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Benthic foraminiferal faunas associated with cold-water coral environments in the North Atlantic realm

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Abstract

Surface benthic foraminiferal assemblages associated with cold-water coral mounds and reefs from the Irish margin and Norwegian shelf (North-east Atlantic) are for the first time compared quantitatively. Results indicate that the considered sites share a common assemblage, dominated by elevated epibenthic and distinct infaunal species. This surface assemblage is typical of environments that are subject to strong bottom-water turbulence with enhanced food availability. It provides a benchmark for comparison with fossil benthic foraminiferal assemblages from past cold-water coral environments. Similar to macrofaunal and megafaunal communities, surface benthic foraminiferal diversity is higher on reefs and mounds than in surrounding off-mound/off-reef sediments. Benthic foraminiferal diversity is highest within the living coral macrohabitat, possibly as a result of enhanced availability and variety of food sources, and ecological niche separation. Indeed, living coral generally thrives on the summits or flanks of reefs and mounds where food availability is most important. The second part discusses the use of fossil benthic foraminiferal assemblages as palaeoceanographic proxies from past cold-water coral environments. The overview of previous observations demonstrates that benthic foraminifera are valuable tools to reconstruct past bottom-water oxygenation, bottom-water currents and surface productivity, all of which are key environmental variables controlling cold-water coral growth. Moreover, the advantages of a detailed investigation of benthic foraminiferal assemblages within cold-water coral environments are compared to other palaeoceanographic proxies. This study highlights that benthic foraminiferal assemblages are an often overlooked proxy within cold-water coral environments, despite yielding valuable information.

KEYWORDS

benthic foraminiferal assemblages, cold-water coral mound, cold-water coral reef, Mediterranean Sea, North Atlantic

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1 | INTRODUCTION

1.1 | Cold-water coral environments

Cold-water coral (CWC) environments (i.e. mounds and reefs) have received growing attention over the last 30 years (Freiwald et al., 1997; Hovland et al., 1994). They have now been reported as relatively common across the world's seas and oceans, although essentially documented in the Atlantic Ocean and Mediterranean Sea (Carranza et al., 2012; Fink et al., 2013; Matos et al., 2015; Mienis et al., 2014; Raddatz et al., 2020; Ramos, et al., 2017; Reolid et al., 2017; Steinmann et al., 2020; Tamborrino et al., 2019; Tracey et al., 2011; Wheeler et al., 2007; Wienberg et al., 2018), and as regionally important contributors to the calcium carbonate budget (Dorschel et al., 2005a; Lindberg & Mienert, 2005; Titschack et al., 2009, 2016). The main framework-forming scleractinian corals in the North Atlantic realm (i.e. North Atlantic and Mediterranean Sea) are the species *Desmophyllum pertusum* (previously known as *Lophelia pertusa*, see Addamo et al., 2016), *Madrepora oculata* (Remia & Taviani, 2005), *Enallopsammia profunda* (Hebbeln et al., 2014), *Solenosmilia variabilis* (Mangini et al., 2010; Raddatz et al., 2020) and *Oculina varicosa* (Reed, 2002). *Desmophyllum pertusum*, *M. oculata* and *S. variabilis* have a cosmopolitan distribution across the North Atlantic realm, although the latter species is scarcer (Roberts et al., 2009). *Oculina varicosa* and *E. profunda* are in contrast restricted to the Western Atlantic (Roberts et al., 2009). Under favourable biological and geological conditions, these species can build widespread CWC reefs (Freiwald et al., 2004; Roberts et al., 2006). The positive topography they form alters local hydrodynamic and sedimentary regimes, whilst providing a refuge for a highly diverse fauna (Buhl-Mortensen et al., 2010; Roberts et al., 2009). Freiwald (2017) reported 5,265 species associated with CWC habitats as of August 2017, of which 420 are new to science. Species endemism appears to be high, to such an extent that CWC habitats are suggested to be major speciation centres (Roberts et al., 2006). They are, as such, considered biodiversity hotspots in the bathyal zone (Corbera et al., 2019; Freiwald et al., 2004; Henry & Roberts, 2007; Linley et al., 2015; Roberts et al., 2006, 2009).

The main parameter controlling the development of CWCs is food availability. Furthermore, substrate availability, temperature, pH, salinity and oxygen availability also play a role (Davies & Guinotte, 2011; Davies et al., 2008; Dorey et al., 2020; Duineveld et al., 2012; Flögel et al., 2014; Freiwald et al., 2002; Maier et al., 2019; Mienis et al., 2012; Naumann et al., 2014; Taviani et al., 2005; Van Engeland et al., 2019). Food availability is in itself governed by a number of environmental variables, such as surface productivity, export production, upwelling and bottom-water currents (De Clippele et al., 2018; Hebbeln et al., 2016; Van Oevelen et al.,

2009; White et al., 2005). The activity of specific bottom-water currents, more precisely internal waves, has in recent years been suggested as a key parameter enhancing lateral food availability at CWC sites (Frederiksen et al., 1992; Lim et al., 2018; Mohn et al., 2014). In addition to providing the necessary food for corals to prosper, enhanced bottom-water currents deliver sediments which are partly retained by the coral framework (Davies et al., 2009; Duineveld et al., 2004; Huvenne et al., 2009a; Mienis et al., 2009; Thiem et al., 2006; White et al., 2005, 2007; Wienberg & Titschack, 2015). The sustained growth of scleractinian CWCs and a simultaneous supply of sediments through bottom-water current transport may over geological time periods lead to the formation of a CWC mound (Roberts et al., 2006; Wienberg & Titschack, 2015). Cold-water coral mounds are formed through the successive deposition of different reef generations, separated by phases of non-reef sedimentation (De Mol et al., 2011; Freiwald et al., 2004; Roberts et al., 2006; Rüggeberg et al., 2007; Wienberg & Titschack, 2015). This long-term build-up process may form mounds reaching heights of over 300 m (De Mol et al., 2002; Mienis et al., 2007). Mounds may or may not be colonised by living CWCs at their summits and on their flanks (Roberts et al., 2009). Thus, a distinction can be made between active and inactive/dormant CWC mounds, respectively, colonised or not by living CWCs (Roberts et al., 2009).

Cold-water coral mounds are considered valuable palaeo-archives (Hebbeln et al., 2016). Indeed, the aragonitic skeleton of CWCs can be accurately dated by the Uranium-series dating method, hence providing a precise time frame of past oceanographic events back to approximately 500 kyr (Cheng et al., 2000; Frank et al., 2011; Robinson et al., 2014). Yet, since CWCs show a discontinuous growth which follows climate cycles, CWC mounds often present a cyclic aggradation interrupted by numerous hiatuses (Dorschel et al., 2005b; Frank et al., 2009; Matos et al., 2017; Stalder et al., 2018; Thierens et al., 2013). To overcome this discontinuous nature of CWC mound records, a twofold approach investigating both cores recovered from the coral mound and from the off-mound contouritic sediments surrounding the coral mounds has been used to reconstruct past environmental conditions (Bahr et al., 2020; Dorschel et al., 2005b; Eisele et al., 2011; Huvenne et al., 2009b; Matos et al., 2017; Rüggeberg et al., 2007; Wang et al., 2019). Theoretically, this strategy allows the discontinuous record provided by CWC mounds to be completed by a more continuous off-mound contourite record. However, as demonstrated by IODP Expedition 307, the surrounding off-mound area is also subject to non-deposition and/or erosive events causing a lack of sedimentary record (Huvenne et al., 2009b; Titschack et al., 2009). As such, CWC mounds and their surrounding sediments do not offer a continuous sedimentary record. Nonetheless, besides these caveats, CWC mounds record intermediate water mass

activity at an extremely high temporal resolution (Fentimen et al., 2020a; Fink et al., 2012; Hebbeln et al., 2016; López Correa et al., 2012; Stalder et al., 2014). Thus, rather than providing a continuous sedimentary record but at a low temporal resolution, CWC mounds yield a highly detailed view of restricted time windows. This complex nature of CWC mound archives requires new and refined pre-existing palaeoceanographic proxies to be developed, such as deep-sea benthic foraminiferal assemblages, in order to fully explore the record they provide.

1.2 | Macrohabitat and microhabitat distributions within CWC environments

Cold water corals are sea floor architects, in the same way as their shallow-water tropical counterparts. They form an intricate ecosystem with different macrohabitats (Freiwald et al., 2002; Roberts et al., 2009). These reef macrohabitats are characterised by their specific faunal and sedimentary attributes (Freiwald, 2002; Roberts et al., 2009). The broad macrohabitat distribution is dictated by the presence or absence of a coral framework and its health (Beuck & Freiwald, 2005; Försterra et al., 2005; Jensen & Frederiksen, 1992). Based on these observations, a reef can be separated between the living coral, dead coral and coral rubble macrohabitats (Roberts et al., 2009). Living coral is generally found on the summit and upper slopes of the reef, where food availability is the highest as a result of the action of bottom-water currents. Dead coral framework is situated beneath living coral and on the lower slopes, whilst coral rubble accumulates at the base of the reef through bioerosion (Davies et al., 2017; Dorschel et al., 2007; Foubert et al., 2011; Heindel et al., 2010; Lim et al., 2017; Roberts et al., 2009; Vertino et al., 2010; Wienberg et al., 2008). Dead coral framework yields the highest associated macrofaunal species diversity. Indeed, in contrast with the living coral macrohabitat, the sediment trapped within the dead coral framework provides niches for infauna (e.g. polychaete worms) (Jensen & Frederiksen, 1992; Margreth et al., 2009; Purser et al., 2013; Roberts et al., 2009). Macrohabitat classifications vary according to reef structure and location. Different studies have thus resulted in contrasting macrohabitat classifications, some studies identifying macrohabitats specific to a given area (Dorschel et al., 2007; Foubert et al., 2005; Freiwald, 2002; Lim et al., 2017; Mortensen et al., 1995; Savini et al., 2014; Vertino et al., 2015). For example, at the base of CWC mounds along the Irish margin, belts of dropstones shape a particular macrohabitat colonised by hydrozoans, agglutinated polychaetes, bryozoans and benthic foraminifera (Lim et al., 2017; Margreth et al., 2009; Vertino et al., 2015). In contrast, the flanks of these CWC mounds close to the summits may be characterised by the presence of sand waves (Margreth

et al., 2009). Cold-water coral environments also provide a great number of microhabitats. For example, Mortensen et al. (1995) distinguished four microhabitats within *D. pertusum* colonies on the Norwegian shelf: the smooth surface of living *D. pertusum*, the detritus laden surface of dead *D. pertusum*, the cavities inside dead *D. pertusum* resulting from sponge borings, and the free space between coral branches.

1.3 | Ecology of deep-sea benthic foraminifera

Among the variety of organisms associated with CWC macrohabitats and microhabitats, benthic foraminifera are a main faunal component, as in all deep-sea marine communities (Gooday, 2014). They play a key role in deep-sea ecology by, for example, processing fresh organic material deposited on the sea floor and providing an essential link between the lower and higher levels of deep-sea food-webs (Gooday, 1993, 2014; Lipps & Valentine, 1970). Benthic foraminifera show a wide variety of feeding strategies (e.g. suspension and deposit feeding, parasitism and symbiosis) and diets (e.g. carnivory, herbivory, detritus feeding and use of dissolved organic matter; Gooday, 2014). Deep-sea species generally feed on organic detritus and bacteria (Gooday et al., 2008). Some species, noticeably in the deep-sea, exhibit an opportunistic behaviour. Indeed, they are capable of suddenly responding to episodic food pulses, such as spring bloom events (Gooday, 1993; Gooday & Hughes, 2002). This opportunistic living strategy leads to the rapid accumulation of an important number of individuals during a short time interval (Gooday, 2014). The composition and density of benthic foraminiferal faunas in the deep-sea is primarily governed by the flux of organic matter reaching the sea floor (Fontanier et al., 2008; Jorissen et al., 2007; Lutze & Coulbourn, 1984) and by the geochemical gradients (oxygen and possibly nitrate) in the sediment pore water (Gooday, 2014; Jorissen et al., 1995). In contrast to shallow-water settings, temperature and salinity only play a minor role on the distribution of benthic foraminifera in the deep-sea (Gooday, 2014; Jorissen et al., 2007). Benthic foraminifera are not restricted to the sediment surface but also occupy distinct depth levels in the sediment (Corliss, 1985; Gooday, 2003). These foraminiferal microhabitats, which become increasingly oxygen depleted as depth increases, extend down to approximately 10 cm depth in the sediment (Fontanier et al., 2008; Jorissen et al., 2007). The balance between food and oxygen availability governs the occupancy of these microhabitats by foraminifera (Jorissen et al., 1995). In oligotrophic regions, which are scarce in food, foraminifera live near the sediment surface where food is concentrated (Jorissen et al., 1995). In comparison, in eutrophic environments, pore water oxygenation rapidly decreases with increasing depth due to the oxidation of organic matter, thus limiting foraminiferal colonisation at depth (Jorissen et al., 1995). The deepest penetration of foraminifera in the sediment is observed in mesotrophic environments where food and oxygen

availability are well balanced (Jorissen et al., 1995). Foraminiferal species can thus be separated between epifaunal species which live above (attached to a substrate) or on the sediment, and infaunal species which live within the sediment. Depending on their living depth in the sediment, a further distinction can be made between shallow (0–1 cm), intermediate (1–4 cm) and deep infaunal (below 4 cm depth) dwelling foraminifera (Gooday, 2014). These microhabitats are not fixed. Indeed, infaunal species are known to migrate laterally and horizontally within the sediment as a function of oxygen and food availability and are influenced by macrofaunal burrowing activities (Gooday, 2014; Heinz & Geslin, 2012). Deep infaunal foraminifera species are more tolerant of oxygen depletion and less dependent on labile organic matter, whereas epifaunal and shallow infaunal species generally necessitate higher oxygen concentrations and fresh organic matter input (Gooday, 2014; Nomaki et al., 2005). Furthermore, the sediment grain size and porosity have been recognised as influencing the distribution of deep-sea foraminifera (Gooday, 2003 and references therein), whilst the intensity of bottom-water currents can also exert control on the composition of benthic foraminiferal assemblages. For example, foraminifera living on elevated substrates are frequently encountered in environments dominated by strong bottom-water currents, such as near seamounts or in contouritic or CWC environments (Margreth et al., 2009; Schönfeld, 1997; Schönfeld et al., 2011). In these areas, the epibenthic suspension-feeding foraminifera profit from food particles transported by the bottom-water currents. The deep-sea substrates colonised by these epibenthic species range from pebbles, corals, hydroids, manganese nodules, to anthropogenic remains such as derelict fishing equipment or macroplastics (Linke & Lutze, 1993; Lutze & Thiel, 1989; Schönfeld, 2002a; Waskowska & Kaminski, 2019; Weston, 1985).

1.4 | Objectives

In addition to reflecting environmental conditions at the sea floor, benthic foraminifera are extremely abundant, highly diverse and well-preserved in the fossil record (Gooday, 1993; Jorissen et al., 2007; Murray, 2006). Benthic foraminiferal assemblages have hence been widely used to reconstruct past environmental conditions (Gooday, 1993; Jorissen et al., 2007 and references therein). Previous studies suggest that benthic foraminiferal assemblages are a useful and promising tool to identify the environmental conditions governing present and past CWC reef and mound development (Fentimen et al., 2018; 2020a; Fink et al., 2012; Margreth et al., 2009, 2011; Rüggeberg et al., 2007; Schönfeld et al., 2011; Stalder et al., 2014, 2015, 2018). However, no integration of these results in one comparative study has yet been done. Thus, the aims of this work are (a) to quantitatively compare within one comprehensive study benthic foraminiferal assemblages from modern CWC reefs and mounds to assess their differences and

similarities, and (b) to better constrain the potential and use of fossil benthic foraminiferal assemblages in CWC mounds as proxies for past surface productivity, bottom-water oxygenation and current velocity.

2 | STUDY AREA AND OCEANOGRAPHIC SETTING

The study of benthic foraminifera associated with CWC environments is still at an early stage and literature on the subject is relatively scarce, thus the material available for this study is limited (Figure 1, Table 1). This is especially true for studies providing quantitative analyses of benthic foraminiferal assemblages and not solely qualitative or individual foraminifera species data sets (Tables 1 and 2). The available data sets are also restricted in their geographic range as they concentrate on the North Atlantic and the Mediterranean Sea (Figure 1, Table 2). Benthic foraminiferal assemblages associated with CWC environments have been investigated from both core (i.e. fossil assemblages) and surface (i.e. living, dead or total (living+dead) assemblages) material (Tables 2 and 3). The oceanographic setting and characteristics of CWC environments considered in this study are described below.

2.1 | Norwegian CWC reefs

Norwegian waters are known to host the highest density of thriving CWC reefs (Freiwald et al., 2002). These occur from 37 m depth in Beitstadfjord (Sneli, 2014) to 400 m depth at Røst Reef (Fosså et al., 2005). *Desmophyllum pertusum* is the dominant scleractinian coral species in these environments (Roberts et al., 2009). All reefs in Norwegian fjords and along the shelf were formed after the retreat of ice-sheets at the end of the last glacial period (Hovland & Judd, 1998; López Corea et al., 2012; Stalder et al., 2014). Surface living and total benthic foraminiferal assemblages have only been documented by Spezzaferri et al. (2013). These authors concentrated on northern Norway CWC-reef sites (Korallen, Lophavet, Stjernesund and Sveinsgrunnen reefs), mid-Norwegian slope CWC-reef sites (Sula, Røst and Trænadjupet reefs), reefs located in Oslo Fjord and adjacent off-mound areas (Table 2). Stalder et al. (2014) further studied fossil benthic foraminiferal assemblages from core material recovered from Lophavet reef (Figure 1; Table 3). Although regional disparities exist, coral reefs in these regions generally develop on pre-existing topographic heights, such as moraine ridges or iceberg plough levees (Fosså et al., 2000; Freiwald et al., 1999, 2002; Mortensen et al., 2001). Living corals colonise the top of these structures, while dead corals are generally found on the flanks (Freiwald et al., 2002; Mortensen

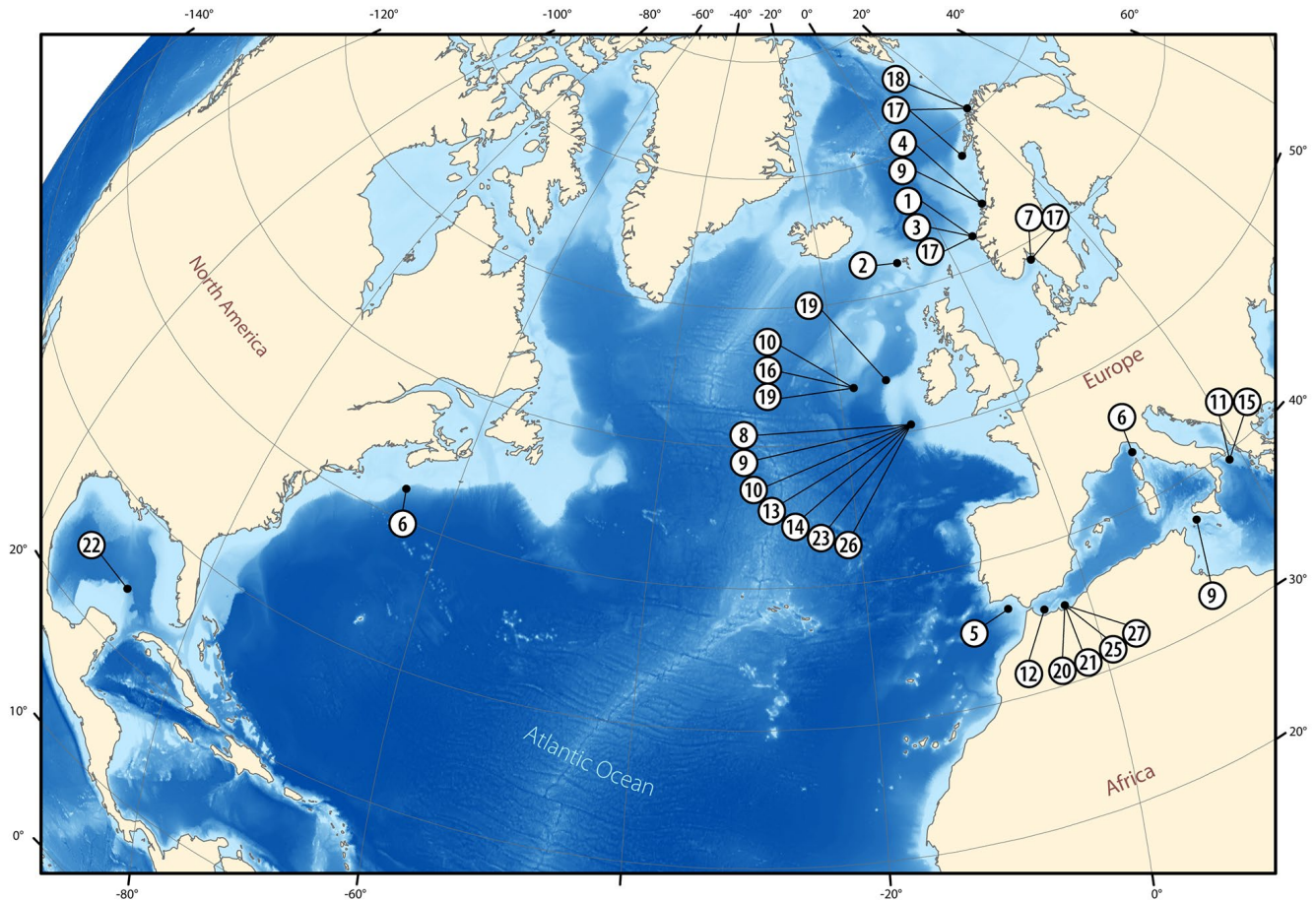


FIGURE 1 Geographical location of foraminiferal studies related to cold-water coral environments. Numbers correspond to studies listed in Table 1

et al., 1995). Norwegian coral reefs may reach tens, hundreds or even thousands of metres across for a thickness of approximately 10 m (Freiwald et al., 2002). A striking example is that of Sula reef, which measures 13 km across for an average framework thickness of 15 m (Fosså et al., 2000; Freiwald et al., 1999). Coral reefs in Norwegian waters are under the influence of the North Atlantic Current which circulates northward (Freiwald et al., 2002). Rüggeberg et al. (2011) demonstrated that at Stjærnesund, coral reefs developed at the boundary between Norwegian Coastal Water and Atlantic Water, thus highlighting the impact of water mass boundary processes on Norwegian coral reef development.

2.2 | Cold-water coral mounds from the Irish margin

The Irish margin, in the same way as the Norwegian shelf, is widely documented to host a great number of CWC localities (Roberts et al., 2009 and references therein). Numerous active, dormant and buried CWC mounds between approximately 450 and 1,150 m depth have been identified around the Porcupine, Rockall and Hatton Banks and in the Porcupine

Seabight (Beyer et al., 2003; Foubert et al., 2005; Huvenne et al., 2002, 2009a; Kenyon et al., 2003; van Weering et al., 2003; Wheeler et al., 2011). *Desmophyllum pertusum*, and to a lesser extent *M. oculata*, are the main framework-forming coral species found at the surface and within these mounds. The region is home to the largest documented CWC mounds, such as in the Rockall Trough, where mounds are over 300 m high (De Mol et al., 2002; Mienis et al., 2007). In contrast, smaller coral mounds not exceeding 10 m in height, such as the Darwin Mounds (northern Rockall Trough) and the Moira Mounds (eastern Porcupine Seabight), are also found in the area (Huvenne et al., 2009a; Wheeler et al., 2011).

For the Porcupine Seabight, surface benthic foraminiferal studies have focused on Galway Mound (Margreth et al., 2009; Schönfeld et al., 2011) and the downslope Moira Mounds (Fentimen et al., 2018 2020b; within the Belgica Mound Province (see Dorschel et al., 2007; Eisele et al., 2008; Lim et al., 2018; Wheeler et al., 2011), Propeller Mound (Margreth et al., 2009; Schönfeld et al., 2011) within the Hovland Mound Province (see De Mol et al., 2002), unnamed buried mounds (Margreth et al., 2009) from the Magellan Mound Province (see De Mol et al., 2002; Huvenne et al., 2007), and adjacent off-mound areas (Figure 1; Table 2). In addition, Rüggeberg

TABLE 1 Published studies focusing on benthic foraminifera associated with cold-water coral environments (modified from Rüggeberg et al., 2015)

Study	Area	Studied material
1. Burdon-Jones & Tambs-Lyche (1960)	Norway	Modern assemblages
2. Jensen & Frederiksen (1992)	Faroe	Foraminifera attached to <i>D. pertusum</i>
3. Cedhagen (1994)	Norway	<i>Hyrrokkin sarcophaga</i>
4. Freiwald & Schönfeld (1996)	Norway	<i>Hyrrokkin sarcophaga</i> on live <i>D. pertusum</i>
5. Schönfeld et al. (2002a)	Gulf of Cádiz	Foraminifera attached to coral fragments
6. Remia & Taviani (2005)	Tuscan Archipelago	Single foraminiferal species, 11 ka
7. Wisshak & Rüggeberg (2006)	Skagerrak	Colonisation experiments at <i>D. pertusum</i> reefs
8. Rüggeberg et al., (2007)	Porcupine	Fossil assemblages, 0–300 ka
9. Beuck et al. (2008)	Norway, Med., Porc.	<i>Hyrrokkin sarcophagi</i>
10. Margreth et al. (2009)	Rockall, Porcupine	Modern assemblages
11. Rosso et al. (2010)	Ionian Sea	Modern assemblages
12. Margreth et al. (2011)	Alboran Sea	Fossil assemblages, 3–15 ka
13. Raddatz et al. (2011)	Porcupine	Single foraminiferal species, ~2.5 Ma
14. Schönfeld et al. (2011)	Porcupine	Modern assemblages
15. Fink et al. (2012)	Ionian Sea	Fossil assemblages, 2–13 ka
16. Morigi et al. (2012)	Rockall Bank	Modern assemblages
17. Spezzaferri et al. (2013)	Norway	Modern assemblages
18. Stalder et al. (2014)	Norway	Fossil assemblages, 2–15 ka
19. Smeulders et al. (2014)	Rockall, Porcupine	Sub-modern assemblages
20. Stalder et al. (2015)	Alboran Sea	Fossil assemblages, 0–13 ka
21. Stalder (2015)	Alboran Sea	Modern assemblages
22. Matos et al. (2017)	Gulf of Mexico	Fossil assemblages, 0–140 ka
23. Fentimen et al. (2018)	Porcupine	Modern assemblages
24. Reolid et al. (2018)	Maldives	Fossil assemblages, 0–22 ka
25. Stalder et al. (2018)	Alboran Sea	Fossil assemblages, 0–33 ka
26. Fentimen et al. (2020b)	Porcupine	Modern assemblages
27. Fentimen et al., (2020a)	Alboran Sea	Fossil assemblages, 0–15 ka

et al. (2007) investigated fossil benthic foraminiferal assemblages from core material recovered from Propeller Mound (Table 3). This is to date the only downcore fossil benthic foraminiferal assemblage data set documented for the Irish margin coral mounds. Coral mounds situated in the Porcupine Seabight demonstrate a number of differences in terms of their water depth, proportions and coral cover. The summit of Galway Mound is situated at 782 m depth and rises 160 m above the seabed (Dorschel et al., 2007). Propeller Mound has similar dimensions with an elevation above the sea floor of 140 m, whilst its summit lies at 680 m water depth (Dorschel et al., 2007; Rüggeberg et al., 2005). The downslope Moira Mounds, with a maximum elevation of 10 m, are much smaller, and also located deeper between 900 and 1,150 m water depth (Wheeler et al., 2011). The Magellan Mounds are, in contrast, situated at shallower depths between 450 and 700 m, and are buried and inactive (De Mol et al., 2002). Living corals colonise the tops of Galway Mound and the Moira Mounds, whilst they are

rather located on the flanks of Propeller Mound (Dorschel et al., 2005b; 2007; Wheeler et al., 2011). Cold-water coral mounds nestled within the Porcupine Seabight are under the influence of the high salinity Mediterranean Outflow Water, circulating northward between 800 and 1,100 m depth, and the Eastern North Atlantic Water flowing above it (Rice et al., 1991; Van Aken & Becker, 1996; White, 2007). The dynamic processes (e.g. internal waves and tides) taking place at the boundary between these two water masses, that deliver food and sediment particles to the coral framework, drive coral mound formation in the area (Juva et al., 2020; Raddatz et al., 2014; White & Dorschel, 2010).

For the Rockall Bank, surface benthic foraminiferal studies concentrated on the Logachev Mounds (Morigi et al., 2012; Smeulders et al., 2014); Franken Mound (Margreth et al., 2009) and adjacent off-mound areas (Table 2). The Logachev Mounds are situated between 550 and 900 m depth and reach heights ranging between tens of metres to more than 300 m

TABLE 2 Sampling details of studies focusing on surface benthic foraminiferal assemblages associated with modern cold-water coral mounds and reefs

Study area (authors)	Specific site	Assemblage type	Number of sites	Sampling interval	Sampling device	Investigated fractions (μm)	Investigation for attached foraminifera
Porcupine Seabight (Margreth et al., 2009)	Franken, Connaught, Propeller, Magellan and Galway Mounds	Total	27	Surface (top 1 cm)	Box-corer	63–125 125–250 > 250	—
Porcupine Seabight (Schönfeld et al., 2011)	Galway and Propeller Mounds	Living* and dead	20	Surface (top 1 cm)	Box-corer	>250	Yes
Rockall Bank (Morigi et al., 2012)	Logachev Mounds	Living* and dead	8	Surface (top 1 cm)	Box-corer	>63	No
Norwegian reefs (Spezzaferri et al., 2013)	Oslo Fjord, Sula, Røst, Trænadjupet, Korallen, LoppHAVet, Stjærnsundet and Sveinsgrunner reefs	Total	32	Surface (top 2 cm)	Grab Box-corer	63–125 125–250 < 250	—
Norwegian reefs (Spezzaferri et al., 2013)	Oslo Fjord, Korallen and LoppHAVet reefs	Living* and dead	7	Surface (top 2 cm)	Submarine Operated grab	63–125 125–250 > 250	–
Rockall and Porcupine Banks (Smeulders et al., 2014)	Logachev and Pelagia mounds	Total	14	Sub-surface (4–5 cm depth)	Box-corer	150–1,000	No
Alboran Sea (Stalder, 2015)	East Melilla Mounds	Living*	5	Surface (top 1 cm)	Box-corer	63–125 125–250 > 250	Yes
Porcupine Seabight (Fentimen et al., 2018)	Moirá Mounds	Living* and dead	20	Surface (top 1 cm)	Box-corer	63–125 125–250 > 250	Yes

The location of study sites is indicated in Figure 1. *Rose-Bengal stained, †: not specified by the authors.

TABLE 3 Studies focusing on benthic foraminiferal assemblages investigated from core material recovered from cold-water coral mounds and reefs

Study area (authors)	Specific site	Water depth of recovered core(s) (m)	Mound height (m)	Dominant coral species	State	Age of core base(s) (ky)	Investigated fractions (μm)
Porcupine Seabight (Rüggeberg et al., 2007)	Propeller Mound	704	160	<i>Desmophyllum pertusum</i>	Active	207.0	>125
Ionian Sea (Fink et al., 2012)	Santa Maria di Leuca Mounds	612 628	Up to 25	<i>Desmophyllum pertusum</i> <i>Madrepora oculata</i>	Active	12.0 13.4	150–500
Norwegian shelf (Stalder et al., 2014)	Lopphavet Reef	225 237	< 10	<i>Desmophyllum pertusum</i>	Active	10.6 15.3	63–125 125–250 >250
Alboran Sea (Stalder et al., 2015)	East Melilla Mounds	251	50–150	<i>Desmophyllum pertusum</i> <i>Madrepora oculata</i>	Dormant	13.0	125–250 >250
Gulf of Mexico (Matos et al., 2017)	Campeche Mounds	573 553 556	20–40	<i>Desmophyllum pertusum</i> <i>Enallopsammia profunda</i>	Active	257.1 7.7 99.1	>150
Alboran Sea (Stalder et al., 2018)	East Melilla Mounds	258 300	50–150	<i>Desmophyllum pertusum</i> <i>Madrepora oculata</i>	Dormant	33.3 11.1	125–250 >50
Alboran Sea (Fentimen et al., 2020a)	East Melilla Mounds	319	50–150	<i>Desmophyllum pertusum</i> <i>Madrepora oculata</i>	Dormant	14.7	>125

The location of study sites is indicated in Figure 1.

(Mienis et al., 2007). They form several kilometre-long elongated ridges perpendicular to the slope (Kenyon et al., 2003; Mienis et al., 2007; Van der Land et al., 2013). Franken Mound lies at 600–675 m depth, its summit rising approximately 90 m above the sea floor. As opposed to the more ovate shaped Galway and Propeller mounds in the Porcupine Seabight, Franken Mound has a more irregular form (Wienberg et al., 2008). Regarding the Porcupine Bank, surface benthic foraminiferal studies have been carried out to the south and north of the Bank, respectively, on the Pelagia (Margreth et al., 2009; Smeulders et al., 2014) and Connaught Mounds (Margreth et al., 2009). The Pelagia Mounds occur between 650 and 800 m water depth and their summits are approximately 100 m above the sea floor (Van Weering et al., 2003). Connaught Mound is situated slightly deeper (860 m water depth) and has a greater elevation (180 m; Margreth et al., 2009). The summits of the investigated mounds from the Rockall and Porcupine Banks are colonised by living coral, essentially the species *D. pertusum* and *M. oculata* (Dorschel et al., 2009; Mienis et al., 2007; Wienberg et al., 2008), and are bathed by the Eastern North Atlantic Water which lies above the low salinity and low temperature Labrador Sea Water circulating below 1,200 m depth (Harvey, 1982; Holliday et al., 2000; Howe et al., 1994; Van Aken & Becker, 1996). In the same way as in the Porcupine Seabight, dynamic processes such as tidal currents and internal waves favour coral mound development on the Rockall Bank (Mienis et al., 2007).

2.3 | Cold-water coral mounds from the North-west Atlantic

Cold-water coral environments dominated by *D. pertusum* also develop in the North-west Atlantic region, noticeably in the Gulf of Mexico, the Florida Straits and off North Carolina (Brooke & Schroeder, 2007; Cordes et al., 2008; Messing et al., 2008; Mienis et al., 2014; Ross & Nizinski, 2007). Yet, no study has documented benthic foraminiferal assemblages from the surface of North-west Atlantic CWC mounds. Fossil benthic foraminiferal assemblages have, however, been investigated from core material from the Campeche CWC province in the southern Gulf of Mexico (Matos et al., 2017; Figure 1; Table 3). These coral mounds have an elongated shape with lengths varying from tens of metres to over 1 km, heights ranging between 20 and 40 m, and are situated between 480 and 600 m depth (Matos et al., 2017). Their summits, colonised by living coral colonies dominated by *D. pertusum* and *E. profunda*, are located at the boundary between the Antarctic Intermediate Water and the overlying Tropical Atlantic Central Water (Matos et al., 2017). The internal waves propagating at the boundary between the two water mass boundaries are suggested to promote coral mound

formation in the area during interglacial times (Matos et al., 2017).

2.4 | Cold-water coral mounds from the Mediterranean Sea

Living scleractinian CWCs have been documented in a number of different settings across the Mediterranean Sea, such as in canyons (Aymà et al., 2019; Fabri et al., 2014; Orejas et al., 2009; Puig & Gili, 2019; Taviani et al., 2015), on overhangs and cliffs (Freiwald et al., 2009; Taviani et al., 2011), or on seamounts (Chimienti et al., 2019; Lo Iacono et al., 2012; Palomino et al., 2011). Mediterranean coral mounds are found in the Northern Ionian Sea (the Santa Maria di Leuca Coral Province; Carlier et al., 2009; Freiwald et al., 2009), the Tyrrhenian Sea (Remia & Taviani, 2005), and in the Alboran Sea (the Melilla Coral Mound Province and the Cabliers Coral Mound Province; Hebbeln, 2019; Iacono et al., 2014; Lo Corbera et al., 2019) (Figure 1). Fossil benthic foraminiferal assemblages have been investigated for both the Santa Maria di Leuca and East Melilla coral mounds (Fentimen et al., 2020a; Fink et al., 2012; Stalder et al., 2015, 2018), whereas surface living benthic foraminiferal assemblages have only been documented for the East Melilla mounds (Stalder, 2015; Figure 1; Tables 2 and 3). The Santa Maria di Leuca mounds are situated at depths between 500 and 900 m and have an elongated shape with a length between 50 and 300 m and a height of 25 m (Freiwald et al., 2009). In contrast, the East Melilla mounds are located in shallower waters between 200 and 450 m depth, while the West Melilla Mounds, which are 1–48 m high and on average 260 m wide, are found at depths between 300 and 590 m (Iacono et al., 2014; Lo Hebbeln, 2019). To the north of the East Melilla mounds, coral mounds occur along three steep 3–20 km long ridges (Hebbeln, 2019). These rise 50–150 m above the surrounding sea floor, which is situated at depths ranging between 375 and 475 m (Hebbeln, 2019). While the Santa Maria di Leuca mounds host thriving colonies of *D. pertusum* and *M. oculata* on their summits and flanks (Chimienti et al., 2019; Freiwald et al., 2009 and references therein), the surface of the East Melilla mounds is only home to scattered occurrences of *D. pertusum* and *M. oculata*. The West Melilla mounds, buried under a 1–12 m thick finer-grained sediment drape, are currently inactive and do not host any living coral colonies (Lo Iacono et al., 2014). Analogous to North-east Atlantic coral mounds, Mediterranean mound development is believed to be tightly linked to hydrodynamic processes (e.g. internal waves, tides) governing the boundary between surface and intermediate water masses, although fluvial input at coral mound sites is also suggested to play a key role (Fentimen

et al., 2020a; Fink et al., 2012; Stalder et al., 2015, 2018; Wang et al., 2019).

3 | MATERIAL AND METHODS

3.1 | Disparities in foraminiferal surface sampling strategies

A number of different methods have been used over the years to investigate benthic foraminiferal assemblages from surface samples (Murray, 2006 and references therein). Cold-water coral environments are no exception and various strategies have been applied when sampling and preparing material from these habitats (Table 2), thus rendering comparisons between studies challenging. Dead, living (Rose-Bengal stained) and total assemblages (dead +living) have all been used, despite yielding different results. Living assemblages represent only a short period of time and are affected by temporal variations in environmental parameters, such as phytoplankton blooms (Fontanier et al., 2002; Gooday, 1993; Jorissen & Wittling, 1999; Ohga & Kitazato, 1997). As such they provide a snapshot of an ecosystem and may not represent the environment over a longer time period. In contrast to living assemblages, dead foraminiferal assemblages are the product of post-mortem processes and of time averaging. Indeed, benthic foraminifera have been widely recognised as undergoing taphonomic processes that affect preservation of the dead assemblage, such as transport and/or test destruction (Berger, 1973; Bourdreau & Canfield, 1993; Duros et al., 2012; Hickman & Lipps, 1983; Jorissen & Wittling, 1999; Murray, 2006). Despite this, the majority of benthic foraminifera (with the exception of soft-shelled tests and delicate agglutinated forms) are well-preserved in the fossil record (Murray, 2006). By reducing the effects of seasonality and patchiness, they provide a temporal average that represents the general state of environmental conditions within an ecosystem (Jorissen et al., 2007). Fossil assemblages from core material yield, in the same way as dead foraminifera from surface samples, a time-averaged record that can be used in palaeoceanographic reconstructions. Total assemblages regroup both living and dead individuals and are hence affected by a combination of aforementioned processes (Murray, 2006). The contribution of living foraminifera to total assemblages varies through time and space. For example during bloom periods, when living foraminiferal standing stocks are the highest, the contribution of living foraminifera to total assemblages will be greater than during other parts of the year. Yet, at the surface of the Moira Mounds (Irish margin), Fentimen et al. (2020b) demonstrated that living foraminifera sampled during the early month of June, that is, at the end of the Spring bloom period, only contribute to approximately 1% of the total benthic foraminiferal

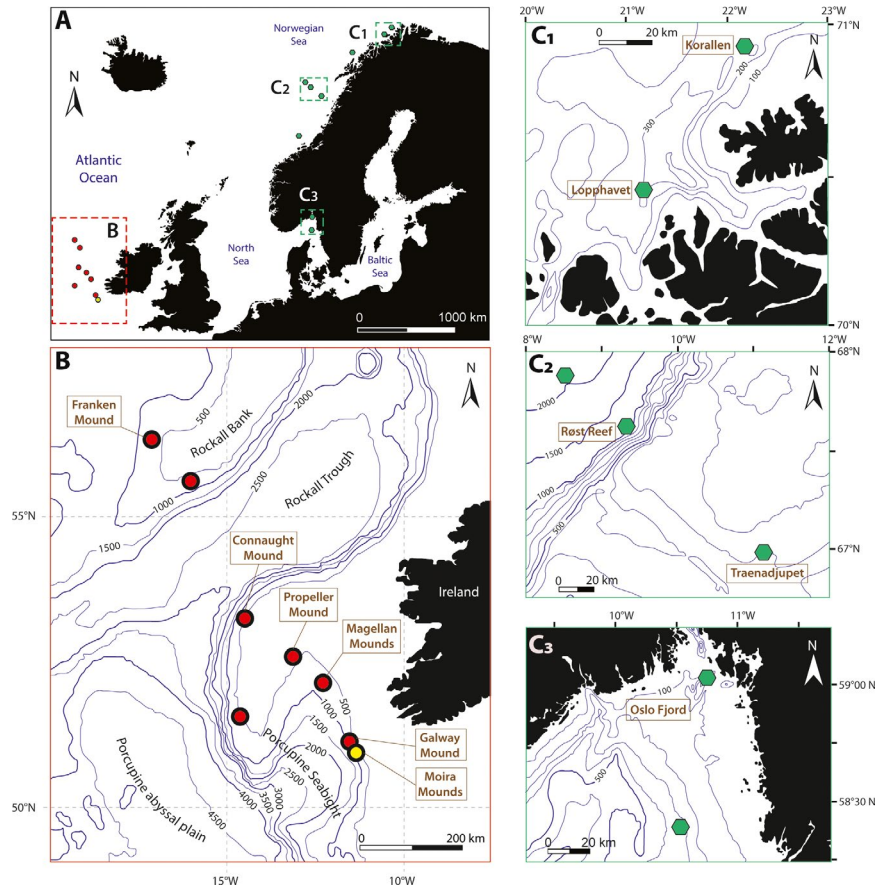
assemblage. Based on these observations, total assemblages at the surface of these Irish CWC mounds may be considered to be essentially composed of dead foraminifera, whilst only receiving a minor contribution of living individuals. Thus, dead and total assemblages may be comparable in a given area.

In addition to differences linked to the type of assemblage (living, dead or total), the choice of the investigated size fraction and, in the case of surface samples, the sampling depth in the sediment, do not follow a uniform sampling protocol (Table 2). For example, Schönfeld et al. (2011) exclusively studied the fraction larger than 250 μm and excluded finer fractions which are considered by other studies (Table 2). Smeulders et al. (2014) focused on total benthic foraminiferal assemblages from 4 to 5 cm depth in the sediment instead of the generally used top first centimetre (Table 2). Furthermore, the investigation of soft-shelled tests (Morigi et al., 2012) or biomineralized tests only (Fentimen et al., 2018; Margreth et al., 2009; Schönfeld et al., 2011; Smeulders et al., 2014; Spezzaferri et al., 2013), or the lack of inspection of bioclasts and pebbles for attached foraminifera (Morigi et al., 2012) can also have an impact on foraminiferal relative abundances. This diversity of sampling protocols handicaps comparisons between studies (Table 2).

3.2 | Data set selection criteria and multivariate analysis

Considering the disparity of sampling strategies used, a selection followed by a normalisation of data sets is necessary to compare quantitatively surface benthic foraminiferal assemblages. The selection criteria were chosen in order to include the most data sets possible in the multivariate analysis, whilst preventing any sampling-related bias in the results. Data sets considering total or both dead and living foraminiferal assemblages, including the smaller size fraction (63–125 μm) and sampled from the top 1 cm of sediment were selected. These criteria hence excluded data sets from Schönfeld et al. (2011), Smeulders et al. (2014) and Stalder (2015) (see Table 2). The data set collected by Morigi et al. (2012) was also excluded due to the scarcity of studied samples and the absence of investigation for living attached foraminifera (Table 2). Data sets from the large Irish mounds (Margreth et al., 2009), Norwegian reefs (Spezzaferri et al., 2013) and Irish Moira Mounds (Fentimen et al., 2018) met the selection criteria and were hence included in the multivariate analysis (Figure 2; Table 2). To minimise biases resulting from diverging foraminiferal taxonomy between these three data sets, determinations were directly compared (all material is stored and available at the Department of Geosciences, University of Fribourg). The data sets were standardised to the size fraction $>63 \mu\text{m}$ and to total assemblages (Annex

FIGURE 2 Study area (A) and overview maps showing the position of surface samples used to compare quantitatively benthic foraminiferal assemblages from modern cold-water coral environments off Ireland (B) and Norway (C₁: Korallen and Lophavet reefs, C₂: Røst and Traenadjupet reefs, C₃: Oslo Fjord reefs). Red circles: large Irish mounds (Margreth et al., 2009); yellow circle: Moira Mounds (Fentimen et al., 2018); green hexagons: Norwegian reefs (Spezzaferri et al., 2013)



S1). The Shannon diversity index was calculated for all samples using the PRIMER6 software (Clarke & Gorley, 2006). Multivariate analyses were performed using the same software. The data were root transformed to partially downscale the contribution of abundant species/genera and increase the contribution of rarer and potentially key indicator species/genera (Field et al., 1982). The Bray–Curtis similarity matrix (Clarke & Gorley, 2006) was then calculated and used to obtain non-metric MultiDimensional Scaling (nMDS) plots. Three different nMDS plots were computed and are illustrated in Figure 3 (stress values are indicated in Figure 3). First, benthic foraminiferal assemblages from both the on-mound/on-reef and off-mound/off-reef habitats from the Norwegian reefs, large Irish mounds and Irish Moira Mounds were quantitatively compared (Figure 3A). A second step consisted of exclusively selecting samples corresponding to the on-reef/on-mound habitat from the three different settings after referring to the characterisations given by the original authors (Fentimen et al., 2018; Margreth et al., 2009; Spezzaferri et al., 2013). Benthic foraminiferal assemblages from the on-reef/on-mound habitat were then compared quantitatively at species level (Figure 3B, Annex S1). Additionally, benthic foraminiferal assemblages were standardised to genus level to form broader ecological groups (Annex S2) and also compared quantitatively (Figure 3C). Similarity Percentage (SIMPER) analyses were

performed to evaluate the contribution of each species/genus to total average similarity within groups and to total average dissimilarity between groups (Annexes S3 and S4). The dissimilarity/standard deviation ratio (Diss/SD) was used to identify discriminating species/genera between clusters (Annexes S3 and S4). The distribution of key on-mound/on-reef species contributing to similarities and dissimilarities between the three different localities and identified with the SIMPER analysis (Annexes S3 and S4) is illustrated in a series of bubble plots (Figure 4).

4 | DISTRIBUTION AND ENVIRONMENTAL SIGNIFICANCE OF BENTHIC FORAMINIFERA ASSOCIATED WITH MODERN CWC ENVIRONMENTS OF THE NORTH ATLANTIC REALM

4.1 | Spatial variability and diversity of benthic foraminiferal assemblages from modern CWC environments

The distribution of total benthic foraminiferal assemblages from Norwegian reefs shows a separation between the on-reef and adjacent off-reef habitats (Figure 3). Although less

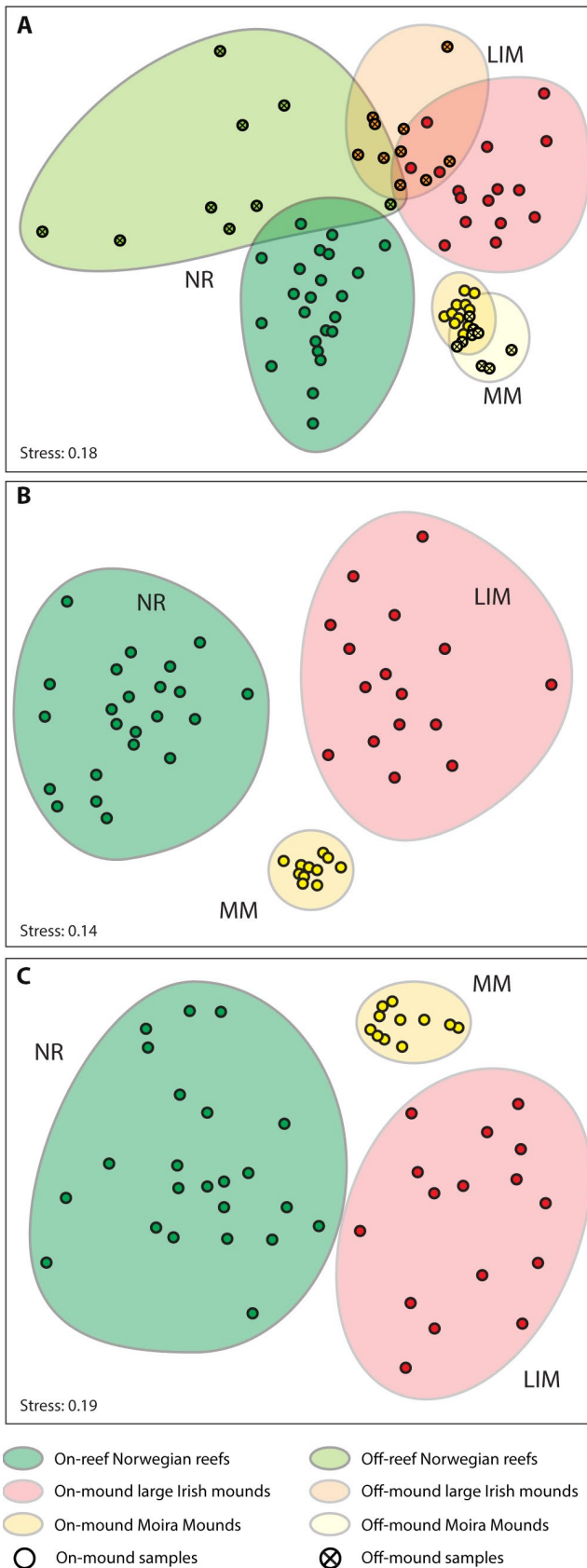


FIGURE 3 Non-metric MultiDimensional Scaling (nMDS) plots obtained for total surface benthic foraminiferal assemblages from selected cold-water coral environments (see Figure 2). (A) nMDS plot obtained for total benthic foraminiferal species assemblages from the on-mound/on-reef and off-mound/off-reef habitats. (B) nMDS plot obtained for total benthic foraminiferal assemblages from solely the on-mound facies, considering foraminiferal species. (C) nMDS plot obtained for total benthic foraminiferal assemblages from solely the on-mound facies, but considering foraminiferal genera. Green dots: Norwegian reef (NR) samples, red dots: large Irish mound (LIM) samples, yellow dots: Irish Moira Mound (MM) samples

observations that total benthic foraminiferal assemblages show a distinct separation between the on-mound/on-reef and off-mound/off-reef habitats on both the Norwegian reefs and large Irish mounds, whilst this separation is less marked on the Irish Moira Mounds (Fentimen et al., 2018; Margreth et al., 2009; Spezzaferri et al., 2013). For all three considered North-east Atlantic settings, surface benthic foraminiferal diversity is highest among the coral-dominated macrohabitats (Figure 5). In contrast, it is the lowest in adjacent off-mound settings around the Norwegian reefs and the Irish Moira Mounds (Figure 5), and within the drop-stone macrohabitat at the base of the large Irish mounds (Figure 5). These results agree with observations from the Rockall and Porcupine Banks, where surface foraminiferal diversity and population density are higher in on-mound habitats than in adjacent off-mound areas (Morigi et al., 2012; Smeulders et al., 2014). Contrasting conclusions were drawn by Schönfeld et al. (2011), who did not report higher living benthic foraminiferal diversity on Galway Mound than in surrounding off-mound sediments. Yet, Schönfeld et al. (2011) focused solely on foraminifera larger than 250 μm (Table 2), most certainly underestimating foraminiferal diversity (Gooday & Goineau, 2019). Overall, past observations combined with those presented in this study indicate that North-east Atlantic benthic foraminiferal diversity is higher on-reef/on-mound than in surrounding off-reef/off-mound sediments, similar to trends commonly reported for megafaunal and macrofaunal communities within CWC environments (Corbera et al., 2019; Henry & Roberts, 2007; Linley et al., 2015; Roberts et al., 2009). This higher benthic foraminiferal diversity on-reef/on-mound reflects the increased food and substrate availability in these areas. Indeed, the variety of elevated substrates (e.g. living and dead corals, shells, coral rubble) and the sediment deposited within and at the base of the coral framework provide a variety of ecological niches for both epibenthic and infaunal foraminifera.

The highest on-reef/on-mound macrofaunal and megafaunal diversity is usually found with dead coral framework, whereas it is lower with live coral (Buhl-Mortensen & Fossa, 2006; Buhl-Mortensen et al., 2010, 2017; Corbera

pronounced, such a distinction between on-mound and adjacent off-mound habitats can also be noticed for the large Irish mounds (Figure 3). These results confirm previous

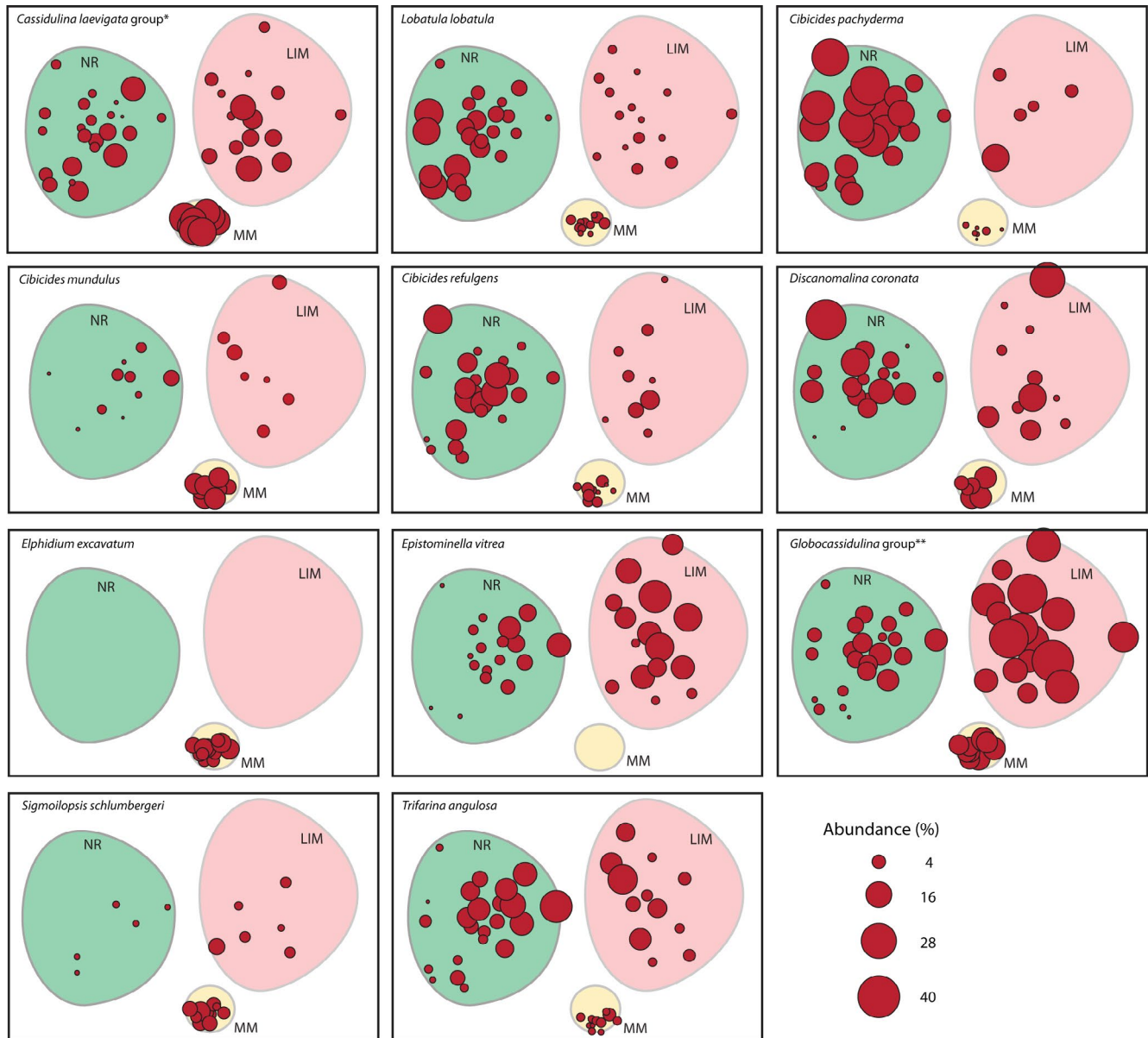


FIGURE 4 Bubble plots illustrating the abundance (in percentage) of key species from modern cold-water coral reefs and mounds. Clusters defined in Figure 3B are overlaid (green: NR—Norwegian reefs; red: LIM—large Irish mounds; yellow: MM—Irish Moira Mounds). The scale of the bubbles in percentages is given to the bottom right. All bubble plots follow the same scale. **Cassidulina laevigata*+*Cassidulina teretis* (Margreth et al., 2009); ***Cassidulina crassa*+*Globocassidulina* spp. (Margreth et al., 2009)

et al., 2019; Jensen & Frederiksen, 1992). This distribution has been linked to microhabitat availability. Indeed, living coral provides less microhabitats than dead coral or coral rubble. The live tissue of scleractinian corals is reported to prevent the attachment of sessile epibenthic macrofaunal species, whilst dead coral offers multiple microhabitats on and in the coral skeleton and within the sediments deposited within the framework (Buhl-Mortensen et al., 2010). As opposed to these observations, the highest benthic foraminiferal diversity is found with living coral, while it is, respectively, the lowest with coral rubble and pebbly sand and with dead coral and dropstone pavements on Norwegian

reefs and on large Irish mounds (Figure 5). Living coral develops in areas where the delivery of suspended food particles by bottom currents is the most important (Roberts et al., 2009 and references therein). This higher concentration of suspended organic matter will in turn favour benthic foraminiferal communities, noticeably epibenthic foraminifera (Figure 5) (Margreth et al., 2009; Schönfeld et al., 2011). Furthermore, Wild et al. (2008, 2009) demonstrated at Tisler Reef (Skagerrak, Norway) that *D. pertusum* communities release high quantities of particulate and dissolved organic matter, in particular mucus (Murray et al., 2019). This coral-derived mucus is an appealing organic

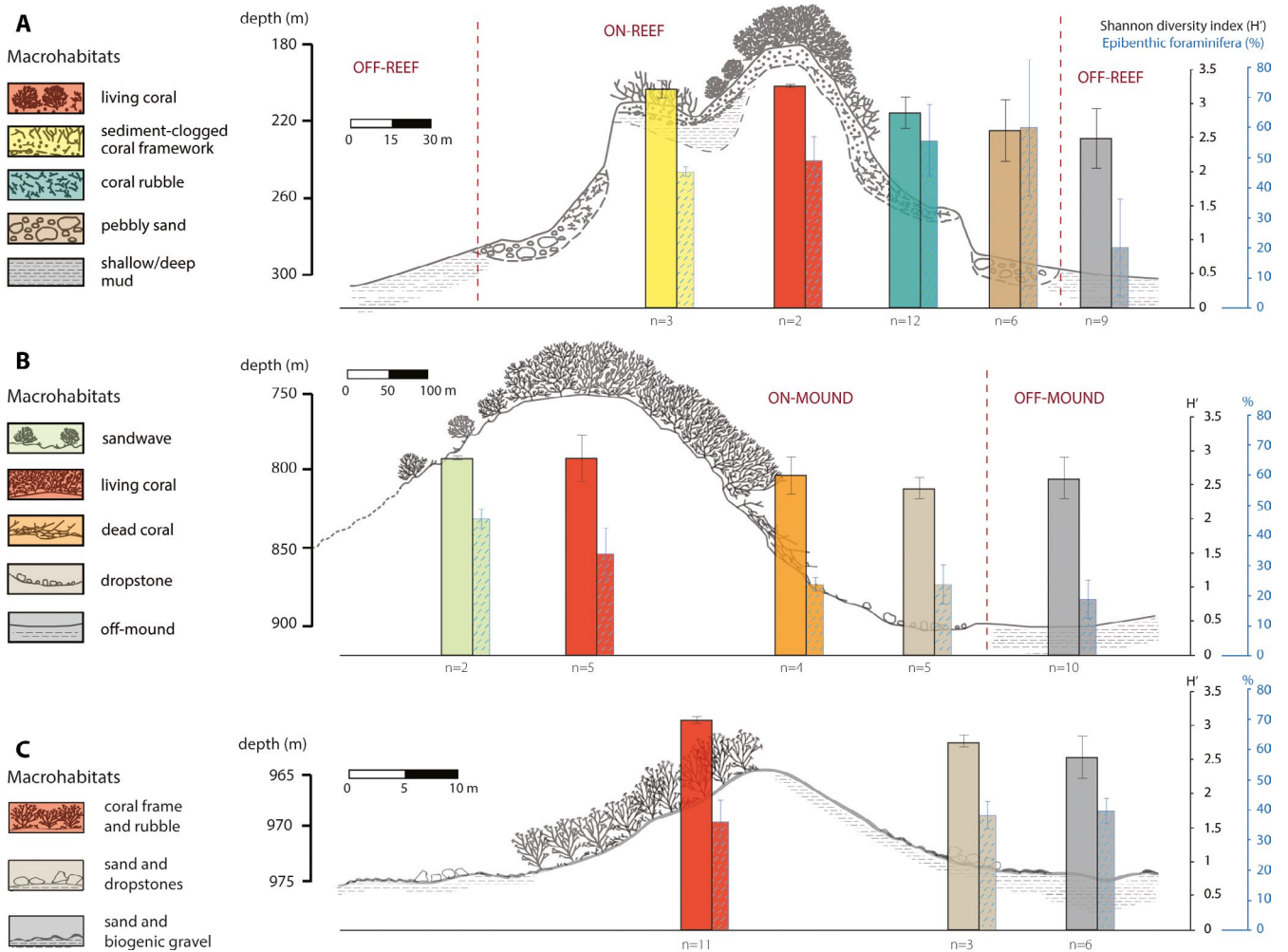


FIGURE 5 Average diversity (wide columns) of surface total benthic foraminiferal assemblages and percentage of epibenthic foraminifera* (narrow dashed columns) associated with cold-water coral macrohabitats on Norwegian cold-water coral reefs (A), the large Irish cold-water coral mounds (B) and the Irish cold-water coral Moira Mounds (C). Panels A and B are modified from Freiwald et al. (2002), Spezzaferri et al. (2013) and Margreth et al. (2009). The macrohabitat distribution follows the original descriptions given by Margreth et al. (2009), Spezzaferri et al. (2013), Vertino et al. (2015) and Fentimen et al. (2018). n : number of samples considered for each macrohabitat. *See Annex S1 for list of epibenthic foraminifera

substrate for planktonic microbial assemblages and stimulates microbial activity in the nearby water column (Wild et al., 2008). Benthic foraminifera are able to adapt to different food sources and can noticeably feed on microbes (Gooday et al., 2008; Murray, 2006). It is suggested here that certain benthic foraminifera feed on the high concentration of microbes within the living coral macrohabitat, the microbes themselves profiting from the coral-derived mucus. As such, benthic foraminifera are possibly an intermediary between microbes and macrofaunal communities and hence an important part of the food-web within the living coral macrohabitat. These observations suggest that food availability and variety (e.g. suspended organic matter, microbes) are the main environmental parameters steering benthic foraminiferal diversity on modern North-east Atlantic CWC environments.

4.2 | Species distribution, microhabitat selection and its association with sea floor environmental conditions

The Norwegian reefs, the large Irish mounds and the Irish Moira Mounds share a similar benthic foraminiferal assemblage (Figures 4 and 6; Annex S3). Epifaunal foraminifera are more abundant on Norwegian reefs and on large Irish mounds than in surrounding off-reef/off-mound sediments, whilst such a trend is not observed on the Irish Moira Mounds (Figure 5). Epibenthic foraminifera are essentially represented by *Discanomalina coronata*, *Cibicid(oid)es* spp. (*Lobatula lobatula*, *C. pachyderma*, *C. mundulus*, *C. refulgens* and *C. aravaensis*), *Hanzawaia boueana*, *Planulina ariminensis* and *Hyrrokin sarcophaga* (Figures 4 and 6; Annex S1). *Cibicides pachyderma* and to a lesser extent *L.*

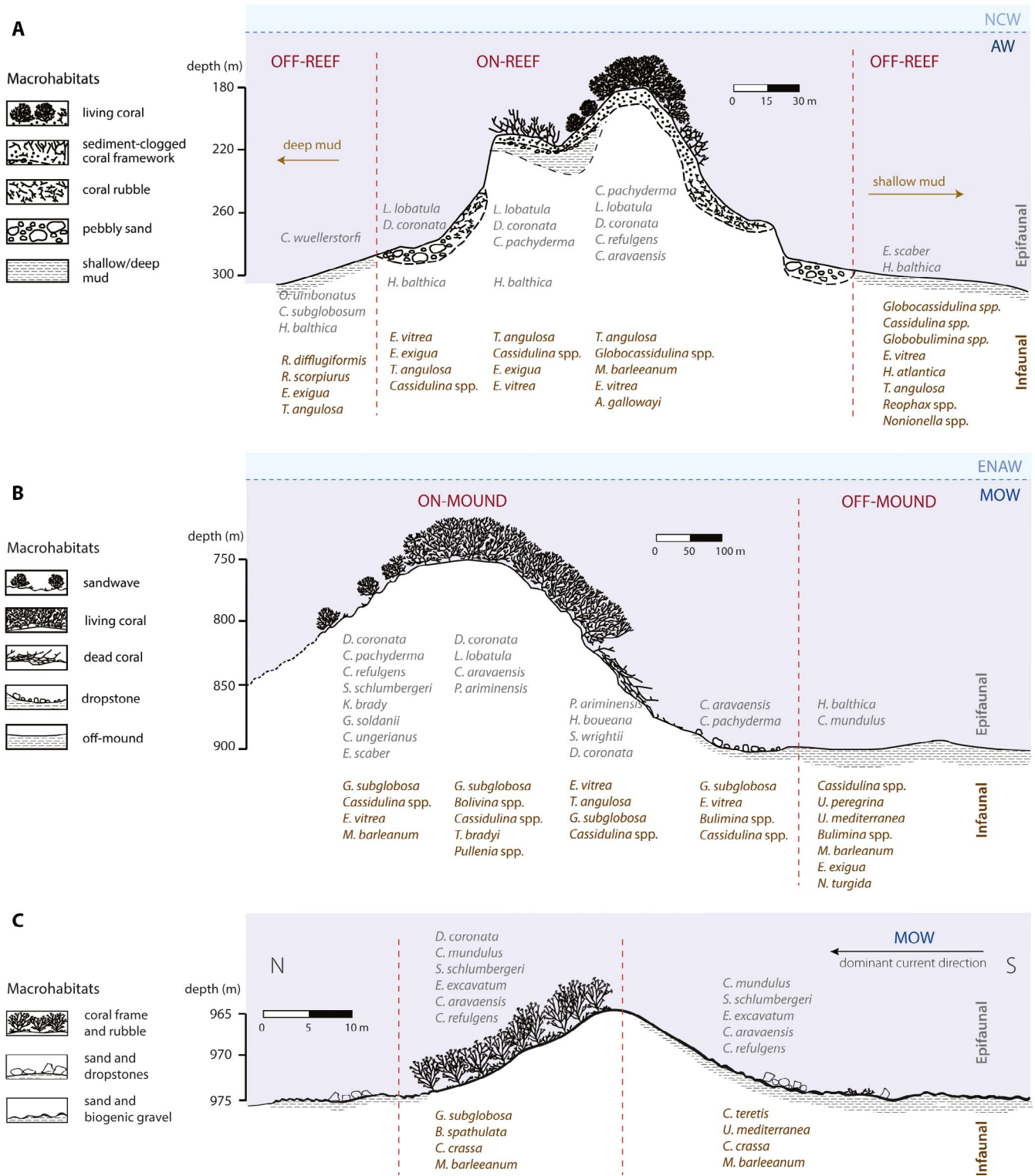


FIGURE 6 Model distribution of macrohabitats in three different modern cold-water coral environments and associated surface benthic foraminifera species. (A) Lophhavet Reef (Norway) modified from Freiwald et al. (2002) and Spezzaferri et al. (2013). (B) Large Irish cold-water coral mound combined from different coral mounds modified from Margreth et al. (2009). (C) Irish Moira Mounds (previously unpublished). Indications on dominant water masses are given: Norwegian Coastal Water (NCW), Atlantic Water (AW), Eastern North Atlantic Water (ENAW) and Mediterranean Outflow Water (MOW). Benthic foraminiferal distributions are based on total surface assemblages

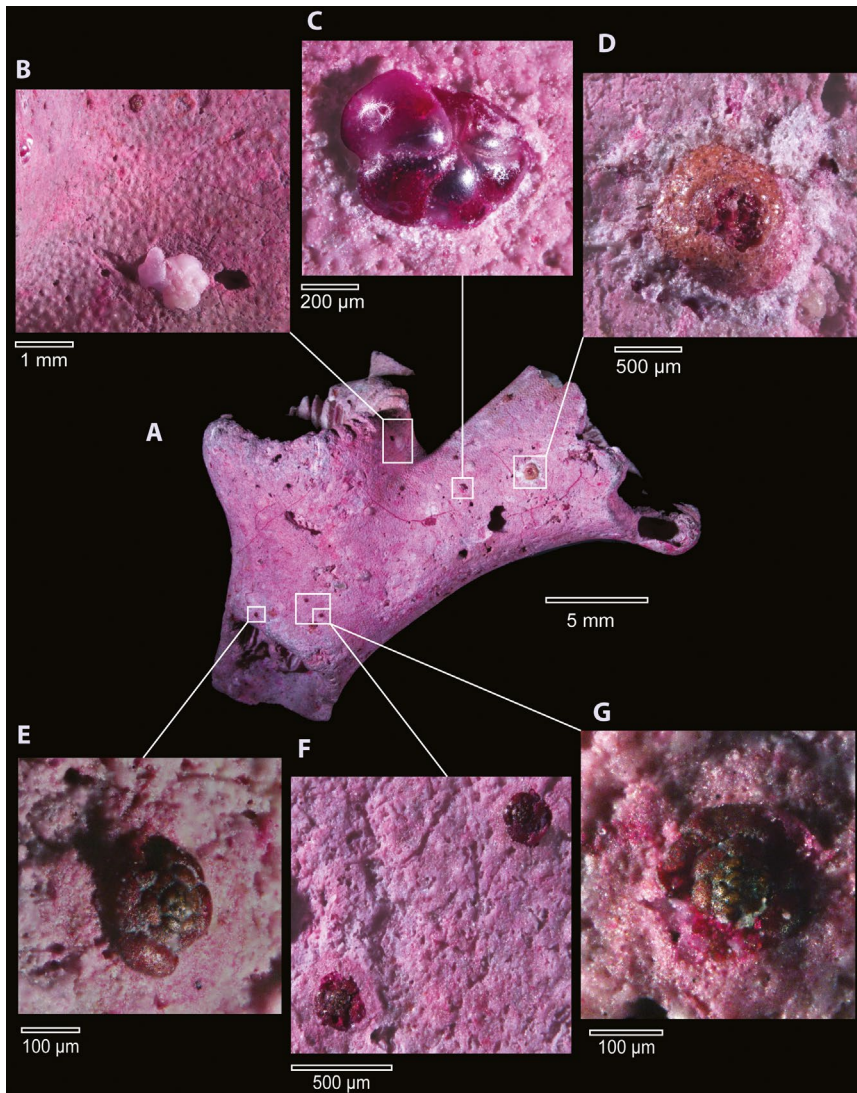


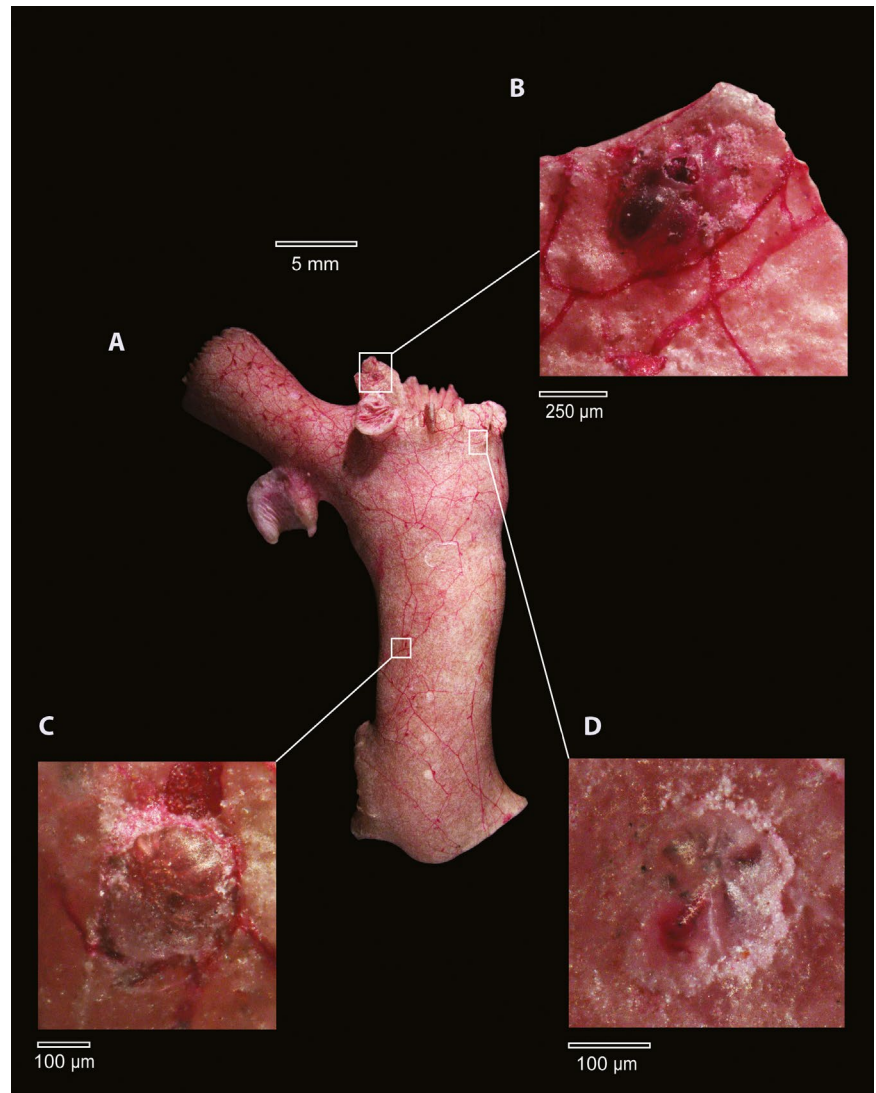
FIGURE 7 Epibenthic foraminifera attached to their substrates from the Irish Moira Mounds (photographed under a Nikon SMZ18 Stereo microscope). (A) Bioeroded dead *Desmophyllum pertusum* (Linnaeus, 1758) fragment; (B, C) *Lobatula lobatula* (Walker & Jacob, 1798); (D) *Tritaxis fusca* (Williamson, 1858); (E–G) *Rotaliammina concava* (Seiglie, 1964)

lobatula are noticeably more abundant on Norwegian reefs (Figures 4 and 6). Based on the SIMPER analyses (Annex S3), the higher abundance of these two species contributes strongly to the dissimilarity between Norwegian reef and Irish mound assemblages (large Irish mounds and Moira Mounds). Assemblages showing high abundances of epibenthic foraminifera have also been observed on Galway, Propeller and Logachev Mounds (Morigi et al., 2012; Schönfeld et al., 2011; Smeulders et al., 2014). The development of this epibenthic community is favoured by the availability of numerous and various substrates to be colonised, together with the strong bottom currents sweeping these mounds (Figure 6). Indeed, *Cibicid(oid)es* spp. and *D. coronata* are suspension feeders, thriving on fresh and labile organic matter in well-oxygenated and high-energy settings (Linke & Lutze, 1993; Margreth et al., 2009). They live attached to coral, coral rubble or to associated elevated biological or geological substrates such as hydroids, sponges, pebbles and dropstones (Figures 7 through 12) (Margreth et al., 2009; Spezzaferri et al., 2015 and references therein). Among cibicidids, *C.*

refulgens shows a preference for the sand veneer and for smooth and stable substrates (e.g. pebbles and dropstone pavements) around Irish coral mounds (Figures 6B,C, 9 and 10) (Fentimen et al., 2018; Margreth et al., 2009; Schönfeld et al., 2011). Schönfeld et al. (2011) suggest that the grazing and filter feeding nutrition strategies of this species may allow it to withstand a highly variable food supply under strong current regimes (Alexander & Delaca, 1987). As such, the abundance of this species may reflect the winnowing at the base of North-east Atlantic coral mounds and the lower food availability than on the upper parts.

In addition to a common epibenthic community, Norwegian reefs, large Irish mounds and the Irish Moira Mounds are characterised by a similar infaunal community (Figures 4 and 6). The sediment trapped within the coral framework provides microhabitats for these species (Figure 6). Common infaunal foraminifera are the species *Trifarina angulosa*, *Trifarina bradyi*, *Melonis barleeaanum*, *Globocassidulina subglobosa* and *Cassidulina* spp. (*C. teretis*, *C. crassa* and *C. laevigata*) (Figures 4 and 6). The

FIGURE 8 Epibenthic foraminifera attached to their substrates from the Irish Moira Mounds (photographed under a Nikon SMZ18 Stereo microscope). (A) *Desmophyllum pertusum* (Linnaeus, 1758) coral fragment; (B) *Lobatula lobatula* (Walker & Jacob, 1798); (C) *Hyrrokkin sarcophaga* (Cedhagen, 1994); (D) *Lobatula lobatula* (Walker & Jacob, 1798)



Globocassidulina group is more abundant on the large Irish mounds, whilst the *Cassidulina laevigata* group is most represented on the Irish Moira Mounds (Figure 4). These differences contribute to the dissimilarity between assemblages from the Norwegian reefs, where both groups of species are less represented, and the large Irish and Moira Mounds assemblages (Annex S3). *Cassidulina* spp. and the species *G. subglobosa* prosper when high-quality labile organic matter is available (Alve, 2010; Gooday, 1993; Murray, 2006; Suhr et al., 2003; Sun et al., 2006), whilst the shallow infaunal *T. angulosa* prefers coarse-grained substrates in high-energy environments (Mackensen et al., 1995; Schönfeld, 2002a). Hence, this infaunal community also reflects the strong bottom currents and the increased availability of labile organic matter within the coral framework (Figure 6). Moreover, the abundance of phytodetritus-feeding species (e.g. *G. subglobosa* and *Epistominella vitrea*) suggests that seasonality plays an important role on the structure of benthic foraminiferal assemblages on North-east Atlantic CWC environments. This hypothesis is supported by the abundance

of living phytodetritus-feeding species, such as *Eponides pusillus* and *Alabaminella weddellensis*, within on-mound sediments from the Propeller Mounds (Morigi et al., 2012) and the Moira Mounds, respectively (Fentimen et al., 2020b). The infaunal *Uvigerina mediterranea* and *Uvigerina peregrina* are more common in adjacent off-mound sediments than on the large Irish and Irish Moira Mounds (Figure 6). Such a distribution trend has also been noticed around Galway and Propeller Mounds (Schönfeld et al., 2011), whereas uvigerinids are rare both on and off Norwegian reefs (Figure 6). The general occurrence of Uvigerinids has been related to finer-grained sediments rich in organic matter (Schmiedl et al., 2000). More specifically, *U. peregrina* appears to respond to pulses of fresh and labile organic matter (Koho et al., 2008). The species *Elphidium excavatum* is solely present at the surface of the Irish Moira Mounds and further explains the dissimilarity between the Moira Mound and Norwegian reef/large Irish mound assemblages (Figure 6). *Elphidium excavatum* is considered to be a nearshore shallow-water dwelling species (Duros et al., 2012; Horton, 1999; Murray, 2006),

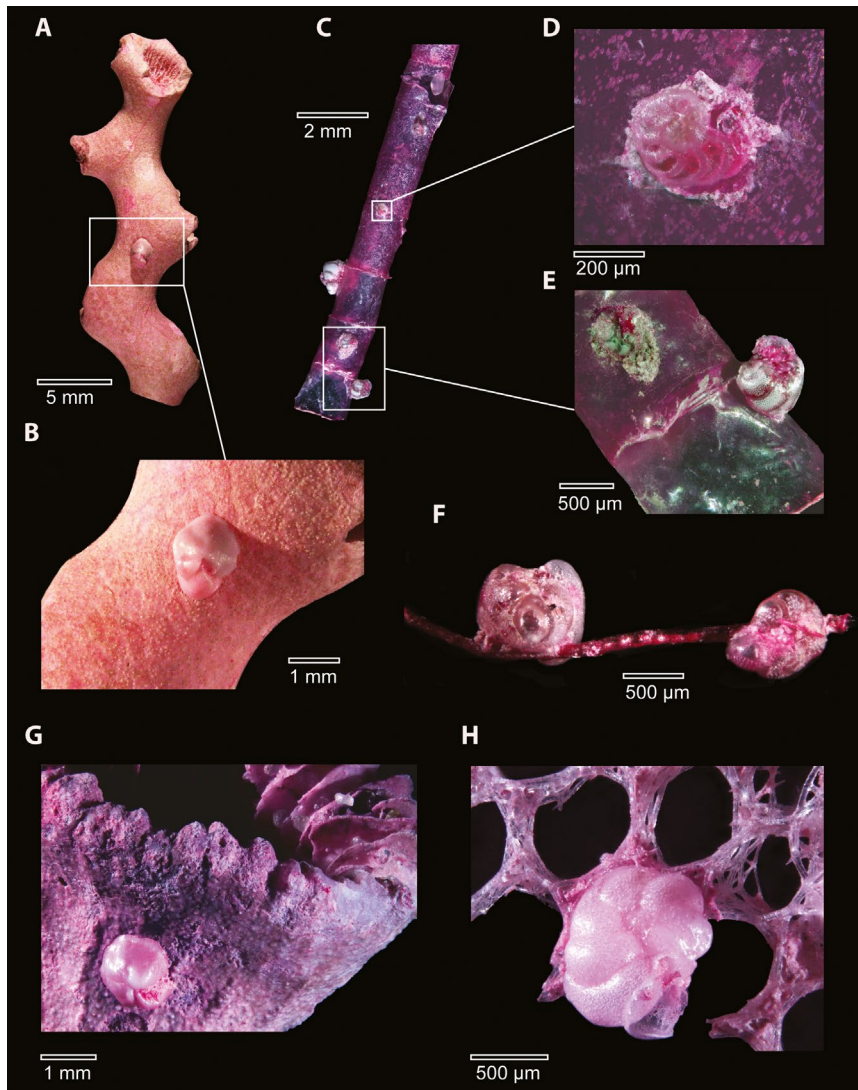


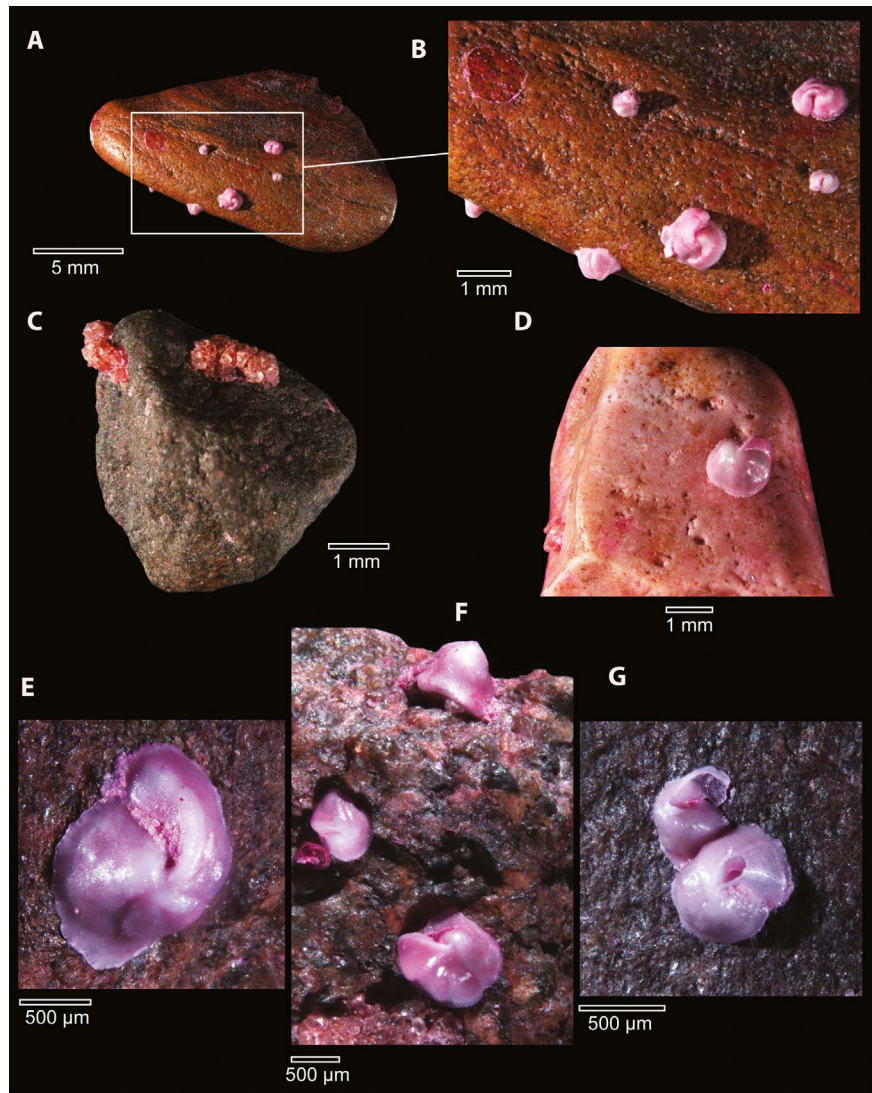
FIGURE 9 Epibenthic foraminifera attached to their substrates from the Irish Moira Mounds (photographed under a Nikon SMZ18 Stereo microscope). (A) *Desmophyllum pertusum* (Linnaeus, 1758) fragment; (B) Close-up of an attached *Cibicides refulgens* (Montfort, 1808); (C) Hydroid fragment with attached *Planulina ariminensis* (D'Orbigny, 1826) and *Discanomalina coronata* (Parker & Jones, 1865); (D, E) Close-up of *Planulina ariminensis* (D'Orbigny, 1826) and two *Discanomalina coronata* (Parker & Jones, 1865) individuals. Notice the veneer of agglutinated material cementing the tests to the substrate; (F) Two *Discanomalina coronata* (Parker & Jones, 1865) clinging to a thin *Pterobranchia* (?) tube fragment; (G) *Cibicides refulgens* (Montfort, 1808) attached near to the septum of a *D. pertusum* fragment; (H) *Hyrrokkin sarcophaga* (Cedhagen, 1994) attached to a sponge fragment

possibly transported to the area through ice-rafting during the last deglacial period (Fentimen et al., 2020b). Thus, its presence at the surface of the Moira Mounds does not represent present-day environmental conditions.

Overall, benthic foraminiferal assemblages indicate that environmental conditions at North-east Atlantic coral reefs and mounds are characterised by important bottom-water turbulence and enhanced food supply. Seasonal input of labile organic matter appears to play an important role on benthic foraminifera distribution on North-east Atlantic CWC environments, whilst oxygen availability and temperature are not limiting parameters at present. In comparison, surface living benthic foraminiferal assemblages from the East Melilla Coral Province (Figure 1; Table 1) are noticeably different (Stalder, 2015). Stalder (2015) reports a high abundance in on-mound sediments of *G. subglobosa* and of the small epibenthic species *Gavelinopsis praegeri* and *Rosalina bradyi*, whilst they are absent or rare in off-mound sediments. Contrary to assemblages from the North-east Atlantic coral

reefs and mounds, the epibenthic foraminifera *Cibicid(oid)* spp. and *D. coronata* are rare or absent in on-mound and off-mound areas (Stalder, 2015). The infaunal opportunistic *Nonionella turgida* is abundant in both on-mound and off-mound sediments (Stalder, 2015). This species is common in the nutrient-rich and oxygen depleted waters of the Rhône prodelta and Adriatic Sea (Barmawidjaja et al., 1995; Diz et al., 2006; Mojtahid et al., 2009). Additionally, experiments have shown that *R. bradyi* responds positively to sporadic pulses of organic matter and can resist extreme salinity changes and oxygen depletion (Fontanier et al., 2008; Heinz et al., 2001). Thus, surface living benthic foraminiferal assemblages, noticeably the absence of large epibenthic filter-feeding species (e.g. *Cibicid(oid)* spp. and *D. coronata*), suggest that turbulence at the East Melilla Coral Province is reduced in comparison to North-east Atlantic reefs and mounds. Moreover, the abundance of *R. bradyi* and *N. turgida* may indicate oxygen depletion at the surface of the East Melilla Coral Province. Oxygen depletion could explain the

FIGURE 10 Epibenthic foraminifera attached to their substrates from the Irish Moira Mounds (photographed under a Nikon SMZ18 Stereo microscope). (A) Numerous *Cibicides refulgens* (Montfort, 1808) attached to a dropstone; (B) Close-up of A. Notice the attachment mark left by a *Cibicides refulgens* (Montfort, 1808) individual (top-left); (C) Two *Rhizammina* sp. 3 (Brady, 1879) attached to a dropstone; (D–G) *Cibicides refulgens* (Montfort, 1808) attached to dropstones. Notice the veneer of agglutinated material cementing the test to the substrate



weaker vitality of coral communities at the East Melilla Coral Province in comparison to more thriving counterparts in the North-east Atlantic (see Section 2.4).

4.3 | Benthic foraminiferal species as bio-indicators of CWC reef health

Benthic foraminifera have successfully been used as bio-indicators of pollution (e.g. industrial waste, heavy metal pollution) within coastal marine environments (Alve & Murray, 1995; Debenay et al., 2015; Frontalini & Coccioni, 2011; Martins et al., 2019; Mojtahid et al., 2008; Prazeres et al., 2019). They have also proved to be an effective tool to trace and monitor the state of tropical coral reefs (Hallock et al., 2003; Uthicke et al., 2010). In the same way as for tropical coral reefs, a number of studies have attempted to identify benthic foraminiferal species reflecting the health state of CWCs (Margreth et al., 2009; Spezzaferri et al., 2013). The

species *D. coronata* has been proposed as an indicator species for living corals on large Irish CWC mounds by Margreth et al. (2009). In contrast, Schönfeld et al. (2011) noticed a higher abundance of *D. coronata* within the coral rubble than on living coral on Propeller and Galway Mounds, while living foraminiferal assemblages from the Moira Mounds did not show a higher abundance of *D. coronata* in the presence of living coral (Fentimen et al., 2018). Observations made by Smeulders et al. (2014) also suggest that the highest abundances of *D. coronata* are associated with coral debris rather than living coral. Moreover, *D. coronata* does not show a preference for coral as a substrate. Indeed, Weston (1985) and Schönfeld (1997) noticed it attached to sponge spicules at the Porcupine Seabight and southern Portuguese continental margin, respectively, whereas it favoured the recruitment of hydroids around Galway Mound (Schönfeld et al., 2011) and at the Moira Mounds (Figure 9). At the surface of Moira Mounds, no *D. coronata* individual was found attached to the investigated coral fragments (Fentimen et al., 2018; Figures 7

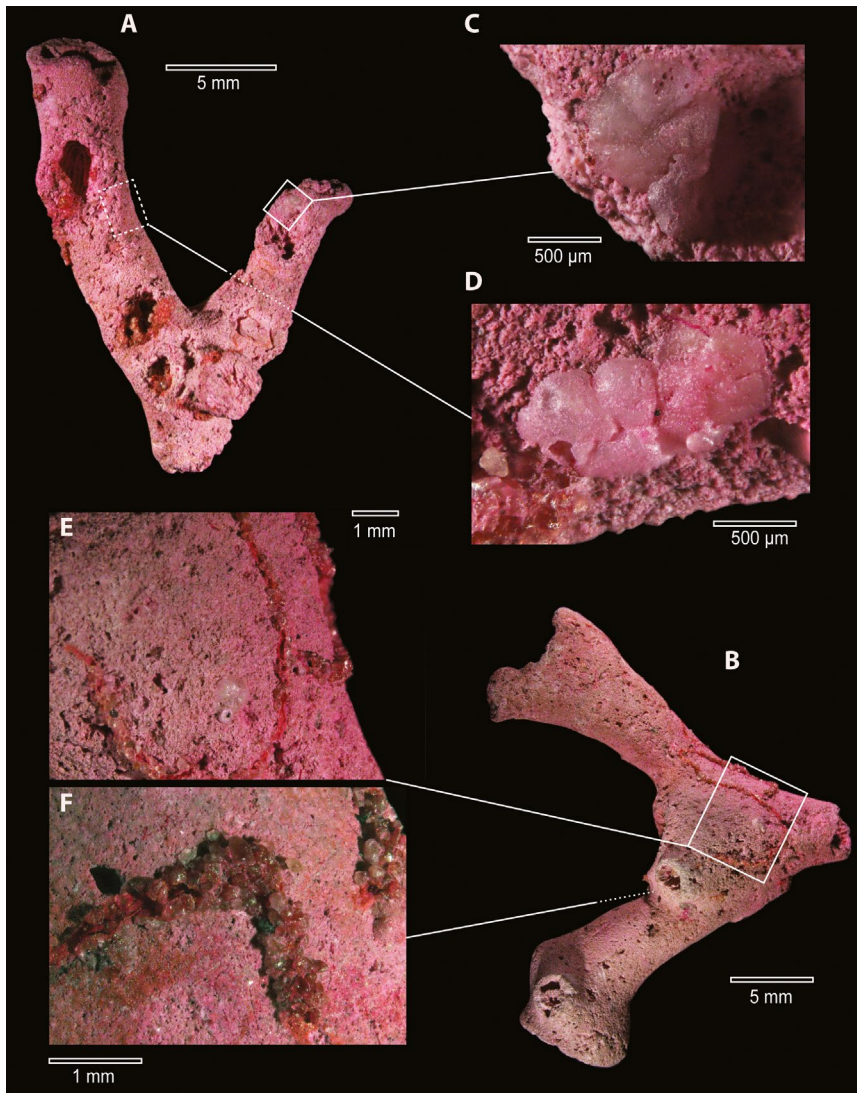


FIGURE 11 Epibenthic foraminifera attached to their substrates from the Irish Moira Mounds (photographed under a Nikon SMZ18 Stereo microscope). (A, B) Strongly bioeroded coral fragments; (C, D) *Lobatula lobatula* (Walker & Jacob, 1798); (E) *Rhizammina* sp. 1 (Brady, 1879); (F) *Rhizammina* sp. 2 (Brady, 1879)

through 12), whilst it was observed associated with communities of the erect cheilostome bryozoan *Buskea dichotoma* in core material from the East Melilla Coral Province (Fentimen et al., 2020a). Thus as it stands, *D. coronata* cannot be used as an indicator for living CWC communities.

The high biodiversity associated with CWC reefs is closely linked to their 3-dimensional structural complexity (Kazanidis et al., 2016; Roberts et al., 2009). Dead coral is an essential part of this construction (Roberts et al., 2009). On-going ocean acidification leads to the dissolution of the coral's aragonitic skeleton (Davidson et al., 2018; Hennige et al., 2015), which weakens individual coral branches and in the long term the entire reef (Hennige et al., 2020 and references therein). Hennige et al. (2020) showed that this loss of dead coral will result in a shift from high 3-dimensional complexity provided by both living and dead coral, to a habitat restricted primarily to live coral colonies with lower 3-dimensional complexity. This phenomenon, given the importance of dead coral as a substratum for epibenthic foraminifera (Figures 7 through 12), may over time reduce benthic foraminiferal macrohabitat and

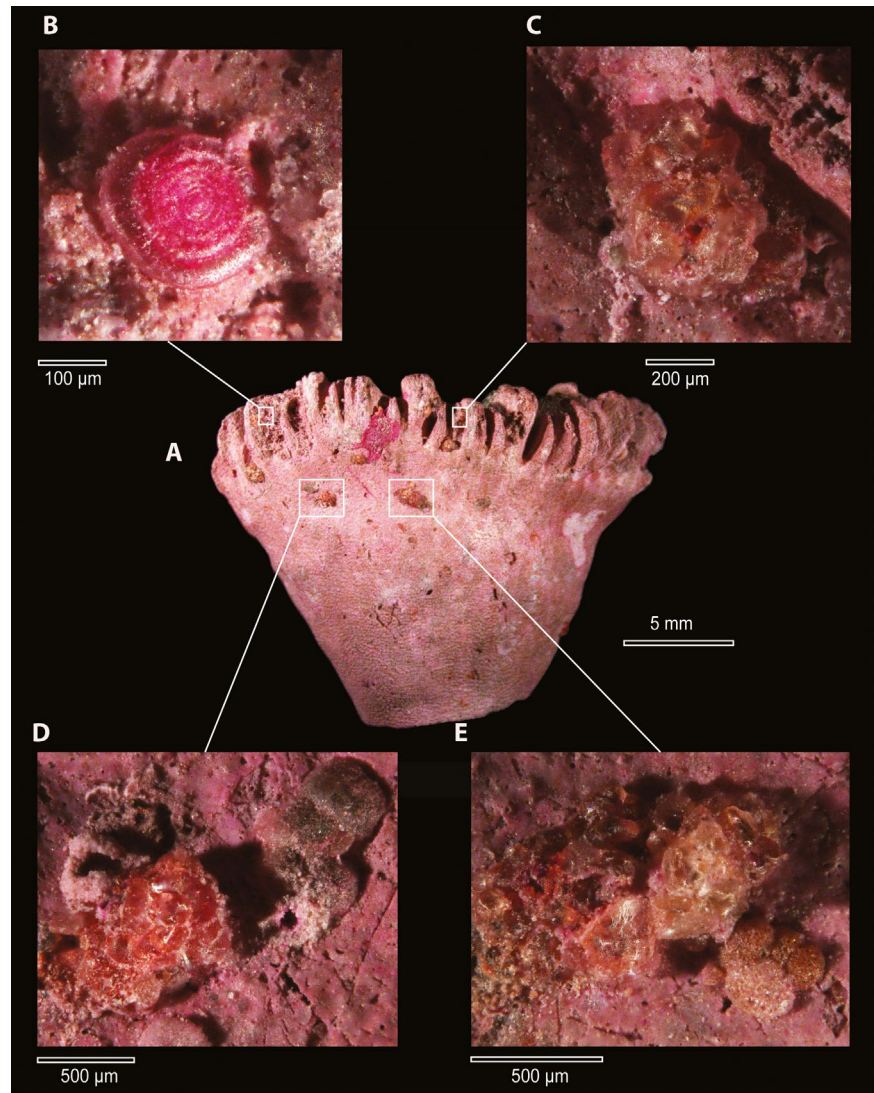
microhabitat availability and ultimately lead to diversity loss within benthic foraminiferal communities. Given their current diversity, benthic foraminiferal assemblages may provide indications of 3-dimensional complexity loss in CWC reefs under the effect of ocean acidification. However, precise sampling and investigation of benthic foraminiferal assemblages from environmentally stressed CWC reefs are needed to assess how promising this approach may be.

5 | BENTHIC FORAMINIFERA AS PALAEOENVIRONMENTAL PROXIES IN PAST CWC ECOSYSTEMS

5.1 | Bottom-water currents

Evaluating past bottom current velocities within CWC mound records is of particular interest since bottom current velocity plays an important role in CWC growth (see Section 2.1).

FIGURE 12 Epibenthic foraminifera attached to their substrates from the Irish Moira Mounds (photographed under a Nikon SMZ18 Stereo microscope). (A) *Desmophyllum dianthus* (Esper, 1794) fragment; (B) *Spirillina vivipara* (Ehrenberg, 1843) attached to the septum of the *D. dianthus* fragment; (C) *Rhizammina* sp. 4 (Brady, 1879) attached to the septum of the *D. dianthus* fragment; (D) *Hemisphaerammina* sp. (Loeblich & Tappan, 1957) and *Placopsilina confusa* (Cushman, 1920) (left and right, respectively); (E) *Hemisphaerammina* sp. (Loeblich & Tappan, 1957) and *Paratrochammina challengeri* (Brönnimann & Whittaker, 1987) (left and right, respectively)



However, there is a lack of palaeocurrent proxies in these environments. Indeed, although the sortable silt mean grain size (10–63 µm; McCave et al., 1995) has been successfully and widely used within (hemi)pelagic and contouritic sediments to evaluate the speed of deep-sea bottom currents (Kleiven et al., 2011; McCave, 2008; McCave & Hall, 2006; McCave et al., 2017; Toucanne et al., 2012), the baffling effect of coral framework on mounds can locally reduce bottom current speed and favour the deposition of fine sediment particles (Dorschel et al., 2007; Fentimen et al., 2020b; Huvenne et al., 2009a). This challenges the applicability of the sortable silt mean grain size as a palaeocurrent proxy in CWC mounds. Past studies have therefore used grain size and sortable silt to evaluate past bottom current velocities in the surrounding off-mound contourites (Fink et al., 2013; Matos et al., 2015; Wang et al., 2019). However, this only documents past current dynamics in off-mound areas and does not necessarily reflect or even record those governing the coral mound itself and the coral communities it hosts. With this in mind,

benthic foraminiferal assemblages appear as a valuable tool to assess past bottom current dynamics in CWC mounds. The abundance of species possessing an elevated lifestyle (e.g. *L. lobatula*, *C. refulgens*, *D. coronata*, *H. sarcophaga*) or resistant to winnowing (e.g. *T. angulosa*) may successfully be used to evaluate qualitatively bottom current velocities affecting CWC mounds (Figures 6 and 13; Annex S5; Fentimen et al., 2020a; Matos et al., 2017; Rüggeberg et al., 2007; Stalder et al., 2014, 2015, 2018). Indeed, in areas where currents are particularly strong, a distinctive benthic foraminiferal assemblage dominated by species living in elevated positions and/or resistant to winnowing can be observed (Schönfeld, 1997, 2002b). Comparing the abundance of high-current indicator species in different CWC mounds from the North-east Atlantic and Mediterranean Sea allows the respective role of bottom currents on coral mound formation to be evaluated (Figure 13). Bottom current velocities derived from foraminiferal assemblages confirm that past CWC growth in the North Atlantic realm is promoted by strong bottom current

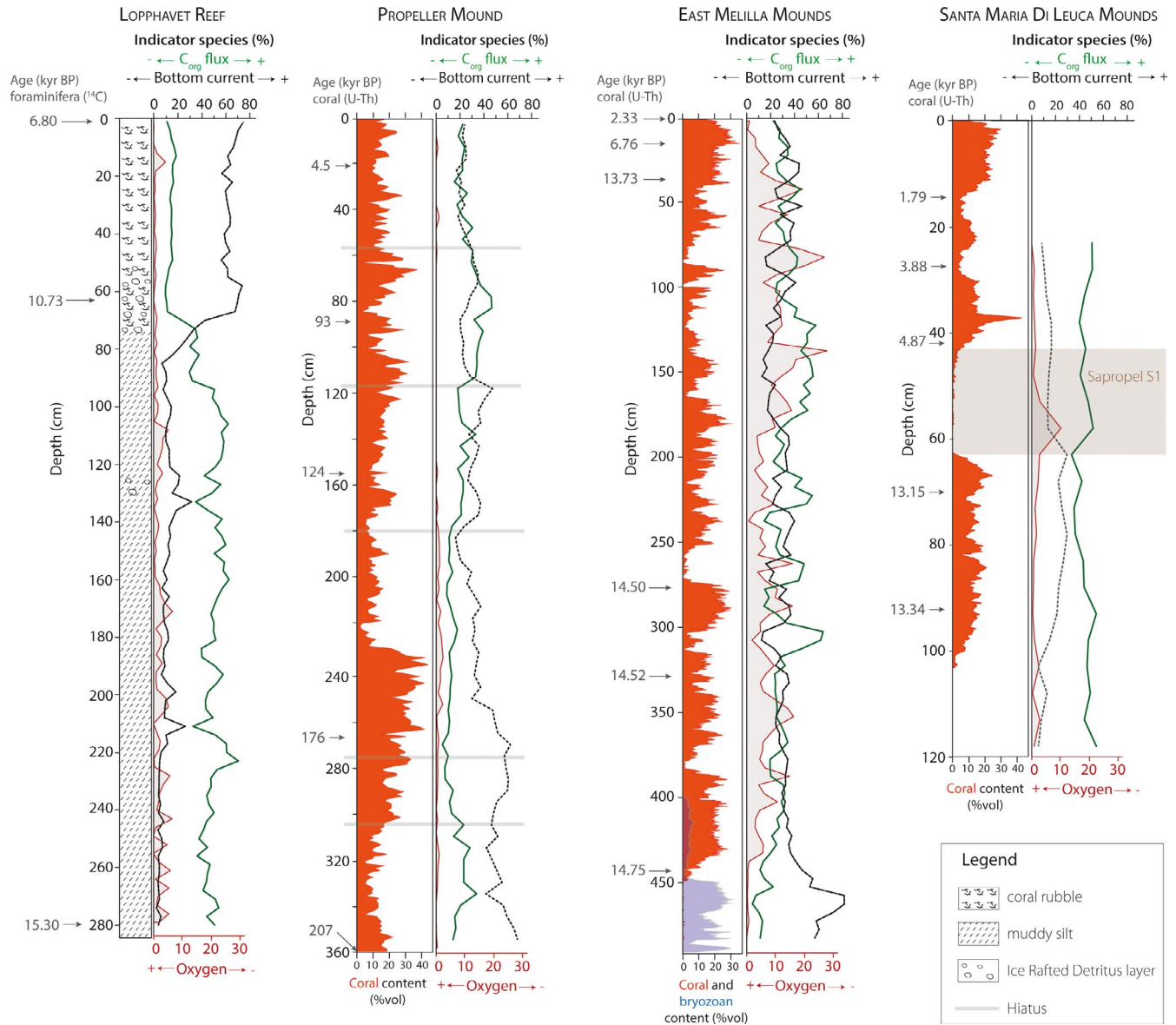


FIGURE 13 Carbon flux (green line), bottom-water current strength (black dashed line) and bottom-water oxygenation (full red line) reconstructions based on the relative abundance of indicator species (Annex S5) for LoppHAVET Reef (Stalder et al., 2014), Propeller Mound (Rüggeberg et al., 2007), the East Melilla Coral Mounds (Fentimen et al., 2020a) and the Santa Maria di Leuca Coral Mounds (Fink et al., 2012). Cold-water coral and bryozoan contents for Propeller Mound (Dorschel et al., 2007), the East Melilla Coral Mounds (Fentimen et al., 2020a) and the Santa Maria di Leuca Coral Mounds (Titschack et al., 2016) are also indicated

velocity (Figure 13). However, strong bottom currents at the East Melilla Coral Province during Greenland Stadial 2.1 appear to have rather favoured the proliferation of the bryozoan species *Buskea dichotoma* (Figure 13; Fentimen et al., 2020a). This observation highlights that other important environmental parameters control CWC proliferation in this area, such as sea floor oxygenation (Fentimen et al., 2020a).

5.2 | Bottom-water oxygenation

Little is yet known about the sensitivity of past *D. pertusum* and *M. oculata* communities to depleted dissolved oxygen

concentrations (DO_{conc}). The lower DO_{conc} limit of *D. pertusum* in the North-west and North-east Atlantic has been assumed to be situated around 2–3.7 ml/l (Brooke & Ross, 2014; Dullo et al., 2008; Freiwald et al., 2009). However, *D. pertusum* has been observed living in the oxygen minimum zones of the subtropical eastern Atlantic (Colman et al., 2005; Le Guilloux et al., 2009), while thriving reefs develop within rather warm waters (6.8–14.2°C) and under hypoxic conditions (0.6–1.5 ml/l) in the oxygen minimum zone off Angola (Hanz et al., 2019; Hebbeln et al., 2020). These discoveries also contrast with laboratory experiments, where individual *D. pertusum* corals from the North-east Atlantic and the Gulf of Mexico could not survive DO_{conc} lower than

40%–50% of the ambient values (Dodds et al., 2007; Lunden et al., 2014). It has been proposed that high food availability compensates the negative effects of hypoxia and high temperatures on *D. pertusum* communities along the Angolan margin (Hanz et al., 2019; Hebbeln et al., 2020). There is, however, a need to better constrain the effects of oxygen depletion on past CWC communities at different temporal scales.

Benthic foraminiferal assemblages from low oxygen environments have a characteristic taxonomic composition, strongly dominated by globobuliminids, chilostomellinids and some other taxa (Bernhard & Sen Gupta, 1999; Sen Gupta & Machain-Castillo, 1993; Smith, 1964). These species become particularly dominant when oxygen concentrations reach values below approximately 1 ml/l (Jorissen et al., 2007). Oxygen-deficient areas are marked by low species numbers but high foraminiferal densities (Gooday, 2014; Gooday et al., 2010). Thus, the composition of benthic foraminiferal assemblages, noticeably the relative abundance of deep-infaunal taxa, can provide information about past DO_{conc} in CWC mounds (Figure 13; Annex S5). For example, based on the relative abundance of deep-infaunal species, Fink et al. (2012) showed that the period of coral absence at the Santa Maria di Leuca coral province coincided with the Early Holocene sapropel S1 event (Figure 13). High relative abundances of low oxygen indicator species are observed within the East Melilla Coral Mounds (Figure 13). These are generally associated with low coral abundances, possibly indicating that short periods of oxygen depletion hindered coral proliferation in the area (Figure 13; Fentimen et al., 2020a). However, these dysoxic events appear to have been rather short-lived and would have alternated with periods of increased DO_{conc} (Figure 13). These observations suggest that Mediterranean CWC communities situated at the East Melilla Coral Province resisted short periods of low DO_{conc} , whereas prolonged periods of oxygen depletion were fatal to corals at the Santa Maria di Leuca Mounds. As opposed to Mediterranean CWC mounds, coral communities situated at the Lophavet Reef (Norwegian shelf) and Propeller Mound (Irish margin) do not appear to have suffered from oxygen depletion (Figure 13).

5.3 | Palaeoproductivity

Constraining past changes in primary production and the export of organic matter to the sea floor is essential to understand the development of CWC mounds through time. Most palaeoproductivity proxies, such as the total organic carbon preserved in the sediment and the benthic $\delta^{13}C$ values, are not only influenced by the quantity of organic matter reaching the sea floor but also by its quality and the

timing of its input (Jorissen et al., 2007). Furthermore, the applicability of total organic carbon as a palaeoproductivity proxy in CWC environments is subject to debate, since CWCs act like a sink for organic matter, reducing its supply to the underlying sediments (Wehrmann et al., 2009). Benthic foraminifera respond rapidly to changes in both the quantity and the quality of exported organic matter (Jorissen et al., 2007). Assemblages dominated by opportunistic species (e.g. *Epistominella exigua*, *A. weddellensis*, *Eponides umbonatus*) and with often a low diversity reflect seasonal pulses of labile high-quality organic matter to the sea floor (Corliss et al., 2009; Gooday, 1993; Gooday & Jorissen, 2012; Sun et al., 2006). Some foraminifera species demonstrate high relative abundances in environments characterised by high organic flux levels. For example, the shallow infaunal *U. mediterranea* and the opportunistic *Bolivina spathulata* are known to demonstrate a positive correlation with organic matter flux (Drinia & Dermitzakis, 2010; Fontanier et al., 2002, 2003; De Rijk et al., 2000; Schmiedl et al., 2000). In the Mediterranean Sea, *Bulimina marginata* is restricted to sites with an organic carbon flux >2.5 g of organic carbon per square metre per year ($gC \cdot m^{-2} \cdot yr^{-1}$), whilst *Bulimina aculeata* is associated with a flux of $3 gC \cdot m^{-2} \cdot yr^{-1}$ (De Rijk et al., 2000). As opposed to buliminids, *G. subglobosa* dominates in areas of the South Atlantic Ocean where the organic carbon flux does not exceed $1 g \cdot cm^{-2} \cdot yr^{-1}$ (Mackensen et al., 1995). An important threshold for many species seems to exist at an organic flux rate of approximately $2-3 g \cdot m^{-2} \cdot yr^{-1}$ (Altenbach et al., 1999; De Rijk et al., 2000; Jian et al., 1999; Weinelt et al., 2001). As such, the relative abundance of species responding positively to high carbon export to the sea floor (uvigerinids, buliminids, bolivinids and cassidulinids; Annex S5) has been used as a palaeoproductivity proxy in CWC mounds (Figure 13; Fentimen et al., 2020a; Stalder et al., 2015, 2018). Benthic foraminiferal assemblages in CWC mounds further prove useful to identify changes in the origin of organic matter, from fresh marine to more refractory organic matter input (Fentimen et al., 2020a; Stalder et al., 2015, 2018). Indeed, certain species (e.g. buliminids) are nowadays dominant in prodelta environments (Jorissen, 1987; Mojtahid et al., 2009). The relative abundance of uvigerinids, buliminids, bolivinids and cassidulinids suggests that enhanced riverine input triggered CWC mound development at the transition between Greenland Stadial 2.1 and Greenland Interstadial 1 at the East Melilla Coral Province (Figure 13; Fentimen et al., 2020a). Thus, despite a certain number of issues hampering their applicability (e.g. the quantification of the carbon flux-dependence of only a few deep-sea foraminifera species), benthic foraminiferal assemblages appear to be a promising palaeoproductivity proxy in CWC mounds.

6 | CONCLUSION

Surface benthic foraminiferal assemblages associated with modern CWC environments from the Irish margin and Norwegian shelf share a similar composition characterised by abundant elevated epibenthic species (e.g. *Lobatula lobatula*, *Cibicides refulgens*, *Discanomalina coronata*) and a distinct infaunal community (e.g. *G. subglobosa*, *T. angulosa*). This assemblage reflects the importance of bottom-water turbulence and enhanced food supply on the development of North-east Atlantic CWC communities. Similar to trends commonly reported for megafaunal and macrofaunal communities from these areas, surface benthic foraminiferal diversity is higher on-reef/on-mound than in surrounding off-reef/off-mound sediments. As opposed to megafaunal and macrofaunal diversity, the highest surface benthic foraminiferal diversity is found with living coral. This higher diversity is possibly the result of higher food availability together with a wider variety of food sources (e.g. microbes thriving on coral-derived mucus, suspended organic matter). Oxygen and temperature do not appear to play a limiting role on the distribution of benthic foraminifera in modern CWC environments from the North-east Atlantic.

The relative abundance of benthic foraminiferal species resistant to weak bottom-water oxygenation suggests that past dysoxic events hampered CWC development at the East Melilla Mounds (south-east Alboran Sea) and at the Santa Maria di Leuca Coral Province (northern Ionian Sea). Corals situated at the East Melilla Mounds were able to withstand the short intervals of oxygen depletion at the sea floor, whereas a more prolonged period of poor oxygenation would have been fatal for CWC communities at the Santa Maria di Leuca Coral Province. This suggests the existence of a temporal threshold under which CWCs can adapt their metabolism to oxygen deficiency. In addition, benthic foraminiferal assemblages may help to reconstruct past bottom-water currents and changes in palaeoproductivity. Overall, benthic foraminiferal assemblages appear as a useful and at present under-exploited proxy to investigate the high-resolution records concealed within CWC mounds.

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CONFLICT OF INTEREST

The authors declare that they have no financial interests or personal relationships that could have influenced the work reported in this paper.

AUTHOR CONTRIBUTIONS

Robin Fentimen: Investigation, Original Draft, Conceptualization and Methodology. Gerhard Schmiedl: Review and Conceptualization. Andres Rüggeberg: Review and Conceptualization. Anneleen Foubert: Review, Conceptualization and Funding Acquisition.

DATA AVAILABILITY STATEMENT

The data that support this study are provided in the Annexes. Benthic foraminiferal assemblages from the Moira Mounds, large Irish mounds and Norwegian reefs are physically stored and available at the Department of Geosciences, University of Fribourg (Switzerland).

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SUPPORTING INFORMATION

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

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