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Sensitivity of a cold-water coral reef to interannual variability in regional oceanography

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Abstract

Aim: We assessed the effects of regional oceanographic shifts on the macrofaunal biodiversity and biogeography of cold-water coral reefs (CWCRs). CWCRs are often hotspots of biodiversity and ecosystem services and are in the frontline of exposure to multiple human pressures and climate change. Almost nothing is known about how large-scale atmospheric variability affects the structure of CWCRs' communities over ecological timescales, and this hinders their efficient conservation. This knowledge gap is especially evident for species-rich macrofauna, a key component for ecosystem functioning.

Location: The Mingulay Reef Complex, a protected biogenic ecosystem in the northeast Atlantic (120–190 m).

Methods: A unique time series (2003–2011) at 79 stations was used to make the first assessment of interannual changes in CWCRs' macrofaunal biodiversity, biogeography and functional traits. We quantified the impacts of interannual changes in North Atlantic Oscillation Index (NAOI)—the major mode of atmospheric variability in the North Atlantic, bottom temperature and salinity alongside static variables of seafloor terrain and hydrography.

Results: Environmental gradients explained a significant amount of community composition (R^2_{adj} = 26.7%, $p < .01$) with interannual changes in bottom temperature, salinity and NAOI explaining nearly twice as much variability than changes in terrain or hydrography. We observed significant differences in community composition, diversity and functional traits but not in species richness across interannual variability in bottom temperature. In warmer years, the biogeographic composition shifted more towards a temperate and subtropical affinity.

Main Conclusions: Our findings highlight the necessity for thorough investigations of faunal communities in CWCRs as they may be sensitive to interannual changes in regional oceanography. Considering the scientific consensus on the substantial warming of North Atlantic by 2100, we recommend the establishment of programmes for the monitoring of CWCRs. This will support an advanced understanding of CWCRs' environmental status over time and will serve their conservation for the future.

1 | INTRODUCTION

Large-scale fluctuations in the atmosphere can affect the water mass characteristics and shape hydrography, biodiversity and food webs that are critical components of the marine environmental status (Mittermeier et al., 2011; Myrberg et al., 2019). In the North Atlantic, the dominant mode of atmospheric variability is the North Atlantic Oscillation (NAO), which can be described through the North Atlantic Oscillation Index (NAOI, hereafter) using an empirical orthogonal function of sea-level pressure anomalies over the Atlantic sector (Hurrell et al., 2003).

The NAO is a major driving force for basin-scale interannual variability in circulation and water mass characteristics. The NAO influences the strength and extent of the subpolar gyre (Lohmann et al., 2009) and upper ocean temperature/salinity values in the subpolar North Atlantic (Hátún et al., 2005; Johnson et al., 2013). A negative NAOI is associated with westward subpolar gyre retraction enabling the intrusion of relatively warm and salty subtropical waters into the eastern North Atlantic (Hátún et al., 2005; Johnson et al., 2013) and subsequently onto the western European shelf (Johnson et al., 2020 and references therein). The NAO can mediate the timing and biomass of primary production (Basterretxea et al., 2018), shifts in zooplankton biogeography and biodiversity (Beaugrand et al., 2002) and cause regime shifts in food webs (Molinero et al., 2008). However, studies on effects of the NAO on benthic marine biodiversity hotspots remain scarce.

Cold-water coral reefs (CWCRs hereafter) are structurally complex ecosystems characterized as hotspots of biodiversity, biomass, elemental cycling and socioeconomic values (Armstrong et al., 2019; De Clippele et al., 2021; Henry & Roberts, 2017). CWCRs' spatial distribution is mainly controlled by the availability of hard substrates, seawater temperature, chemistry and hydrodynamics which facilitate the supply of food (Roberts et al., 2006; Hebbeln et al., 2019). As a response to their environmental requirements, CWCRs are often found in the (upper) bathyal zone and continental shelves.

CWCRs in the continental shelves and the bathyal zone are exposed, in overall, to multiple pressures such as physical damage (e.g. bottom trawling, oil & gas activities), ocean warming, deoxygenation and contaminants (Clark et al., 2019; Hennige et al., 2020; Roberts et al., 2016; Sweetman et al., 2017; Weinnig et al., 2020). While CWCRs located at relatively shallow depths on the continental shelf might act as refugia for the effects of ocean acidification (Turley et al., 2007), they are still threatened by warming, physical damage and microplastics (Bindoff et al., 2019; La Beur et al., 2019). As human activities expand, adaptive spatial management measures are required. This, in turn, needs a better understanding of variability in biodiversity and ecosystem functioning over space/time as well

as the development of integrated monitoring programmes (Cormier et al., 2019).

Macrofauna are a key constituent in ecosystem functioning globally: they are extremely species-rich (Grassle & Maciolek, 1992) and shape benthic elemental cycling (Janas et al., 2019). Macrofaunal biodiversity and functional traits are usually correlated with a system's capacity to buffer environmental stressors and offer a useful proxy of marine ecosystem health (Gunderson, 2000; HELCOM, 2018; Hooper et al., 2005). Studies have examined the effects of size and type of biogenic habitat (Bourque & Demopoulos, 2018; Jensen & Frederiksen, 1992; O'Hara et al., 2008) as well as bathymetric and hydrographic gradients in shaping macrofaunal biodiversity (Henry et al., 2013; Kazanidis et al., 2016). Notably, these studies focussed on a single time point, and work examining macrofaunal communities in CWCRs over time is lacking. This is a major knowledge gap that hinders our understanding about the response of macrofauna to temporal environmental changes. Addressing this knowledge gap is crucial as studies over geological timescales have found compelling links between the decline of CWCRs' biodiversity and climatic/oceanic perturbations (Douarin et al., 2014).

Our work aims to advance our understanding on the effects of spatial gradients in seafloor characteristics and current speed as well as the effects of interannual variability in regional oceanography on CWCRs' macrofauna. We focus on the Mingulay Reef Complex, a hotspot of marine biodiversity on the western European shelf. Mingulay Reef Complex is included in the East Mingulay Marine Protected Area (Figure 1). Increasing our understanding on the functioning of CWCRs enables efficient implementation of marine policies and the protection of these extremely fragile ecosystems for the future.

2 | METHODS

2.1 | Study area

The Mingulay Reef Complex (MRC, hereafter) is one of the best-studied CWCRs in the world and is located on the northeast Atlantic continental shelf, in western Scotland (e.g. Henry et al., 2013; Roberts et al., 2005). The MRC contains reef mounds that are 13–60 m wide, 16–108 m long and between 2 to 34 m tall, which are formed by the cosmopolitan scleractinian coral *Lophelia pertusa* (De Clippele et al., 2017). X-ray computed tomography of seabed cores revealed cycles of different ecosystem phases (reef initiation, framework expansion, framework collapse, coral rubble) over the mid-Holocene to late Holocene (Douarin et al., 2014).

Today, the MRC is primarily bathed by North Atlantic Water which is a warm (10.0–10.5°C), salty (35.4 psu) water mass that flows
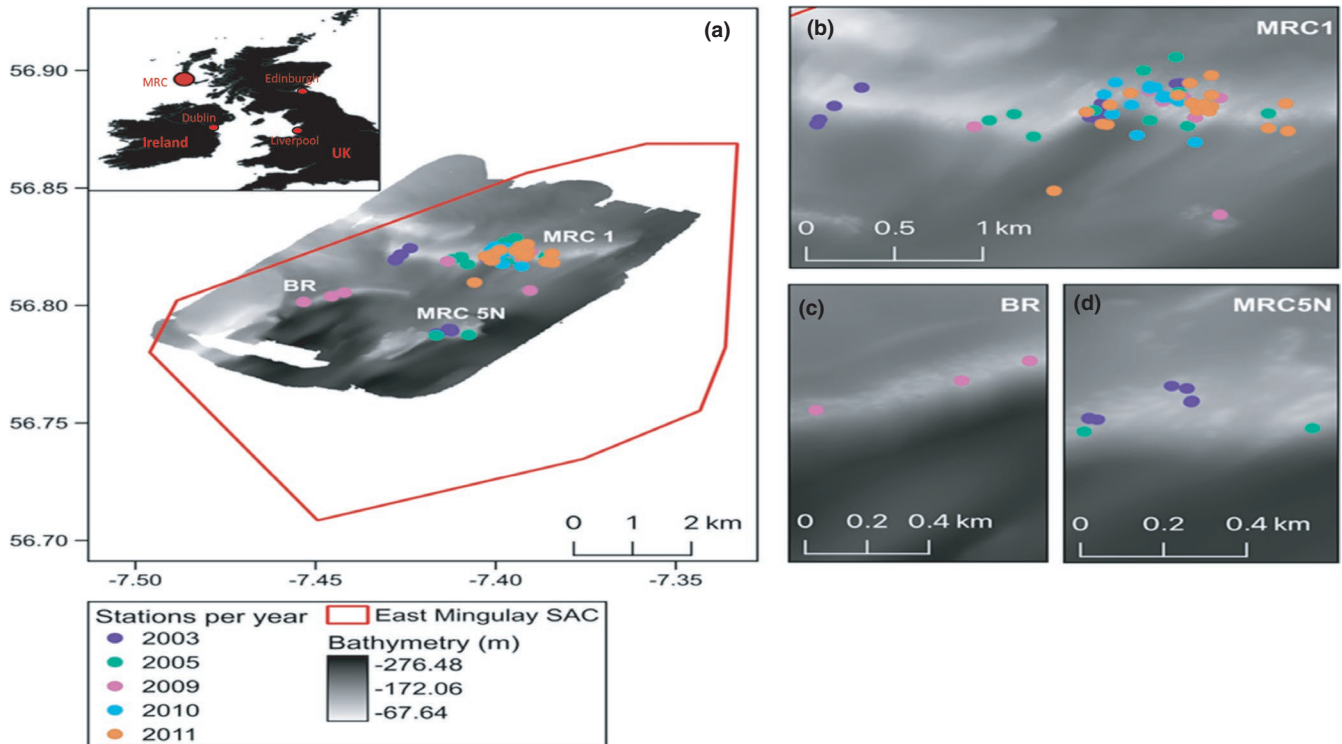
FIGURE 1 (a) Location of the Mingulay Reef Complex (total area ~100 km²) in the Sea of the Outer Hebrides (northeast Atlantic), with the red polygon delineating the east Mingulay Marine Protected Area. Colourful circles represent the years of sampling. (b) Locations of sampling stations at Mingulay Reef Complex 1 (MRC1), (c) at Banana Reef (BR) and (d) at Mingulay Reef Complex 5 North (MRC5N). Colour shading represents bathymetry, see legend. For more details on stations, see Table S1

onto the European Shelf from the eastern subpolar North Atlantic (Johnson et al., 2013; Porter et al., 2018). Over multi-annual time scales, the bottom temperatures and salinities at MRC show a statistically significant inverse relationship with the NAOI (Johnson et al., 2020). Specifically, in years with weak atmospheric forcing and a negative NAOI, warmer and more saline bottom conditions are found at MRC, while cooler and fresher bottom values are seen during a positive NAOI (Johnson et al., 2020). In contrast, the fresher Scottish Coastal Current has a minor influence at the MRC, particularly at the seabed (Inall et al., 2009).

Acoustic surveys of the MRC using multibeam echosounders combined with seabed video revealed mounds of *L. pertusa* in five Mingulay sites, in water depths ranging from 120 to 190 m. These five reefs include the following: Mingulay Reef Complex 1 (MRC1, hereafter), Mingulay Reef Complex 5 North (MRC5N, hereafter), Mingulay Reef Complex 5 South, Banana Reef and Four Mounds (Duineveld et al., 2012; Roberts et al., 2009). As MRC1, MRC5N and Banana Reef are the most data-rich reefs in terms of environmental and macrofaunal data, we used these sites to investigate links between spatial and temporal environmental variability and marine ecosystem structure and function (Figure 1).

We analysed macrofaunal communities and environmental data from 79 stations sampled between 2003 and 2011 (Figure 1; Table S1). The number of stations sampled per year is as follows: 18 in 2003, 14 in 2005, 14 in 2009, 15 in 2010 and 18 in 2011 (Figure 1;

Tables S1–S2). Sampling in remote, CWCRs is logistically challenging, and thus, the MRC stations that have been sampled to date may not be fully representative of the whole Marine Protected Area (Figure 1). It should be clarified though that (a) the Marine Protected Area itself contains also soft sediments and (b) our stations have been carefully selected for sampling CWCRs habitats of which the MRC1, Banana Reef and MRC5N are the most-well developed that we know of.

Considering data resolution and previous findings at MRC (NAOI—Hurrell et al., 2003; temperature, salinity—Findlay et al., 2013; bathymetry, topography, current speed, macrohabitat—Roberts et al., 2009; Henry et al., 2013), we classified a priori the bathymetry, topography and current speed as "spatial variables" (i.e. mainly changing across space), and the bottom potential temperature (hereafter mentioned as "bottom temperature"), bottom salinity and the NAOI as "temporal variables" (i.e. variables mainly changing across time).

2.2 | Benthos

Benthic samples (total $n = 79$) were collected using a modified Van Veen Grab (sampling 0.1 m² per deployment) in 2003, 2005, 2009, 2010, 2011 (Figure 1; Table S1). Samples were sieved at 1 mm, macrobenthos collected and stored in 4% seawater formalin and

transferred to 70% industrial methylated spirit. Specimens were identified to the lowest possible taxonomic level using best available taxonomic keys for North Atlantic marine invertebrates and guidance from expert taxonomists.

Accounting for the existence of both colonial and solitary taxa, we have recorded species' presence/absence (Henry et al., 2013). We acknowledge that the use of presence–absence (and not abundance/biomass) data may have some effect on the outcomes of our analyses but these effects are not expected to be major (Buchner et al., 2019). Furthermore, we feel that presence–absence data was the optimal approach as for many species (e.g. encrusting bryozoans) measurements on abundance and/or biomass would not be accurate. Following previous biodiversity studies at MRC (Henry et al., 2013), we have also excluded sponges due to a lack of taxonomic resolution across this group. Presence/absence data were assembled in a species assembly matrix using PRIMER (Clarke & Gorley, 2015).

Ecological functional traits reflecting species' functions in the ecosystem were considered (after Bates et al., 2017). Specifically, specimens were assigned to a feeding type (i.e. suspension/filter feeder, deposit feeder/grazer, predator, omnivore), mobility/orientation type (i.e. sessile encrusting, sessile horizontal, sessile erect, mobile) and body size (i.e. 0–10, 10–50, 50–100, >100 mm) using the information in Henry et al. (2013), Kazanidis et al. (2016), Hayward and Ryland (2017).

Specimens identified at the species level were also assigned to one of the 30 biogeographic realms identified by Costello et al. (2017) using the information on each species' geographic distribution from the Ocean Biodiversity Information System (https://obis.org/). Information for each species' bathymetric distribution, temperature and salinity ranges was then extracted from the Ocean Biodiversity Information System and recorded.

2.3 | Spatial variables: bathymetry, topography and current speed

Topographic terrain variables were calculated from bathymetric data (depth). Specifically, the following metrics were derived from the bathymetry data: slope, ruggedness (equivalent to rugosity), northness and eastness (via aspect), standardized broad- and fine-scale bathymetric position index (inner radius of 1 and outer radius of 5 and 3 cells, respectively). We used these bathymetry-related variables to have a good coverage of the seabed terrain parameters that change across space and to quantify their role in macrofaunal biodiversity patterns. Previous studies at the MRC (Henry et al., 2010, 2013) and elsewhere (e.g. Savini et al., 2014; Sundahl et al., 2020) have shown that bathymetry-related variables such as bathymetric position index and slope have a significant contribution in explaining spatial patterns in cold-water coral communities.

The Spatial Analyst and Benthic Terrain Modeler toolboxes in ArcGIS were used in this study as they are toolboxes widely used in the literature for similar studies (Henry et al., 2010, 2013; Woodall et al., 2015; Lacharite and Metaxas, 2018; Murillo et al., 2020 amongst others). The average values of each spatial variable were extracted

using the ArcGIS v.10.6.1 spatial Analyst Toolbox. In addition, average and maximum current speed (m/s) were also obtained at each station from a high-resolution 3D ocean model created for MRC. Average and maximum current speed values (m/s) were extracted using the ArcGIS v. 10.6.1 Spatial Analyst toolbox using data generated by a high-resolution 3D ocean model created for the MRC by Moreno Navas et al. (2014). The nested system consisted of a coarse-resolution outer model which covers part of the Sea of the Hebrides and, a fine-scale inner model covering the MRC (horizontal resolution ~100 m).

Macrohabitat was also treated as a spatial variable. Based on previous studies at MRC (Henry et al., 2010, 2013), macrohabitat was classified in six types, representing six levels of structural complexity. These types were as follows: "muddy sand" (i.e. the least structurally complex macrohabitat), "rubble," "rock," "live coral," "dead framework" and "mixed live and dead framework" (i.e. the most structurally complex habitat).

2.4 | Temporal variables: Bottom temperature, bottom salinity and NAOI

Following previous studies (e.g. Birchenough et al., 2018; Zettler et al., 2017), we have used data for the winter NAOI (December-January-February-March) (Hurrell et al., 2003). These data were downloaded from the National Center for Atmospheric Research/University Corporation for Atmospheric Research website (climate-dataguide.ucar.edu). This was done both for the year of biological sampling (noted as "same year") and for the year prior to it (noted as "previous year"), following Zettler et al. (2017) (Table S2). Annual averages of bottom temperature (±0.01) and bottom salinity (±0.001) for the same and previous year were extracted from the grid point nearest to MRC in the UK Meteorological Office's EN4 objectively analysed observational data set (Good et al., 2013).

2.5 | Data analysis

To avoid statistical bias and Type I error inflation, all explanatory variables were checked for correlation (R package "corrplot" version 0.84; Wei & Simko, 2017) and variables with significant correlation scores (Pearson's $r > .7$ or $<-.7$) were discarded (Figure S1). The species data were Hellinger-transformed, giving lower weights to rare species and maintaining linear correlations between species and gradients of environmental variables (Legendre & Gallagher, 2001).

The variance of macrofaunal communities explained by spatial and temporal environmental variables was examined using redundancy analysis (RDA). This multivariate statistical method combines regression and principal component analysis and can model response variables as a function of multiple explanatory variables (Borcard et al., 2018). The RDA model was built with the species assembly matrix as the response variable and all the non-correlated environmental variables as the explanatory variables. A forward stepwise selection was applied to retain the statistically significant explanatory variables (R package "vegan"

version 2.5-6; Oksanen et al., 2019). In order to quantify the variance of macrofaunal communities explained by (a) spatial, (b) temporal and (c) interactions between spatial and temporal variables, a series of RDA and partial RDA (pRDA) models were constructed (Borcard et al., 1992). The significance of fitted environmental vectors was determined by calculating the goodness of fit defined as the squared correlation coefficient r^2 using permutation tests with the command envfit() of package "vegan" (Oksanen et al., 2019). Species under the influence of each specific environmental variable were identified through visual inspection of the total RDA and pRDAs biplots, with species selection based on RDA scores (R package "vegan" and "RcolorBrewer" version 1.1-2; Neuwirth, 2014). All RDA and pRDA analyses were conducted in R. R code is provided in the Supporting Information.

Species richness (SR), Margalef diversity index (d) and average taxonomic distinctness (Δ^+) were measured in PRIMER with values of SR and Δ^+ being normalized to the number of samples collected each year (Clarke & Gorley, 2015; Table S1). Statistical differences in SR, d, Δ^+ and functional traits across (a) interannual changes in bottom temperature, bottom salinity, NAOI (same year), NAOI (previous year) and (b) areas (i.e. MRC1, MRC5N and BR) were examined in R. First, the normality of the distributions was checked with the Shapiro–Wilk test and the equality of variances with the Bartlett test. In the case of normal distribution and equal variances, the hypothesis that the groups have the same mean was tested through one-way analysis of variance. In the case of normal distributions and unequal variances, the hypothesis that the groups have the same mean was tested through one-way analysis of means. In the case that the normal distribution criterion did not hold, the hypothesis that the groups have the same median was tested through the Kruskal–Wallis test. These tests were followed by pairwise comparisons to identify the presence of statistically significant differences in pairs of groups. In the case of one-way analysis of variance, multiple comparisons were carried out through the Tukey's test. In the case of one-way analysis of means, the comparisons were carried out through the Games Howell test (Burk, 2018). When the Kruskal–Wallis test was used, the pairwise comparisons were carried out through the Dunn test (Dinno, 2017). Accounting for the multiple comparisons, the p values were adjusted using the Bonferroni correction (Armstrong, 2014).

3 | RESULTS

3.1 | Macrobenthos taxonomic, mobility and functional traits' composition

In total, 342 taxa were identified across 13 phyla, with 62% of the taxa being identified to species level (Table S3). Phyla with the highest number of taxa were Annelida (37.6% of total taxa), Bryozoa (24.3%), Arthropoda (16.0%) and Mollusca (10.1%). Almost half of the 342 taxa were suspension- and filter-feeding species (48.5%) followed by deposit feeders/grazers (25.1%), predators (20.5%) and omnivores (0.1%). In terms of mobility/orientation, most of the taxa were mobile (54.1%), followed by sessile erect (19.9%), sessile encrusting (16.1%) and sessile horizontal (9.6%). Finally, in terms of

TABLE 1 Results of the permutation test on the partial redundancy analyses (RDA) showing the amount of variance explained by each of the statistically significant temporal and spatial variables. r^2: squared correlation coefficient (goodness of fit statistic)

	RDA1	RDA2	r^2	p Value
Temporal variables (13.7%)				
Bottom temperature (same year)	−0.91210	0.40997	.5685	.001
Bottom salinity (same year)	−0.16893	0.98563	.5738	.001
NAOI (same year)	−0.64973	−0.76016	.5734	.001
NAOI (previous year)	−0.92202	−0.37003	.1333	.007
Spatial variables (7.2%)				
Bathymetric position index	0.95996	−0.28013	.3073	.001
Ruggedness	−0.56025	−0.82833	.2293	.003
Macrohabitat	0.28145	−0.95958	.1415	.005
Average current speed	0.05328	−0.99858	.0892	.045

Abbreviation: NAOI, North Atlantic Oscillation Index.

body size, most of the taxa were 0–10 mm (42.7%), followed by those at 10–50 mm (31%), 50–100 mm (14%) and >100 mm (12%).

3.2 | Drivers of macrobenthic community structure

The forward stepwise selection of environmental variables retained four spatial and four temporal variables that had a statistically significant contribution ($p < .05$) in explaining macrofauna variance. In total, 26.7% of the variance was explained: 13.7% by the temporal variables, 7.2% by the spatial variables and 5.7% by the interactions between spatial and temporal variables. The spatial and temporal variables with a statistically significant contribution in explaining macrofaunal variance can be seen in Table 1.

3.3 | Species richness (SR), Margalef diversity index (d), average taxonomic distinctness (Δ^+) and community composition across time and space

Statistically significant differences were seen for Margalef diversity index (d) values across bottom salinities and NAOI values (same and previous year) and marginally across the different bottom temperatures (Figure 2; Table S4). Average taxonomic distinctness (Δ^+) showed statistically significant changes over the interannual shifts in bottom temperature, bottom salinity and NAOI and across the areas (Figure 2; Table S4). These maximum Δ^+ values (seen in 2005) were significantly different from the Δ^+ values seen in years with
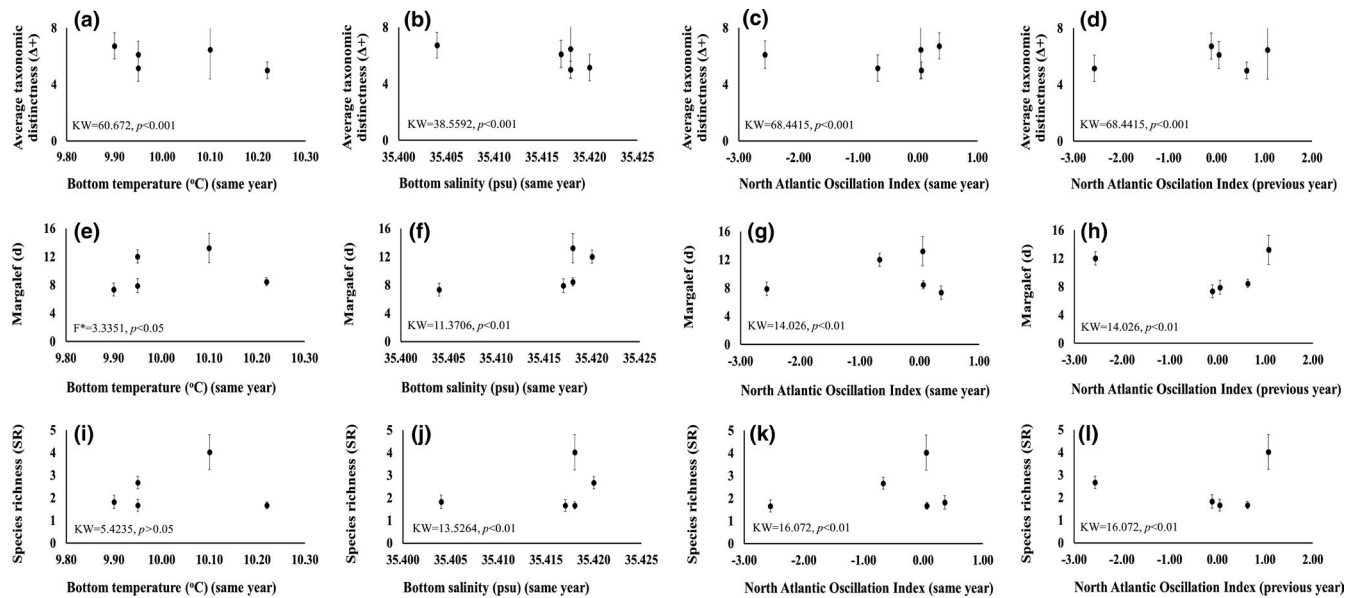
FIGURE 2 (a–d) Average taxonomic distinctness [Δ⁺], (e–h) Margalef diversity index [d] and (i–l) species richness [SR] across interannual changes in bottom temperature (same year), bottom salinity (same year), North Atlantic Oscillation Index (NAOI; same year) and NAOI (previous year) at the Mingulay Reef Complex. Annual average values (circles), standard error (error bars), outcomes of statistical tests (*F* = one-way ANOVA; *F**=one-way analysis of means not assuming equal variances; KW = Kruskal–Wallis rank sum test) and *p* values are given. The outcomes of the pairwise comparisons are shown in Table S4
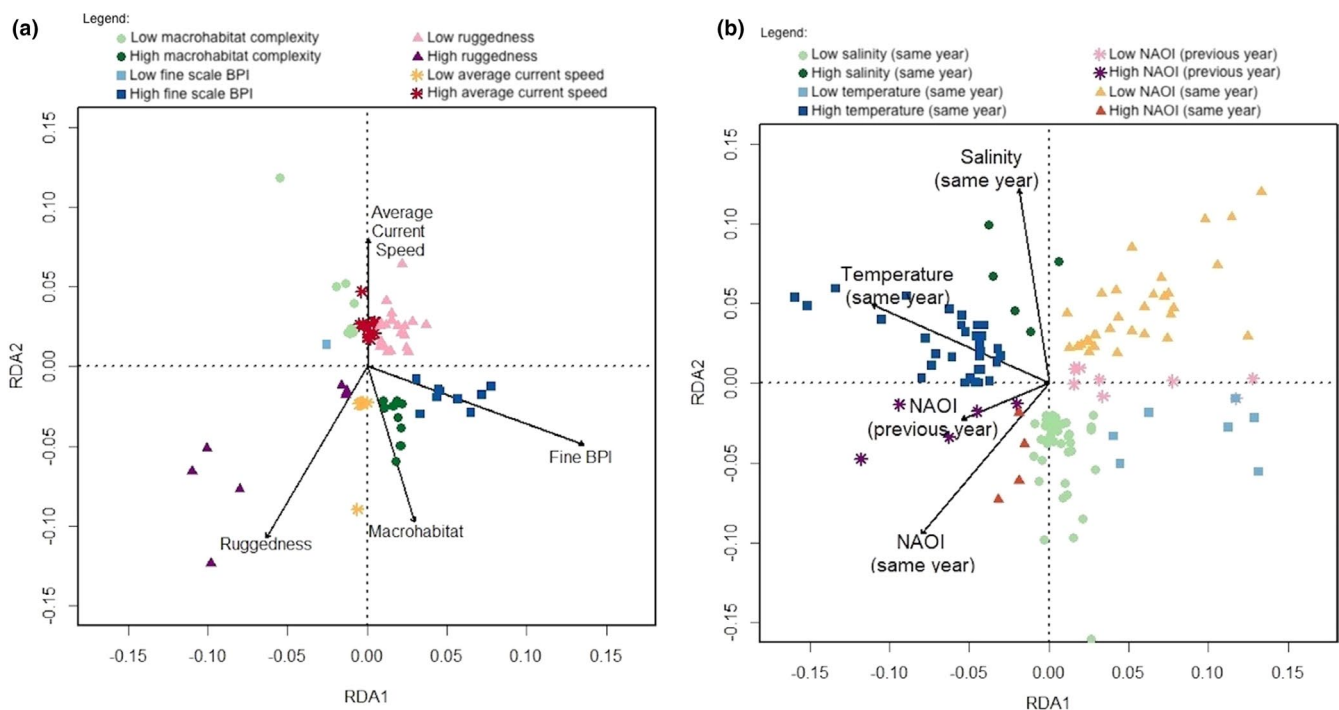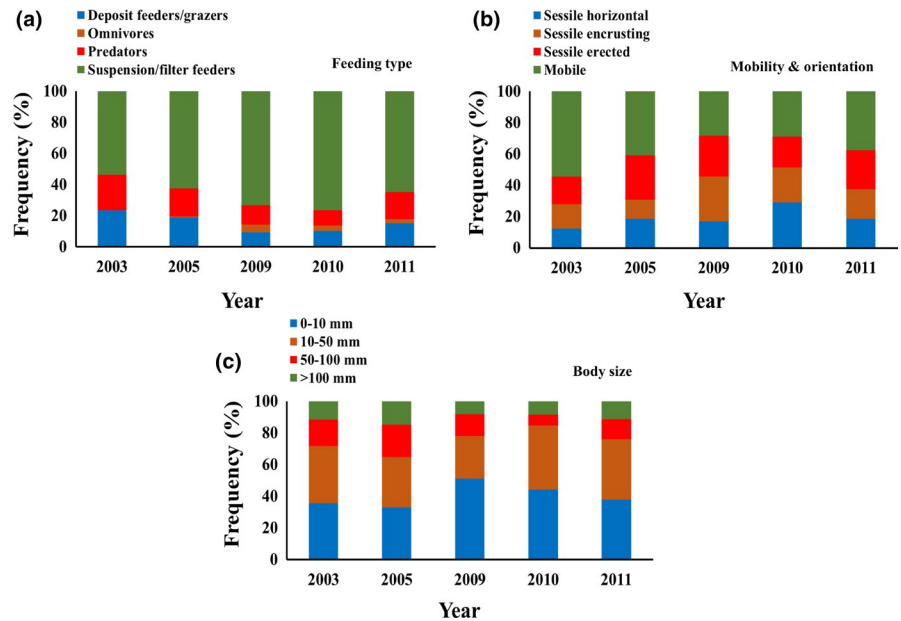

FIGURE 3 Biplots of pRDA model showing species associated with (a) the spatial variables [fine-scale bathymetric position index (BPI), macrohabitat, ruggedness, average current speed] and (b) the temporal variables [bottom temperature, bottom salinity, North Atlantic Oscillation Index (NAOI; same year) and NAOI (previous year)] at the Mingulay Reef Complex. Each symbol colour combination represents a group of species associated with a state of an environmental variable (see legend). For species names, see Figure S2 and Tables S5, S6

higher bottom temperatures, higher bottom salinities, lower values of NAOI (same year) and lower and higher values of NAOI (previous year) (Figure 2; Table S4).

Species richness (SR) did not show statistically significant changes over the interannual changes in bottom temperature (Figure 2; Table S4). SR, however, showed statistically significant shifts over the interannual

FIGURE 4 Changes in (a) feeding types, (b) mobility/orientation types and (c) body size across years at the Mingulay Reef Complex. The outcomes of the pairwise comparisons are shown in Table S7

3.4 | Macrofaunal groups under the influence of environmental gradients across space

Species linked to higher fine-scale bathymetric position index values were mainly sessile suspension feeders, while those associated with structurally complex macrohabitats included a rich mixture of functional traits with predators (e.g. *Porania (Porania) pulvillus*, *Eunice norvegica*), mobile deposit feeders/grazers (e.g. *Galathea strigosa*) and sessile suspension- and filter-feeding species (e.g. the bivalve *Hiatella arctica*) (Figure 3a; see also Figure S2a and Table S5). Species found in highly rugged areas were mainly erect suspension feeders with larger more robust morphologies (e.g. the anthozoan *Parazoanthus anguicomus*), while about one-third of species found in less rugged areas were encrusting bryozoans (e.g. *Schizomavella (Schizomavella) linearis*). Species linked to high average current speed areas were mainly suspension- and filter-feeding species (the erect bryozoan *Buskea dichotoma*) and omnivores, while those in low average current speed areas were mainly deposit feeders (e.g. the isopod *Uromunna petiti*). In areas with higher structural complexity, there were more predators than suspension- and deposit-feeding species; on the contrary, in areas with lower structural complexity there were more suspension-feeding species than predators and deposit-feeding species (Figure 3a; see also Figure S2a and Table S5).

3.5 | Macrofaunal groups under the influence of environmental gradients across time

A single assemblage seemed to be associated with higher bottom temperatures (13 species) and another one associated with lower

bottom temperatures (seven species) (Figure 3b; see also Figure S2b and Table S6). Species associated with higher bottom temperatures at the MRC (e.g. the polychaete *Lysidice unicornis*) are commonly found in warmer areas like the Caribbean, Indo-Pacific Seas, Gulf of Suez and Red Sea biogeographic realms. In contrast, species associated with lower bottom temperatures (e.g. the bryozoan *Disporella hispida*) are also found in cooler areas like the Norwegian Sea and the Arctic Seas biogeographic realms (Figure 3b; See also Figure S2b and Table S6).

Three species were associated with higher bottom salinity values (e.g. the isopod *Janira maculosa*) while 29 species (molluscs, polychaetes, bryozoans and echinoderms) (Figure 3b; see also Figure S2b and Table S6) were associated with slightly fresher bottom waters. Seven species were associated with the higher NAOI (same year) (e.g. the suspension-feeding polychaete *Serpula vermicularis*) and the higher NAOI (previous year) values (e.g. the erect anthozoan *Parazoanthus anguicomus*). In contrast, a much larger number of species ($n = 22$) were associated with the lower values of the NAOI (same year). These were mainly encrusting suspension feeders (e.g. the bryozoan *Amphiblestrum flemingii*), small suspension feeders (e.g. the bivalve *Modiolula phaseolina*) and deposit feeders (e.g. the ophiuroid *Amphipholis squamata*) (Figure 3b; see also Figure S2b and Table S6).

3.6 | Macrofaunal functional traits

Almost all the groups of functional traits showed statistically significant changes over the interannual changes in bottom temperature, bottom salinity and NAOI (Figure 4; Table S7). The frequency (%) of the suspension/filter feeders and the sessile erect organisms had their lowest values during highest bottom temperatures (Figure 4). This lowest frequency of suspension/filter feeders and sessile erect organisms was statistically different ($p < .05$) from the frequencies

recorded under lower temperatures (Figure 4; Table S7). On the contrary, the frequency of predators had its maximum values under the highest bottom temperatures (Figure 4); this peak in the distribution of predators was statistically different from the frequency of predators recorded under lower bottom temperatures (Figure 4; Table S7).

4 | DISCUSSION

This study has unravelled the effects of both spatial and temporal environmental gradients on macrofaunal communities in a cold-water coral reef. Interannual changes in regional oceanography explained almost double the variance explained by spatial gradients, the latter which were solely considered in previous studies. (Bourque & Demopoulos, 2018; Buhl-Mortensen et al., 1995; Cordes et al., 2008; Henry et al., 2013). Interestingly, there were no significant changes in SR over bottom temperature changes but there were changes in community composition, Δ^+ and functional traits and marginal changes for d. This highlights the necessity for thorough examinations of macrofaunal communities to identify changes in ecosystem structure and functioning.

Due to the relatively short time series examined here, it is challenging to draw a definite conclusion on the effects of temperature, salinity, and NAOI interannual variability on CWCR macrofauna. Models predict an increase of up to 2.0°C for bottom temperatures at Mingulay by 2100 (Findlay et al., 2013) while temperatures between 200–1,000 m in the North Atlantic are predicted to rise, on average, by 1.8°C over the same period (Puerta et al., 2020; Sweetman et al., 2017). Considering that changes in biodiversity and functional traits were observed over a range of 0.32°C, we highlight the need for the establishment of monitoring programmes at MRC and at CWCRs in general.

4.1 | On the role of spatial gradients

Many species associated with topographic highs or high average current speed were sessile suspension feeders suggesting that these conditions are highly favourable, possibly due to enhanced food supply (Davies et al., 2009; Kazanidis & Witte, 2016).

Macrohabitat was also an important driver of species distribution. Areas dominated by live and dead coral framework hosted a richer mixture of functional traits than areas with muddy sand. This is likely related to the fact that higher structural complexity increases the number of ecological niches (Tews et al., 2004). The presence of predators (e.g. *Eunice* polychaetes) is also possibly related to the fact that they feed on anthozoans and tunicates which are abundant in coral framework (Kazanidis & Witte, 2016). Regarding ruggedness, larger sized and erect suspension feeders were found in highly rugose areas while encrusting delicate forms proliferated in smoother areas. Large/erect/robust body forms likely proliferate in rugose areas under turbid waters due to enhanced food capture rates. In contrast, low-lying and delicate forms are preferably found in less energetic environments (Henry et al., 2013).

4.2 | On the role of temporal gradients in water mass characteristics and regional oceanography

A recent study showed a statistically significant inverse relationship between bottom conditions in the eastern North Atlantic and the strength of the NAO (Johnson et al., 2020). The westward retraction of the subpolar gyre during a weak NAO (Lozier & Stewart, 2008), enables the northward extension of warm and salty subtropical waters (Hátún et al., 2005, 2017; Johnson et al., 2013). A similar signal was observed at the MRC, with warmer and more saline bottom conditions again observed during a weak NAO (Johnson et al., 2020). The similarity in time series from the two areas suggests that bottom conditions at the MRC reflect changes observed in the wider eastern North Atlantic. It appears that subpolar gyre dynamics affect the MRC and contribute to biodiversity changes over ecological timescales.

Shifts in faunal biogeographic affinity are probably related to changes in water mass characteristics. Most of the species associated with the higher values of bottom temperature are also found in temperate areas on both sides of North Atlantic as well as in subtropical areas. Two possible scenarios are suggested. First, warmer conditions enhance species' reproductive success (Byrne, 2011; Holopainen et al., 2016; Lewis et al., 2002; Rupp, 1973). Second, during a weak NAO/westward retraction of the subpolar gyre, the northward expansion of the warm and salty North Atlantic Water facilitates the extension of species from lower to higher latitudes. Most species associated with warmer waters at MRC are mobile polychaetes and arthropods. Their higher mobility and pelagic larvae (Iannotta et al., 2007) could support their dispersal.

NAOI (same year) had a stronger contribution than the NAOI (previous year) in explaining biological variability, suggesting a relatively rapid response of macrofauna to NAOI. This mirrors findings from the intertidal/upper subtidal zone in the North Sea (Birchenough et al., 2018 and references therein), the Mediterranean bathyal (Cartes et al., 2009) and the abyssal northeast Atlantic (Smith et al., 2009) where the winter NAO caused shifts in the structure and functioning of benthic communities in subsequent seasons and years.

A high-resolution ocean model shows that the NAO has a positive correlation with bottom kinetic energy at the MRC (Johnson et al., 2020). A high NAOI/increased kinetic energy likely enhances food supply supporting the proliferation of some suspension/filter feeders such as *P. patelliformis* and *S. vermicularis* (Table S6). In contrast, deposit feeders and encrusting organisms (Table S6) were associated with a low NAOI/decreased kinetic energy which likely enhances the food capture by these low-lying species.

It is important to note that a large part of biological variability remains unaccounted for. About 80% of the polychaetes species are distributed over a relatively wide range of bottom temperatures and salinities (OBIS, 2019). Thus, environmental gradients experienced at the MRC are likely within their niche envelope and will not explain any variability. Unexplained variability could also be linked to limited dispersal. Indeed, 40% of the species not associated with

environmental gradients were found at only one station. Limited dispersal obscures any relationship between biological and environmental sampling scales (Bullock et al., 2006; Selmoni et al., 2020). Third, the temporal resolution of environmental sampling may be somewhat coarse and biased towards species with perennial life spans.

4.3 | Implications for biogenic ecosystem functioning

The changes seen at the MRC macrofauna over time, including common species (Henry et al., 2013; Kazanidis et al., 2016), indicate that the macrofauna may be susceptible to interannual changes in water mass characteristics. When the MRC was subjected to higher bottom temperatures, there was a significant decrease in suspension/filter feeders and a significant increase in predators (Figure 4; Table S7). The mechanisms driving these shifts are not known, and longer time series are needed to draw a firm conclusion. It is noteworthy, though, that ~70% of the suspension/filter-feeding species that were not recorded during higher temperatures have to date also not been recorded in (sub)tropical areas. This indicates their preference for higher latitudes and colder waters (Hayward & Ryland, 2017; Jensen & Frederiksen, 1992; Klitgaard, 1995). In addition, predators recorded during higher bottom temperatures at MRC have been found in (sub)tropical areas indicating their affiliation with a wide range of bottom temperatures (Froglia & Speranza, 1993; Simon et al., 2014).

Suspension and filter feeders are usually primary consumers which channel organic matter from the lower to the higher trophic levels. Studies in tropical reefs and CWCRs have shown their key role in food web functioning through the high assimilation of dissolved organic carbon and its conversion to biomass (de Goeij et al., 2017; Rix et al., 2016). Their role is also pronounced in areas where strong bottom currents prevail, for example CWCRs, as they trap food sources which otherwise would have been transported away (Gili & Coma, 1998; Roberts et al., 2009).

Experimental work has shown that ocean warming has negative impacts on the health status of some suspension/filter feeders (bivalves, Mackenzie et al., 2014; tunicates, Nagar & Shenkar, 2016; sponges, de Goeij et al., 2017) affecting thus their important role in ecosystem functioning (Bell et al. 2018). Recent studies have shown the negative impacts of increased temperatures on the abundance of low-trophic level consumers (Garzke et al., 2015) and biomass transfer from secondary production to fish stocks, globally. This reduced efficiency is expected to be more severe in cold-water ecosystems. Studies at ecosystems for which we have a relatively advanced understanding compared to CWCRs (e.g. plankton, macroalgae, fish, marine mammal and seabird systems; Beaugrand et al., 2008; Poloczanska et al., 2016; Ramírez et al., 2017) have given insights into how the rapid northwards expansion of tropical species can lead to substantial shifts in temperate marine ecosystem functioning (Vergés et al., 2014).

4.4 | Implications for CWCR conservation

Our findings contribute to the conservation of the MRC in several ways. Firstly, the European Union's Marine Strategy Framework Directive has set 11 descriptors for the achievement of Good Environmental Status (European Commission, 2017). Biodiversity (Descriptor 1), non-indigenous species (D2), food webs (D4) and seafloor integrity (D6) are four key descriptors in this Directive. The present study advances our knowledge about biodiversity, habitat integrity and food web structure at MRC Marine Protected Area over time and space serving conservation and achievement of Good Environmental Status. Furthermore, sampling benthos over the years has served the establishment of baselines for marine litter (D10 in the Directive) at MRC (La Beur et al., 2019). Furthermore, improving the understanding about the effects of interannual variability on MRC fauna could help improve predictions of the ecosystem functioning under future scenarios. This progress serves the establishment of monitoring programmes at MRC, which are currently missing. Indeed, the current study has shown that MRC may be sensitive to interannual changes in water mass characteristics, and thus, the establishment of regular monitoring programmes is necessary for reef conservation. Our findings contribute also to the conservation of CWCRs on a regional scale. Specifically, biological and environmental (meta)data from MRC are archived in online repositories (e.g. PANGAEA) serving the upscaling of findings from the local to the regional level, which is necessary for the achievement of Good Environmental Status (Kazanidis et al., 2020). In addition, our findings contribute to the identification and management of climate change refugia, a mitigation strategy for the conservation of species susceptible to climate change (Morelli et al., 2016). The shoaling of the aragonite saturation horizon by 2100 (Orr et al., 2005) is expected to cause major reductions in habitat suitability for North Atlantic CWCRs as they will be bathed in more acidic waters (Morato et al., 2020). However, CWCRs on the continental shelf, such as the MRC, are expected to be less affected by the shoaling of the aragonite saturation horizon, and thus, they may serve as climate change refugia (Morato et al., 2020; Turley et al., 2007). Data continuity, accessibility and affordability are important obstacles in the identification of fine-scale climate change refugia (Morelli et al., 2016). Advancing knowledge on the temporal dynamics of continental shelves' CWCRs and sharing of gathered (meta)data serve the establishment of monitoring programmes and CWCR conservation for the future.

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BIOSKETCH

Georgios Kazanidis is a marine zoologist who studies the impacts of human activities and changing environmental conditions on the structure and functioning of marine ecosystems. Since 2012, he has focussed on the ecology of deep-sea ecosystems. The authors of the present study (affiliated with ATLAS and iAtlantic projects) formed a multidisciplinary team and advanced human knowledge about the effects of interannual variability of regional oceanography and seafloor terrain on the biodiversity and biogeography of cold-water coral reefs. This serves the assessment of cold-water coral reefs health status and their conservation for the future.

Author contributions: LAH and JMR collected samples. GK and LAH sorted and identified macrofauna. LAH, JMR, CJ, JV and LDC provided data on the environmental variables. GK and JV analysed the data and made the graphs. GK wrote the manuscript with editorial help from LAH, JV, CJ, LDC and JMR.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.