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COELENTERATE BIOLOGY

Distribution of nine cold-water coral species (Scleractinia and Gorgonacea) in the cold temperate North Atlantic: effects of bathymetry and hydrography

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Abstract The distribution of nine cold-water corals in the cold temperate North Atlantic is described based on existing records. The species studied are *Lophelia pertusa, Madrepora oculata, Paragorgia arborea, Primnoa resedaeformis, Paramuricea placomus, Acanella arbuscula, Isidella lofotensis, Radicipes gracilis* and *Acanthogorgia armata.* The compiled number of records were 5,854, of which 4,875 were obtained from databases and 979 from publications. Distribution maps were produced and temperature, broad-scale topography and current patterns were considered to understand the distribution patterns and conditions at which the species thrive. Currents connecting shelves and slopes above 500 m can explain the wide spatial distribution of *L. pertusa, P. arborea* and *P. resedaeformis.* However, *L. pertusa* is scarce on the western side of the North Atlantic, *P. arborea* has only few records off Iceland and *A. arbuscula* and *A. armata* are not found on the Norwegian shelf. The differences in distribution patterns between species indicate that they are differently affected by the topographic barrier between the North Atlantic and the Nordic Seas. Present knowledge of dispersal ability of cold-water corals does not allow a firm causal explanation to the observed distribution patterns. These, however, are indicative of biogeographic provinces relevant to cold-water corals and their habitat requirements.

Keywords Cold-water corals · N Atlantic distribution · Gorgonian corals · Lophelia · Temperature requirement · Depth distribution · Biogeographic provinces

Introduction

Cold-water corals are found in all of the world's oceans and in some adjacent seas, commonly at depths between 200 and 1,000 m (Kramp, 1932; Broch, 1935; Madsen, 1944; Zibrowius, 1980; Tendal, 1992; Tyler & Zibrowius, 1992; Rogers, 1999; Heifetz, 2002; Mortensen et al., 2006; Stone, 2006; Watling, 2011). Some coral species are more common at greater depths with recorded maximum depths of ca 4,000 and 6,328 m for the Northeast Atlantic (Grasshoff, 1981) and the North Pacific (Keller, 1976), respectively. In general, cold-water octocorals are extremely stenothermal and unable to live in depth with significant variation in temperature (Madsen, 1944; Bett, 2001; Freiwald, 2002). Over the last decades, there has been increased interest on cold-water corals, with the main

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focus on the reef-forming species *Lophelia pertusa*. However, studies on cold-water corals on both sides of the North Atlantic date back more than 100 years. Marine scientists in the beginning of last century were well aware of *Lophelia* reefs and gorgonian corals in the North Atlantic (Storm, 1901, 1909; Broch, 1912a, b; Nordgaard, 1912; Kiær & Wollebæk, 1913; Grieg, 1914; Jungersen, 1915; Jungersen, 1917; Broch, 1922; Joubin, 1922a, b; Verrill, 1922; Pratje, 1924; Wahrberg & Eliason, 1926; Nordgaard, 1929; Dons, 1933a, b, 1935; Deichman, 1936; Madsen, 1944). This pioneering work provided large amounts of data, such as geographical position and depth of each coral record and biogeographical information.

In recent decades, the interest for cold-water corals has been revitalized by new technology (mainly involving unmanned underwater platforms, such as remote operated vehicles), thus making it easier to observe and collect corals. This has promoted awareness that corals are species-rich habitats (for a review see Buhl-Mortensen & Mortensen, 2004) threatened by commercial fishing and other human activities (e.g. petroleum exploitation, mining and cable laying). As a result, many reports and databases providing information on coral distribution have become available over the last 15 years [e.g. OSPAR (http://www.ospar.org/), and Seamounts Online (http://seamounts.sdsc.edu/)]. Many physical factors (i.e. temperature, salinity, currents, substratum and topography) have been proposed to be important in influencing the spatial distribution of cold-water corals. The relative importance of these factors seems to vary between regions and taxonomic groups (Strömgren, 1970; Frederiksen et al., 1992; Mortensen et al., 2001, 2006).

In this study, we present the distribution of nine coral species: *Lophelia pertusa, Madrepora oculata, Paragorgia arborea, Primnoa resedaeformis, Paramuricea placomus, Acanella arbuscula, Isidella lofotensis, Radicipes gracilis* and *Acanthogorgia armata* in the cold temperate North Atlantic based on existing records. These species are common cold-water corals belonging to the orders Scleractinia and Gorgonacea with a large number of records in the study area. The aim of this study is to:

(1) describe the distribution patterns of these species in the Cold temperate North Atlantic,
(2) identify environmental correlates on a regional scale,
(3) explore the geographic differences in coral distribution in the arctic and cold temperate N Atlantic that may reflect the biogeography in the larger region and
(4) characterize the topographic/hydrographic barriers that may restrict their spatial distributions.

For this purpose, we have analysed new and unpublished data and existing published information.

By relating the distribution pattern of these species to the environmental characteristics (temperature and depth) and ocean current patterns, we aimed to identify the water masses where they occur and the most important driving forces that influence their distribution.

There has been some effort to define biogeographic regions in the Atlantic Ocean based on corals and other megafauna. Watling et al. (2013) have proposed general biogeographic provinces in the deep areas of the world, including the Atlantic. However, the spatial resolution for the northern part of the Atlantic has been poor (Cairns & Chapman, 2001; see Fig. 1A) and regional provinces are not well established for cold-water corals. Working Group of deep-water ecology (WGDEC) did a preliminary cluster analysis of similarity between regions in the North Atlantic based on the presence of coral species (ICES, 2012). The geographic groups of corals found by WGDEC (ICES, 2012) were similar to the regions defined by Hischock (1996). Their analysis also showed that the species compositions of corals from the waters off the Iberian Peninsula and Azores were similar to each other but very different from the remaining regions in the North Atlantic. We have selected the areas for this study based on this information, and these include the waters off Canada, north to the Davis Strait, south of Iceland, Faroese waters, Great Britain, Norway, Arctic waters and with the addition of the Mid-Atlantic Ridge.

Materials and methods

Sources of coral records

Records of the corals *L. pertusa, M. oculata, P. arborea, P. resedaeformis, P. placomus, A. arbuscula, I. lofotensis, R. gracilis* and *A. armata* (Fig. 2) were compiled from an extensive set of sources covering large areas in the arctic and boreal North

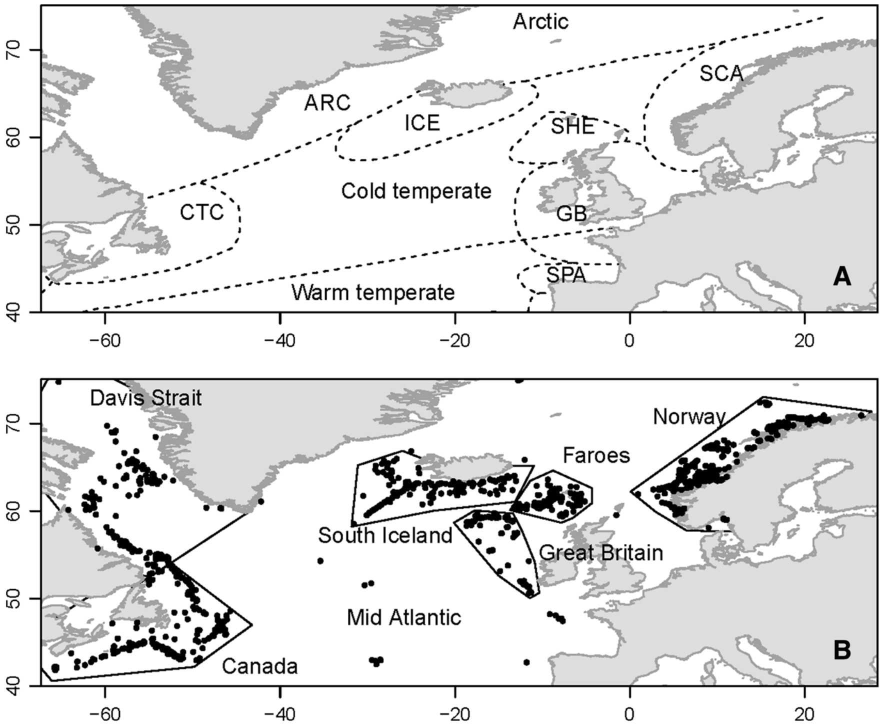

Fig. 1 **A** Identified biogeographic regions relevant to the study area. Biogeographic regions identified from scleractinian distribution by Cairns and Chapman (2001). *CTC* Cold temperate Canadian coast; *SCA* Scandinavia, coast of Norway; *ICE* Iceland, Reykjanes Ridge; *GB* North Sea and coast of Great Britain, Ireland and France; *SHE* Shetland, Faroe, Orkney, New Hebrides Islands, Rockall Banks; *ARC* Arctic, off Labrador, Newfoundland and Greenland; *SPA* Southern Bay of Biscay. **B** Geographic distribution of the records of cold-water corals in this study, see also Table 1. *Polygons* indicate areas for which data have been grouped for regional comparison

Atlantic (Tables 1, 2; Fig. 1B). Data were extracted from several databases from Norway, Iceland and Faroe Islands. Datasets from Iceland included the Icelandic Benthos Database, that holds data from the Benthic Invertebrates of Icelandic waters project (BIOICE), and unpublished data from coral surveys by the Marine Research Institute (MRI, Iceland). Data from Norway used in this study included the following: coral database of the Institute of Marine Research (IMR) (contains data from various Norwegian surveys and observations over time); unpublished data from the MAREANO project and from Norwegian offshore petroleum-related surveys. Datasets from the Faroes and Canada were the Marine Benthic Fauna of the Faroe Islands programme (BIOFAR) and data from by-catch surveys by Fisheries and Oceans Canada (DFO), respectively. We also extracted data from the Seamounts online database (Thomson, 1927; Zibrowious, 1985; Bouchet & Metivier, 1988; Kiriakoulakis et al., 2005; Van Duyl & Duineveld, 2005; Narayanaswamy et al., 2006) and finally, records were extracted from the literature, including published data from early expeditions. For analysis and comparison, we have grouped the areas in 6 regions: Canada (Atlantic Canada, including Newfoundland); Davis Strait (Labrador, W Greenland); S Iceland (south of the Greenland–Scotland Ridge, GSR); Faroes (the region around Faroe Islands); Great Britain (Irish waters, Rockall and Shetlands islands) and Norway.

Depth and temperature data

Depth data were not available for a large proportion of the records ($n = 2{,}340$, 40.6%). For these records, depth was estimated from the data from the Global Multi-Resolution Topography (GMRT) Synthesis database, version 2.5 (Ryan et al., 2009). Temperature data were only available for 642 records (9.6%

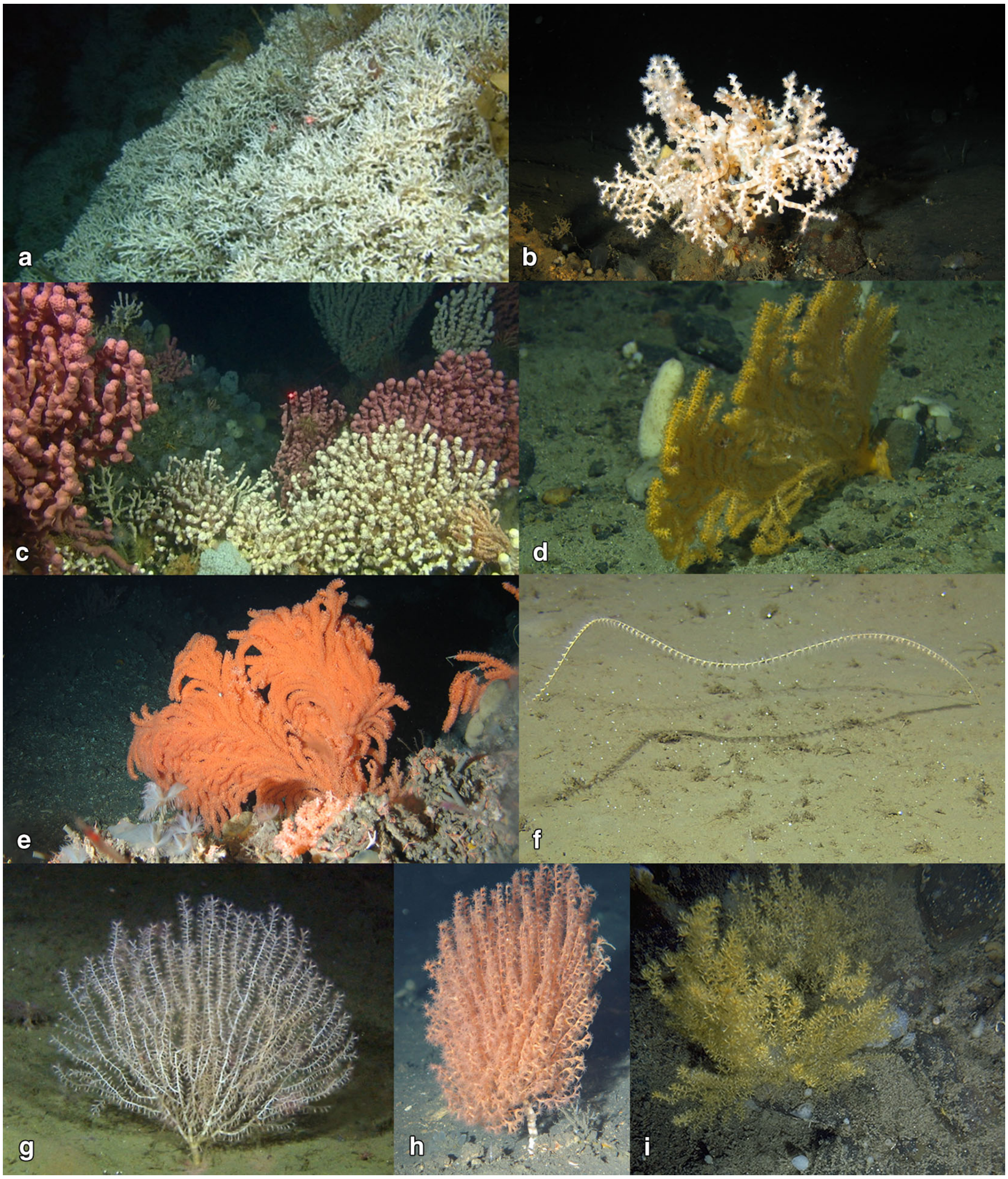

Fig. 2 The coral species included in this study: **a** *Lophelia pertusa,* **b** *Madrepora oculata,* **c** *Paragorgia arborea,* **d** *Paramuricea placomus,* **e** *Primnoa resedaeformis,* **f** *Radicipes gracilis,* **g** *Isidella lofotensis,* **h** *Acanella arbuscula* and **i** *Acanthogorgia armata.* Photo credits for *Lophelia, Paragorgia, Paramuricea, Isidella* and *Radicipes* to Institute of Marine Research, Bergen, Norway, for *Acanella, Madrepora* and *Primnoa* to Marine Research Institute, Reykjavik, Iceland, and for *Acanthogorgia* to Department of Fisheries and Ocean, Dartmouth, Canada

of records). Temperature data were obtained from the World Ocean Atlas 2013 (WOA13, Locarnini et al., 2013). We extracted temperature data as twelve monthly composites and as a single annual composite, obtained by averaging the six decadal means available in the database. At each node of the latitude/longitude grid, the temperature records at the deepest depth level were considered indicative of the near-bottom temperatures. A map of minimum bottom temperatures was obtained by plotting the

Table 1 References to information on occurrence of the coral species used to produce distribution maps

Data (literature and data bases)	*A. arbuscula*	*A. armata*	*I. lofotensis*	*L. pertusa*	*M. oculata*	*P. arborea*	*P. placomus*	*P. resedaeformis*	*R. gracilis*
Projects and databases									
The Icelandic Benthos Database (2007)	52	3		51	22	3		1	4
IMR coral database			56	2,602	26	591	61	311	19
MAREANO			33	11		16	12		
MRI coral surveys				42	24	5	3	25	
BIOFAR (1987–1991)				26	11	6		13	
Seamounts online	10	1		388	200	2	2	3	
Fisheries and Oceans Canada (DFO)	182	86				27		8	9
Literature									
Bruntse & Tendal (2001)								20	
Carlgren (1939)				3	2				
Copley et al. (1996)				18	12	6		5	
Frederiksen et al. (1992)				65					
Gilkinson & Edinger (2009)	1					1		15	
Grasshoff (1981, 1986)	1	4							
Henry & Roberts (2007)				6	6				
Jungersen (1917)	3		2	4		1	4	1	
Jørgensen et al. (2013)	16	5				6	4	2	3
Kramp (1939)							3		
Madsen (1944)	22	5	1			2	7	4	5
Mayer & Piepenburg (1996)			3						
Mercier & Hamel (2011)								15	
Mortensen et al. (2008)	7					5		2	
Mortensen et al. (2006)	27			11		166		350	9
Thomson (1927)	5	2							
Stephens (1909)	6	1		8	5				
Wienberg et al. (2008)		1							
Tendal (1992)						18			
Tendal et al. (2013)				1					
Number of records	332	108	95	3,236	308	855	96	775	49
% No. of records	5.7	1.8	1.6	55.3	5.3	14.6	1.6	13.2	0.8
Number of reports	12	9	5	14	9	14	8	15	6

Table 2 Number of registrations of the nine coral species in the different regions defined in Fig. 1

Species	Canada	Davis Strait	S Iceland	Faroes	Great Britain	Norway	Total
Lophelia pertusa	11	1	112	141	344	2,584	3,193
Madrepora oculata			60	13	183	26	282
Primnoa resedaeformis	349	40	31	36		312	768
Paramuricea placomus		4	7	8		72	91
Paragorgia arborea	181	27	16	14		609	847
Acanella arbuscula	163	72	63	4	6		308
Acanthogorgia armata	57	34	8		2		101
Isidella lofotensis							
Radicipes gracilis	18	5	7			19	49
Number of records	779	183	304	216	535	3,714	5,731
Number of species	6	7	8	6	4	7	

minimum values of the monthly composites on each node of the grid.

Temperature–depth profiles for seven regions representative of hydrographical setting off Canada, David Strait, S Iceland, N Iceland, Faroes, Great Britain and Norway were generated to indicate bottom temperature at different depths on the continental margin in these areas. The profiles were obtained by extracting the data of each region in the annual composite. The annual temperature composite was also utilized to estimate the temperature for the records in the coral database, given that most records did not contain in situ temperature measurements ($n = 5{,}119$, 88.9%). To do this, we extracted the temperature record at the deepest available layer in the latitude/longitude node closest to the location of each coral record.

Results

The total number of records compiled for the nine species was 5,854 (Table 1). A total of 4,875 records were from various databases, while 979 records were obtained from the literature including reports from early expeditions. Only a minority of the records (1.6%) did not have records of depth. Most records were for *L. pertusa* ($n = 3{,}167$ records, 55.0%), followed by *P. arborea* ($n = 853$, 14.8%), and *P. resedaeformis* ($n = 772$, 13.4%). The rarest species were, *I. lofotensis* ($n = 95$, 1.6%), *P. placomus* ($n = 94$, 1.6%) and *R. gracilis* ($n = 49$, 0.9%).

The number of records of each species within the six regions within the North Atlantic is shown in Table 2. The amount of records provides both an indication of the relative abundance of each species and how well each region has been mapped for corals. Most records originated from Norwegian waters followed by the waters off Atlantic Canada, Great Britain and Iceland. Iceland had records for eight of the nine species, lacking only *I. lofotensis,* a species that appears to be almost endemic to Norway. Davis Strait and Norway had seven species each. *Acanella arbuscula* and *A. armata,* have not been recorded off Norway, while both species were present off Canada and Iceland. *Paragorgia arborea*, *P. resedaeformis* and *P. placomus* are found in Canadian waters, in the Davis Strait, in Norway and south of Iceland but were absent from the Great Britain region. However, records of *P. arborea* were relatively few off S Iceland compared to records of *L. pertusa* and *P. resedaeformis* which often co-occur with this species, which is surprising as it is found frequently in the regions west and east of Iceland. On the other hand, there were surprisingly few records of *L. pertusa* from Atlantic Canada, although *P. arborea* and *P. resedaeformis* were frequently recorded. *R. gracilis* is not recorded in Faroes and Great Britain regions indicating that these areas are located south of its distribution limit.

Distribution maps for the nine coral species in the Arctic–Boreal North Atlantic are shown in Fig. 3A–I

Most of the species included in this paper have been found south of the Davis Strait and the GSR but also along the shelf of Norway. Based on the distribution patterns, species can be grouped as follows:

Species recorded mainly in the east North Atlantic and off Norway: *L. pertusa, M. oculata* and *P. placomus;* species found in the whole North Atlantic including

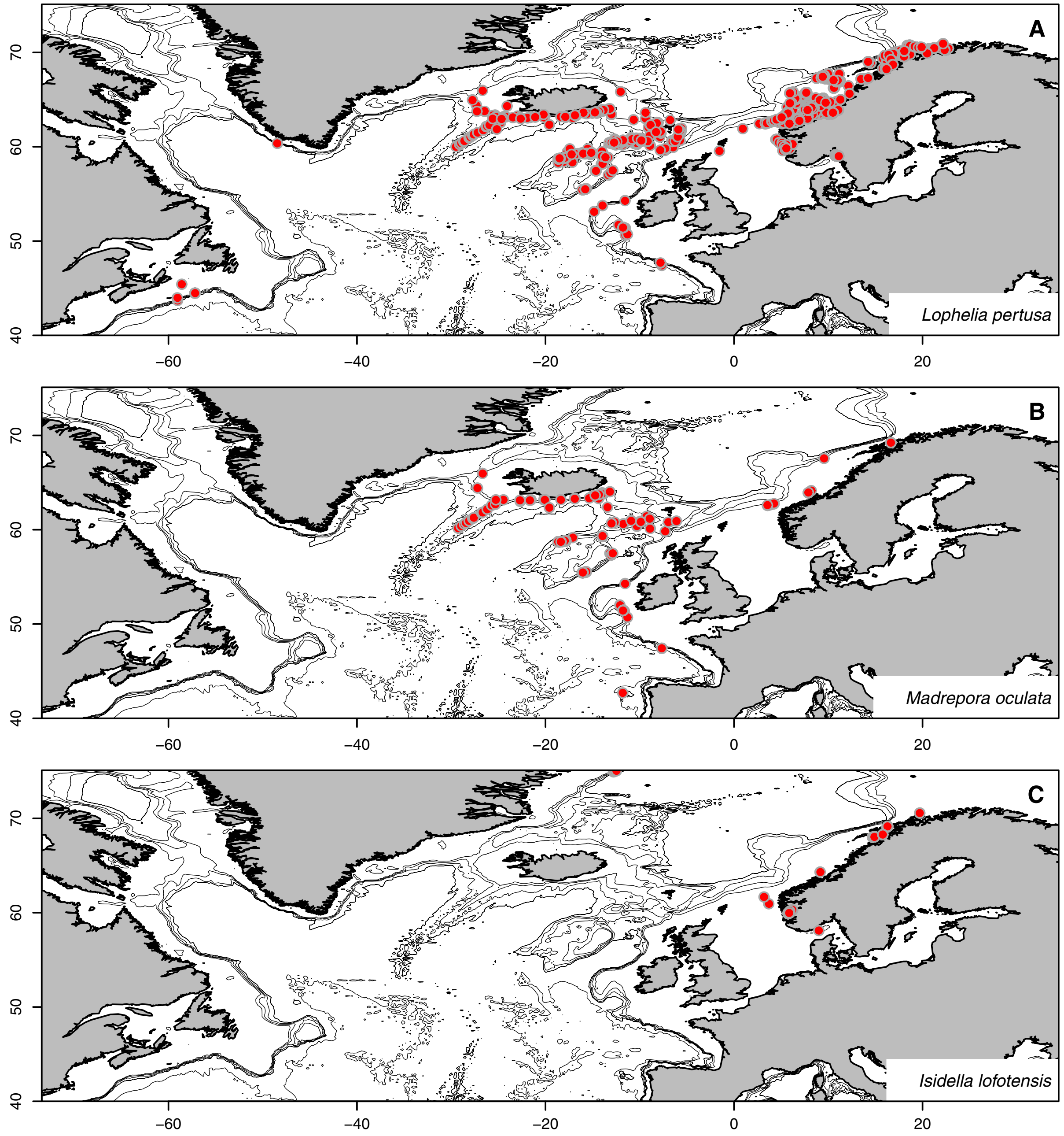

Fig. 3 Distribution of the scleractinians *Lophelia pertusa* (**A**) and *Madrepora oculata* (**B**) and the gorgonians *Isidella lofotensis* (**C**), *Paramuricea placomus* (**D**), *Primnoa resedaeformis* (**E**), *Paragorgia arborea* (**F**), *Acanella arbuscula* (**G**), *Acanthogorgia armata* (**H**) and *Radicipes gracilis* (**I**) in the arctic–boreal North Atlantic based on information compiled from the sources listed in Table 1. Depth contours every 500 m down to 2,000 m

Norway: *P. arborea* and *P. resedaeformis,* and species present in the whole North Atlantic but absent from the Norwegian shelf: *A. arbuscula* and *A. armata*, of which the latter is also not recorded in the Faroes region. In addition, we compiled few observations of *R. gracilis,* generally from deep and cold locations, while *I. lofotensis* was (except a single observation) only recorded off Norway.

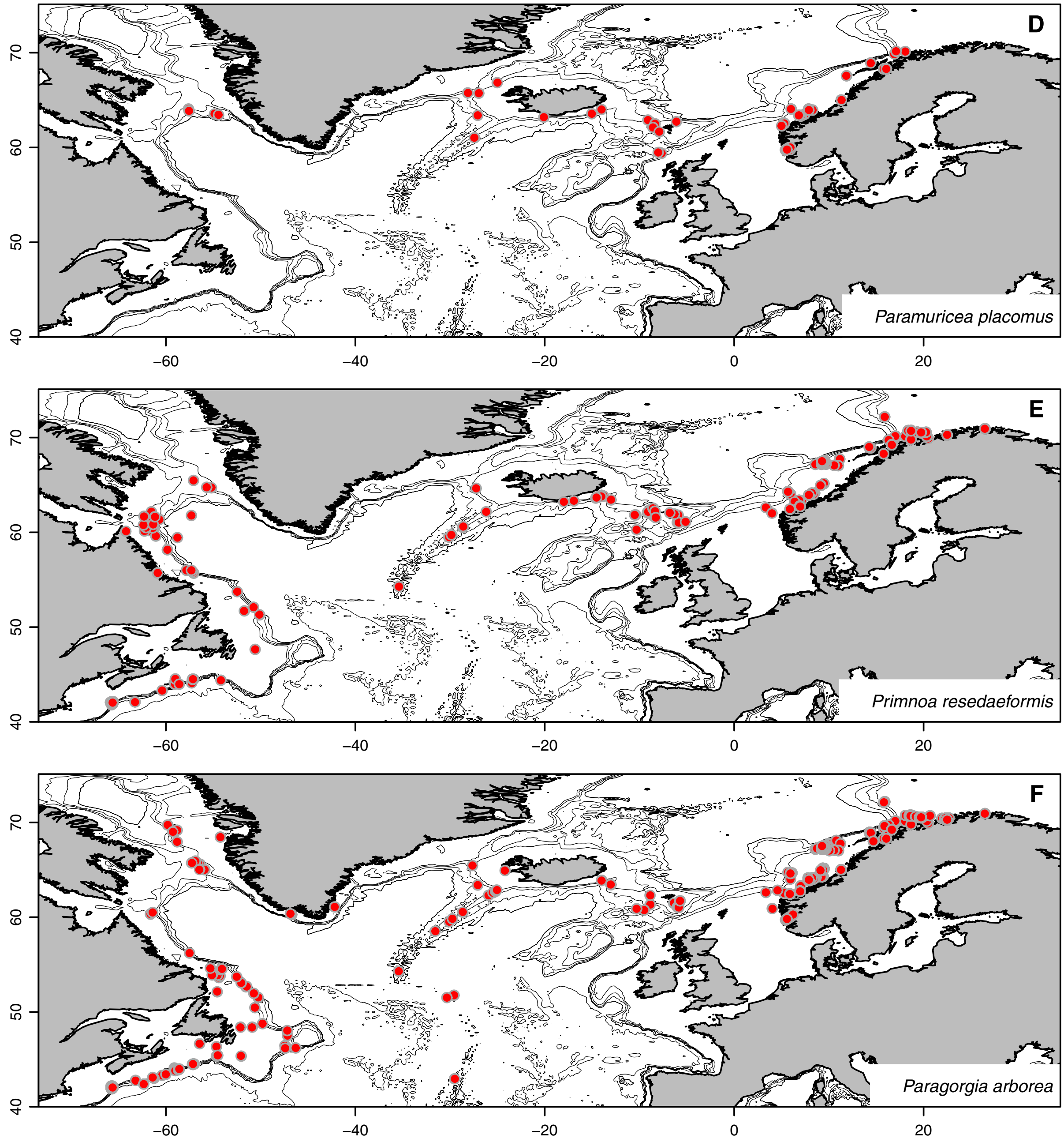

Fig. 3 continued

Species recorded mainly in the east North Atlantic and off Norway: *L. pertusa, M. oculata* and *P. placomus*

Lophelia pertusa has been widely recorded on the eastern side of the North Atlantic, south of the GSR and along the Norwegian coast. It is almost absent from the western side of the North Atlantic. In Canada, there are only few records, occurring at 166 m depth in Jordan basin (Gass & Willison, 2005) and at 260–400 m at Stone Fence (Mortensen et al., 2006). There are no known records north of Nova Scotia on the W Atlantic side, even though extensive registration of by catches from fisheries has been undertaken in

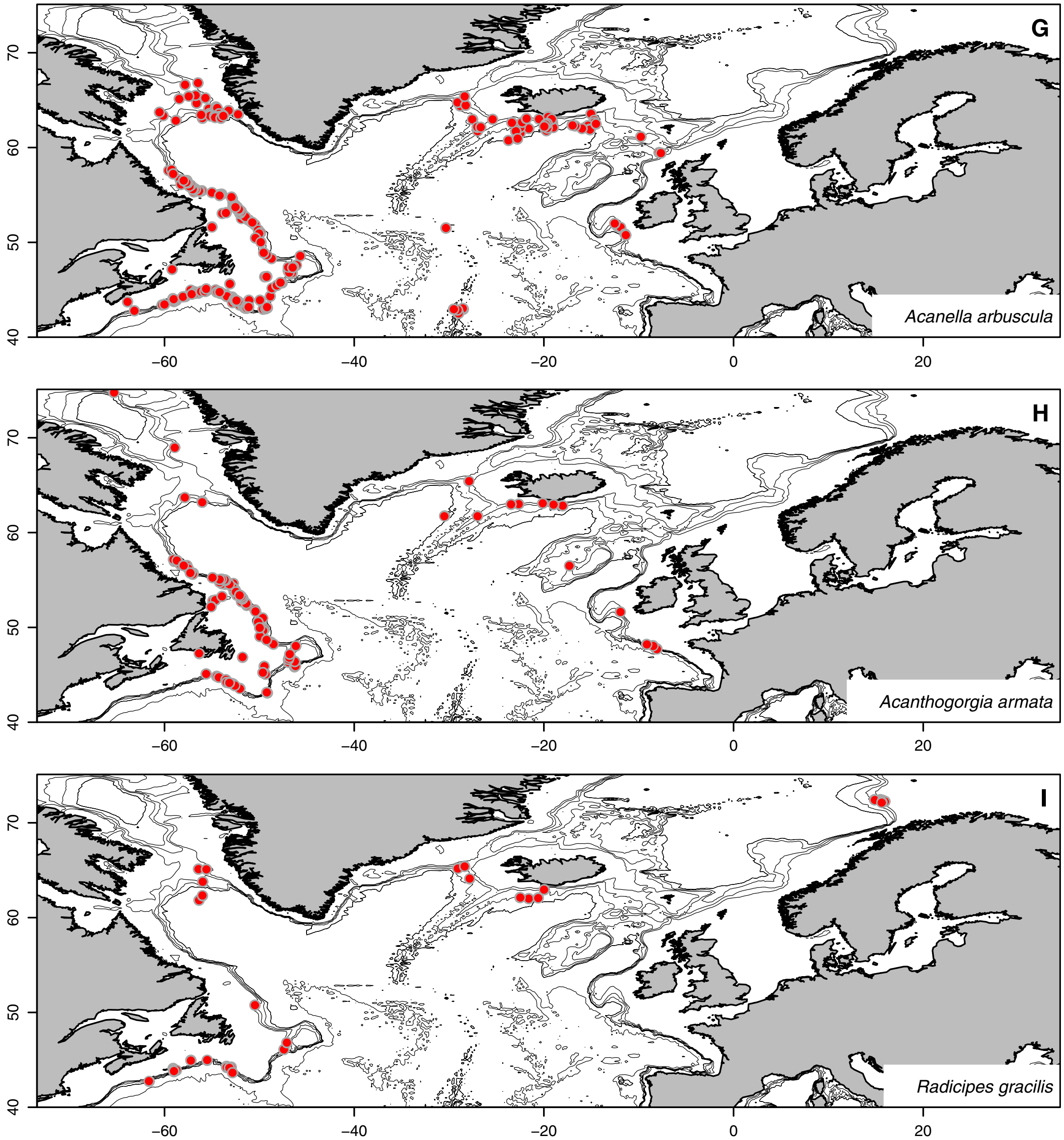

Fig. 3 continued

this area (Mortensen et al., 2006; Gilkinson & Edinger, 2009). It was recently found west of Greenland, in the Davis Strait region, at 900 m (Tendal et al., 2013). In the Great Britain region, it was recorded on the continental shelf and slope at 700–1,355 m (Stephens, 1909; Henry & Roberts, 2007). Most records were from locations shallower than 1,000 m and most commonly from 200 to 300 m depth (Figs. 3A, 4). However, there were clear differences in depth distribution between the six regions (Fig. 5). Records from south of Iceland and the Faroes are mostly between 200 and 800 m whereas deeper in the Great Britain region, mainly below 400 m. In Norway, the coral was mainly found between 200 and 400 m on the continual shelf or slope. The shallower maximum depth off Norway compared to the other regions where it has been recorded is probably related to regional hydrographical setting affecting temperature at depth patterns rather than suitable to feeding or substrate conditions. The general temperature tolerance of *L. pertusa* ranges from 4 to 14°C (Mortensen et al., 2001). This agrees with the records of *L. pertusa* mainly found above 6°C (Fig. 4). The cold temperature north of Iceland could explain the lack of occurrence in otherwise suitable habitats (Fig. 3A). *Lophelia pertusa* was recorded by Jungersen (1917) from 0.3 to 13.6°C, however, this lower temperature limit has not been confirmed. The upper threshold for survival of *L. pertusa* is generally accepted to be 12–14°C, while recent experimental and in situ data suggested that the upper temperature limit for short-term exposure to warm water is near 15°C (Brooke et al., 2013).

Madrepora oculata shows a similar distribution pattern as *L. pertusa* (Fig. 4B). It is common in the NE Atlantic, south of the GSR, along the south continental slope of Iceland, west of the Faroe Islands and off Great Britain along the Irish continental margin. It is recorded from Norway but not frequently and there are no references for the NW Atlantic part of our study area. Most records were from above 1,000 m (Fig. 5). South of Iceland, it was recorded at 264–1,642 m (Carlgren, 1939, The Icelandic Benthos Database, 2007), in the Faroes at 200–1,000 m (Frederiksen et al., 1992) and west of Ireland and UK (Hatton and Rockall bank), it was recorded at 130–1,350 m depth (Stephens, 1909; Wilson, 1979a, b). On the Norwegian shelf, it was found at a narrow depth range between 200 and 300 m. This species has been found at a temperature range similar to *L. pertusa*, from 2.8° and to about 13°C; in our records, the temperature range was 1–12°C with most observations from above 6°C (Fig. 4).

Paramuricea placomus is, like the previous species, absent from Canadian waters (Fig. 3D), but corals reported as *Paramuricea* spp. have been frequently registered off Newfoundland (Gilkinson & Edinger, 2009). A few old records of *P. borealis* (former species name) exist from Canada that according to Opresko (1980) probably is *P. grandis.* Off Norway, it has been recorded from Lofoten to Skagerrak (Madsen, 1944) with northern limit at Arnø 67°11′N, 14°2′E near Bodø (Jungersen, 1917) and from Faroes to Denmark Strait (Madsen, 1944). In Icelandic waters,

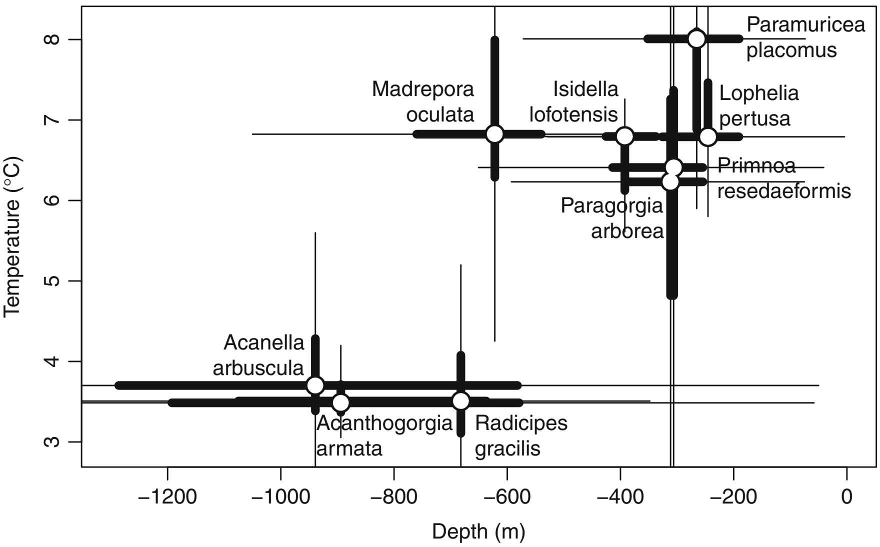

Fig. 4 Depth and temperature distribution of nine coral species in the cold temperate North Atlantic, based on information compiled from the sources listed in Table 1 and estimated from the Global Multi-Resolution Topography Synthesis database (depth) and World Ocean Atlas 2013 (temperature) databases. The *circle line* indicates the median value, *thick lines* extend to the 25 and 75% quantiles and *thin lines* are approximations to the 95% confidence interval for the median

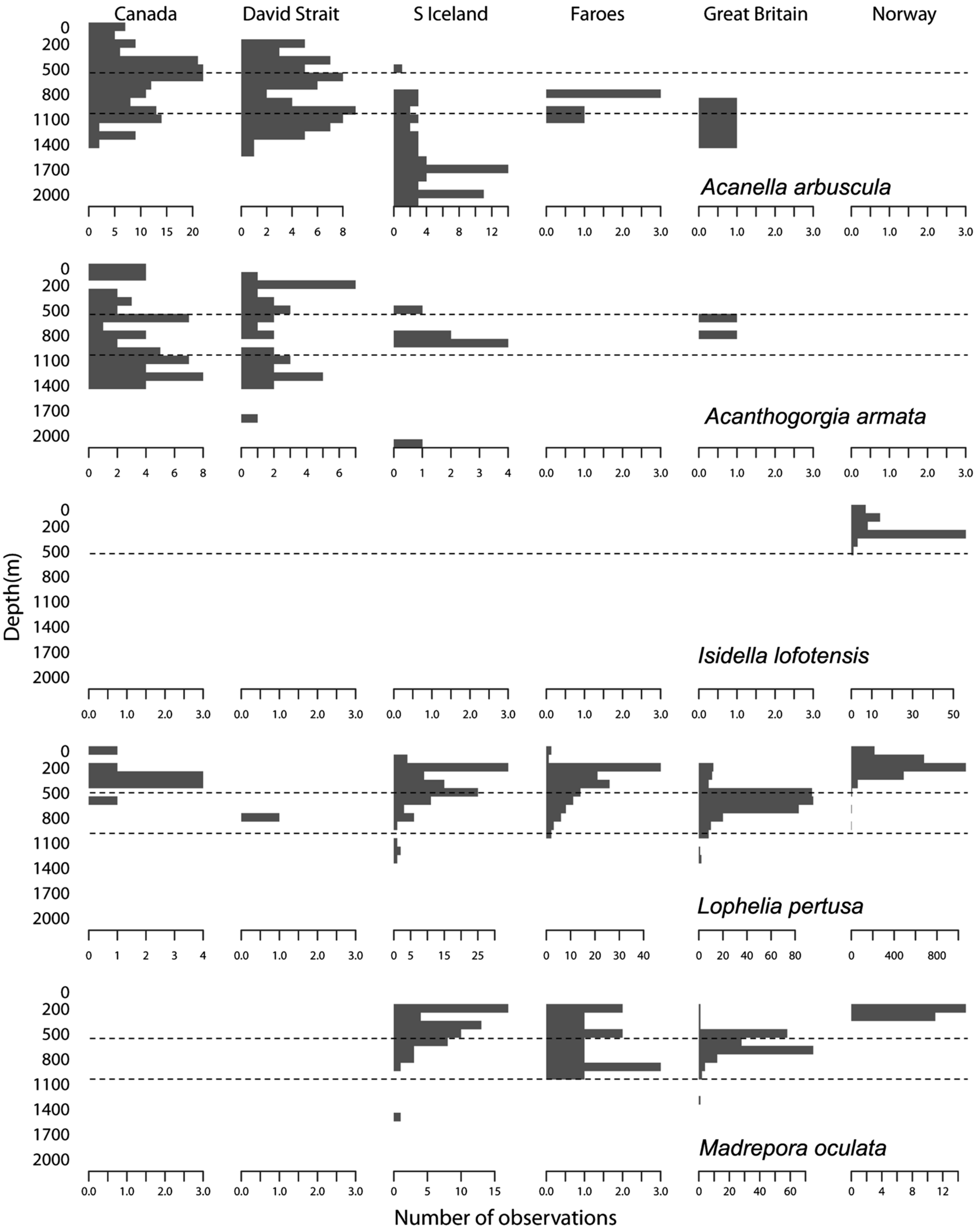

Fig. 5 Number of observations at different depths for the coral species studied divided by region (see Fig. 1B). *Dotted lines* indicate 500 and 1,000 m depth

P. placomus is found off the north-west coast, where the influence of the Irminger current (IC) results in high temperature (Kramp 1939). It was recorded from the same depth range in Iceland and Faroes 100–1,200 m, at 800–1,100 m in Davis Strait but shallower (100–500 m) in Norwegian waters (Fig. 5). Most data are from Norway where the main temperature range is 6–9°C (Fig. 4).

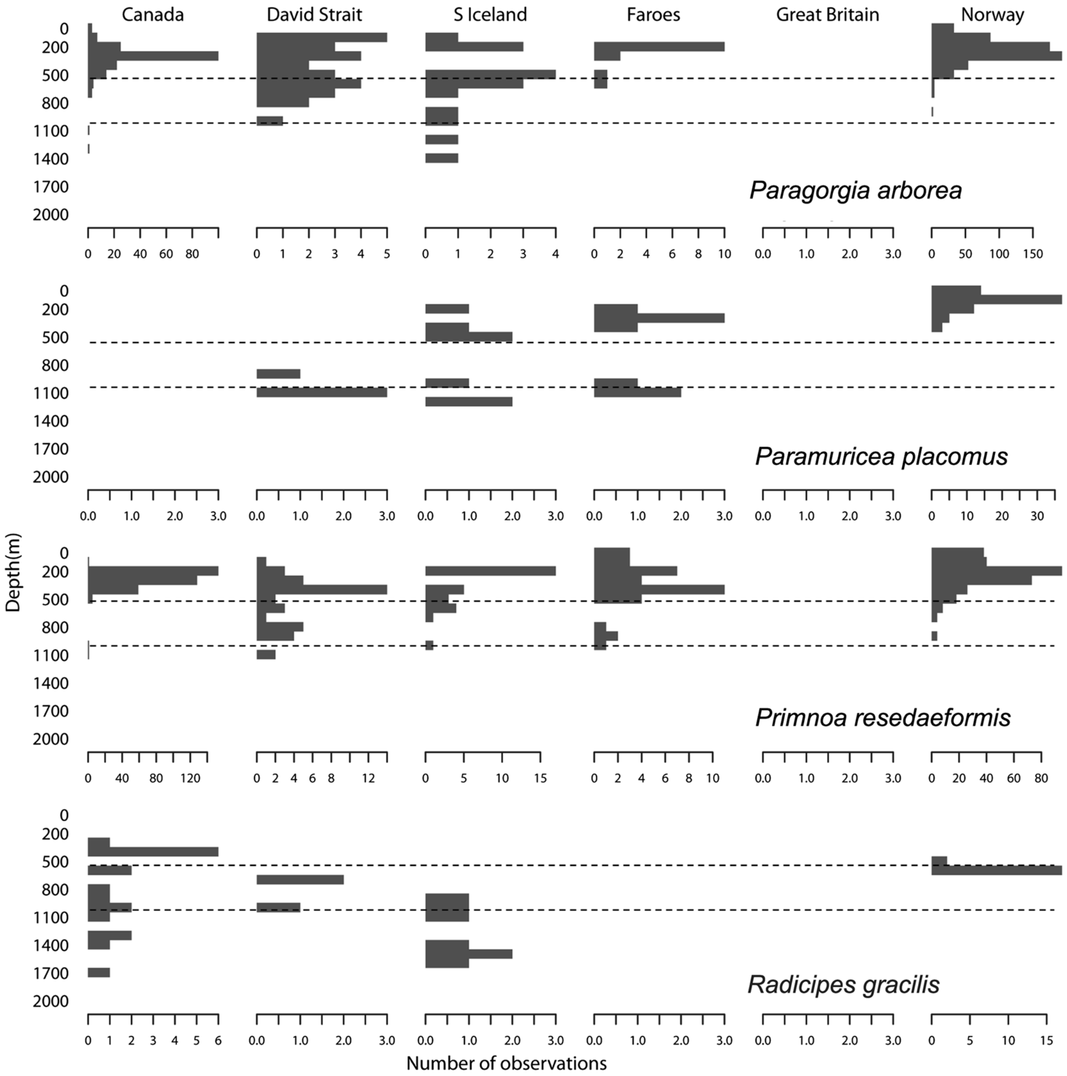

Fig. 5 continued

Species found in the whole North Atlantic including Norway: *P. arborea* and *P. resedaeformis*

Paragorgia arborea has an extensive distribution (Fig. 3F) both in the NW and NE Atlantic. It has been recorded off Canada, in Davis Strait and reaching into the Baffin Bay and on the west slope of Greenland, as well as south off Iceland and in Faroe waters (BIOFAR data) and along the Norwegian shelf and slope. In the older literature, it was concluded that this species was not recorded in Iceland and the Faroes (Jungersen, 1917; Kramp, 1939). Copley et al. (1996) found it at seven stations along the Mid-Atlantic Ridge south of Iceland. This species is mainly found above 600 m in all regions (Fig. 4). In Davis Strait and Canada, the depth range is 250–750 m (Gass & Willison, 2005; Mortensen et al., 2006; Jørgensen et al., 2013) and the depth range south of Iceland is 200–1,200 m (Copley et al., 1996, The Icelandic Benthos Database, 2007) (Fig. 5). *Paragorgia arborea* is recorded from a wide temperature range of 1–11°C (Fig. 4) in Norway and Atlantic Canada where most records were available and it is mainly found at 3–8°C.

Primnoa resedaeformis is one of the most often reported deep-water gorgonians according to Cairns &

Bayer (2005). It is known to be warm North Atlantic species from 150 to 900 m (Jungersen, 1917). It is in general much more common than *P. arborea* even though their general distribution patterns are almost identical (Fig. 3E). In NW Atlantic, it is mainly found along the continental slope of Canada, Labrador and west Greenland. South of Iceland, it is found along the Reykjanes Ridge and the south-east continental slope, along the Iceland–Faroe Ridge and the shelf and slope of the Faroes and the shelf of Norway.

Although known from Icelandic waters since 1915 (Jungersen, 1915; Kramp, 1939), only few specimens had been found prior to a recent habitat mapping off Iceland, which has shown this species to be common along the south continental slope and mainly associated with *L. pertusa*. It is known from the study area at depths of 95–1,020 m (Grasshoff & Zibrowius, 1983; Cairns & Bayer, 2005), but occurs mainly above 500 m (Figs. 4, 5). Like *P. arborea*, it is found within a wide temperature range of 1–11°C (Fig. 4), while it is mostly recorded at temperature between 5 and 7°C.

Species present in the whole North Atlantic but absent from the Norwegian shelf: *A. arbuscula* and *A. armata*

Acanella arbuscula is widely recorded around the North Atlantic in relatively deep waters (600–1,200 m). Its spatial distribution appears to be restricted by the cold water north of the GSR and north of Davis Strait (Fig. 3G). Madsen, (1944) considers it as very common in the North Atlantic between the equator and the submarine ridges connecting Scotland, Iceland and Greenland and predicted that it should occur in deeper parts of the entire Atlantic Ocean. His observations fit well with newer observations with the exception of the area north of the ridge dividing the Norwegian Sea from the deep basin of the North Atlantic, where there are no records. It is common off Nova Scotia and the western side off Greenland north to Davis Strait. It is also common south of Iceland and is found in Faroes and Irish waters but has not been observed on the Norwegian continental shelf and slope. In Nova Scotia and Newfoundland *A. arbuscula* occurs on the slope but in Iceland it seems to be more associated to the basin. This species seems to have two main depth ranges. In the NW Atlantic, it is recorded from rather shallow waters down to 1,400 m in Canada and Davis Strait (Gass & Willison, 2005). In the NE Atlantic, the Faroes and Great Britain regions, it is found between 800 and 1,400 m but south of Iceland, it is found at broader depth range (500 to >2,000 m), (Fig. 5). It is mainly found at temperatures between 2 and 6°C with occasional records from 1 to 3°C, however, in the Great Britain region, it is found at 8–10°C (Fig. 4).

Acanthogorgia armata is abundant in Atlantic Canada (Newfoundland, Flemish Cap and Labrador and as far north as to Davis Strait) (Madsen, 1944; Gass & Willison, 2005; Wareham & Edinger, 2007; Murillo et al., 2010; Baker et al., 2012) (Fig. 3H). It has recently been observed west of Greenland (Jørgensen et al., 2013). The species is found south and south-west of Iceland in the NE Atlantic and in Celtic waters (Stephens, 1909; Wienberg et al., 2008), but there are no records of this species in the Norwegian area or north of the GSR. It has a wide depth range from 100 to over 2,000 m (Fig. 4). Its depth range in Canada is 171–1,415 m (Wareham & Edinger, 2007), in the Davis Strait at depths between 484 and 1,445 m (Jørgensen et al., 2013) and south off Iceland at 557–2,137 m (Madsen, 1944; The Icelandic Benthos database, 2007) (Fig. 5). Its temperature range is from 1 to 12°C, however, most occurrences are within 3–4°C (Fig. 4).

Species with restricted distribution patterns within the North Atlantic: *I. lofotensis* and *R. gracilis*

Isidella lofotensis is found in Norwegian waters from Skagerrak to Lofoten (Madsen 1944) (Fig. 3C). Outside Norwegian waters, it has only been identified from underwater photographs taken at 365–775 m depth, on the upper slope east off Greenland at 75°N (Mayer & Piepenburg, 1996). According to Jungersen (1917), it is closely related to *Isidella elongata* from the Mediterranean Sea and the Bay of Biscay. Bathymetric distribution for Norway according to Madsen (1944) is 200–700 m (Figs. 4, 5). In East Greenland, the temperature where this species was found ranges from 0 to 1.3°C, which is markedly lower than in Norwegian waters where the mean temperature is 7.6°C (Fig. 4).

Radicipes gracilis is found on both sides of the North Atlantic but appears to be relatively uncommon (Fig. 3I). It is found south of Iceland, Davis Strait, Canada and was recently found in high concentrations on the Norwegian continental slope in the Barents Sea between Bear Island and the Norwegian mainland (MAREANO data). There is a gap in the distribution in the Faroes and the Great Britain regions where it seems to be absent. Off Canada, it occurs at 300–1,700 m depth, south of Iceland at 800–1,400 m, while the first record off Norway is from 700 m in the Barents Sea and in Davis Strait, it is recorded >700 m (Fig. 5). The temperature range is 0–7°C (Fig. 4). In Norway (the Barents Sea) and in Davis Strait, it is found between 1 and 5°C but in Canada it is found at 3–7°C. According to Madsen (1944), this species is belonging to the cold temperature boreal group and not found north of the ridges in the Davis strait, Denmark Strait and between Iceland and the Faroes and that it is mainly found at depths >1,000 m and at temperatures around 3°C (1.5–6.1°C).

Discussion

Cold-water corals in the north Atlantic have a wide geographic distribution (Madsen 1944). Recent coral mapping off Canada (Mortensen & Buhl-Mortensen, 2004; Mortensen et al., 2005; Mortensen & Buhl-Mortensen, 2005; Mortensen et al., 2006), Iceland (Copley et al., 1996, BIOICE; MRI unpublished data) and Norway (MAREANO) shows several examples of similarities in species composition between these waters, indicating strong connectivity. This is also the case for many of the species in this study and the most common species, *P. arborea* and *P. resedaeformis*, have an almost continuous occurrence from off George's Bank, Nova Scotia, Grand Banks, Davis Strait, southern Greenland, south of Iceland, Faroes, the coast of Norway. However, some species seem to have a northern distribution limit in the North Atlantic defined by large ridges such as the Davis Strait, Denmark Strait, the Iceland–Faroe Ridge and the Wyville Thomson Ridge. The differences in the spatial distribution patterns of the nine coral species reflect their response not only to changes in environmental variables (temperature, substratum, currents and food availability) along depth gradients but also the connectedness of suitable habitat for adults and larvae i.e. their possibility to colonise.

Topography and hydrography

This section describes the topography, near-bottom temperature and major current patterns of the North Atlantic (Fig. 6) in order to provide the necessary background to interpret coral distribution patterns.

The Arctic and Nordic Seas are separated from the North Atlantic Ocean by the GSR. The bathymetry is an important factor influencing the flow of water and the mixing of currents. This can be observed as the flow direction of currents often follows different bathymetry features like the continental slope, underwater canyons and ridges. The shallow David Strait and the GSR, along with the continental slopes, are important topographical features that have direct influence on current systems, especially deep water currents, and the separation and blending of water masses. As a result, these topographical features could influence the large-scale distribution of cold-water corals.

A cold water mass flows from the polar region into the Arctic and the Nordic Seas and enters the North Atlantic partly in the form of deep water currents or overflows. The cold polar water also flows south to the Baffin Sea where it meets the Labrador current (LC). The warm N Atlantic current (NAC) branches off the Gulf Stream, coming from the east coast of USA and Canada, and supplies the area with warm water (Figs. 6, 7).

In the NE Atlantic, the NAC splits west of Ireland and UK in the Rockall trough where a branch of it keeps onwards to Norway forming the Norwegian Atlantic current (NwAC), while the other branch that turns to west forms the IC that forms a branch that flows to the west coast of Iceland in north direction and subsequently passes the southern part of Greenland. The NwAC has a two-branched structure that appears throughout the Nordic Seas, with the Atlantic water confined to a 200–600 km wide wedge (Orvik & Niiler, 2002).

The cold East Greenland current (EGC) comes from north and meets the IC west of Iceland. The volume of this flow is regulated with the amount of the cold polar water coming from north. The EGC turns into West Greenland current (WGC) and this current goes into the Labrador Basin and then turns south to join the Gulf Stream again at the Grand Banks.

In the intermediate depths south of Iceland, the Labrador and Irminger Sea water from the west flowing over the Reykjanes Ridge and the overflow bottom water from the north enter the basin through the Faroe–Shetland and the Faroe Bank Channels and flow along the south continental slopes westwards,

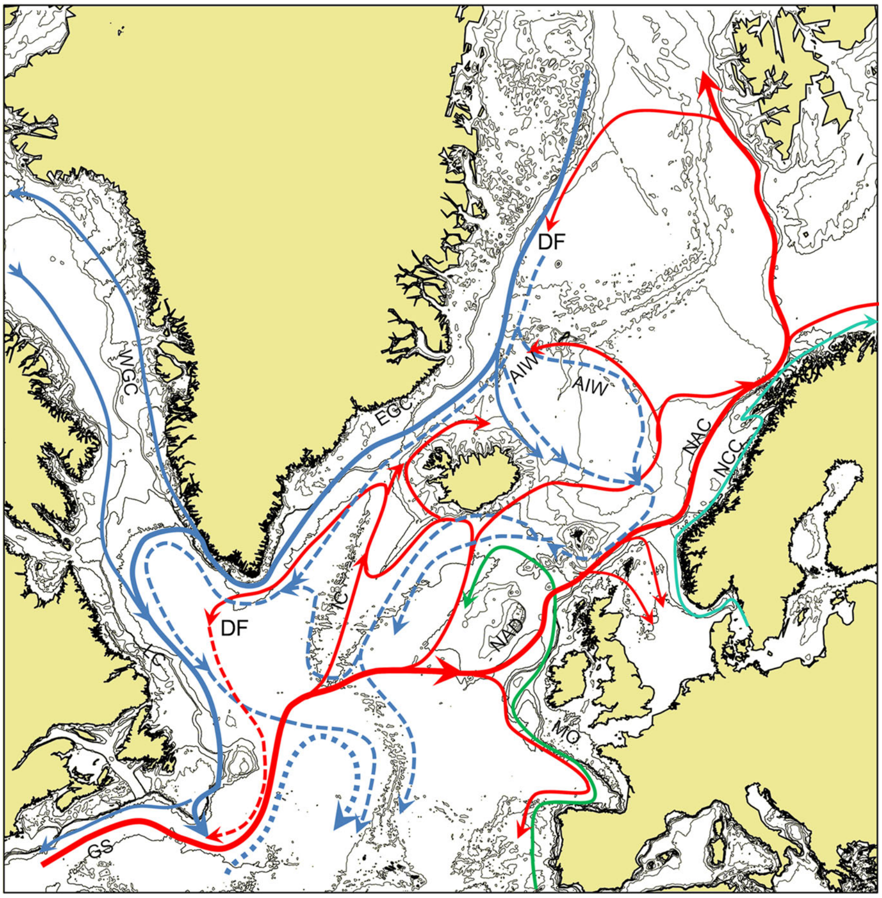

Fig. 6 General current patterns in the North Atlantic area relevant to this study. *Red lines* are warm surface currents, whereas *blue lines* are cold deep currents. *DF* deep-water formation, *AIW* Arctic intermediate water, *NAC* North Atlantic current, *NAD* North Atlantic drift, *IC* Irminger current, *NCC* Norwegian coastal current, *EGC* East Greenland current, *WGC* West Greenland current, *LC* Labrador Current, *GS* Gulf Stream, *MO* Mediterranean outflow

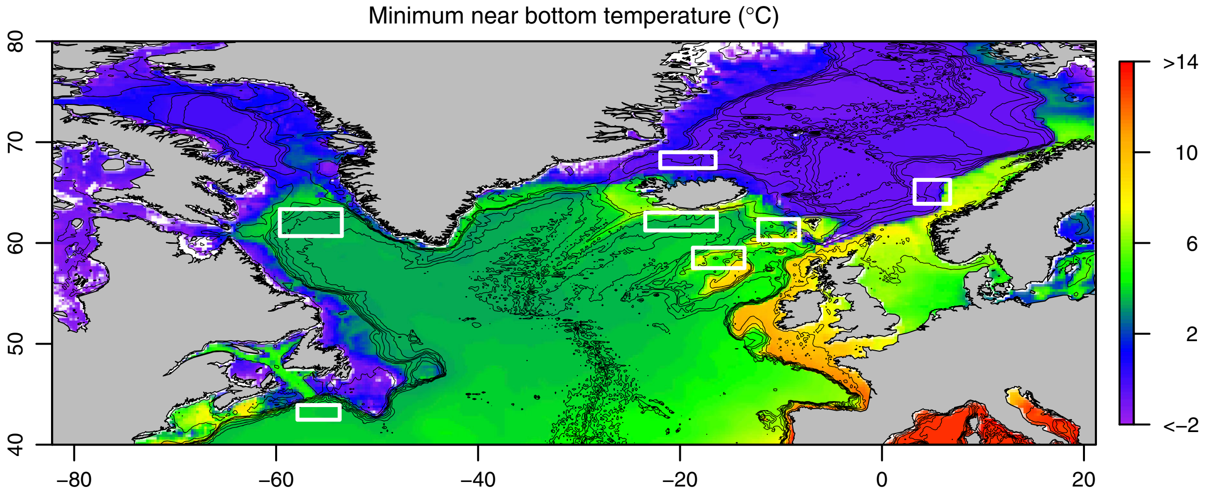

Fig. 7 Minimum near-bottom temperature (°C) in the cold temperate North Atlantic, based on data from the World Ocean Atlas 2013. Data for temperature by depth profiles (Fig. 5) were extracted for representative areas marked by *white boxes*. Depth contours every 500 m down to 2,000 m

then south along the Reykjanes Ridge and enter into the Irminger Sea (Malmberg, 2004).

The east and west Greenland sinking zones are important for the deep and cold water formations in the North Atlantic and for the global sea water circulation. Overflows crossing the Greenland–Scotland through the Denmark Strait and the Faroe–Shetland Channel have been shown to enter the Labrador Basin (Yashayaev & Dickson, 2008). The North East Atlantic, the Nordic seas and the Arctic Ocean are dominated by cold water below 500 m depth, which is the general sill depth of the GSR (Hansen & Østerhus, 2000; Hansen et al., 2001). The Faroe Bank channel has a sill depth of around 840 m, and the deepest part >600 m has an outward flowing water mass with a temperature <0.5°C (Hansen et al., 2001).

Depth, temperature and vertical zonation of the corals

Mortensen & Buhl-Mortensen (2004) suggests that upper temperature tolerance may restrict the upper bathymetric distribution range of cold-water corals, while at low temperatures and food supply may control the lower distribution.

The depth ranges of the different corals may differ between provinces, depending on the zonation of water masses with different temperatures (Figs. 7, 8). Roughly, the corals can be arranged in three groups with respect to water temperature: (1) Cold water, −1 to 3°C, (2) Intermediate water, 3–6°C and (3) Warm water 6–8°C. It is clear that these nine species can be split into two groups based on the depth ranges, six of them occurring at temperatures >5°C and depths <600 m while the rest occur at temperatures <5°C and at depths >600 m (Fig. 4).

Globally, *L. pertusa* occurs within a wide depth range (39–3,380 m). Regionally, however, it occurs in narrower, fairly well-defined depth zones parallel to the shelf break, or the rim of offshore banks and seamounts. It is most common at intermediate depths (200–1,000 m) in oceanic water (>35 S), with temperatures between 4 and 12°C (Teichert, 1958; Zibrowius, 1980; Frederiksen et al., 1992). *Lophelia* occurs in North Atlantic water which in some areas is mixed with Mediterranean Outflow Water, or Coastal Water (Teichert, 1958; Zibrowius, 1980; Frederiksen et al., 1992; Mortensen et al., 2001). South-west of the Faroe–Shetland Channel, where Atlantic Water is found down to ~1,000 m (van Aken, 2000), *Lophelia* is recorded down to the same depth (Chesher, 1987; Frederiksen et al., 1992). *Madrepora oculata* has frequently been recorded together with *Lophelia* in the North East Atlantic, but it is found in higher abundance in the Mediterranean Sea (Freiwald et al., 2009) as it seems to tolerate higher temperature (Wienberg et al., 2009).

Regional maximum depths of *Lophelia* in such offshore areas generally reflect different maximum depths of water masses with suitable temperatures (Frederiksen et al., 1992; Mortensen et al., 2001). Off the Norwegian coast, *Lophelia* reefs are most abundant at depths between 200 and 400 m, and in water with salinities >34 S, and temperatures between 4 and 8°C (Dons, 1944; Mortensen et al., 2001). The deepest occurrences of *Lophelia* on the continental slopes off mid-Norway (around 500 m) coincide with the shallowest occurrences of the boundary layer between the relatively warm NwAC and the cold Norwegian Sea Arctic Intermediate Water. The depth of this boundary layer varies due to the presence of internal tidal waves (Blindheim, 1990). The warm Atlantic Water is also found in the basin south of Iceland where *Lophelia* and *M. oculata* are found down to over 1,000 m (mostly dead samples, BIOICE data). The upper depth limit of *Lophelia* offshore does not seem to be controlled by temperature or salinity.

Paragorgia arborea and *P. resedaeformis* have very similar distribution patterns. Mortensen & Buhl-Mortensen (2004) found that the different bathymetric distribution patterns for these common gorgonians in the Northeast Channel (Nova Scotia) could be related to different maximum bottom temperatures. *Paragorgia arborea* was not observed in water with maximum temperatures >10°C, whereas *P. resedaeformis* was found shallower at depths with maximum temperatures up to 12°C. The shallower occurrence of *P. resedaeformis* compared with *P. arborea* has previously also been noted by Kramp (1932) and Madsen (1944).

Radicipes gracilis, *A. arbuscula* and *A. armata* are predominately found at lower temperatures than the the other species, around 3°C (1.5–6.1°C). Several of the species that are found on and south off the submarine ridges in the North Atlantic are also distributed in the warmer area of the Norwegian Sea (from Skagerrak to Lofoten). Amongst the species selected in our analyses, is *Paramuricea placomus*.

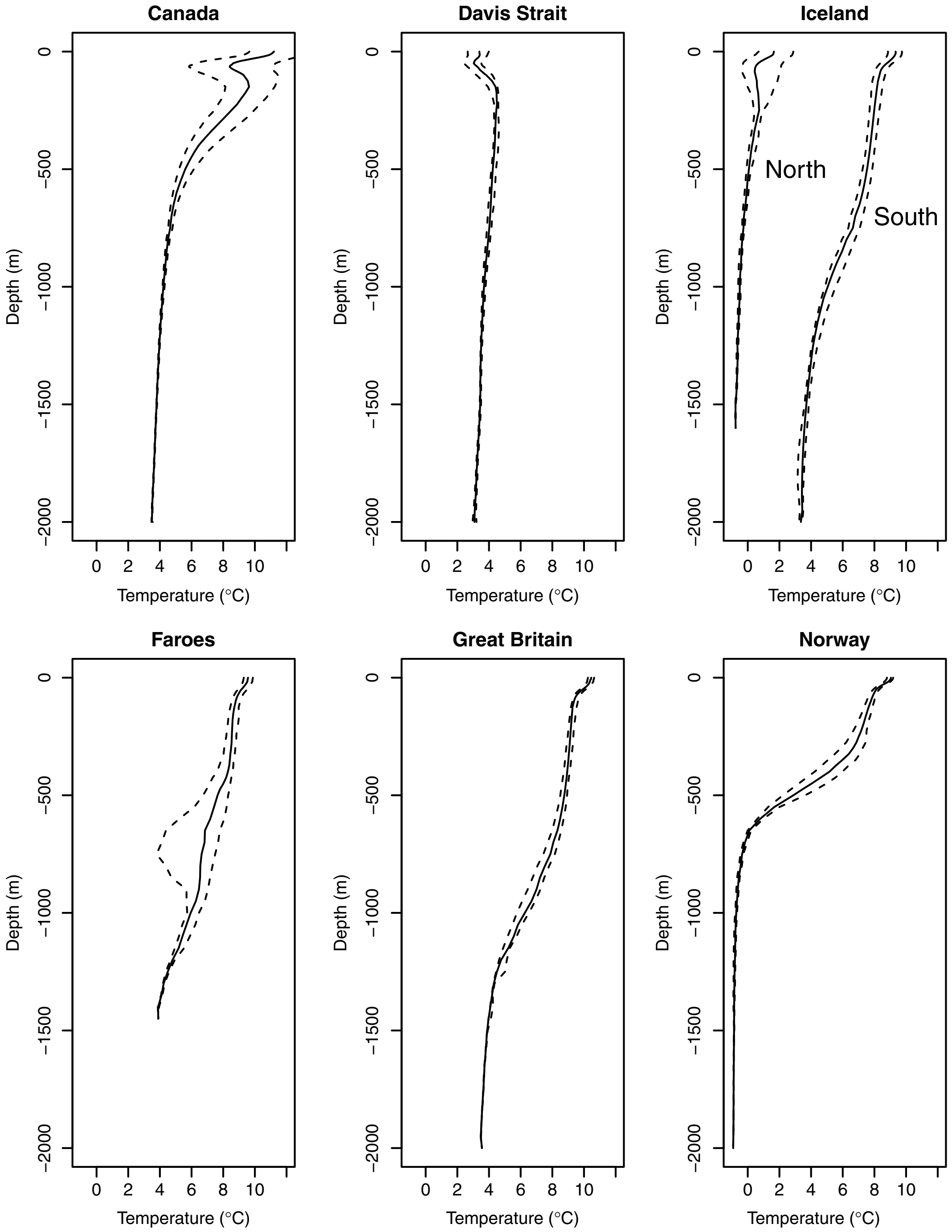

Fig. 8 Temperature at depth profiles for seven representative areas in the cold temperate North Atlantic, based on data from the World Ocean Atlas 2013. The lines show the 10th, 50th and 90th quantiles of the temperature records at each depth

This intermediate to warm water group occurs predominately at temperatures between 3 and 8°C and includes *Isidella lofotensis* (found only in Norway) and *Primnoa resedaeformis* and *Paragorgia arborea* at 5–8°C (these are also found in the boreal Pacific).

Biogeographic regions and groups

Three groups of corals could be identified based on similar distribution patterns: species recorded mainly in the east North Atlantic and off Norway: *L. pertusa, M. oculata* and *P. placomus*, species found in the whole North Atlantic including Norway: *P. arborea* and *P. resedaeformis* and species present in the whole North Atlantic but absent from the Norwegian shelf: *A. arbuscula* and *A. armata.* The gorgonian *I. lofotensis* is almost exclusively restricted to Norwegian fjords, with some few records from the Norwegian shelf.

The distribution of these species suggests that the border between the arctic and cold temperate Atlantic should be moved further north on both sides of Greenland (see Fig. 9). This is supported by the presence of six of the nine coral species studied in the Davis Strait of which all are lacking in the Arctic deep water of the Norwegian Sea and cannot sustain the low temperature of arctic waters.

For the deeper part of the study area, this border between the arctic and cold temperate Atlantic is similar to the division of lower bathyal (>800 m) provinces in the North Atlantic into Arctic and Northern Atlantic Boreal provinces by Watling et al. (2013). However, this area displays great bathymetrical variation and different environments and the larger parts of the cold temperate region should be divided into sub-regions as described below.

The southern limit of the cold temperate region suggested by Cairns & Chapman (2001) is in this study represented by the Great Britain region. Both the widely distributed gorgonians, *P. resedaeformis* and *P. arborea,* are lacking in this region. The presence of a rich fauna of gorgonian species off Ireland is well known and most of these species have not been collected during Nordic expeditions, one exception is *A. arbuscula* (Madsen, 1944). The explanation suggested by Madsen (1944) is that most of the species found off Ireland require temperatures above 8°C and their distribution in the eastern part of the Atlantic Ocean is limited by the 8°C isotherm at ~1,000 m depth.

Sub-regions in the cold temperate Atlantic

Cold-water corals are widely distributed in the cold temperate part of North Atlantic due to good connectivity between continental slope and shelf areas via currents below 200 m (Fig. 6), nevertheless, our results indicate that this region can be divided into sub-regions. Based on the depth, distribution and temperature tolerance of the studied species, we have identified four sub-regions that correspond well with the sub-regions that were described by Cairns and Chapman (2001) for the cold temperate part of North Atlantic based on the distribution of scleractinia (Fig. 9):

(1) Slope and basin of North Atlantic below 600 m (identified as cold temperate by Cairns and Chapman (2001)). Here, the three deep sea and stenotherm corals *A. arbuscula, A. armata* and *R. gracilis* have been widely recorded.

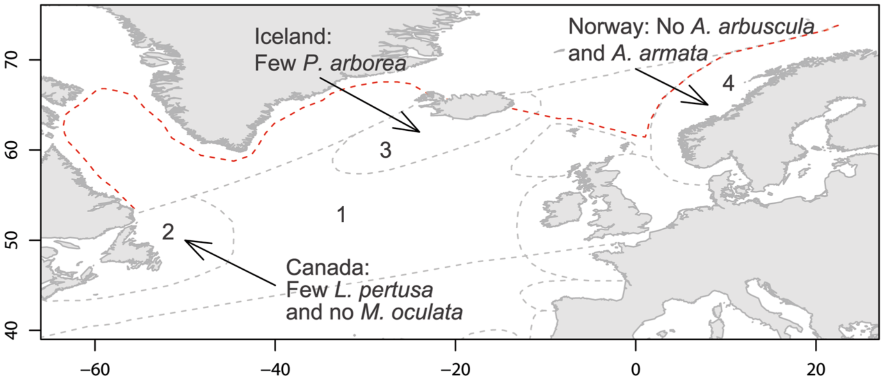

Fig. 9 Modified from Cairns & Chapman (2001). *Red dotted line* indicates the border between the arctic and cold temperate Atlantic below 200 m based on distribution of the nine cold-water corals (seven gorgonians and two scleractinian) included in this study. The four biogeographic regions supported by the distribution of the nine corals are indicated with numbers 1–4 referred to in the discussion section

(2) The Canadian and Newfoundland shelf and slope above 600 m with very few records of *L. pertusa,* no *M. oculata* and *I. lofotensis*, but many records of *P. resedaeformis, P. arborea, A. arbuscula, A. armata* and *R. gracilis*. This area is identified as CTC in Cairns and Chapman (2001).

(3) Iceland shelf and Reykjanes Ridge (identified as ICE in Cairns and Chapman (2001)) had many records of *L. pertusa,* and a rich coral fauna including *A. arbuscula, A. armata, M. oculata, P. resedaeformis,* and *R. gracilis*. Records of *P. arborea* were very few and no registrations were found for *I. lofotensis.*

(4) The Scandinavian Norwegian shelf and slope (identified as SCA in Cairns and Chapman, 2001) had uniquely high records of *L. pertusa* and many records of *P. resedaeformis* and *P. arborea* and some records of *I. lofotensis M. oculata, R. gracilis* but *A. arbuscula* and *A. armata* were not recorded.

Area 4 has a topographical barrier, the Greenland–Scotland, to the deep North Atlantic (area 1), while areas 2 and 3 are in open contact with area 1. The Greenland–Scotland topographical barrier presumably represents an environment with a temperature range, currents and substrates that restrict the transport of larvae of *A. arbuscula* and *A. armata* and do not allow their colonization of the Norwegian coast (area 4), which has otherwise a suitable habitat for these species. In contrast, the deep-sea soft-sediment species *R. gracilis* that presumably can tolerate lower temperatures than *A. arbuscula* and *A. armata* and occur deep in the North Atlantic basin has been recorded off Norway. We also find the presumably endemic species *I. lofotensis* within the study area.

It is also remarkable that *L. pertusa* is rare off Canada and *P. arborea* is rare off southern Iceland, since these areas had a rich coral fauna of species that are known to co-occur with them. This could be explained by availability of larvae that presumably are transported by the major current systems in the area. *L. pertusa* becomes increasingly more common going eastward across the Atlantic. The strong NAC, originated as the Gulf Stream coming from the east coast of USA, heading towards the East Atlantic could explain the connectivity of the eastern areas. There it feeds the warm waters to Great Britain, through the Faroe–Shetland Channel to Norway, to Iceland and some of it also reaches the southern tip of Greenland. The absence of *L. pertusa* from Canada and Davis Strait can thus be explained by the strong LC from north towards south that prevents the warm Gulf Stream to reach the continental margins, which prohibits further northward colonization of this coral species. This also suggests that other current systems than the NAC could explain the distribution pattern of other coral species, like the cold overflow from the Nordic Seas passing the Faroe–Shetland Channel at the seafloor, preventing the dispersal of *A. arbuscula* and *A. armata* to Norway.

Reproduction and dispersal barriers

It is mainly the corals occurring deeper than ca 1,000 m that are restricted by geographical barriers (Mortensen et al., 2006). Larva distribution and food supply are probably the most important factors controlling the distribution of cold-water corals. Food supply may vary locally depending on topography of the seabed (Mortensen et al., 2001), whereas larval transport is probably controlled by more broad-scale features such as ocean currents and broad-scale topographic structures (ridges and basins). Mortensen et al. (2006) conclude that the distribution of cold-water corals within broad-scale shelf intrusions, such as canyons and shelf troughs coincide with areas of out-flowing nutrient-rich and hydrographically stable shelf water.

Based on the limited available literature on reproduction and dispersal for cold-water corals, these appear to adopt several examples of different reproduction strategies and thus dispersal abilities. The deep-sea octocorals belonging to the genera *Primnoa* are ovo-viviparous, releasing fertilized eggs (larvae). This should have implications with regard to dispersal abilities. As an example, *L. pertusa* is a broadcast spawner with long larvae stage and dispersal range (Brooke & Järnegren, 2013; Larsson et al., 2014). *Madrepora oculata* is gonochoric spawner with periodic production or release and has inferred lecithotrophic larvae (Waller et al., 2005).

L. pertusa being very common on the Norwegian coast does not experience the GSR as a barrier. Presumably, the eastern branch of the NwAC feeds *Lophelia* larvae to the Norwegian continental shelf.

The two branches pass one at each side of the Faroes and have a common origin below the Irish–Scottish continental shelf at 53°N. *L. pertusa* has been frequently observed to colonise oil platform legs at 60–80 m indicating availability of larva at this depth. *L. pertusa* is gonochoric and inferred spawner with lecithotropic larvae (Waller et al., 2005). The larvae have been studied to be floating in the sea for 3–5 weeks whereafter they seek down to the bottom to settle (Larsson et al., 2014). The occurrence of isolated patches, such as those on the Swedish west coast suggests that its larvae can be dispersed planktonically over long distances, such as from the Shetland–Faroe channel to inner Skagerrak.

Acanella arbuscula It is found to produce lecithotrophic larvae and is believed to be a broadcast spawner (Beazley, 2011). This would allow the dispersal to be wide. Beazley (2011) suggests that the high reproductive success of this species could be due to the high mean polyp fecundity compared to other deep-water gorgonians. The distribution pattern of *A. arbuscula* indicates that its larva is not transported widely in upper water masses like *L. pertusa* and cannot colonise the Nordic Seas by the GSR and the Faroe Bank channel that has a sill depth of around 840 m but with the deepest part (>600 m) having an outward flowing cold (<0.5°C) water mass (Hansen et al., 2001).

Conclusions

- The currents connecting shallow (<500 m) and warm (>3°C) areas, on the North Atlantic continental shelves explain the wide distribution of many species.
- Species that are restricted to deeper (>800 m) waters in the Eastern and Western basin of the North Atlantic are absent from the Nordic Seas due to a combination of topographical barriers (the Greenland–Iceland–Scotland ridge) at ~500 m, and cold (<3°C) bottom water deeper than 500 m in the Faroe Bank Channel.
- The distribution of species that only can sustain temperatures >3°C and species that survive temperatures down to 1.5°C are affected differently by the topographic barriers in the North Atlantic.
- The observed distribution of cold-water corals in this study suggests that the border between the arctic and cold temperate Atlantic should be moved further north on both sides of Greenland.

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