

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, *Syringamina 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 µm 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 grain 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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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 %).

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 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 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 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 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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(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. fourth 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 *Ophiocten 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.

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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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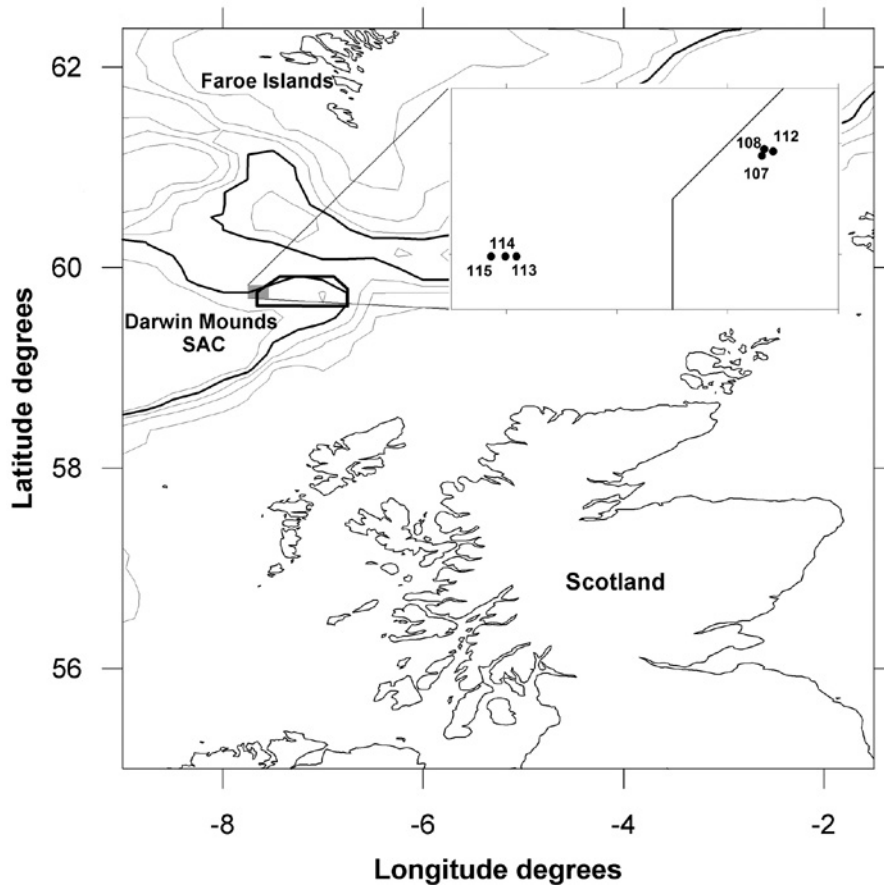


Fig. 1. Study area showing the sampling locations inside (stations 107–108 and 112) and outside (stations 113–114 and 115) the SAC. The SAC area and the 800 m contour are showed in bold.

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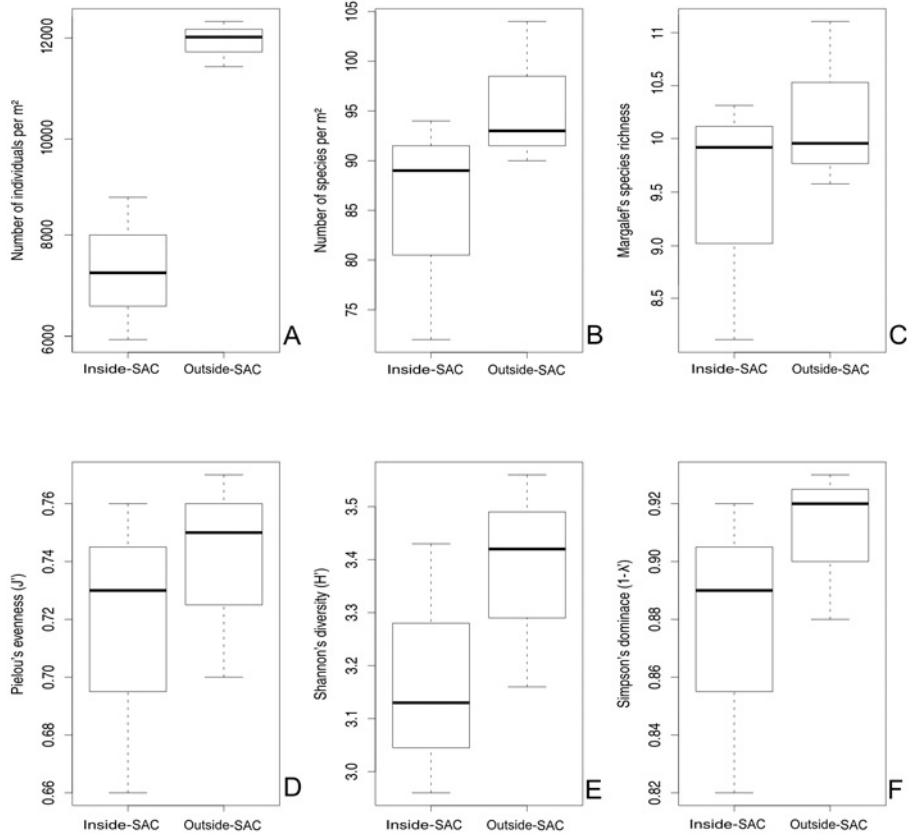


Fig. 2. Box-whisker plots of number of individuals (**A**) and biodiversity indices (**B–F**) inside and outside the SAC.

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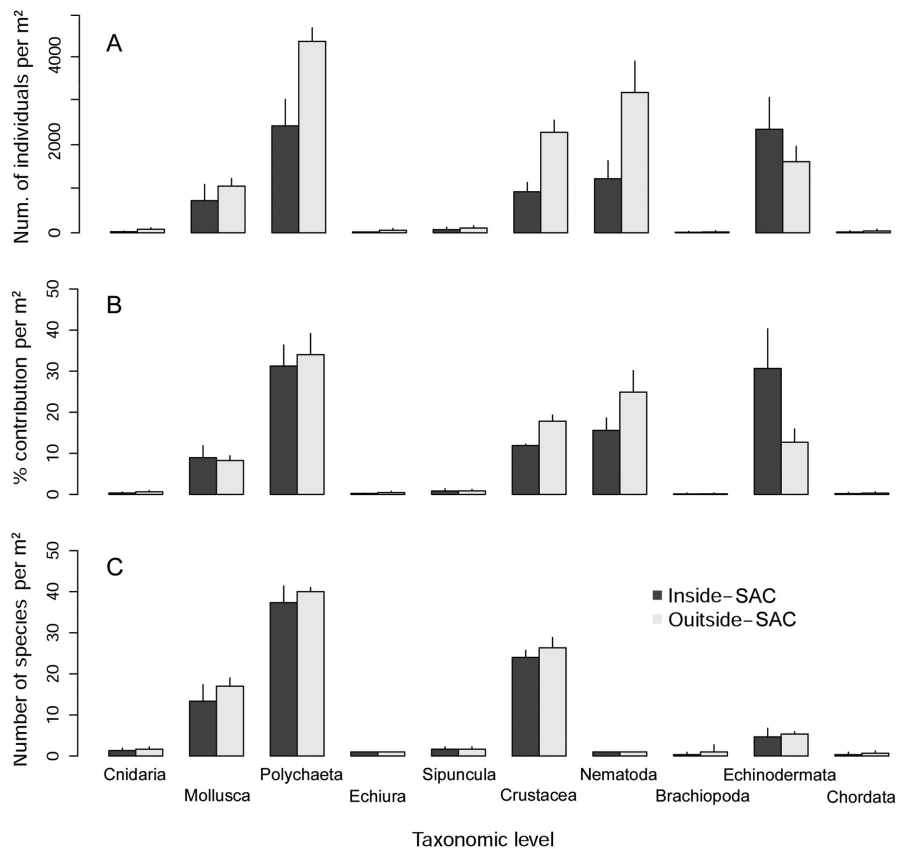


Fig. 3. Number of individuals **(A)** percentage contribution **(B)** and species **(C)** per m² and per taxonomic level inside and outside the SAC (mean \pm SD).

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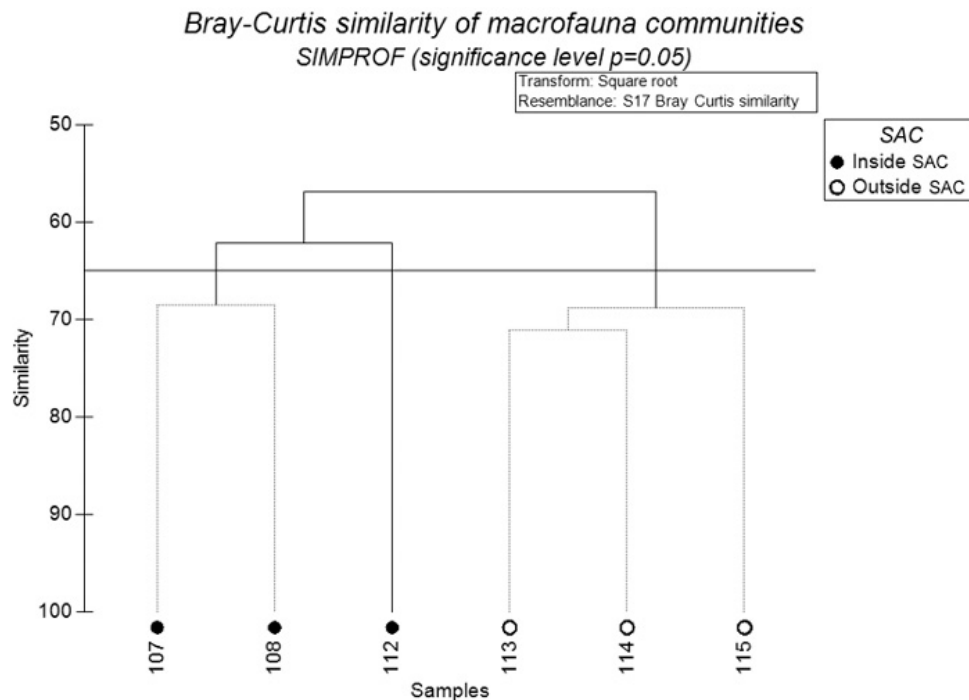


Fig. 4. Cluster analysis and SIMPROF test of macrofaunal species compositions inside ● and outside (○) the SAC. Dotted lines connected stations that did not show statistical differences in the multivariate community structure.

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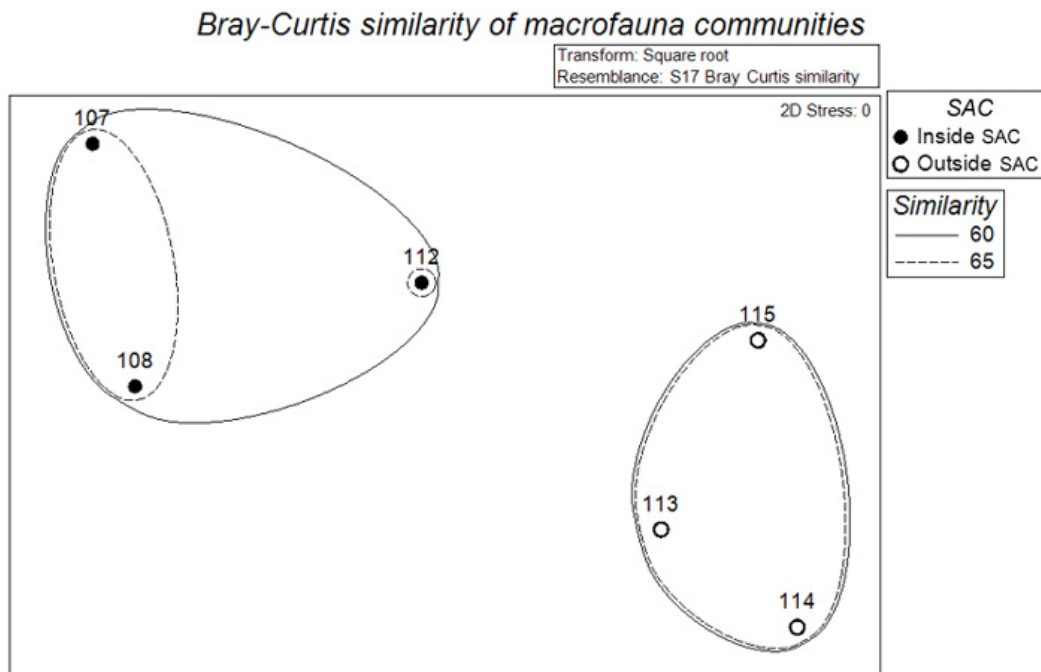


Fig. 5. MDS of macrofaunal species compositions inside ● and outside (○) the SAC.

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