitats and faunal assemblages

The SUCS was used as a tool allowing insight into the conditions of the underwater landscape and investigation of the micro-scale topography of the benthic environment. SUCS imagery can also be used to estimate faunal richness and density of the benthos.

The SUCS consists of three units: (1) the laboratory-based imaging control; PC with monitor (for camera and lighting control), a cable-metering sheave indicator and deck box; (2) the deck-based deployment control; winch, underwater cable, deck monitor and metering sheave on the mid-ships gantry; and (3) the underwater camera lander unit; tripod frame with underwater housed video and stills camera, booster and power distribution board and the underwater lights.

The SUCS was deployed from the mid-ships gantry on a fibre-optic cable connected to a motorized winch system, dropping at a rate of 30 m min^{-1} until it sat and stabilized on the seabed, video and photo stills were taken using the SUCS software. The system allows high-resolution photo stills (2448×2050 pixels), with a field of view fixed to 0.25 m^{-2} on a flat surface, and video footage (2448×2050 pixels) to be taken simultaneously that produces a live feed in full colour and in HD (2448×2050 pixels). A photo was taken as soon as the system was settled on the seabed, the system was then lifted clear of the bed and moved $\sim 5 \text{ m}$ in one direction, this was repeated to achieve 20 photos (i.e. 5 m^{-2}) taken over an approximate horizontal distance of 100 m. The SUCS was deployed a total of 21 times at approximate depths of 100, 250, 500, 750 and 900 m (Table 1).

Sessile and mobile benthic fauna observed in SUCS photos were distinguished according to morphotype, as a proxy for taxonomic group (species, genus or class), and enumerated. To allow faunal assemblage structure to be related to benthic habitat characteristics, SUCS photos were categorized according to (1) roughness, on a scale from 0 (smooth mud or fine sand) to 5 (complex 3-dimensional cover), and (2) dominant substratum type, on a scale from 0 (silt) to 8 (boulders or bedrock; Table 2).

Data analyses

For each transect, faunal counts were summed and divided by accumulated photo area to obtain densities of individual morphotypes, which were used to calculate morphotype richness (S) and evenness (Simpson's $1 - \lambda$) (Table 3). Owing to an exceptionally low sample size ($N = 7$), the 500 m-depth transect at site 5 (SUCS21) was excluded from further analyses.

Transects were ranked according to average roughness, determined from the mean of the ordinal roughness categories (Table 2) assigned to individual photos. Additionally, the relative proportions of photos within the nine substratum categories (Table 2) were used to estimate the per cent cover of different substrata (i.e. silt, fine sand, coarse sand, small

Table 2. Classifications used for roughness and substratum identification across SUCS imagery.

Roughness	Description
0	Completely smooth (mud/fine sand)
1	Sand waves/ripples/small pebbles
2	Scattered rocks
3	Scattered larger rocks/bedrock
4	Scattered larger rocks/bedrock covering >50% of image
5	Complex 3-D cover
Substratum	Description
0	Silt
1	Fine sand
2	Coarse sand
3	Fine pebbles
4	Coarse pebbles
5	Cobbles
6	Rocks
7	Large rocks
8	Boulder/bedrock

pebbles, large pebbles, cobbles, small rocks, large rocks and boulders/bedrock) along each transect. Thus, nine separate variables, each representing the per cent cover of a different substratum type, were assigned to individual transects.

Subsequent analyses focussed on the relationships of environmental variables (transect depth, average roughness and percent cover of substrata) with (1) univariate faunal abundance and diversity indices (average density [i.e. the sum of the densities of individual morphotypes], richness and evenness of morphotypes, each represented by a single value per transect) and (2) multivariate faunal assemblage structure.

Table 3. SUCS transect depths, average faunal densities and univariate diversity indices (morphotype richness and evenness). Density, richness and evenness are overall values calculated for each transect as a whole; richness is not standardized by transect area.

Transect	Depth (m)	Density (m^{-2})	Richness (S)	Evenness ($1 - \lambda$)
SUCS1	880	1.2	4	0.72
SUCS2	770	3.6	8	0.82
SUCS3	500	3.6	10	0.86
SUCS4	220	7.8	12	0.77
SUCS5	110	24.6	9	0.48
SUCS6	120	6.4	13	0.81
SUCS7	260	23.8	23	0.89
SUCS8	340	17.2	20	0.87
SUCS9	750	1.4	6	0.82
SUCS10	890	4.6	14	0.91
SUCS11	110	21.2	16	0.55
SUCS12	210	41.4	24	0.65
SUCS13	500	154.8	19	0.11
SUCS14	800	43.2	19	0.41
SUCS15	1020	6.5	11	0.88
SUCS16	280	46.4	24	0.63
SUCS17	670	2.6	10	0.88
SUCS18	480	313.8	18	0.08
SUCS19	850	22.8	16	0.72
SUCS20	280	19	15	0.82
SUCS21	500	34.3	13	0.72

Spearman rank correlations were used to determine whether average density, richness and evenness varied with transect depth and average roughness. For the purpose of these analyses, richness was standardized by transect area to account for differences in the number of photos among transects (i.e. between SUCS₁₅ and the others). To test for relationships between the same three univariate indices and substratum characteristics, Mantel tests were performed on Euclidean distance matrices derived from both response data and multivariate substratum per cent cover data (i.e. nine variables), with 9999 permutations of the response matrix to evaluate significance (Legendre & Legendre, 2012).

Prior to multivariate analyses, pairwise Spearman rank correlations were used to assess the extent of collinearity among environmental variables (i.e. average roughness and nine substratum variables). Average roughness showed strong ($\rho \geq |0.70|$) positive correlations with per cent cover of small rocks ($r = 0.85$) and large rocks ($r = 0.79$); therefore, roughness was excluded from further analyses. Subsequently, the biota-environment (BIOENV; Clarke & Ainsworth, 1993) routine was used to identify the optimal subset of environmental variables accounting for variability in faunal assemblage structure, via maximization of the rank correlation between environmental and biological distance matrices. The variables identified by the BIOENV analysis were then used in a canonical analysis of principal coordinates (CAP; Anderson & Willis, 2003) to enable dissimilarities in faunal assemblages among transects to be visualized in the context of key environmental variables. The resulting ordination plot incorporated vectors representing Spearman rank correlations between environmental variables and the first two CAP axes. The significance of the overall model (based on the sum of all eigenvalues) and of constraining variables (marginal terms) were assessed via ANOVA-like permutation tests involving 9999 permutations. Spearman rank correlation coefficients between individual morphotype densities and CAP axes (Anderson & Willis, 2003) were calculated to identify the most important morphotypes (i.e. $|\rho| \geq 0.5$) contributing to variability in assemblage structure. Additionally, non-metric multidimensional scaling (nMDS) plots, unconstrained by environmental variables, were produced to show the overall pattern of faunal dissimilarities and variation in morphotype densities among transects.

Multivariate analyses were performed using Euclidean distances calculated from environmental data, which were z-standardized to account for scaling differences between depth and substratum variables, and Bray–Curtis dissimilarities calculated from individual morphotype densities, which were $\log_{10}(x + 1)$ -transformed to downweight the influence of numerically dominant species. Exclusion of rare morphotypes (i.e. overall mean density $\leq 0.01 \text{ m}^{-2}$) did not alter results substantially; therefore, analyses incorporated all morphotypes.

All analyses were conducted in R (version 3.2.0; R Core Team, 2015), in particular, using the functions *mantel()*, *bioenv()* and *capscale()* in the *vegan* package (version 2.3–5; Oksanen *et al.*, 2016).

Benthic specimen collection

An Agassiz trawl (AGT) was used to sample the larger macro- and mega-fauna from the benthic environment. The AGT had a mesh size of 1 cm and a mouth width of 2 m. The cable

length used was 1.5 times the water depth and was towed at 1 knot for 5 min from the ship's stern. The AGT was deployed seven times across depths of ~250, 500, 750 and 900 m (Table 1), where practicable, given the steep and abrasive topography. Samples were brought on-board and identified according to lowest possible taxonomic unit. Subsequent analysis of samples and photography records were undertaken back at the Ascension Island Government Fisheries Laboratory in the days following the cruise. Specimens that could not be identified were sent to taxonomic specialists.

RESULTS

Fine scale bathymetry

Near-complete bathymetric coverage for ocean depths from 100 to 1000 m around Ascension Island resulted from the survey (data available on request from the Polar Data Centre). Typically, the seabed is a narrow extension radiating from the island to a depth of ~450 m (Figure 2A). On the north-west and especially the south-west of the island, the seabed extends out to 450 m in a plateau which at its widest point is 7 km offshore, beyond 450 m depth the angle of the slope of the seabed increases considerably reaching 1000 m depth within 1 km (Figure 2B). This drop-off is most pronounced along the north-west coast of the island (and to the east of the large south-eastern plateau) where the seabed inclination reaches a near-vertical 78°. The slope around the island is punctuated by large topographic features rising from depths over 1000 m to, in places on the south coast, as shallow as 250 m. This complexity in the topography creates regions of high rugosity (roughness) over broad spatial scales (50 m) (Figure 2C) and large variation in TPI (Figure 2D), which may equate to greater habitat variability.

Temperature and salinity profiles

Temperature profiles around Ascension were characterized by warm surface waters (24 °C), with the top 80 m of the water column falling in a narrow temperature range of 22–24 °C. A sharp thermocline at ~80 m was identified at all deployments, with temperatures rapidly dropping to 17 °C and then continuing to drop to ~12 °C by 200 m. Below 200 m water temperature decreased to 10 °C at 300 m, 8 °C at 500 m and 5 °C at 900 m. At all deployments temperatures were seen to stabilize at ~5 °C below 800 m (Figure 3).

Salinity was recorded at 36.2 psu from 0–40 m water depth at all sites. Salinity increased between 50 and 60 m, peaking at ~36.5 psu, before decreasing with depth to ~35.0 psu at 200 m. Salinity stabilized at 34.5 psu deeper than 600 m (Figure 3).

Benthic habitats and faunal assemblages

A total of 95 morphotypes were distinguished using SUCS footage obtained from depths of 110–1020 m, of which 57 could be assigned preliminarily to genus, representing 21 identifiable classes within 12 Phyla (Supplementary Material, Table S1). Images revealed a series of characteristic faunal assemblages associated with particular substratum types that varied across the range of depths sampled (Figure 4A–F). Across all 21 transects, mean (\pm SE) average faunal density

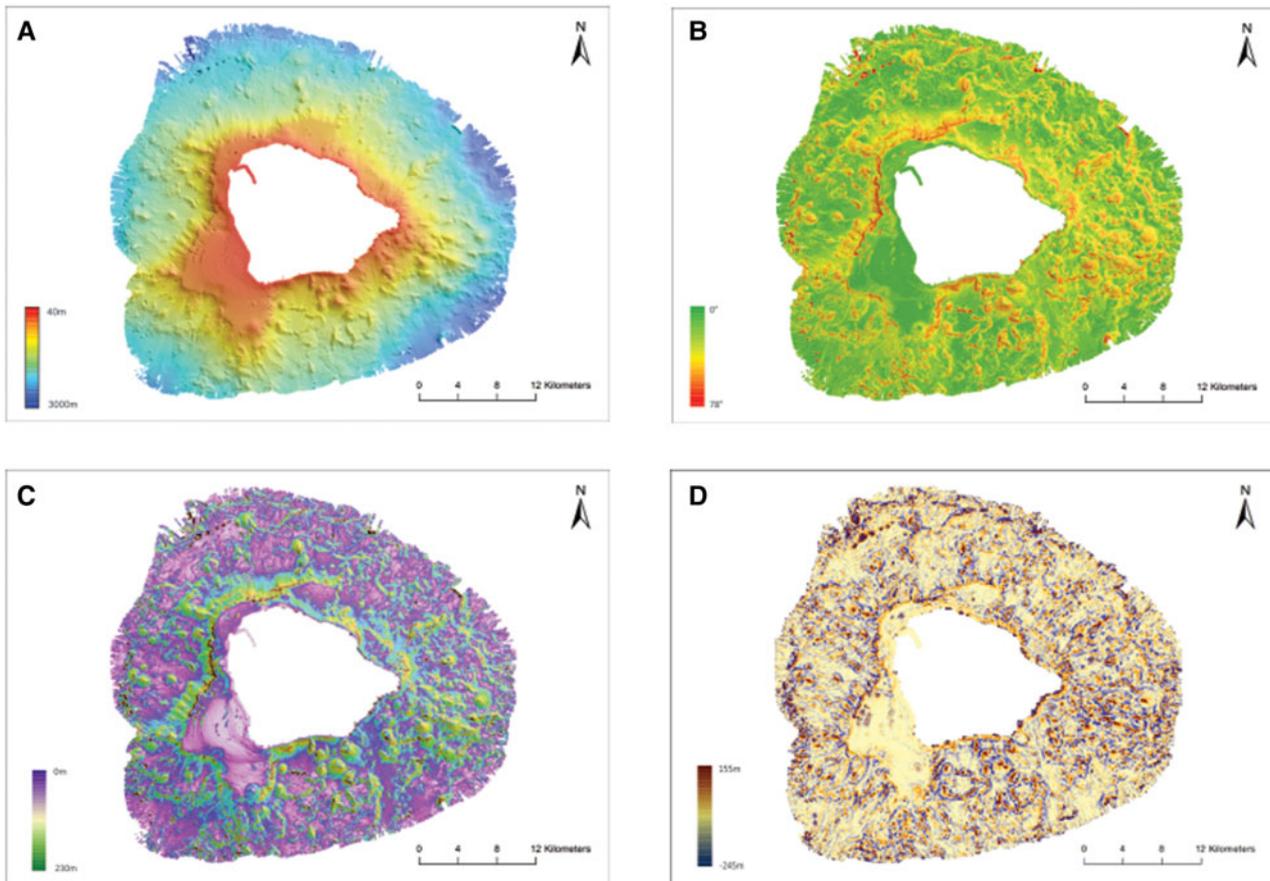


Fig. 2. (A) Bathymetry dataset gridded to 50 m resolution; (B) the measure in degrees ($^{\circ}$) of the inclination of the seabed; (C) Terrain Ruggedness Index (TRI); (D) Topographic position index (TPI).

was $38.1 \pm 15.6 \text{ m}^{-2}$ (range 1.2–313.8), while mean morphotype richness and evenness were 14.5 ± 1.3 (4–24) and 0.7 ± 0.1 (0.1–0.9), respectively (Table 3).

The most abundant morphotype was the brittle star *Ophiacantha* sp., observed on 10 transects, with an overall mean (\pm SE) density of $22.2 \pm 15.6 \text{ m}^{-2}$ (maximum 300.6 m^{-2} , transect SUCS18; Figure 4C). Other relatively abundant morphotypes were sabellid polychaetes ($2.6 \pm 1.7 \text{ m}^{-2}$; Figure 4E), black corals (*Antipatharia* sp.; $1.5 \pm 1.0 \text{ m}^{-2}$; Figure 4A) and, on particular transects, squat lobsters identified as *Munida micropthalma* (2.8 m^{-2} , SUCS18) and a shrimp-like giant mysid, likely *Gnathophausia zoea* (1.8 m^{-2} , SUCS7 and SUCS16).

Polychaetes identified as *Serpula* sp. (mean density $1.3 \pm 1.1 \text{ m}^{-2}$) represented the most widespread morphotype, observed on 12 transects. Other commonly encountered morphotypes (≥ 10 transects) included the shrimp *Nematocarcinus* sp. ($0.4 \pm 0.1 \text{ m}^{-2}$; Figure 4D) and scleractinian corals belonging to the genera *Caryophyllia* ($1.6 \pm 1.3 \text{ m}^{-2}$; Figure 4B) and *Lophelia* cf. *pertusa* ($1.1 \pm 0.4 \text{ m}^{-2}$; Figure 4F).

The only significant relationship found with respect to average faunal density was that it correlated positively with average roughness ($\rho = 0.51$, $P = 0.021$). There was no correlation between average density and either substratum characteristics (Mantel test; $\rho = -0.03$, $P = 0.578$) or depth ($\rho = -0.38$, $P = 0.097$), but there was an apparent peak in density at 480–500 m, driven by elevated densities of

Ophiacantha sp. within transects SUCS13 and SUCS18 (Table 3; Figure 4C). Neither morphotype richness nor evenness correlated significantly with either depth (richness: $\rho = -0.17$, $P = 0.461$; evenness: $\rho = 0.32$, $P = 0.176$) or substratum (richness: $\rho = 0.06$, $P = 0.225$; evenness: $\rho = -0.05$, $P = 0.654$). Further, while evenness was not related to roughness ($\rho = -0.27$, $P = 0.258$), there was only a marginally significant positive correlation between richness and roughness ($\rho = 0.41$, $P = 0.075$).

Transect depth and per cent cover of coarse sand and large pebbles were identified as the most important environmental variables underlying variability in faunal assemblages (BIOENV; $\rho = 0.65$). All three constraints in the CAP were significant (depth: pseudo- $F_{1,16} = 3.35$, $P < 0.001$; coarse sand: pseudo- $F_{1,16} = 2.90$, $P < 0.001$; large pebbles: pseudo- $F_{1,16} = 1.87$, $P = 0.012$). Depth showed a strong negative correlation with CAP axis 1 ($\rho = -0.90$), the converse of which was true for per cent cover of pebbles (Figure 5A). The importance of depth in explaining overall dissimilarities among faunal communities was also emphasized by the unconstrained MDS plot (Figure 6A). Per cent cover of sand correlated positively with CAP axis 2 ($\rho = 0.65$), which separated transects with the lowest average roughness (i.e. SUCS1, 3, 4, 7, 9 and 17) from the rest of the samples (Figure 5A).

A total of nine morphotypes showed strong relationships ($|\rho| \geq 0.5$) with CAP axes 1 and 2 (Figure 5B). Deeper transects were associated with greater densities of *Nematocarcinus* sp., which was not found shallower than 500 m (Figure 6B),

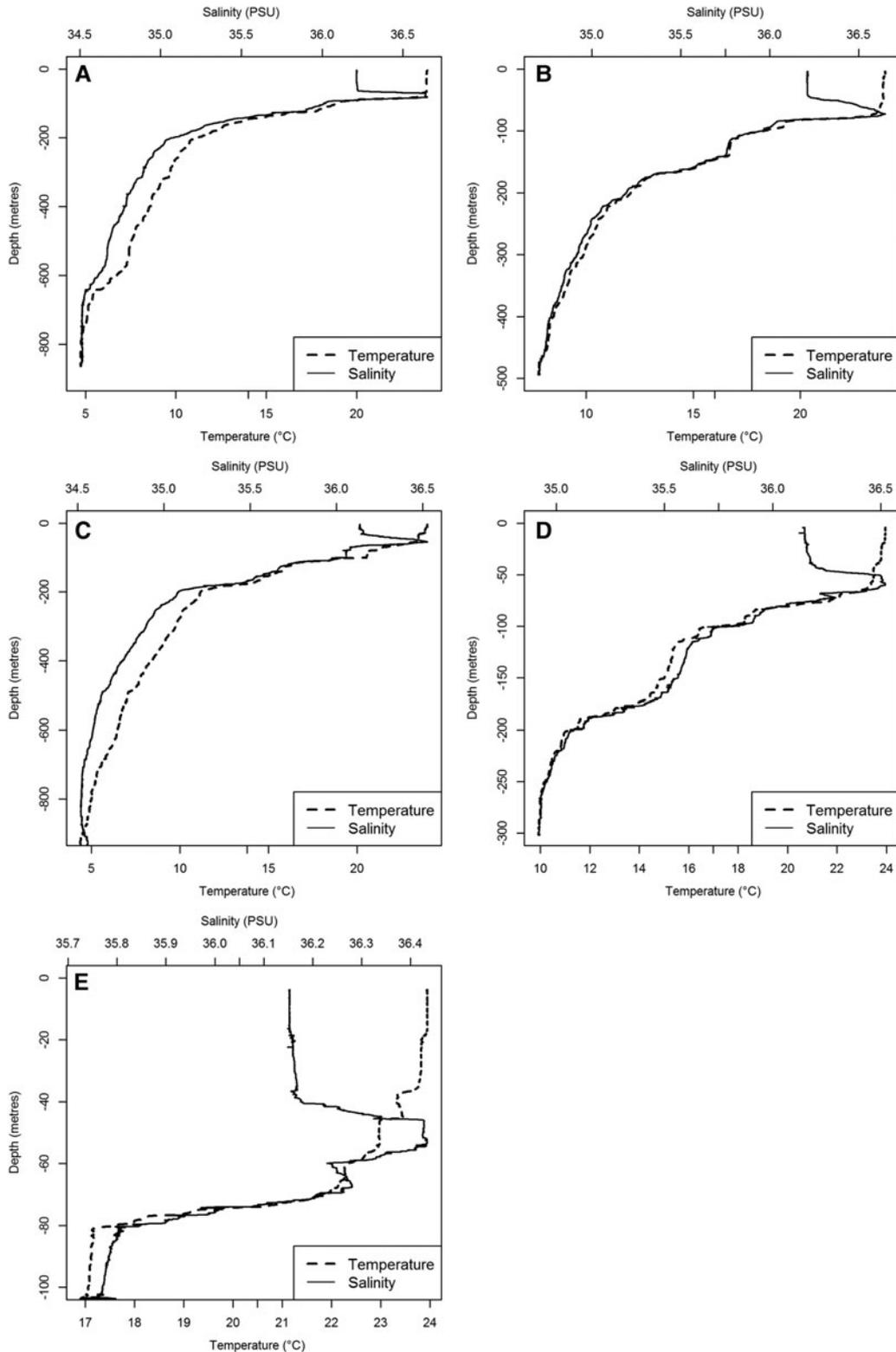


Fig. 3. CTD derived temperature and salinity profiles for each of the five deployments: (A) CTD 1; (B) CTD 2; (C) CTD 3; (D) CTD 4; (E) CTD 5.

and, to a lesser extent, sabellid polychaete and crinoid morphotypes (Figures 4E & 6C, D). While sabellid polychaetes reached relatively high densities at 800–850 m depth (SUCS14 and SUCS19; Figure 6C), they were also found on shallower transects with lower per cent cover of sand (Figure 5A). *Antipatharia* sp. and orange encrusting sponge

(*Demospongiae* sp. indet.; Figure 6E) were more characteristic of shallower transects (Figure 4A) with greater per cent cover of pebbles. Although the density of *Serpula* sp. was partly related to depth (Figure 6B), this morphotype was abundant on shallower, less sandy transects (e.g. SUCS12; Figure 6F). Where present, the sea pen *Virgularia* sp. was more abundant



Fig. 4. Representative SUCS images of benthic habitats across a range of depths: (A) rocky substrata covered with black coral (*Antipatharia* sp.), encrusting algae and orange sponge (Demospongiae) at 100 m (transect SUCS5); (B) fine sediment with abundant sea urchins (*Cidaris* sp.) and scleractinian corals (*Caryophyllia* sp.) at 250 m (SUCS16); (C) large rocks with high densities of brittle stars (*Ophiacantha* sp.) at 450 m (SUCS18); (D) coarse sediment and fine pebbles inhabited by sea pens (*Virgularia* sp.), shrimps (*Nematocarcinus* sp.) and gastropod molluscs at 500 m (SUCS3); (E) large rocks associated with sabellid polychaetes and feather stars (Crinoidea) at 700 m (SUCS14); (F) boulders and bedrock supporting reefs of the scleractinian coral *Lophelia* sp. at 800 m (SUCS19). Scale bar represents 20 cm.

on transects with a higher per cent cover of sand (Figures 4D & 6B).

Benthic specimen collection

In all, the 213 specimens collected were identified into 60 morphotypes (Supplementary Material, Table S2). Samples were

separated by class as follows (including the number of specimens collected in each case): Alcyonaria (4), Anthozoa (3), Bivalvia (3), Brachiopoda (2), Cirripedia (4), Crinoidea (11), Crustacea (21), Demospongia (11), Echinoidea (7), Gastropoda (5), Hexactinalida (8), Hydrozoa (2), Malacostraca (57), Ophiuridae (20), Pisces (9), Polychaetes (18), Scyphozoa (6), Sipunculida (2), Thaliacea (2),

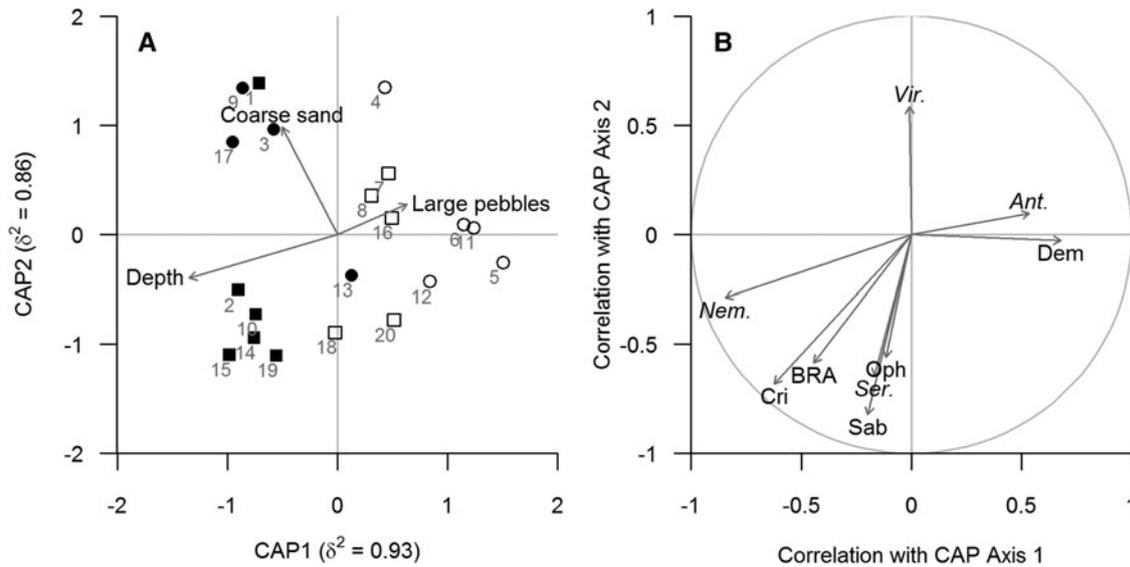


Fig. 5. (A) CAP ordination plot of faunal assemblage structure according to environmental variables (vectors represent Spearman rank correlation coefficients with axes). Point labels correspond to SUCS transect number and symbols depth category (○, 100–249 m; □, 250–499 m; ●, 500–750 m; ■, >750 m). (B) Spearman rank correlation coefficients between CAP axes and individual morphotypes for which $|\rho| \geq 0.5$ (Ant., *Antipatharia* sp.; BRA, *Brachipoda* sp. indet.; Cri, *Crinoidea* sp. indet.; Dem, *Demospongiae* sp. indet.; Nem., *Nematocarcinus* sp.; Oph, *Ophiuroidea* sp. indet.; Sab, *Sabellidae* sp. indet.; Ser., *Serpula* sp.; Vir., *Virgularia* sp.).

Zoantharia (18). All individuals were identified to class or lower, sorted, photographed and sent to taxonomic experts for formal identifications where necessary. Two specimens of Grenadier fish preliminarily identified as *Malacocephalus laevis* (Lowe, 1843) and *Ventrifossa* sp. (Macrouridae) are likely new records for Ascension Island.

One of the most commonly encountered species found in trawls around Ascension Island were shrimps of the genus *Nematocarcinus*, identified as *N. gracilipes* (Filhol, 1884), found between depths of 500 and 1000 m and representing 15–40% of invertebrates larger than 0.5 cm collected in samples. At a depth of 700–1000 m, most of the specimens were adults, whereas at 500 m most were juveniles. Also identified at 500 m and shallower were *N. tenuipes* (Spence Bate, 1888) and *N. faxoni* (Burukovsky, 2001). Other crustaceans also identified included a galateid *Munida* sp. (likely *Munida micropthalma*). Shrimps including *Stylopandalus richardi* (Coutière, 1905) (Pandalidae) and *Sergia* spp. (Sergestidae) and crabs *Chaceon* sp. (Geryonidae) also occurred regularly, mostly on rocky habitats between 100 and 500 m.

DISCUSSION

While our understanding of shallow marine ecosystems surrounding Ascension Island has only recently begun to improve (e.g. Weber *et al.*, 2014; Brewin *et al.*, 2016; Wirtz *et al.*, 2017), the current study represents the first detailed examination of physical and biological characteristics of Ascension's marine environment at substantially greater depths. In addition to providing extensive fine scale bathymetric data to 1000 m depth, this study generates new insight into how benthic habitats and faunal community structure vary throughout Ascension's shelf area at depths of 100–1000 m. Further, the collection of biological specimens addresses the critical lack of knowledge regarding deeper-water marine

biodiversity associated with this unique and isolated oceanic island.

The detailed map of seafloor topography resulting from this study enables the quantification of benthic habitat variability at a greater scale and resolution than was previously possible for Ascension Island. These data potentially provide a basis for inferring wider distribution patterns of substratum types and faunal assemblages, and for directing future oceanographic and benthic ecological research within Ascension's marine zone. Additionally, while the number of CTD deployments was limited by logistical constraints, temperature and salinity profiles spanned the range of depths sampled for benthic habitat types and faunal assemblages, representing sites lying both north and south of Ascension Island. There is still, however, much scope for the collection of additional data to characterize variation in physical oceanographic parameters in Ascension's waters in greater detail.

Our results from the SUCS image analysis showed that the average density of benthic fauna increased with substratum roughness (rugosity), perhaps not unexpected considering that the structure of marine benthic communities and habitat heterogeneity are recognized as being inextricably linked (McClain & Barry, 2010). Further, increased habitat complexity, including roughness, is often associated with greater diversity in benthic systems (e.g. Beck, 2000; Downes *et al.*, 2000; Thrush *et al.*, 2001). However, we found no relationship between substratum roughness and measures of faunal diversity (richness and evenness) at the level of individual transects in the current study. Despite this result, benthic species diversity may be influenced by other habitat characteristics, such as sediment particle size diversity (Etter & Grassle, 1992), measured at much finer scales. It should also be noted that diversity was probably underestimated in most habitats, as many cryptic or infaunal taxa are likely to have remained undetected in SUCS imagery. This bias towards more conspicuous morphotypes could in turn mask biological patterns and their relationships with environmental variables.

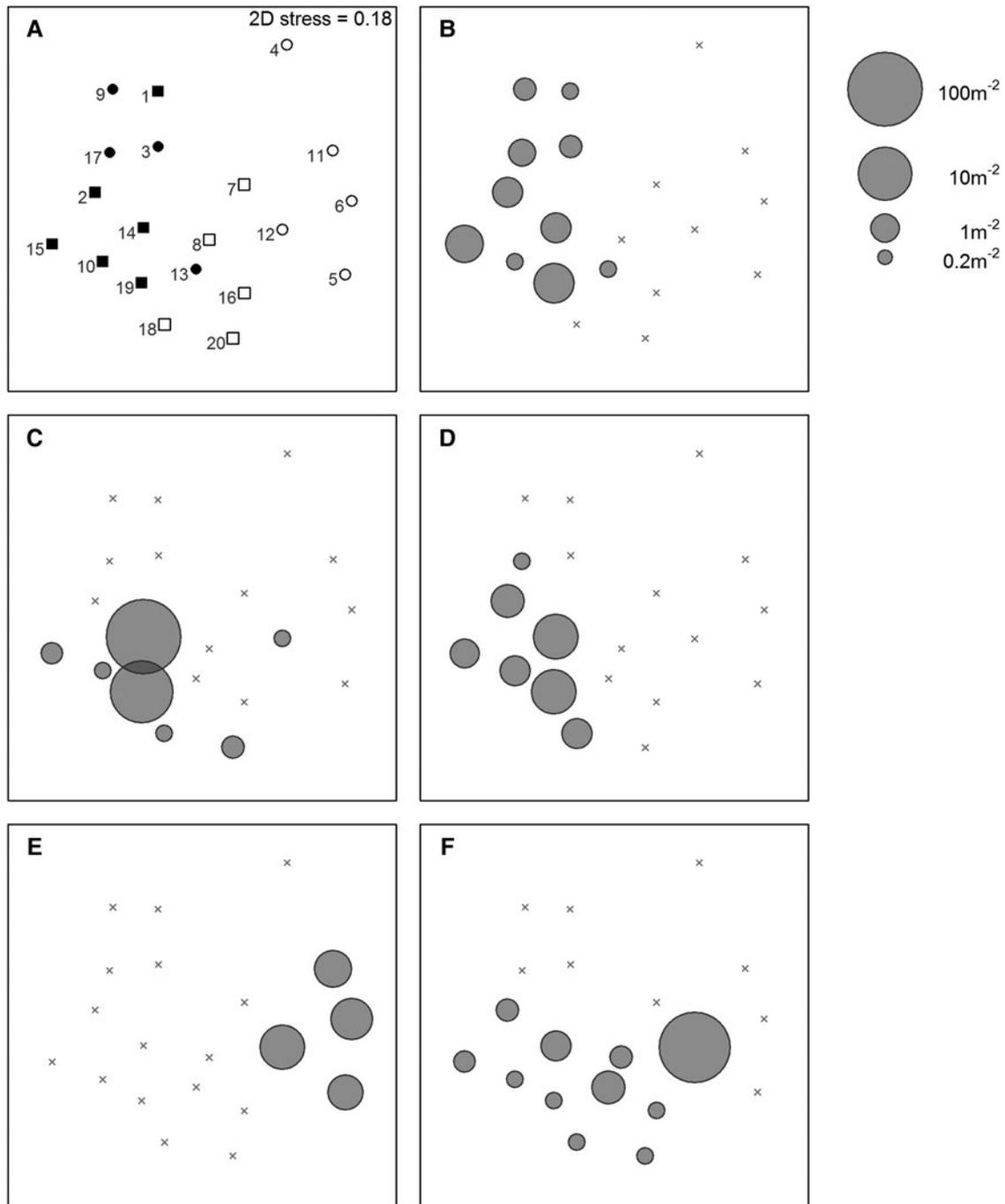


Fig. 6. (A) Non-metric MDS plot of faunal assemblage structure, based on $\log_{10}(x + 1)$ -transformed morphotype densities. Point labels correspond to transect number and symbols designate depth category (○, 100–249 m; □, 250–499 m; ●, 500–750 m; ■, >750 m). (B–F) The same MDS plot with superimposed circles representing densities of morphotypes exhibiting the strongest correlations ($|\rho| > 0.75$) with CAP axes: (B) *Nematocarcinus* sp.; (C) *Sabellidae* sp. indet.; (D) *Crinoidea* sp. indet.; (E) *Demospongiae* sp. indet.; (F) *Serpula* sp.

While neither roughness *per se* nor depth were related to univariate measures of diversity, the structure of benthic faunal assemblages inhabiting Ascension Island's shelf varied according to depth and substratum type. Previous studies conducted in offshore benthic habitats at comparable depths have demonstrated the importance of depth and proportional covers of different substratum types in explaining spatial variation in faunal community structure (e.g. Buhl-Mortensen *et al.*, 2009; Robert *et al.*, 2014). In addition to depth, the cover of coarse sand and large pebbles appeared to be important determinants

of community structure, and we identified nine faunal morphotypes driving changes in assemblage structure across benthic habitats. Black corals (*Antipatharia* sp.) characterized the shallowest sites, a common feature of which was a relatively high cover of complex rocky substratum, with the potential to support a diverse array of epilithic and epizootic species (Warner, 1981) such as the encrusting sponges (Demospongiae) that were also recorded in abundance.

Surveys at intermediate depths revealed diverse habitats characterized by a range of sessile and mobile species. The

sea pen *Virgularia* sp. was only encountered on five transects (SUCS 3, 4, 7, 8 and 9), all of which consisted predominantly of coarse sediment – thus, there was a clear association between this species and this particular substratum type. The analysis also identified an association between sabellid polychaetes and hard substrata, as this morphotype was found at particularly high densities on SUCS transects 14 and 19, for which the majority of photos were characterized by rocks, large rocks and boulders/bedrock. These transects, however, showed considerable heterogeneity in terms of substratum type, including a number of photos characterized by sediment, in which large numbers of sabellid polychaetes were also counted. This illustrates how species–substratum associations can depend on the spatial resolution of data (in this case, at the level of transect as opposed to individual photographs) and care should be taken when using such relationships to extrapolate across different scales (Williams *et al.*, 2010).

The cold-water coral *Lophelia* cf. *pertusa*, encountered on around half of all transects, was recorded as deep as 1020 m, exhibiting particularly high densities on transects shallower than 350 m. In addition to occurring in the Pacific and Indian Oceans, *L. pertusa* is distributed widely throughout the Atlantic, with relatively high abundances on the continental shelves of Europe and south-eastern North America (Roberts *et al.*, 2009). However, deep-water coral communities (including *L. pertusa*) are less well known from the South Atlantic (e.g. Arantes *et al.*, 2009; Carranza *et al.*, 2012). The current study provides the first record of substantial aggregations of reef-building scleractinian corals from Ascension Island's shelf. Currently regarded as one of the most structurally complex habitats in the deep ocean, cold-water coral reefs support high levels of biodiversity and act as potential speciation centres, while providing trophic links between the surface and seafloor and enhancing benthic carbon accumulation (Roberts *et al.*, 2006). Owing to the ecological importance of cold-water corals and associated taxa, deep sea coral reefs are regularly categorized as Vulnerable Marine Ecosystems (VMEs; e.g. Auster *et al.*, 2010; Jones & Lockhart, 2011) requiring protection from destructive fishing practices and seabed extractive operations, in addition to agents of global environmental change. Our findings indicate the importance of Ascension Island in terms of supporting cold-water coral reefs, enhancing our understanding of the distribution of these ecosystems within the South Atlantic. Additional species identified during this study can also be considered as indicator taxa for VMEs, such as cup corals (*Caryophyllia* sp.), sea whips (*Stichopathes* sp.) and erect sponges.

Nematocarcinid shrimps (mostly *Nematocarcinus gracilipes*, with lower abundances of *N. tenuipes* and *N. faxoni*) were observed frequently on transects at greater depths, particularly those deeper than 500 m, although one juvenile specimen was obtained from ~250 m. Members of this genus are widespread across the Atlantic and tend to inhabit soft muddy substrata, where they feed on detritus (Cardoso & Burukovsky, 2014). Owing to their observed abundance at Ascension Island, *Nematocarcinus* spp. may provide a staple food source for deep-sea fishes and other predators. While the distribution of *N. gracilipes* is largely within the Atlantic, *N. tenuipes* can also be found in the Indian and Pacific Oceans (Burukovsky, 2003). Thus, in this case, Ascension Island represents a zone of contact among species with

different, yet overlapping, regional distributions, whose coexistence may be supported by high local productivity.

Island biodiversity is expected to increase with island size, age and proximity to continents (MacArthur & Wilson, 1963). Although Atlantic island biogeographic patterns have been evaluated for shallow marine taxa (Hachich *et al.*, 2015), fewer generalizations can be made regarding species inhabiting deeper waters. For the relatively small, young and isolated island of Ascension, we might expect comparatively low benthic biodiversity, particularly in the context of the Atlantic Ocean and of tropical regions in general. However, with morphotype (cf. species) richness averaging 14.5 m^{-2} across all samples (maximum 24 m^{-2}), this may not be the case, perhaps reflecting an overall latitudinal gradient of increasing benthic diversity towards the equator (Rex *et al.*, 2000). Additionally, species inhabiting the shallow waters surrounding Ascension Island represent a unique mixture of western and eastern Atlantic taxa (De Grave *et al.*, in press; Tsiamis *et al.*, 2017; Wirtz *et al.*, 2017), but in the case of deeper marine ecosystems, different processes may govern species ranges and connectivity among regions (McClain & Hardy, 2010). The description of benthic communities and new species records arising from this study will provide valuable clues as to the biogeographic origins of deep-water taxa inhabiting the central Atlantic. On a smaller scale, while this study revealed a number of distinct benthic habitats characterized by particular faunal communities, taxonomic abundance and diversity were found to be very patchy within transects, emphasizing the importance of local variability in environmental variables in driving biological patterns. For example, we found high faunal densities ($>300\text{ m}^{-2}$) in certain areas, which may coincide with high productivity and/or substratum stability. Overall, the relative importance of environmental variables in structuring benthic marine communities varies according to scale (Williams *et al.*, 2010); although the main aim of our primarily descriptive study was to characterize the physical and biological features of Ascension's shelf environment, the results will also contribute to a more general understanding of the processes structuring deep-water ecosystems.

This study has greatly enhanced our knowledge of Ascension Island's marine environment beyond 30 m depth. The detailed physical and biological data collected here will enable the identification of ecologically important and/or vulnerable benthic habitats, which in turn will assist in the delimitation of zones for protection. These data also constitute a critical baseline against which to assess potential future ecological responses to local- and large-scale environmental change. Deep-sea ecosystems are vital to ocean biogeochemical and ecological processes, and the loss of benthic biodiversity is a serious threat to marine ecosystem functioning (Danovaro *et al.*, 2008). Additionally, confirmation of the identities of species collected in deep-water samples will increase biodiversity estimates and contribute to our understanding of biogeographic processes structuring Ascension's marine communities. While there is scope for further analysis of data from the current study to investigate relationships between environmental and biological variables in more detail, future surveys should aim to incorporate larger scales and greater depths to assess the generality of our findings. Overall, our understanding of the biogeography and functioning of deep-sea ecosystems remains limited, largely as a result of the technical and logistical challenges involved in collecting

data from such large-scale, inaccessible environments. In addition to addressing this critical lack of understanding, scientific researchers must work closely with conservation bodies, industry and policymakers to ensure the successful management of these important marine ecosystems (Ramirez-Llodra *et al.*, 2010).

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315417000820>

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