

This discussion paper is/has been under review for the journal Biogeosciences (BG).
Please refer to the corresponding final paper in BG if available.

Macrofauna community inside and outside of the Darwin Mounds SAC, NE Atlantic

N. Serpetti^{1,2}, E. Gontikaki², B. E. Narayanaswamy³, and U. Witte²

¹Oceanlab, Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, AB41 6AA, UK

²SAMS, Scottish Marine Institute, Oban, Argyll, PA37 1QA, UK

Received: 13 November 2012 – Accepted: 13 November 2012
– Published: 29 November 2012

Correspondence to: N. Serpetti (natalia.serpetti@sams.ac.uk)

Published by Copernicus Publications on behalf of the European Geosciences Union.

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Abstract

Over the past two decades, growing concerns have been raised regarding the effects of towed fishing gears, such as trawls and dredges, on deep-sea biodiversity and ecosystem functioning. Trawling disturbs the benthic communities both physically and biologically, and can eliminate the most vulnerable organisms and modify habitat structure; chronically disturbed communities are often dominated by opportunistic species. The European Union is under obligation to designate a network of offshore Special Areas of Conservation (SACs) and Marine Protected Areas (MPAs) by the end of 2012 based on the perceived expectation that these networks will help protect marine biodiversity and that within these areas, faunal abundance and diversity will be higher than the surrounding fished areas.

The Darwin Mounds, only discovered in 1998, are located in the Rockall Trough, NE Atlantic at a depth of ~1000 m. Deep-water trawling regularly took place in the region of the Darwin Mounds; however in 2004 the mounds were designated as the first offshore SAC in UK and the area is now closed to bottom trawling. As part of the HERMIONE programme the influence of human impact on the Oceans was one of the key themes and in June 2011, an investigation of the macrofaunal community structure at comparable sites both inside and outside of the Darwin Mound SAC was undertaken.

Macrofaunal communities were found to differ significantly, with the difference mostly driven by changes in the abundance of polychaetes, crustaceans and nematodes whilst no significant differences were seen for the other phyla. Whereas overall macrofaunal abundance was higher outside the SAC compared to within, this pattern varies considerably between phyla. Diversity indices showed no significant differences between protected and unprotected sites. This could indicate that a few years of preservation are not enough time to determine a recovery by the macrofaunal community of cold-water ecosystems and that a continued monitoring over a longer term is necessary to fully understand the impact of fishery closures.

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1 Introduction

Marine sediments are a major reservoir in the global carbon (C) cycle and the cycling or burial of organic matter (OM) in marine sediments are key terms in the global C, N and P cycles, linked to ocean nutrient budgets and productivity, and to climate. Although the bathyal continental margins constitute only 7 % of the surface area of the oceans, approximately 30 % of all organic matter remineralisation, and thus nutrient recycling, occurs here (Middelburg et al., 1997). At the same time, the biodiversity of continental margin sediments is remarkably high diverse, and is hypothesized to be a source of biodiversity for both the shallow continental shelves and the deeper ocean basins (Danovaro et al., 2008). The macrofaunal organisms that live within these sediments are known to be ecosystem engineers that, via their feeding activities and burrow structures, significantly alter the habitat structure, geochemical setting and food supply for other organisms. In many deep-sea systems, macrofauna are of primary importance in the early stages of organic matter (OM) diagenesis and recycling (e.g. Witte et al., 2003; Hunter et al., 2012), and the super-abundance of megafauna can even prevent the accumulation of phytodetritus on the sea floor (Billet et al., 2001; Bett et al., 2001). Echiurans, polychaetes and sipunculans, in particular, have been found to be keystone species that through their feeding and foraging activities supply deeper living micro- and macro-organisms with labile, easily degradable organic matter (Levin, 1999). Thus, the biodiversity and activity of seafloor macrofaunal communities and the cycling of OM and regeneration of nutrients at the seafloor are intimately linked. In addition, the benthic communities that live on and within the sediments of the continental margins provide important habitat and food resources (direct or indirect) for demersal fish.

Continental margin habitats are, however, also being increasingly altered by human activities, and the consequences of anthropogenic impacts on benthic biodiversity and ecosystem functioning in the deep-sea are almost completely unknown (Levin and Dayton, 2009; Levin et al., 2010). Over the past two decades growing concerns have been raised about the effects of towed fishing gears such as trawls and dredges. Trawling

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disturbs benthic communities both physically and biologically, eliminating the most vulnerable organisms and modifying habitat structure (Clark and Rowden, 2009; Puig et al., 2012). Several studies suggest that chronically disturbed communities are dominated by opportunistic communities (de Juan et al., 2007), which may remove important food sources for commercially important fish, reduce biodiversity and have strong implications for biogeochemical processes such as nutrient regeneration (Puig et al., 2012).

A recent evaluation has identified fishing as the human activity with the largest footprint in the deep North Atlantic (Benn et al., 2010), and deep-water fishing has been shown to have disproportionately large effects on the targeted ecosystems, diminishing fish populations living up to 2000 m deeper than the fished stocks (Bailey et al., 2009; Priede et al., 2010) and causing the re-suspension and subsequent relocation via lateral transport of surficial sediments (Martin et al., 2008; Puig et al., 2012).

The Darwin Mounds are situated in the North-east section of the Rockall Trough, ~ 180 km to the North-west of Scotland and were first discovered in 1998 (Bett, 2001). The mounds are found at a depth range of 900–1060 m (Masson et al., 2003), cover an area of about 1500 km² and each mound is approximately 5 m high and 100 m in diameter (Bett, 2001). The Darwin Mounds are thought to be quite unique as they have “tail-like” formations associated with each mound. The sandy substrate of the mounds have been colonised by corals, including high numbers of *Lophelia pertusa* and *Madrepora oculata* (Gubbay et al., 2002). The mounds are also colonised by a diverse group of suspension feeders as well as infauna; some of the more unusual fauna include the large fragile xenophyophore, *Syringammina fragilissima* (Masson et al., 2003; Van Gaever et al., 2004). Increasing evidence of destruction from bottom trawling and concerns regarding the damage from potential hydrocarbon exploration (Wheeler et al., 2005) eventually lead to the Darwin Mounds being designated by the European Council in 2004, as the first offshore Special Area of Conservation (SAC) in the UK. A total area of 1300 km² is now permanently closed to bottom trawling (European Council, 2004) but not as yet to pelagic trawling.

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In this study, the sediment macrofaunal communities were analysed in sites comparable with regard to depths, sediment type and OM content located both inside and outside the Darwin Mounds SAC in order to evaluate potential differences in the community structures and assess possible ecological macrofaunal responses in term of ecosystem resilience and recovery.

2 Material and methods

2.1 Study site and sample collection

In order to assess the effect of deep-water trawling on benthic macrofaunal communities, sediment samples were collected from both inside and outside the Darwin Mounds SAC during the RRS James Cook cruise 060 in May–June 2011. To ensure comparability, the stations sampled inside the SAC were outwith of the mounds themselves, and associated coral colonies as those outside the SAC. The stations outside the SAC were situated to the southeast of the Darwin Mounds. The maximum distance between all the stations, both within and outside of the SAC was ~ 18 km. In total, 48 megacorer barrels were taken at six stations at a depth of ~ 800 m, (Table 1, Fig. 1) using the NOC megacorer (i.d. of cores: 10 cm). All cores were characterised by a top layer of up to 10 cm of sandy-mud overlying glacial mud (as seen by Masson et al., 2003). The cores were sliced into 0–5 cm and 5–10 cm depth horizons. The fauna were elutriated through a 250 μ m mesh sieve and the resultant residue preserved in 10 % formalin solution. A subsample of 10–20 ml was taken from one additional core per deployment and frozen at -20°C for total organic carbon (TOC), total nitrogen (TN) and grain size analysis. The macrofauna were sorted in the laboratory, identified to the lowest possible taxonomic level and preserved in ethanol. Nematodes were included in our analysis due to the high number of individuals. However the specimens were not identified to species level and the phylum was used as a single entity in the diversity calculations.

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2.2 Statistical analysis

Analysis of the macrofaunal communities was undertaken using PRIMER V6 (Clarke and Warwick, 2001). Univariate analysis was carried out on sediment properties (TOC, TN, median gran size and mud content) and on macrofaunal community indices, (including Margalef's species richness (d), Pielou's evenness (J'), Shannon's diversity (H') and Simpson's dominance ($1-\lambda'$), Clarke and Warwick, 2001). An ANOVA test was used to evaluate the significant differences between samples collected inside and outside the SAC. Multivariate analysis was undertaken using cluster analysis and non-metric multi-dimensional scaling (MDS). In order to weight the importance of dominant and rare species, we applied a square-root transformation of the species abundance data (Clarke and Warwick, 2001). A similarity profile test (SIMPROF) was used to determine if there were significant differences in the internal macrofaunal multivariate structure between all the samples. A similarity percentage test (SIMPER) was carried out to evaluate the role of individual species in contributing to the group separations (Clarke and Warwick, 2001; Clarke and Gorley, 2006).

3 Results

3.1 Univariate analysis

No significant differences were found for TOC%, TN% and percentage of mud content when comparing the stations inside and outside of the SAC. Median grain size at the stations inside the SAC was significantly higher ($p < 0.05$) than stations outwith of the SAC (Table 1). The number of individuals was significantly higher outside than inside the SAC ($p < 0.01$). Mean values for the other macrofaunal community indices did not show significant differences in terms of diversity (number of species, Margalef's, Pielou's, Shannon's Simpson's) (Table 2 and Fig. 2).

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The difference in the total macrofaunal community abundance between stations collected outside and within the SAC was mostly driven by significant changes in abundances of the polychaetes ($p < 0.05$), crustaceans ($p < 0.01$) and nematodes ($p < 0.05$) whilst no significant differences were seen for the other taxonomic levels (Fig. 3a).
5 Polychaetes were found to be the most dominant macrofauna collected both within and outwith of the SAC (Fig. 3a). However, the standardised polychaete abundance did not change significantly ($p > 0.05$) when comparing stations outside and within the SAC. This indicates that the proportion of polychaetes collected within and outside the SAC is similar (ranging from 25–40% (Fig. 3b)). The same trend as seen for the
10 polychaetes was found for the nematodes (Fig. 3b). Crustaceans, however, contributed significantly to the community composition outside of the SAC ($p < 0.01$), and this was caused by one dominant species, *Haploops setosa* (contributing ~220 to ~335 individuals per m²). By comparison *H. setosa* had a notably lower presence inside the SAC with the number of individuals found ranging from ~16 to ~32 individuals per m².
15 Echinoderms, dominated by the ophiuroid *Ophiocten gracilis*, were the only taxa which had a significantly higher contribution ($p < 0.05$) to the community composition inside the SAC compared to outside (Fig. 3b). The number of species collected per phylum did not show any significant variation across the samples (Fig. 3c).

3.2 Multivariate analysis

20 The cluster analysis and the SIMPROF permutation test showed a high similarity between the samples (Fig. 4). At 57% similarity, two main groups were identified as having a significantly different internal multivariate structure ($p < 0.001$). These two groups corresponded to samples collected inside and outside the SAC. At 62% similarity, station 112 was found to be significantly different ($p < 0.05$) from the other sampling sites
25 located inside the SAC (stations 107 and 108). No statistical evidence for any other sub-structure was found (samples connected with a dotted line).

The similarity patterns described were also evident in the MDS showing two distinct major groups (2-D stress: 0) corresponding to inside and outside the SAC with a

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similarity of > 57% (e.g. 60% in Fig. 5). At a similarity of > 62% (e.g. 65% in the Fig. 5) stations 107 and 108 inside the SAC clustered in another sub-group. The average similarity between samples from outside the SAC (69.6%) was slightly higher than those from inside the SAC (64.3%).

5 The SIMPER test revealed that the overall dissimilarity (43%) between the samples collected inside and outside the SAC was driven by small contributions of most species. Nematoda (3.5%), the amphipod *H. setosa* (2.4%), the Ostracoda sp.1 (1.9%) and the polychaete *Aricidea* sp.1 (1.7%) were the species that contributed most to the overall dissimilarity (cut off applied at 10% cumulative dissimilarity). Abundances outside the
10 SAC were up to three, five and 20 times higher than within the SAC for nematoda, *Aricidea* sp.1 and Ostracoda sp.1, and *H. setosa*, respectively.

High abundances found at station 112 (within the SAC) also separated this site from the other two located inside the SAC (107 and 108), resulting in a 38% dissimilarity. Ostracoda sp.1 (2.1%), Nematoda (2%), the polychaete *Prionospio* sp.1 (2%) and the scaphopod *Pulsellum* sp.1 (1.8%) were the most important species that contributed to
15 this dissimilarity (cut off applied at 10% cumulative dissimilarity).

4 Discussion

Many deep-water ecosystems, such as seamounts, knolls and pinnacles, have been increasingly exploited in the last two decades for their fish resources and the use of
20 destructive fishing gears can badly damage sessile habitat-building fauna (Pitcher et al., 2010). The role of these habitats on maintaining biodiversity, marine food webs, and larval settlement underlined the necessity to protect and manage them at global, regional, and national levels (e.g., Probert et al., 2007; Santos et al., 2009). The overarching goal of the European integrated maritime policy, known as Marine Strategy
25 Framework Directive is to achieve a “Good Environmental Status” by 2020 across the offshore Europe’s SACs and MPAs network defined by 2012 (JNCC website: <http://jncc.defra.gov.uk/>). Protection of open waters areas, beyond national jurisdiction,

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is also underway with 330 000 km² already closed to bottom fisheries in five areas of the Mid-Atlantic Ridge (NEAFC, 2009). Although these initiatives are a positive step forward, the percentage of the world's deep water ecosystems being scientifically monitored and effectively managed is still exceptionally low (Probert et al., 2007).

5 Marine protected areas and special areas of conservations are generally created to protect specific targets, e.g. fish stocks, coral species, and peculiar geomorphological structures such seamounts and as hydrothermal vents. But although there is an expectation that regulating the human activities in these areas will protect faunal biodiversity and abundance, we are far from understanding the efficiency of these closures
10 in particular on an ecosystem level. Previous studies, found that unfished sites (or less fished in terms of trawling impact) showed higher mega- (Clark and Rowden, 2009) and macrofaunal (Kaiser and Spencer, 1996; Duineveld et al., 2007; de Juan et al., 2011) abundance and diversity compared to fished ones (or high trawling impact sites). However, there have been relatively few studies investigating the impact and effects of
15 trawling in the deep sea (Clark and Rowden, 2009) and there are even fewer studies which assess the macrofaunal community (Duineveld et al., 2007), or recovery times of benthic infaunal communities after intensive trawling.

Unfortunately, collecting samples in the deep sea is still a challenge and coring in sandy sediments is often impossible in shallow water. The relatively coarse sediments
20 at much of the sampling area unfortunately prevented a random sampling design and restricted the number of samples we were able to retrieve. However, this study offered the opportunity to undertake a preliminary assessment of the effect of the first deep water SAC on macrofaunal community in an area that has already been damage by trawling and that has subsequently been protected.

25 In contrast to previous findings, our results did not show an increase in abundance and biodiversity of the benthic community inside the SAC. On the contrary, significantly higher species abundance was found outside the SAC than within. However, these studies were carried out in different geographic areas, and using different sampling approaches.

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Trawls, epibenthic sledge, Day grab and box corer were generally used to evaluate the trawling impact on the benthic community in shallow (Kaiser and Spencer, 1996; Demestre et al., 2008; de Juan et al., 2011) and deep waters (Clark and Rowden, 2009) and to assess community diversity (Bremner et al., 2003), whereas in our study a
5 megacorer was used. Moreover, the trawl and the epibenthic sledge both generally used a 10 mm cod-end mesh, or coarser mesh, to assess the epifaunal community therefore the fauna collected are species that are generally classed as megafauna instead of macrofaunal species (Kaiser and Spencer, 1996; Bremner et al., 2003; Demestre et al., 2008; Clark and Rowden, 2009; de Juan et al., 2011). By comparison
10 the Day grab and box core were used to assess the fishing impact on the infaunal community in shallow waters (Queirós et al., 2006; Duineveld et al., 2007); however it is known that both of these gears usually underestimate both faunal abundance and biomass (Bett, 2000).

In our study, the macrofauna were retained on a 250 µm sieve mesh. Using a fine
15 mesh sieve is a key factor for deep water infaunal analysis where the specimens tend to be particularly small (Kaariainen and Bett, 2006; Ramirez-Llodra et al., 2010), however this makes it more difficult to compare our results with other "macrofaunal" community studies where a coarser mesh (generally 1 mm) has generally been used (Kaiser and Spencer, 1996; Jennings et al., 2002; Queirós et al., 2006; Duineveld et al., 2007; de
20 Juan et al., 2011).

Other factors that are important drivers of macrofaunal abundance are sediment grain size distribution, OM contents and depth. However, no significant differences were found in terms of sediment percentage of mud and OM contents between stations collected outside and within the Darwin Mounds SAC. The sediment collected in
25 our study was classed as being moderately well sorted fine sand, confirming the findings of Huvenne et al. (2009). Median grain size was found to be significantly lower outside the SAC compared to within, but still in the range of fine sand. This difference could be due to the fact that samples outside the SAC have been collected in a pock-mark area characterized by the presence of finer sediments (Huvenne et al., 2009).

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However, there is no evidence that the pockmark area adjacent to the Darwin Mounds is currently active (Masson et al., 2003) and our results did not show any differences in biodiversity between the pockmark area (outside the SAC) and within the SAC. None of the macrofaunal species identified here was known as components of deep cold-seep communities. Station 108 (within the SAC) was an exception with higher concentration of mud content compared to the other sampling sites, but this attribute did not single out this site in term of macrofaunal community composition. Other studies showed that the macrofaunal abundances and biomass in the Rockall Trough were variable with depth (Bett et al., 2001), however the relative variability in abundances that we found between inside and outwith the SAC were five times higher than previously recorded. So the abundance difference that we found in this study could be driven by presence/absence of trawling activity.

Despite the differences in macrofaunal abundances, our results showed high similarity level (57 %) of the communities across the samples compared to other studies (Clark and Rowden, 2009; Narayanaswamy et al., 2005, 2010) with no differences in terms of biodiversity indices. However the number of individuals per m^2 was significantly different between samples collected inside and outside the SAC. Total abundance for both within and outside the SAC (~ 6000 up to $12\,400$ individuals per m^2) was higher than the abundances, at comparable depths, found in the Faroe-Shetland Channel (~ 3000 individuals per m^2 ; Narayanaswamy et al., 2005), in the north-east Rockall Trough (the comparison has been made with selected sampling stations with similar grain size, OM characteristics and geographical coordinates to our study area: AFEN 2000) and in the North Sea at the same latitude (~ 6000 individuals per m^2) (Basford et al., 1990), however a coarser mesh size was used in these studies. When the same size of mesh (i.e. $250\ \mu m$) was used, our total abundance was in the same order of magnitude as that found in the Rockall Trough ($\sim 10\,000$ individuals per m^2 ; Gage et al. 2002), but our polychaete abundance (up to 4650 individuals per m^2) was still higher than the findings in the Faroe-Shetland Channel (Narayanaswamy, 2000). Biodiversity values however, were comparable with those at a similar depth in the Faroe-Shetland Channel

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(Narayanaswamy et al. 2005; 2010), higher than the findings in the north-east Rockall Trough (AFEN 2000), but lower compared to macrofauna collected in the Rockall Trough by Gage et al. (2002).

Long-term effect of fishing generally determined changes in larger and usually less abundant species and significant differences across sampling sites are more difficult to assess in a multivariate analysis that, when using strong data transformations, tends to down-weight the presence of common larger species with low abundances (Duineveld et al., 2007). Because the high abundances of small species in our samples we used the square root transformation instead of stronger ones. Same results were obtained using no transformation of the data. When strong data transformations were applied (e.g. forth root, logarithm or presence/absence) the similarity across the samples increased even more due to the high abundances of small nematodes and polychaetes in our samples.

The trawling activity can damage or even completely destroy fragile specimens, which in turn quickly attract infaunal detritivore species (Kaiser and Spencer, 1996). Kaiser et al. (2000) also underlined the prevalence of opportunistic species in areas disturbed by fishing. These aspects could explain why higher abundances of nematodes and the generally smaller opportunistic polychaete families, such as the Paraonids, Spionids, and Capitellids were observed in our study and hence their importance in structuring the macrofaunal community.

However, because the effect of fishing has a greater impact on larger species, i.e. the removal of the megafauna and demersal fish predators by fishing gears, the significant difference of species abundances observed inside and outside the SAC could represent an ecological response to the reduced predation pressure on macro- and meio- faunal species. This may explain the high abundances of large specimens (up to $100\ mm$) and hence more desirable to megafauna and demersal fish species, of the amphipod *Haploops setosa* on fished sites. *H. setosa* was also identified by the SIMPER test as one of the main species contributing to the dissimilarity between the samples collected outside and within the SAC, with the community outside the SAC

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being dominated by this species. The specimens collected in this study were found living in pouch-like tubes as described for the first time by Shields and Hughes (2009). Echinoderms, mostly consisting of *Ophiosten gracilis* species, were the only phylum that showed a higher percentage contribution of abundances inside the SAC sites compared to outside (Fig. 3b) indicating that this species may be particularly vulnerable to damage or disturbance by beam-trawling. To shed light on underlying mechanisms of benthic community responses to the impact of demersal fisheries in terms of biodiversity and abundances it is therefore important that the size spectra ecological concept (size-abundance relationships) (Kaariainen and Bett, 2006) and the predator-prey interactions within benthic communities are considered.

None of the community diversity indices investigated (number of species, species richness, Pielou's evenness and Shannon and Simpson indices) showed significant differences across the sites; however mean values were lower inside the SAC stations. This reduction in diversity inside the SAC was most apparent for Shannon's diversity index indicating that at the SAC the diversity of rare species was lower inside the SAC than outwith of the SAC. Kaiser and Spenser (1996) also noted that the decrease in abundances of rare species contributed most to the difference between fished and unfished areas.

Increasing diversity in fished areas may be also an ecosystem response to intermediate levels of disturbance following the "intermediate disturbance hypothesis" (Connell, 1978) and the "dynamic equilibrium theory" (Huston, 1979) where competitive exclusion was impeded, promoting co-existence in potentially competing species.

The closure of the Darwin Mounds to bottom trawling seems to be fairly well respected, with a reduction in trawl marks within the SAC area. However, the Darwin Mounds still appear to be covered in mainly dead coral, especially the region towards the east, and overall there was little evidence of recovery (Huvenne, 2011). We also have to highlight that the Darwin Mounds SAC was only established in 2004 (European Council, 2004) and a period of just seven years may not be sufficient to determine a full recovery of the benthic community in particular in deep-water, low resilient benthic

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ecosystems. The multivariate analysis showed a higher degree of dissimilarity between the samples collected within the SAC than outside. Increased variability among samples possibly indicates communities from a disturbed environment (Clark and Rowden, 2009), however it can also indicate changes due to the ecosystem recovering.

Acknowledgements. The research leading to these results has received funding from the European Community's Seventh Framework Programme (FP7/2007–2013) under the HERMIONE project, grant agreement no. 226354. Our thanks go to our colleagues Veerle Huvenne and Brian Bett (NOC, Southampton) who contributed to various aspects of the discussion and to Niels Jobstvogt (Oceanlab) for his help in collecting the samples.

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Table 1. List of sampling stations inside and outside the Darwin Mound SAC.

Station	Latitude	Longitude	Depth	Location
107	59°47.724	07°34.043	815	inside SAC
108	59°47.364	07°34.147	816	inside SAC
112	59°47.582	07°33.538	823	inside SAC
113	59°41.905	07°47.462	773	outside SAC
114	59°41.907	07°48.071	771	outside SAC
115	59°41.894	07°48.844	769	outside SAC

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Table 2. Sediment properties (TOC, TN, median grain size and mud content) and macrofaunal community indices (number of individuals, number of species, Margalef's, Pielou's, Shannon's, Simpson's) at each station collected inside (Stations 107, 108 and 112) and outside the SAC (113, 114 and 115).

Station	Sediment properties				Macrofauna community indices					
	TOC (%)	TN (%)	Median grain size (μm)	Mud content (%)	Number of individuals per m^2	Number of species	Species richness (d)	Pielou's evenness (J')	Shannon ($H' \log_e$)	Simpson ($1-\lambda'$)
107	0.205	0.044	190.7	17.2	5894	72	8.2	0.7	3.1	0.9
108	0.212	0.04	170.4	30.1	7261	89	9.9	0.7	3.0	0.8
112	0.186	0.036	192.8	16.1	8806	94	10.2	0.8	3.4	0.9
113	0.212	0.046	139.9	16.3	11 481	93	9.8	0.7	3.4	0.9
114	0.243	0.046	153.9	16.5	12 404	104	11.2	0.8	3.6	0.9
115	0.27	0.029	158.7	13.3	12 086	90	9.5	0.7	3.2	0.9

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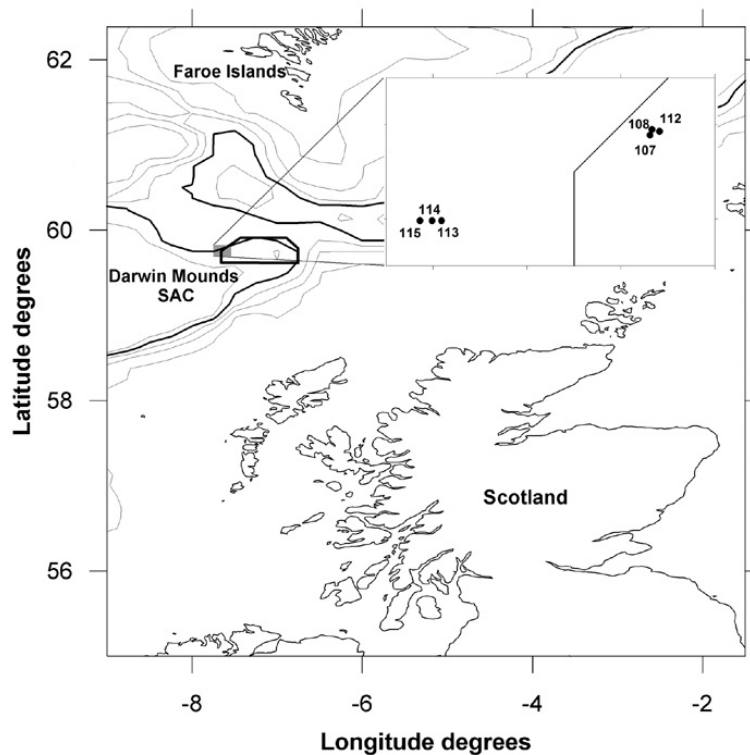


Fig. 1. Study area showing the sampling locations inside (stations 107–108 and 112) and outside (stations 113–114 and 115) the SAC. The SAC area and the 800 m contour are showed in bold.

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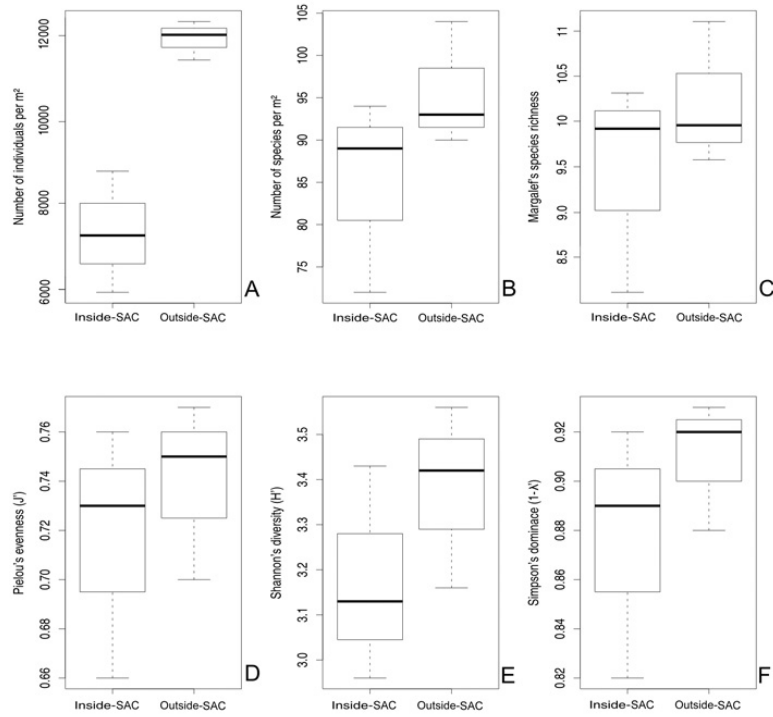


Fig. 2. Box-whisker plots of number of individuals (**A**) and biodiversity indices (**B–F**) inside and outside the SAC.

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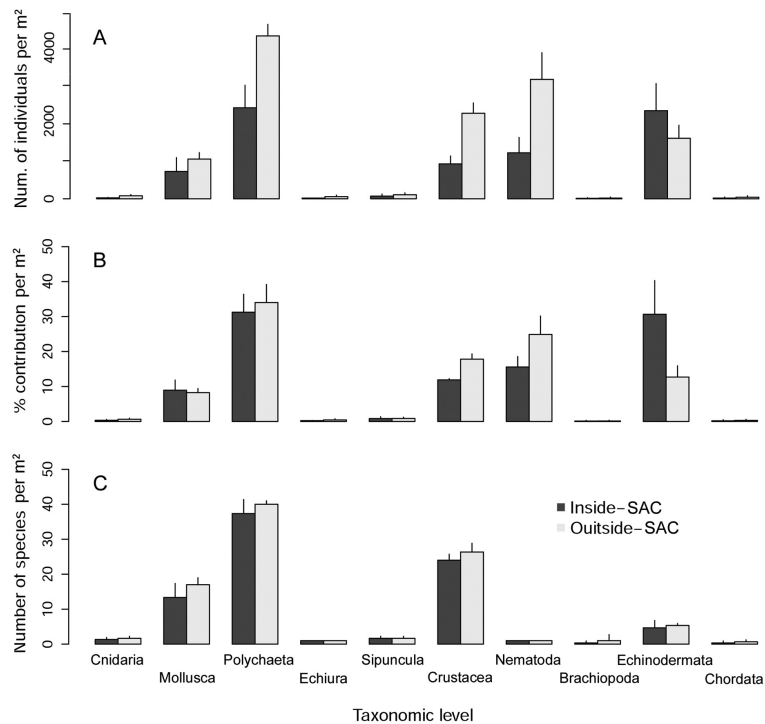


Fig. 3. Number of individuals (**A**) percentage contribution (**B**) and species (**C**) per m² and per taxonomic level inside and outside the SAC (mean ± SD).

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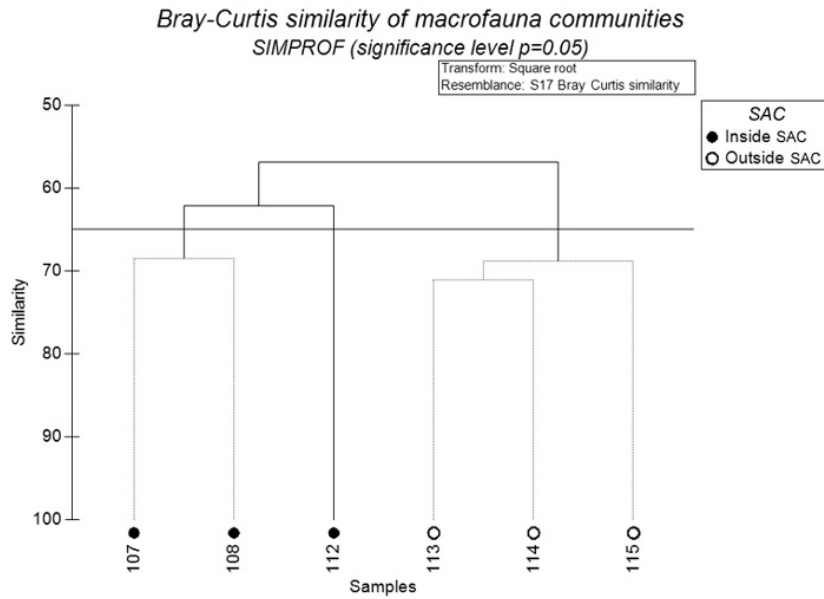


Fig. 4. Cluster analysis and SIMPROF test of macrofaunal species compositions inside ● and outside (○) the SAC. Dotted lines connected stations that did not show statistical differences in the multivariate community structure.

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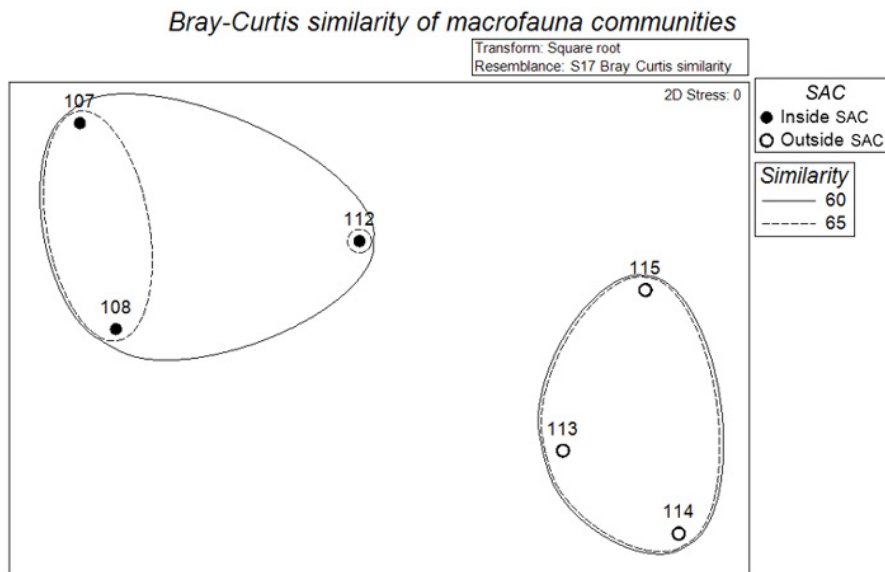


Fig. 5. MDS of macrofaunal species compositions inside ● and outside (○) the SAC.

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