



Distribution and biodiversity of cold-water corals in Icelandic waters at the boundaries of the N-Atlantic and the Arctic

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Abstract

This work presents a comprehensive compilation of cold-water coral records from within Iceland's exclusive economic zone (EEZ). The resulting database includes 2,710 records across two classes, Octocorallia (orders Malacalcyonacea and Scleractinia) and Hexacorallia (orders Scleractinia and Antipatharia). Data sources include records from the Danish Ingolf expedition (late 19th to early twentieth century), specimens held at the Natural Science Institute of Iceland (NSII), the BIOICE project (1991–2004), bycatch data from groundfish trawl surveys conducted by the Marine and Freshwater Research Institute (MFRI, 2015–2020), underwater images from MFRI's Benthic Habitat Mapping programme (2004–2021), and records from published literature. Cold-water corals are distributed widely within Icelandic waters, with a taxonomic diversity of 77 species across 27 families. Records were obtained at locations with mean temperature ranging from -1.0 to 9.0 °C and at depths of 15 to 2,710 m., with most observations recorded in waters deeper than 600 m. Three distinct species assemblages were identified: group A, consisting of a few species present both north and south of Iceland and including species predominantly located in the cold waters north of Iceland; group B and group C, comprising species found in the warmer waters south and west of Iceland. The Icelandic coral fauna displays mixed geographic affinities. Scleractinia show significant similarities to coral faunas of the Shetland, Faroe, Orkney, New Hebrides Islands and Rockall Bank, as well as to those of the western North Atlantic from Canada to the Gulf of Maine. The geographic affinity of octocorals aligns more closely with the boreal eastern Atlantic and northern Mid-Atlantic Ridge, as well as the western North Atlantic fauna from east off Canada to Cape Hatteras.

Keywords Cold-water corals · Sea pens · Hexacorallia · Octocorallia · Biogeography

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Introduction

Cold-water corals (CWCs) belong to a polyphyletic assemblage of several distantly related sessile cnidarians that generally live in deep (> 200 m), aphotic and cold marine waters. Cairns (2007) defines corals as “animals in the cnidarian classes Anthozoa and Hydrozoa that produces either calcium carbonate (aragonite or calcitic) secretions, resulting in a continuous skeleton or as numerous microscopic, individualised sclerites, or that have a black, horn-like, proteinaceous axis”. By this definition, the group includes over 5,500 species (WoRMS 2024).

Unlike tropical corals, cold-water corals are heterotrophic and lack symbiotic algae (zooxanthellae); they rely instead on food particles and zooplankton transported by surrounding water masses. Because they lack symbiotic algae, CWCs do not experience bleaching in response to stress as tropical corals do. Cold-water corals include species from the orders

Scleractinia (stony corals) and Antipatharia (black corals) within the class Hexacorallia, from various groups within the class Octocorallia (soft corals, gorgonians, and sea pens), and from the family Stylasteridae (hydrocorals) in the class Hydrozoa (Roberts et al. 2009). They are present in all of the world's oceans (Freiwald et al. 2021), with most species occurring at temperatures ranging between 4 to 12 °C and depths of 200 to 1000 m (Roberts et al. 2009; Balogh 2023). Their habitat includes fjords, continental slopes, canyons, deep shelves, the flanks of oceanic banks, seamounts and abyssal depths (Cordes et al. 2016; Yesson et al. 2012), and occasionally shallower waters of around 40 m (Mortensen and Fosså 2001). CWC aggregations form functional habitats characterized by structural complexity, high biodiversity, biomass, and metabolic activity, including coral reefs, mounds, coral gardens, and seapen field. (Buhl-Mortensen et al., 2015; Lockhart and Hocevar 2021; Maier et al. 2023).

In the North Atlantic, the scleractinian corals *Desmophyllum pertusum* (Linnaeus, 1758) (syn. *Lophelia pertusa*), *Solenosmilia variabilis* Duncan, 1873 and *Madrepora oculata* Linnaeus, 1758 form biogenic reefs. These are reported primarily along the continental slopes of Europe and North America, but also in sub-arctic waters near the Faroe Islands (Jensen and Frederiksen 1992), south of Greenland (Jørgensen et al. 2013), and south and west of Iceland (Ólafsdóttir et al. 2020). In Norway, CWC reefs are found north of the Arctic Circle (Järnegen and Kutti 2014). Various physical factors, including temperature, salinity, currents, substratum and topography, have been proposed as important in shaping CWC distribution, though their relative importance seems to vary between regions and taxonomic group (Mortensen et al. 2001, 2006; Burgos et al. 2020; Tong et al. 2023).

Cold-water corals habitats are vulnerable to human impacts including bottom trawling, fossil fuel extraction, seabed mining, and climate change (Althaus et al. 2009; Ramirez-Llodra et al. 2011; Ragnarsson et al. 2017). The reef-building and habitat-forming characteristics of CWCs contribute to their slow recovery, as they have slow growth rates, long life spans (Andrews et al. 2002; Roark et al. 2009), late age of maturity, and low or unpredictable recruitment (Lacharité and Metaxas 2013). As a result, most CWC habitats are classified as Vulnerable Marine Ecosystems (VMEs) under the criteria set by the Food and Agriculture Organization (FAO 2009) and are included in the OSPAR list of Threatened and/or Declining Species and Habitats (OSPAR 2015). Protection and conservation of these habitats is therefore essential (Cordes et al. 2016; Montseny et al. 2021), and enhancing our understanding of CWC species composition and distribution is crucial for designing effective conservation measurements (Baker et al. 2012; Gros et al. 2022).

The diversity of CWC fauna in Icelandic waters likely reflects the steep environmental gradients between the cold

Arctic seas to the north and the milder North Atlantic waters to the south. These contrasting environmental conditions influence the species distribution across major taxa and constitute a significant part of the biogeographic boundary between the Arctic and the southern Boreal regions (Ekman 1953; Spalding et al. 2007; UNESCO 2009; Costello et al. 2017). The earliest scientific records of CWC in Icelandic waters date back to the late nineteenth century, primarily from the Ingolf Expeditions (1895–1896), the surveys by the R/V Michael Sars (1900–1902), and the Thor expeditions (1903–04). In the 1990s, comprehensive sampling of benthic fauna during the BIOICE project (Guðmundsson et al. 2014; Steingrímsson et al. 2020) significantly increased knowledge of CWC taxonomy and distribution, which has been further expanded since 2004 through underwater video surveys for habitat mapping (Ólafsdóttir et al. 2020).

The objective of this paper is to compile a comprehensive review of the occurrence and distribution of CWCs in Icelandic waters, drawing on all available data sources. It focuses on four orders within the classes Octocorallia and Hexacorallia: Malacalcyonacea, Scleractinia, Antipatharia, and Scleractinia, and excludes the hydrozoan family Stylasteridae.

Materials and method

Study area

The records compiled for this study are limited to the Icelandic Economic Exclusive Zone (EEZ), which covers approximately 758,000 km², with water depths reaching 3000 m and near-bottom temperatures ranging from −1.0° to 8.9 °C.

Iceland is a volcanic island at the intersection of the Mid-Atlantic Ridge (MAR) and the Greenland-Iceland-Scotland Ridge (GISR). These submerged oceanic ridges create a complex system of near bottom currents with diverse hydrographic properties (Fig. 1) (Hansen and Østerhus 2000; Beaird et al. 2013). Water temperatures differ markedly on either side of the GISR, with average near-bottom water temperature of approximately 4 °C south of the GISR, while temperatures between 1° and −1 °C in the basins located north of the GISR (Jochumsen et al. 2016). The Iceland-Scotland Overflow Water (ISOW) and the Denmark Strait Overflow (DSO) are the main channels for water masses originating from the Arctic Ocean and the Nordic Seas into the North Atlantic (Lozier et al. 2022). These strong near-bottom currents flow over the GISR at its deepest points in the Denmark Strait (> 800 m), between Iceland and the Faroe Islands (> 500 m), and in the Faroe-Shetland Trough (> 1900 m) (Fig. 1). The warm, saline surface currents of the Irminger Current, a branch of the North Atlantic Current, influence shelf waters along Iceland's southern and

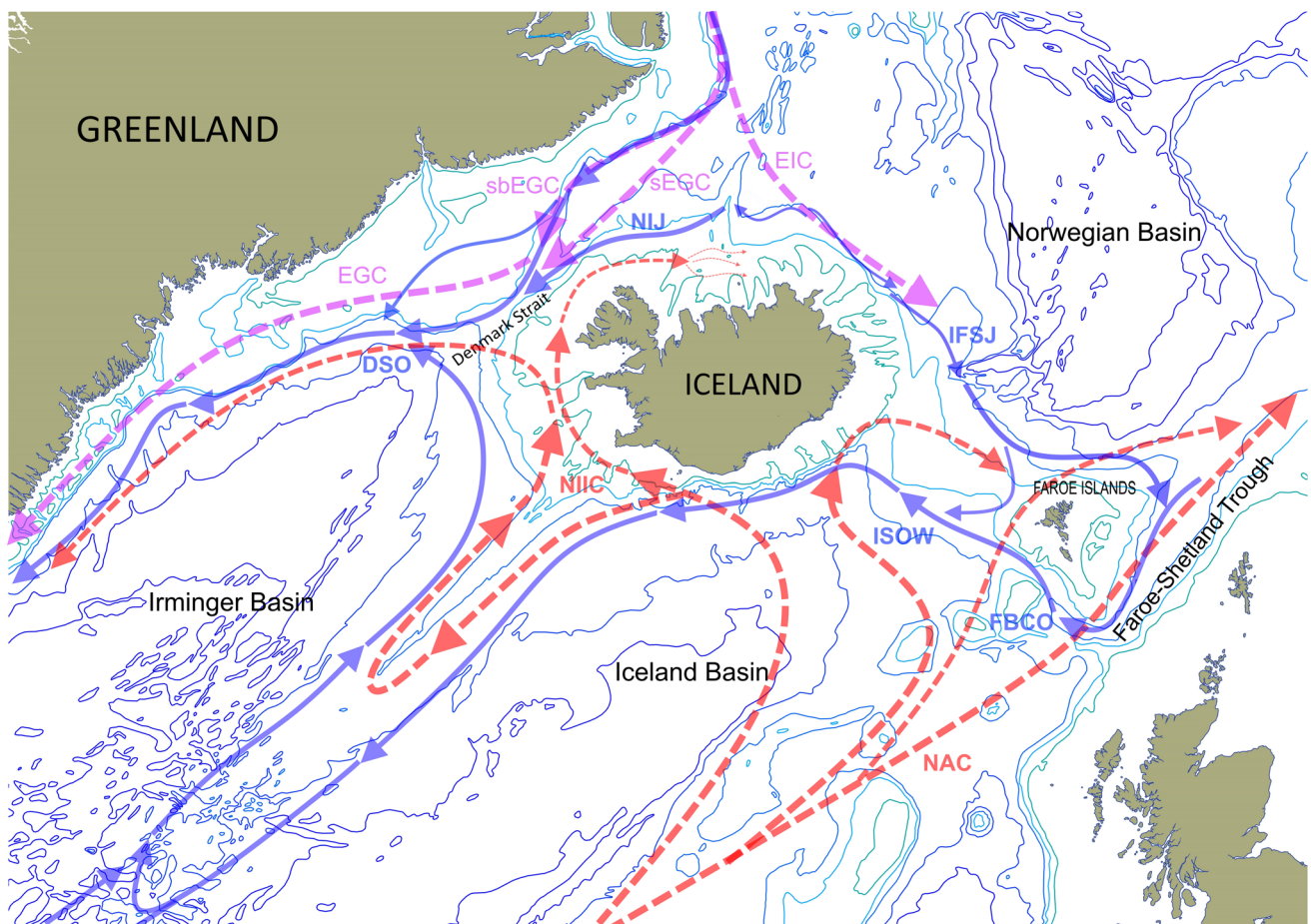


Fig. 1 Main currents around Iceland. The acronyms are: The Iceland-Scotland Overflow Water (ISOW), the Denmark Strait Overflow Water (DSO), East Greenland Current (EGC), North Icelandic Jet (NIJ), Shelfbreak East Greenland Current (sbEGC), Separated EGC

(sEGC), North Iceland Irminger Current (NIIC), East Icelandic Current (EIC), Iceland-Faroe Slope Jet (IFSJ) and Faroe-Bank Channel Overflow (FBCO)

western coasts (Chafik and Rossby 2019). The Irminger Current branches into the North Iceland Irminger Current (NIIC), carrying these waters through the Denmark Strait towards northwest and northern Iceland (Semper et al. 2022). In contrast, the northeastern and eastern shelves are influenced by surface currents of relatively cold waters from the East Icelandic Current (EIC) (Valdimarsson et al. 2012; Semper et al. 2020).

Data sources

Cold-water corals (CWCs) records within the Icelandic EEZ were obtained from multiple sources. Pioneer contributions include publications by H.F.E. Jungersen, who reported the first records of Pennatulida (Jungersen 1904), Scleractinia (Jungersen 1915, 1917), and *Anthomastus* (Jungersen 1927). Kramp (1939) and Calgren (1939) compiled new and existing records of Octocorallia and Madreporaria for the Zoology of Iceland report series,

while Madsen (1944) reported on Octocorallia collected during the Ingolf and Thor expeditions. Dons (1944) noted two coral reefs sites south off Iceland but did not specify exact locations. Zibrowius (1980) reported on coral specimens collected during cruises on board the FRV Anton Dorn in 1970 and the CSS Dawson in 1971. Copley et al. (1996) published records of Alcyonacea and Scleractinia from the Reykjanes Ridge, some of them within the Icelandic EEZ. More recently, Korfhage et al. (2022) identified Hexacorallia and Octocorallia in Icelandic waters using molecular methods.

The most extensive benthic sampling initiative in Icelandic waters since the Ingolf Expedition was the BIOICE project (Benthic Invertebrates of Icelandic waters), which aimed to document the biodiversity and distribution of benthic invertebrates within the Icelandic EEZ (Guðmundsson et al. 2014; Guðmundsson 2023). Between 1991 and 2004, a total of 1,031 zoological samples were obtained at 579 locations using four gear types: Agassiz trawl, Snell sledge, RP sledge,

and triangle dredge (Steingrímsson et al. 2020). Scleractinians from the BIOICE project were identified by Helmut Zibrowius (unpublished) and Octocorallia by Pablo Lopez-Gonzales, with results published by Sanmartín Payá (2004) and including recent adjustments of some groups. For this compilation, a coral species sampled at the same BIOICE station with different gear types are listed as a single record for that locality.

In 2004, local fishermen's knowledge of coral reef locations and extents was acquired through questionnaires (Steingrímsson and Einarsson 2004). Guided by this information, the Marine and Freshwater Research Institute (MFRI) began mapping coral reefs the same year. Since then most CWC data has been collected using underwater camera systems, including ROVs and towed camera platforms. Between 2004 and 2019, MFRI's Benthic Habitat Mapping programme conducted over nine surveys capturing CWC observations. Multiple observations of a coral species within a single video transect were considered as a single record, as this study focuses on mapping the presence of cold-water corals at broad scales. Findings from underwater imagery

have informed management actions to protect CWC habitats on Iceland's southern shelf and shelf break (Steingrímsson and Sólmundsson 2004; Ólafsdóttir and Burgos 2012).

Additional records were obtained as bycatch during MFRI's annual bottom trawl groundfish surveys (2015–2018), and flatfish surveys (Ólafsdóttir and Guðmundsson 2019; Thorlacius et al. 2024). Multiple specimens of the same species in a single trawl were considered as a single record. A small number of unpublished catalogue records were also obtained from the Natural Science Institute of Iceland (NSII). The distribution of all observations is shown in Fig. 2.

Nomenclatural updates follow recent revisions by Moore et al. (2017), Molodtsova (2013), and López-González and Drewery (2022), supplemented by personal consultations with Pablo López-González and Catherine S. McFadden regarding Umbellulidae, Clavulariidae, Tubiporidae and Sarcodictyonidae. Synonymies of coral species from previous publications were standardized against accepted names in the World Register of Marine Species (WoRMS, Horton et al. November 2022, McFadden et al. 2022).

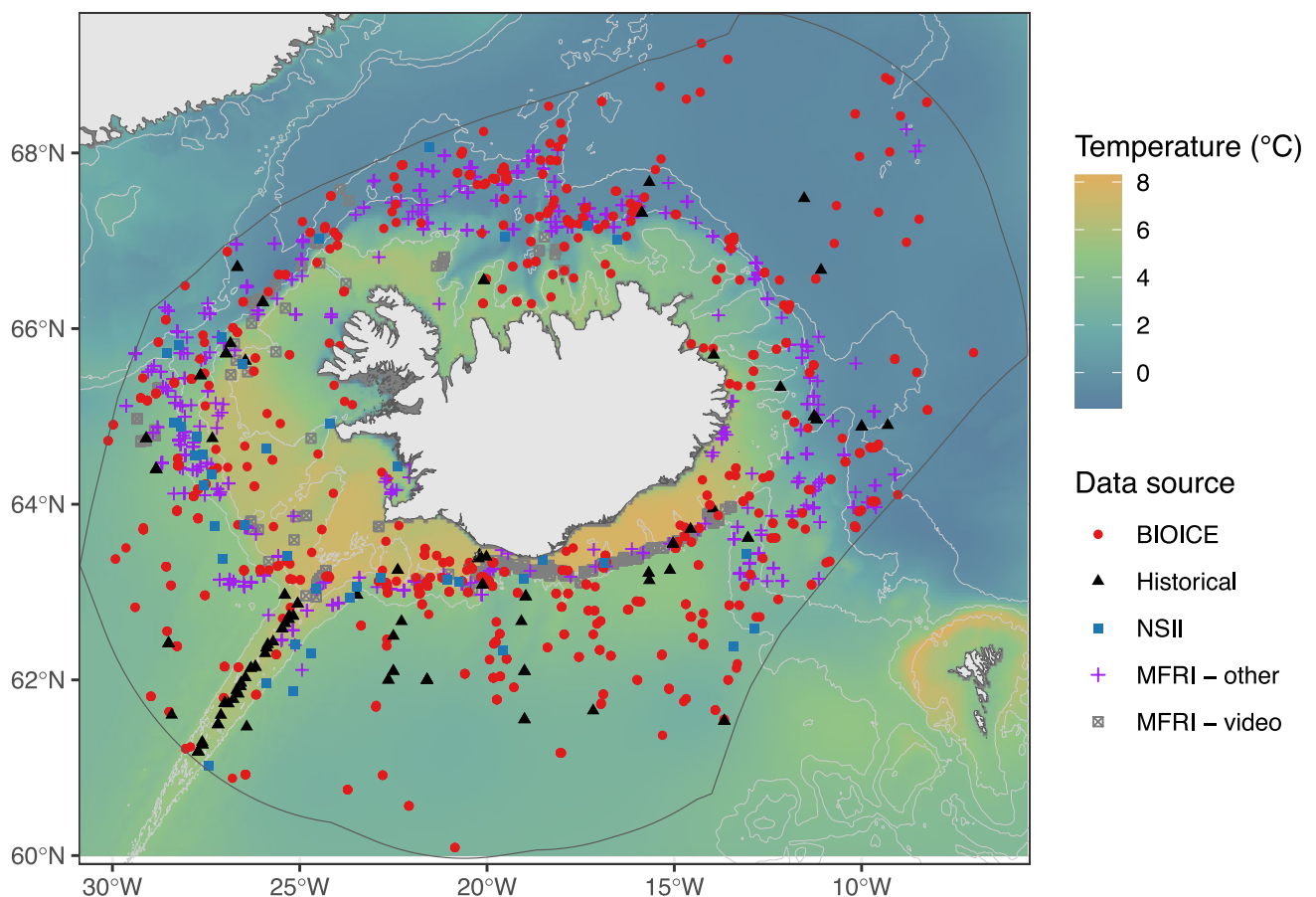


Fig. 2 Mean bottom temperature of the region around Iceland and locations of coral records included in this study. Data sources include the BIOICE project (BIOICE), records from historical sources including the Ingolf, Thor and Dana expeditions (Historical), obser-

ventions compiled by the Natural Science Institute of Iceland (NSII), and records obtained by the Marine and Freshwater research institute during underwater video (MFRI—video) and other surveys (MFRI – other)

The majority of the recorded occurrences include *in-situ* near-bottom water temperature measurements ($n = 1860$, 79.5%). Where these were unavailable, temperatures were estimated from nearby MFRI measurements. Where depth data was absent, depths were derived from a digital elevation model combining multibeam echosounder data, crowd-sourced bathymetry data, and data from GEBCO (GEBCO Bathymetric Compilation Group 2020). Depth and temperature ranges for each taxon were presented as two-dimensional boxplots showing median values, 25th and 75th percentiles, and minimum–maximum ranges.

Species assemblages and species richness

To delineate cold-water coral assemblages, we compiled species occurrence data into a regular hexagonal grid with 50 km² cells. This spatial aggregation was necessary because most samples in our database were collected with gears having small footprints, resulting low species counts per individual sample. Taxa not recorded in a cell were considered absent, though this absence cannot be confirmed given the mismatch between sample scale and cell area. The number of taxa per samples per cell was used to map broad patterns of species richness. We identified species assemblages through hierarchical clustering of taxa per each cell using Ward's minimum distance, utilizing the R packages Cluster (Maechler et al. 2022) and Factoextra (Kassambara and Mundt 2020). To reduce statistical bias, taxa with fewer than ten occurrences were removed from the analysis, leading to the identification of assemblages based on a total of 56 taxa.

Results

The current inventory of cold-water corals in Icelandic waters includes 2,710 records, comprising 1,141 records of Malacalcyonacea, 1,099 records of Scleralcyonacea, 457 records of Scleractinia, and 13 records of Antipatharia (Table 1).

Most records ($n = 1,060$, 39%) originated from the BIOICE project, where corals were observed at 197 stations, accounting for 34% of all sampled BIOICE stations. Bycatch from the MFRI groundfish surveys contributed 752 records (28%). Records from underwater images or videos totalled 620 (23%), while compiled records from published sources amounted to 218 (8%). Additionally, there were 60 (2%) records of museum specimens in NSII.

Taxonomic richness

A total of 77 taxa were identified to the species level. Scleralcyonacea accounted for the highest number of species,

totalling 31 (40%), across 14 families with three additional species yet to be fully identified. Malacalcyonacea accounted for 23 species (30%) from 7 families. Scleractinia comprised 19 species, with one identified to genus level (25%), spanning 5 families. Antipatharia included three species (one species and two identified only at the genus level) in a single family (5%).

The five most frequently recorded species were *Umbellula encrinus* (Linnaeus, 1758) with 181 records, *Gersemia fruticosa* (Sars, 1860) with 152 records, *Drifa glomerata* (Verrill, 1869) with 151 records, *Duva florida* (Rathke, 1806) with 148 records, and *Desmophyllum pertusum* (Linnaeus, 1758) with 125 records (Table 1).

CLASS OCTOCORALLIA.

Order Malacalcyonacea

This order encompasses twenty-three species across seven families.

Family Acanthogorgiidae

Genera: *Acanthogorgia* (1 species), *Muriceides* (2 species), *Paramuricea* (2 species), *Placogorgia* (1 species).

Six species from four genera belong to the family Acanthogorgiidae (Table 1, Fig. 3A and B). These species occur in a depth range of 83–1957 m, mostly located south of the Greenland-Iceland-Faroes Ridge (GIFR). Few specimens belonging to *Paramuricea* (remain to be identified further) are found north of Iceland. Identification from images is difficult to lower level than family though with good image quality it is possible to go further in some cases.

Family Alcyoniidae

Genera: *Alcyonium* (1 species), *Anthothela* (1 species), *Gersemia* (2 species), *Lateothela* (1 species).

Five species from four genera belong to the family Alcyoniidae (Table 1, Figs. 3C and 4A). These species have a wide range of depth, with three of them reaching 2000 m, and including the shallow water species *Alcyonium digitatum*. These species are both in the warmer and colder waters.

Family Capnellidae

Genera: *Drifa* (1 species), *Duva* (2 species), *Pseudodrifa* (2 species).

Four species belonging to three genera are included in the family Capnellidae (Table 1, Fig. 4B and C). These species are distributed around Iceland at depth range of 65–1700 m. The species of *Pseudodrifa* are primarily concentrated on the ridge systems between Greenland and Iceland as well as between Iceland and the Faroes Islands.

Family Ceratocaulidae

Genus: *Ceratocaulon* (1 species).

Ceratocaulidae is a monotypic family recently established by López-González et al. (2024).

Table 1 List of cold-water coral records from published source, the BIOICE project, various records in the NSII database, bycatch records from stock assessment survey and records from images and video captured by underwater cameras. Depth and temperature range and registration of the taxa within biogeographic zones

Taxa	Published data	BIOICE	NSII	MFRI by-catch	Image Video	Total no. of Records	Depth range (m)	Temp. Range (°C)	Recorded in the biogeographic zones in Watling et al 2011 and Cairns and Chapman 2001
OCTOCORALLIA									
ORDER MALACALYCONACEA									
Acanthogorgiidae Gray, 1859									
<i>Acanthogorgia armata</i> Verrill, 1878	4	5		7	9	25	290–1308	3.3–7.7	IIA, IIC, IIIA
<i>Muriceides kuekenhali</i> (Broch, 1912)		3				3	271–976	4.7–7.3	IIB
<i>Muriceides sceptrum</i> (Studer, 1891)	1					1	540	4.8	IIIA
<i>Muriceides</i> sp(p)	3					3	595	5.9	
<i>Paramuricea biscaya</i> Grasshoff, 1977		4				4	1087–1957	2.5–4.5	IIC, IIIA
<i>Paramuricea placomus</i> (Linnaeus, 1758)	10		2			12	200–1294	0.1–7.7	IIA, IIB, IA, IIIA
<i>Paramuricea</i> sp(p)		7		3	21	31	119–1296	4.2–7.8	
<i>Placogorgia graciosa</i> (Tixier-Durivault & d'Hondt, 1974)		2				2	689–983	3.3–4.7	IIIA
Acanthogorgiidae									
		18			66	84	83–1808	–5.7–8.9	
Alcyoniidae Lamouroux, 1812									
<i>Alcyonium digitatum</i> Linnaeus, 1758	11	2		12	1	26	15–80	7–8.7	IIA, IIB
<i>Anothothela grandiflora</i> (Sars, 1856)	3	3				6	240–2515	3.1–8.1	IIA, IIB, IIC, IIIA
<i>Gesernia</i> sp(p)	3			2	36	41	489–638	–0.3	
<i>Gesernia fruticosa</i> (Sars, 1860)	7	62		83		152	80–2003	–0.9–6.2	
<i>Gesernia rubiformis</i> (Ehrenberg, 1834)	7	37		39	1	84	45–1957	–0.5–9.0	IIA, IIB
<i>Lateothela grandiflora</i> (Tixier-Durivault & d'Hondt, 1974)	1					1	510	7.7	
Anthothelidae									
				4	21	25	216–906	4–6	
Capnellidae McFadden, van Ofwegen & Quattrini, 2022									
<i>Drifa glomerata</i> (Verrill, 1869)	14	58	5	55	19	151	65–1693	–0.3–8.9	IIA, IIB
<i>Duva florida</i> (Rathke, 1806)	9	58		71	10	148	80–1335	–0.8–8.4	IIA, IIB, IIIA
<i>Duva multiflora</i> (Verrill 1879)			6			6	117–197		
<i>Pseudodrifia groenlandica</i> (Molander, 1915)		2		47		49	170–1137	–0.5–6.7	
<i>Pseudodrifia raemosa</i> (Studer, 1891)		14	7			21	179–1673	–0.5–7.2	
<i>Pseudodrifia</i> sp.				17	3	20	295–939	–0.3–6.9	
Former Nephthelidae group	3			18	53	74			
Ceratocaulidae López-González, San Martín-Payá & Williams, 2024									
<i>Ceratocaulon wandeli</i> Jungersen, 1892	5	45		33	3	86	260–1223	–0.9–3.9	IIIA
Clavulariidae Hickson, 1894									
<i>Clavularia alba</i> (Grieg, 1888)	2					2	552–1484	–0.5–3.5	IIA, IIB

Table 1 (continued)

Taxa	Published data	BIOICE	NSII	MFR by-catch	Image Video	Total no. of Records	Depth range (m)	Temp. Range (°C)	Recorded in the biogeographic zones in Watling et al 2011 and Cairns and Chapman 2001
4 <i>Clavularia arctica</i> (Sars, 1860)	1	39				40	87–2051	−0.1–6.7	IIB, IIIA
<i>Clavularia borealis</i> Koren & Daniels-sen, 1883	1					1	847	5.5	IIB, IIIA
<i>Clavularia griegii</i> Madsen, 1944	1	2				3	913–1570	3.4–6.1	IIB
<i>Clavularia</i> sp(p)		11	1		10	22	130–1884	−0.5–7.2	
Plexauridae Gray, 1859									
<i>Swiftia borealis</i> (Kramp, 1930)	8					8	83–1630	2.9–6.6	IIB
Tubiporidae Ehrenberg, 1828									
<i>Scyphopodium ingolfi</i> (Madsen, 1944)		10				10	639–1809	2.6–6	IA, IIIA
ORDER SCLERACYONACEA									
Chrysogorgiidae									
<i>Chrysogorgia agassizii</i> (Verrill, 1883)	2	4	1			7	1057–2192	2.7–4.8	IIA, IIIA
<i>Chrysogorgia</i> sp.		3				3	1308–2083	2.8–3.8	
<i>Chrysogorgiidae</i>					1	1	1277–1340	4	
<i>Radicipes gracilis</i> (Verrill, 1884)	4	4				8	955–1717	2.7–4.8	IIA, IA, IIIA
<i>Radicipes</i> sp.				1	1	2	1206–1277	4–5.6	
Coralliidae Lamouroux, 1812									
<i>Anthomastinae</i> Verrill, 1922	5	4		7	7	23	450–2051	2–7.9	
<i>Anthomastus grandiflorus</i> Verrill, 1878		1	2	1		4	613–2399	2.1–6.6	IIA, IIB, IIC, IA, IIIA
<i>Anthomastus purpureus</i> (Koren & Daniels-sen, 1883)		31	3			34	570–2400	2.1–8	
<i>Heteropolypus</i> cf. <i>sol</i> Molodtsova, 2013	1	12		17		30	203–2709	2.3–7.9	
<i>Pseudoanthomastus</i> sp. Tixier-Durivault & d'Hondt, 1974	3	10		7	4	24	408–1717	2.4–7.6	
<i>Paragorgia arborea</i> (Linnaeus, 1758)	4		3	2	4	13	180–1740	1.3–6.8	IIA, IIB, IIIA
Keratoisidae									
<i>Acanella arbuscula</i> (Johnson, 1862)	12	28		25	15	80	237–2192	−0.6–8.1	IIA, IIB, IIC, IIIA
<i>Keratoisididae</i>			1	2	2	5	440–1036	−0.3–6.8	
Primnoidae									
<i>Primnoa resedaeformis</i> (Gunnerus, 1763)	5	1			16	22	180–600	4.7–7.8	IIA, IIB
<i>Convexella jungersenii</i> (Madsen, 1944)		1				1	2177	3.1	
<i>Primnoidae</i> sp. 1					1	1	350		
<i>Primnoidae</i> sp. 2					2	2	574–650		

Table 1 (continued)

Taxa	Published data	BIOICE	NSII	MFR by-catch	Image Video	Total no. of Records	Depth range (m)	Temp. Range (°C)	Recorded in the biogeographic zones in Watling et al 2011 and Cairns and Chapman 2001
Superfamily Pennatuloidea McFadden, van Ofwegen & Quattrini, 2022									
Anthoptilidae Kölliker, 1880									
<i>Anthoptilum grandiflorum</i> (Verrill, 1879)			1	6	2	9	250–1293	3.8–7.5	
<i>Anthoptilum murrayi</i> Kölliker, 1880	4	36		7		47	293–2085	2.3–8	
<i>Anthoptilum</i> sp.					5	5	262–291	6.7–7.6	
Balticinidae Balss, 1910									
<i>Balticina christii</i> (Koren & Danielssen, 1848)			1		1	2	570–703	−0.6–7.3	
<i>Balticina finnarchica</i> (Sars, 1851)	1		1	1		3	658–1789	−0.1–6.5	
<i>Balticina</i> sp(p)		9	1		26	36	165–2085	−0.7–7.8	
Funiculinidae Gray, 1870									
<i>Funiculina quadrangularis</i> (Pallas, 1766)		13		29	2	44	292–2269	0.8–7.7	
Kophobelemnidae Gray, 1860									
<i>Kophobelemn stelliferum</i> (Müller, 1776)	3	15	3			21	264–2350	−0.8–7.8	
<i>Kophobelemn</i> sp.		42		7	61	110	37–2400	−0.9–7.8	
Pennatulidae Ehrenberg, 1834									
<i>Pennatula aculeata</i> Danielssen, 1860	4	12			3	19	125–2709	2.5–7.3	
<i>Pennatula phosphorea</i> Linnaeus, 1758	3			1	1	5	109–770	5.6–7.8	
<i>Pennatula phosphorea</i> var. <i>candida</i> Marshall & Fowler, 1888	2					2	94–120	6.7	
<i>Pennatula</i> sp(p)		9		8	24	41	133–2400	2.1–7.9	
<i>Ptilella grandis</i> (Ehrenberg, 1834)		8	3	7	18	36	193–1677	2.6–7.8	
Protoptilidae Kölliker, 1872									
<i>Distichoptilum gracile</i> Verrill 1882	1	9				10	126–2345	2–3.3	
<i>Protoptilum carpenteri</i> Kölliker, 1872	1					1	1591	3.3	
<i>Protoptilum thomsoni</i> Kölliker, 1872		1				1	1083	4.8	
Pseudumbellulidae López-González in López-González & Drewery 2022									
<i>Pseudumbellula scotiae</i> López-González & Drewery, 2022		3		4		7	300–1840	3.2–7.2	
Umbellulidae Kölliker, 1880									
<i>Umbellula encrinus</i> Linnaeus, 1758	2	29	2	142	6	181	166–2083	−0.9–7.3	
<i>Umbellula</i> sp. 1				3		3	677–935	4.5–6.2	
<i>Umbellula</i> sp. Unid				8	2	10	247–1331	−0.4–7.3	
Virgulariidae Verrill, 1868									
<i>Glaciaptilum steenstrupii</i> Kölliker, 1870	1	23		1		25	141–995	−0.6–4.5	

Table 1 (continued)

Taxa	Published data	BIOICE	NSII	MFR by-catch	Image Video	Total no. of Records	Depth range (m)	Temp. Range (°C)	Recorded in the biogeographic zones in Watling et al 2011 and Cairns and Chapman 2001
<i>Stylatura elegans</i> (Danielssen, 1860)	2	11				13	124–960	5.5–7.2	
<i>Virgularia mirabilis</i> (Müller, 1776)	11	40				51	90–1122	–0.6–7.7	
<i>Virgularia tuberculata</i> Marshall, 1883	3	20				23	124–1018	–0.8–7.9	
<i>Virgularia</i> sp(p)		43		2	4	49	121–1809	–0.6–7.7	
Virgulariidae				11	41	52	140–1005	–1.1–7.6	
Sarcodictyonidae McFadden, van Ofwegen & Quattrini, 2024									
<i>Telestula septentrionalis</i> Madsen, 1944	4	29				33	166–2177	2.5–6.4	IIA, IIB, IIIA
HEXACORALLIA									
ORDER ANTIPATHARIA									
Schizopathidae									
<i>Bathypathes</i> sp.		2		2	1	5	630–1286	5.5–7.3	
<i>Parantipathes</i> sp.					1	1	1087		
<i>Stauropathes arctica</i> (Lütken, 1871)		2		4	1	7	838–1407	3.7–5.5	
ORDER SCLERACTINIA									
Caryophylliidae									
<i>Caryophyllia</i> (<i>Caryophyllia</i>) <i>ambrosia</i> Alcock, 1898		6				6	1568–1950	3.0–3.6	IIA, IIB, SHE, IIIA
<i>Caryophyllia</i> (<i>Caryophyllia</i>) <i>atlantica</i> (Duncan, 1873)		6				6	845–1188	3.7–5.5	SHE, IIB, IIIA
<i>Caryophyllia</i> (<i>Caryophyllia</i>) <i>sarsiae</i> Zibrowius, 1974		1				1	1398	3.9	BER, IIB, MED, IIIA
<i>Caryophyllia</i> (<i>Caryophyllia</i>) <i>smithii</i> Stokes & Broderip, 1828						1			SHE, IIB, IIIA, IIIB, IIID
<i>Caryophyllia</i> (<i>Caryophyllia</i>) <i>seguenzae</i> Duncan, 1873		1				1	895–914	5.5	SHE, IIIA, IIIC, IIID
<i>Caryophyllia</i> sp(p)		1		1		3	233–1539	3.2–8.1	
Caryophyllidae					7	7	290–580		
<i>Desmophyllum dianthus</i> (Esper, 1794)	1	14	1	2	4	22	267–2071	2.7–7.8	BER, IA, IB, IC, IIA, IIB, IIIA, IIIB, IIID
<i>Desmophyllum pertusum</i> (Linnaeus, 1758)	15	23	11	22	54	125	115–1360	1.9–7.9	IA, IB, IC, IIA, IIB, IIIA, IIIB, IIIC, IIID
<i>Premocyathus cornuformis</i> (Pourtales, 1868)		21				21	851–2006	2.4–5.2	BER, IA, IB, IC, ID, IIA, IIB, IIIA
<i>Solenosmilia variabilis</i> Duncan, 1873	2	5	1	3	6	17	547–1678	3.4–6.3	BER, IA, IB, IC, ID, IIB, IIIA, IIIB

Table 1 (continued)

Taxa	Published data	BIOICE	NSII	MFR by-catch	Image Video	Total no. of Records	Depth range (m)	Temp. Range (°C)	Recorded in the biogeographic zones in Watling et al 2011 and Cairns and Chapman 2001
<i>Stephanocyathus (Stephanocyathus) moseleyanus</i> (Sclater, 1886)		5		15		20	317–952	5.2–7	SHE, IIB, IIIA, IIID
<i>Stephanocyathus (Odontocyathus) nobilis</i> (Moseley in Thompson, 1873)		4		3		7	905–1678	3.6–4.1	SHE, IIB, IIIA, IIIB, IIIC
<i>Stephanocyathus</i> sp.		3				3	913–1829	3.2–5.7	
<i>Vaughanella</i> sp.	1	25				26	815–1710	2.5–5.5	
Dendrophylliidae									
<i>Leptopsammia britannica</i> (Duncan, 1870)	16	8				24	114–858	5.4–7.5	SHE
Flabellidae									
<i>Flabellum (Ulocyathus) alabastrum</i> Moseley in Thompson, 1873		18	1	2		21	593–1829	−0.5–6.3	IA, IIA, SHE, IIIA, IIIB, IIIC, IIID
<i>Flabellum (Ulocyathus) angulare</i> Moseley, 1876		4				4	2269–2400	2.1–3.1	IA, IIA, SHE, IIIA
<i>Flabellum (Ulocyathus) macandrewi</i> Gray, 1849		6				6	255–952	5.2–7.7	IA, IIA, SHE, IIB, IIIA, IIIC
<i>Flabellum</i> sp(p)				1	7	8	240–550		
<i>Javania caillietii</i> (Duchassaing & Michelotti, 1864)		3		1		4	1157–1398	3.7–4.1	BER, IA, IB, IC, ID, IIA, IIIA, MED
Fungiacyathidae									
<i>Fungiacyathus (Fungiacyathus) fragilis</i> Sars, 1872		24				24	296–1962	2.7–7.0	IIA, IIB, IIIA, IIID
<i>Fungiacyathus (Bathyactis) marenzelleri</i> (Vaughan, 1906)		29				29	336–2709	2.3–7.0	IB, SHE, IIB, IIIA, IIIC, IIID
Oculinidae									
<i>Madrepora oculata</i> Linnaeus, 1758	10	16	2	6	37	71	227–1643	2.8–8.9	IA, IB, SHE, IIB, IIIA, IIIB, IIIC, IIID, MED
Total number of records	218	1060	60	752	620	2710			
Number of taxa	48	72	23	48	47	105			14 IIA, 30 IIB

Table 1 (continued)

Remarks on species taxonomy:

- ¹Two known species of *Paramuricea* have been recorded in Iceland. Some of the collected specimens still need further examination and identification. For underwater images, identification to species level is impossible, and recognizing this uncertainty, they have been labelled *Paramuricea* sp(p). We realize some of those underwater specimens could also belong to *Placogorgia*
- ²In a taxonomic revision of Anthothela (Moore et al. 2017) the authors described a new genus: *Lateothela* Moore et al. 2017. The authors stated that many specimens previously identified as *Anthothela grandiflora* are in fact *Lateothela grandiflora*, including one specimen from the “Thor” expedition in Icelandic waters. Both species are found south of Iceland (Fig. 3a). Based on this revision, all observations from video were recorded as Anthothelida, that is now unaccepted. As it is impossible to identify between these species from video, we keep the old common family name for now
- ³Identifications from underwater images and video have often been recorded as “Nephtheidae”, including the genera *Drifta*, *Duva*, *Gersemia* and *Pseudodrifa*. Now these split into the families Capnellidae and Alcyoniidae. A more detailed work would be needed to re-identify these specimens from the underwater material
- ⁴Four species of *Clavularia* have been recorded in Iceland. Madsen (1944) recorded three species from five stations but none of these species were reported by the BIOICE project, that only recorded *C. arctica*. This suggests that *Clavularia* specimens in Icelandic waters need re-examination
- ⁵Primnoidae sp. 1 resembles *Narella* sp. and sp. 2 resembles *Callogorgia* sp. but this has not been confirmed
- ⁶In a re-examination of the BIOICE samples, based on the paper of Molodtsova (2013), we found that *Anthomastus grandiflorus* were mostly *Heteropolypus sol* Molodtsova 2013 and *Pseudanthomastus* sp. Jungersen (1927) identified the samples he found during the Ingolf Expedition as *Anthomastus grandiflorus* but it is evident from the plates that these specimens also belong to *Heteropolypus* cf. *sol* and *Pseudanthomastus* sp
- ⁷Jungersen (1904) reported *Umbellula lindahlia* Kölliker, 1875 from a single sample of the Ingolf expedition within Icelandic waters, but it was not included in our review because his description seems to be rather speculative and this species has not been reported again from these waters. MFRI data include an unknown species labelled *Umbellula huxleyi* but this needs revision
- ⁸Jungersen (1917) reported on *Caryophyllia* (*Caryophyllia*) *smithii* (as *Caryophyllia clavus* Sacchi, 1835) from Iceland but did not include positions or other information so the occurrence of this species in Icelandic waters is unknown

The sole species, *Ceratocaulon wandeli* (Jungersen 1892), was described from a material collected northwest of Iceland. Its geographic distribution extends from NW Iceland to the Faroe Islands, north of the GIFR and into the Davis Strait in the eastern Canadian Arctic (Jungersen 1892; Madsen 1944; de Moura Neves et al. 2025).

Family Clavulariidae

Genus: *Clavularia* (4 species).

Four species belong to single genera in the family Clavulariidae (Table 1, Fig. 5B). *Clavularia arctica* is most widely distributed, ranging from shallow < 100 m to deep waters > 2000 m.

Family Plexauridae

Genus: *Swiftia* (1 species).

A single species, *Swiftia borealis* (Kramp, 1930), belonging to the family Plexauridae (Fig. 5C) is found south and north of Iceland. It was described by Kramp (1930), and the species had then been found in Greenland, Iceland and the Faroe Islands.

Family Tubiporidae

Genus: *Scyphopodium* (1 species).

Scyphopodium is a monotypic genus including the single species *Scyphopodium ingolfi* (Madsen, 1944) (Table 1, Fig. 6A). The species was described from a specimen collected southeast of Iceland.

Order Scleralcyconacea.

This order includes thirty-one species across fourteen families, with nine of them belonging to the superfamily Pennatulioidea.

Family Chrysogorgiidae

Genera: *Chrysogorgia* (2 species), *Radicipes* (1 species).

Specimens belonging to two genera of the family Chrysogorgiidae are distributed in the deep waters south of Iceland (Table 1, Fig. 6B).

Family Corallidae

Genera: *Anthomastus* (2 species), *Heteropolypus* (1 species), *Pseudoanthomastus* (1 species), *Paragorgia* (1 species).

The subfamily Anthomastinae represents three genera, all recorded in the deep waters south and west of Iceland, south of the GIFR (Table 1, Figs. 6C and 7A). A single species belonging to the fourth genus of *Paragorgia* (Fig. 7A), has also been documented occurring south of the GIFR.

Family Keratoisididae

Genus: *Acanella* (1 species).

The species *Acanella arbuscula* (Johnson 1862) is widely distributed south of Iceland (Fig. 7B).

Fig. 3 Observations of species in the families Acanthogorgiidae; (A and B), Alcyoniidae; (C), in the order Malacalcyonacea

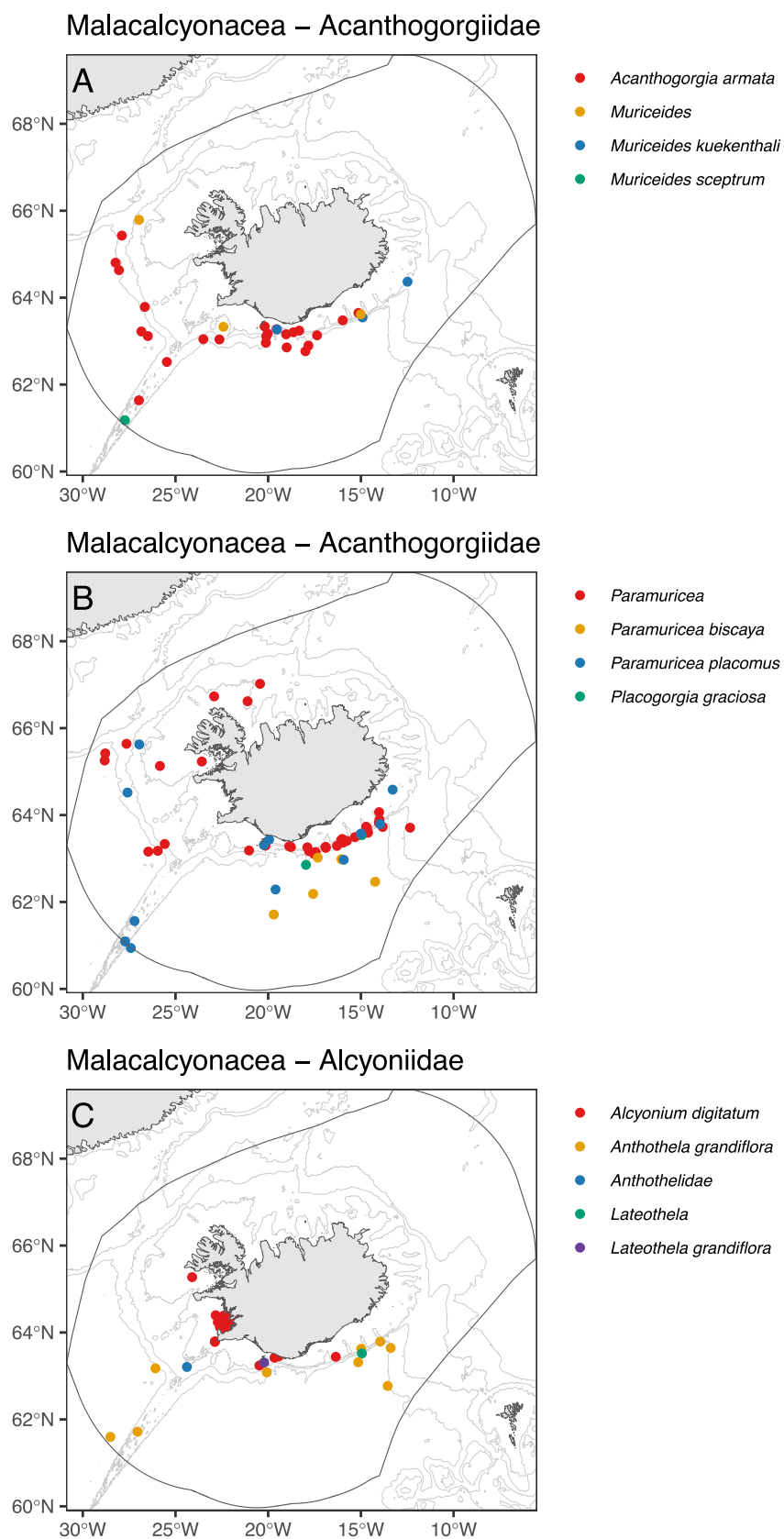


Fig. 4 Observations of species in the families Alcyoniidae; (A), Capnellidae; (B and C), in the order Malacalcyonacea

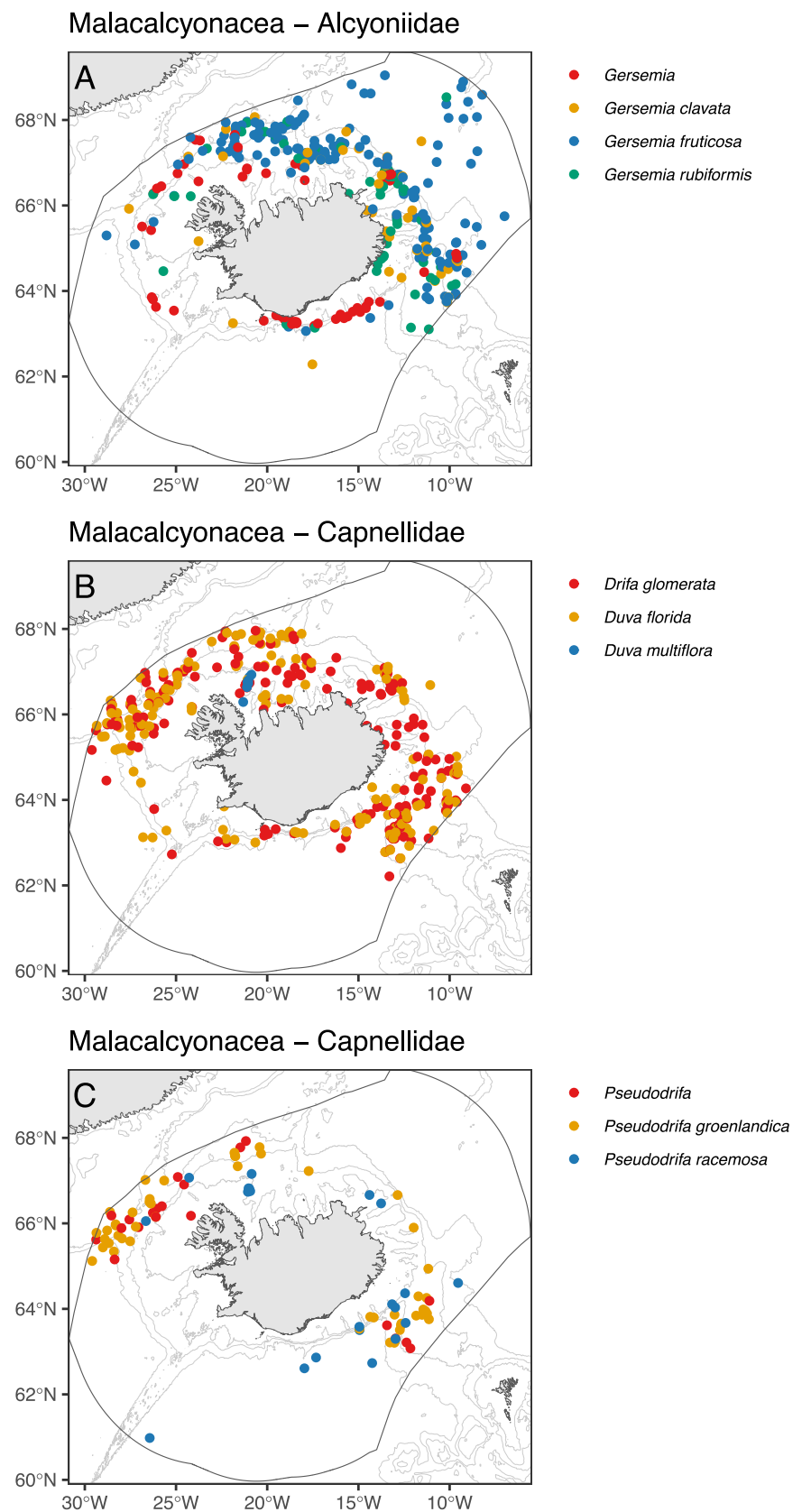


Fig. 5 Observations of species in the families Ceratocaulidae; (A), Clavulariidae; (B), and Plexauridae; (C), in the order Malacalcyonacea

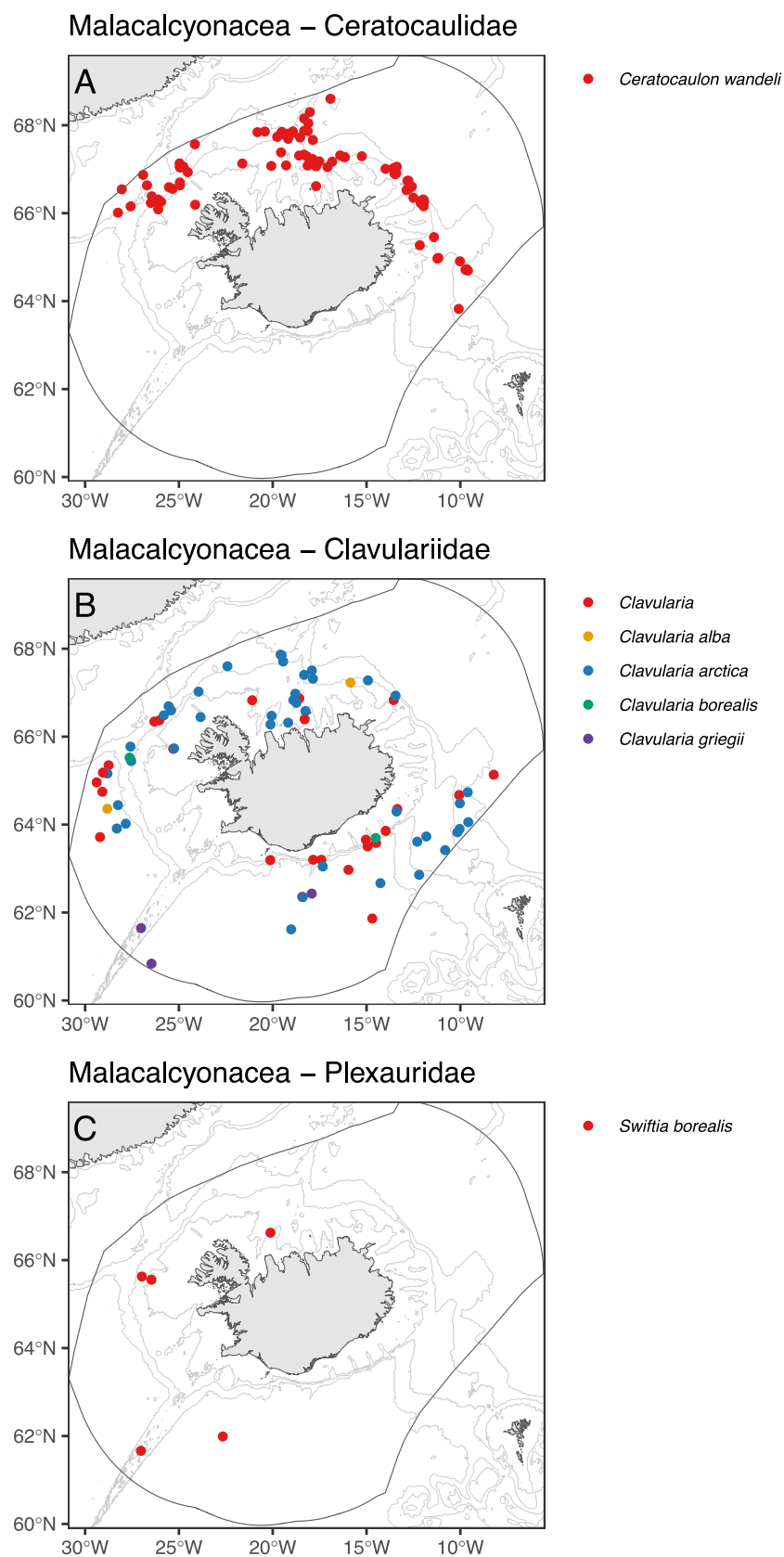


Fig. 6 Observations of species in the family Tubiporidae, order Malacalcyonacea; (A), and in the families Chrysogorgiidae; (B) and Coralliidae; (C) in the order Scleralcyonacea

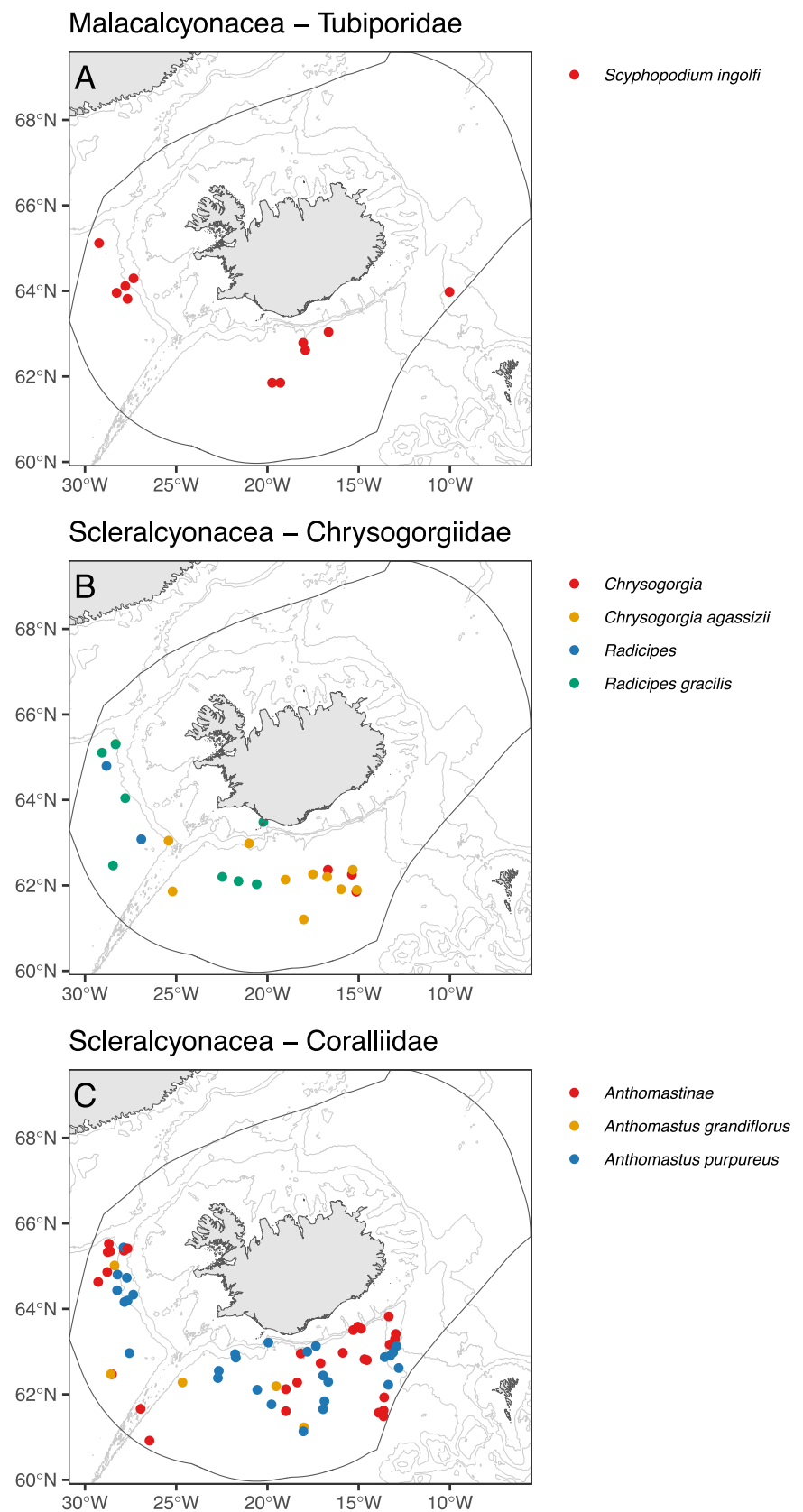
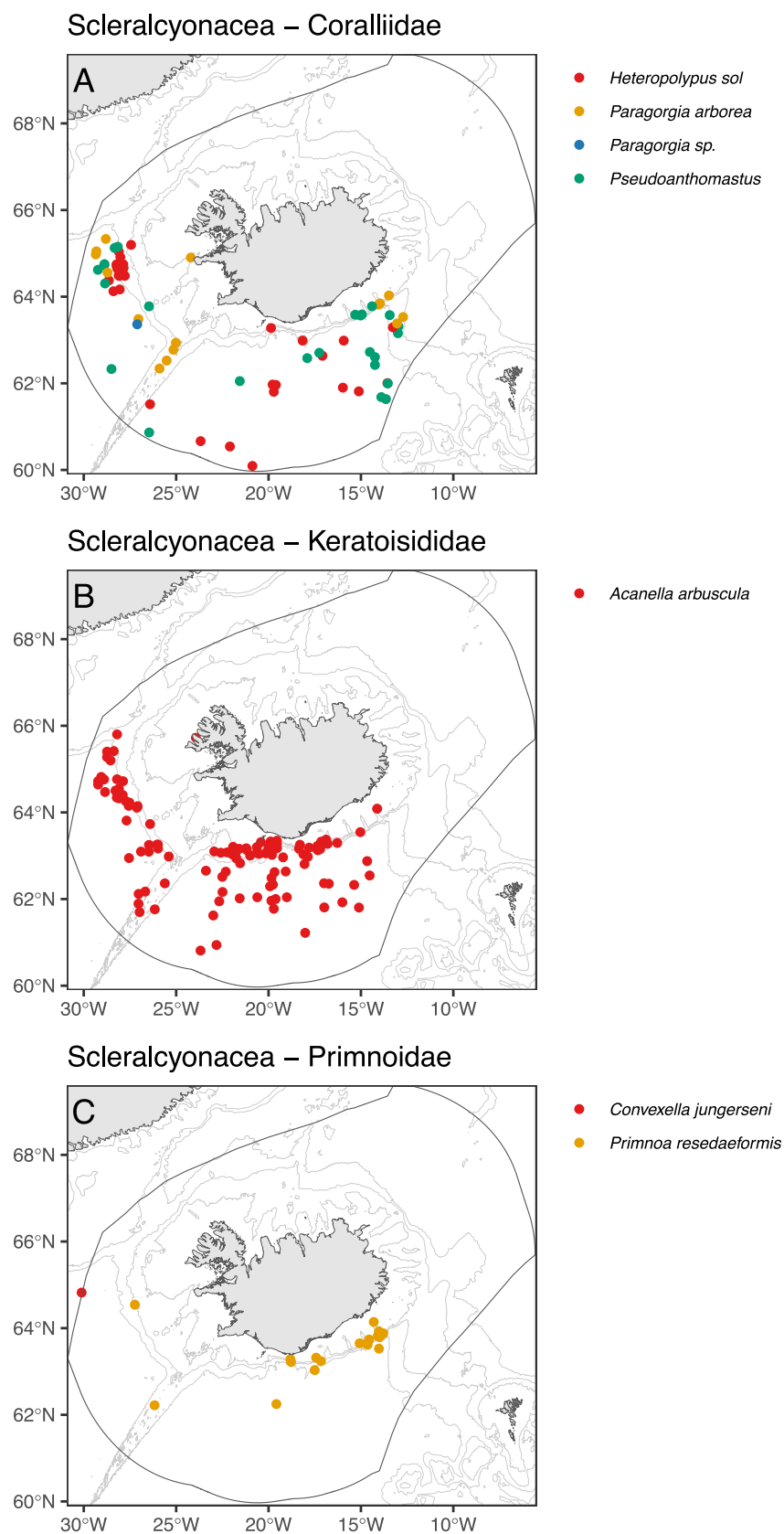


Fig. 7 Observations of species in the families Coralliidae; (A), Keratoisididae; (B), and Primnoidae; (C) in the order order Scleralcyonacea



Other species belonging to the family Keratoisididae have been collected and additional specimens have been observed on underwater images, but these specimens remain unidentified pending further taxonomic examination.

Family Primnoidae

Genera: *Convexella* (1 species), *Primnoa* (1 species).

Two species representing two genera of the family Primnoidae have been recorded (Table 1, Fig. 7C). Underwater imagery shows two additional types that most likely belong to the family; however, as no physical samples were obtained, they could not be properly identified.

Superfamily Pennatuloidea. Nine families belong to this superfamily and are commonly referred to as sea pens.

Family Anthoptilidae

Genus: *Anthoptilum* (2 species).

A single genus with two species belonging to the family Anthoptilidae are distributed in the deep waters south and west of Iceland (Table 1, Fig. 8).

Family Balticinidae

Genus: *Balticina* (2 species).

A single genus with two species belonging to the family Balticinidae are distributed along the shelf break south of Iceland as well as in the deeper waters (Table 1, Fig. 8B).

Family Funiculinidae

Genus: *Funiculina* (1 species).

A single species of the family Funiculinidae is mainly distributed in the Denmark Strait, west of Iceland (Table 1, Fig. 8C).

Family Kophobelemnidae

Genus: *Kophobelemn* (1 species).

A single species of the family Kophobelemnidae has been identified, with several records only to genus level of *Kophobelemn* (Table 1, Fig. 9A). The main distribution is south of Iceland, with some records in the deep waters north of Iceland.

Family Pennatulidae

Genera: *Pennatula* (2 species and one variety), *Ptilella* (1 species).

Three species and one variety belonging to the family Pennatulidae are distributed along the continental slope south of Iceland and in the deep waters south of the GIFR (Table 1, Fig. 9B and C).

Family Protoptilidae

Genera: *Distichoptilum* (1 species), *Protoptilum* (2 species).

Three species belonging to the family Protoptilidae were observed in the waters deeper than 1000 m south of Iceland, with a single record at 126 m depth (Table 1, Fig. 10A).

Family Pseudumbellulidae

Genus: *Pseudumbellula* (1 species).

In 2022, López-González and Drewery, described the monotypic family Pseudumbellulidae, with the sole species *Pseudumbellula scotiae*. This species is recorded west of the Reykjanes Ridge (Table 1, Fig. 10B).

Family Umbellulidae

Genus: *Umbellula* (1 species). A single species has been identified, *Umbellula encrinus* Linnaeus 1758, however, specimens have been collected that are of different species (one or more) that remain to be revised (Table 1, Fig. 11A).

Family Virgulariidae

Genera: *Glaciaptilum* (1 species), *Stylatula* (1 species), *Virgularia* (2 species).

Three genera belonging to the family Virgulariidae are distributed in Iceland (Table 1, Fig. 11B). The genus *Glaciaptilum* was described in 2025 by López-González and Ólafsdóttir, with a new name for the species *Virgularia glacialis* as *Glaciaptilum steenstrupii* (Kölliker 1870). This is an Arctic species, only distributed north of the GIFR, and the only species belonging to the family that is exclusively in the north, while species belonging to the genus *Virgularia* are distributed around Iceland and the species belonging to the genus *Stylatula* are in more shallow waters in the south (Table 1, Fig. 11B).

Family Sarcodictyonidae

Genus: *Telestula* (1 species).

In 2024, McFadden, van Ofwegen and Quattrini described the family Sarcodictyonidae which is represented by a single species in Icelandic waters, *Telestula septentrionalis* Madsen 1944 (Table 1, Fig. 10C).

CLASS HEXACORALLIA

Hexacorallia in Icelandic waters consist of two orders: Antipatharia and Scleractinia. Their known spatial distribution to date is shown in Figs. 11, 12, 13, and 14.

Order Antipatharia.

Black corals (order Antipatharia) are rare in Icelandic waters, with three species recorded across 13 locations.

Family Schizopathidae

Genera *Bathypathes* (1 species), *Stauropathes* (1 species), *Parantipathes* (1 species).

Three species from three genera belonging to the family Schizopathidae have been recorded in deep water, mostly west of Iceland (Table 1, Fig. 11C).

Fig. 8 Observations of species in the families Anthoptilidae; (A), Balticinidae; (B), and Funiculinidae; (C) in the order Scleralcyonacea

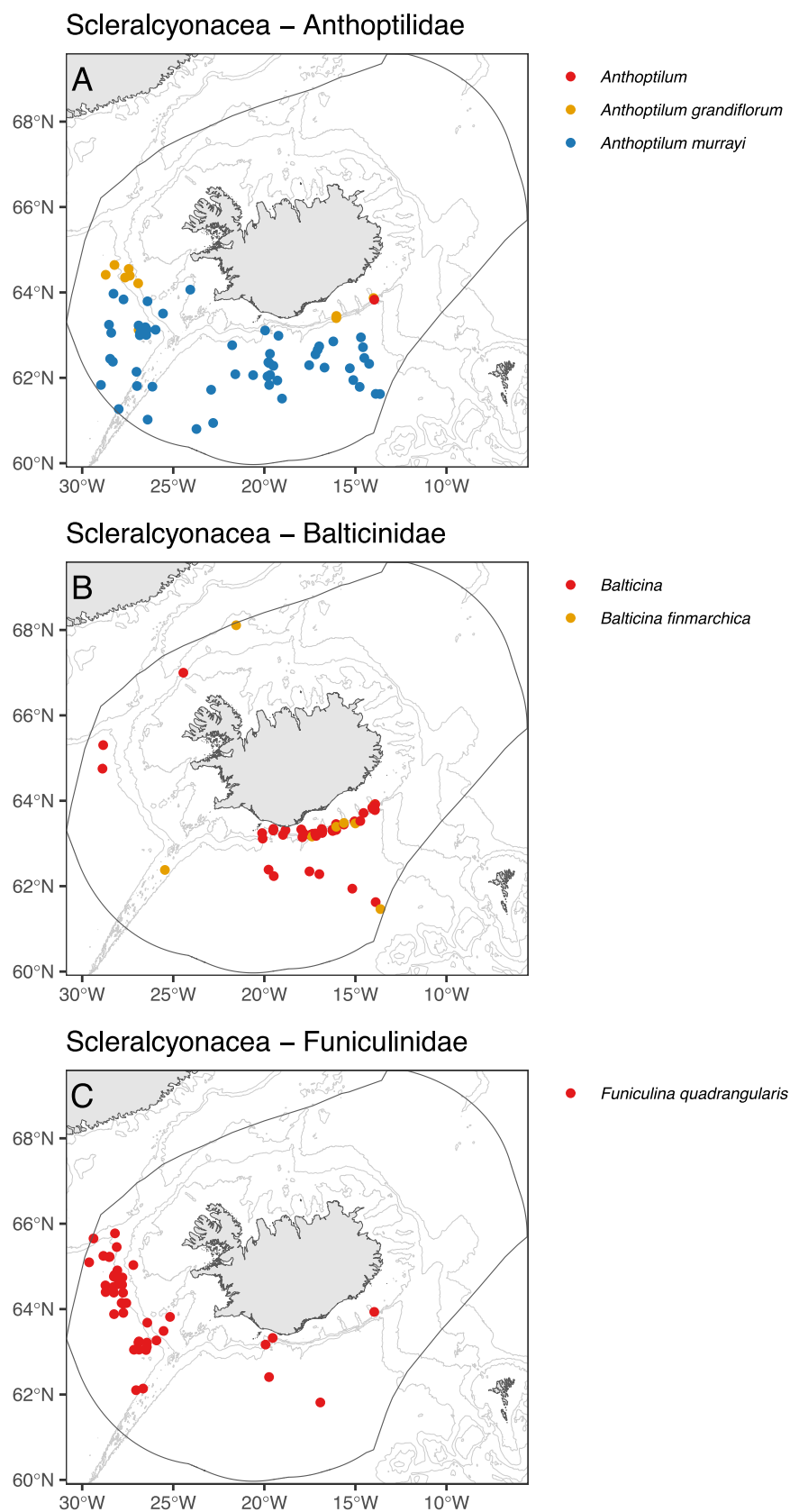


Fig. 9 Observations of species in the families Kophobelemnidae; (A) and Pennatulidae; (B and C) in the order Scleralcyonacea

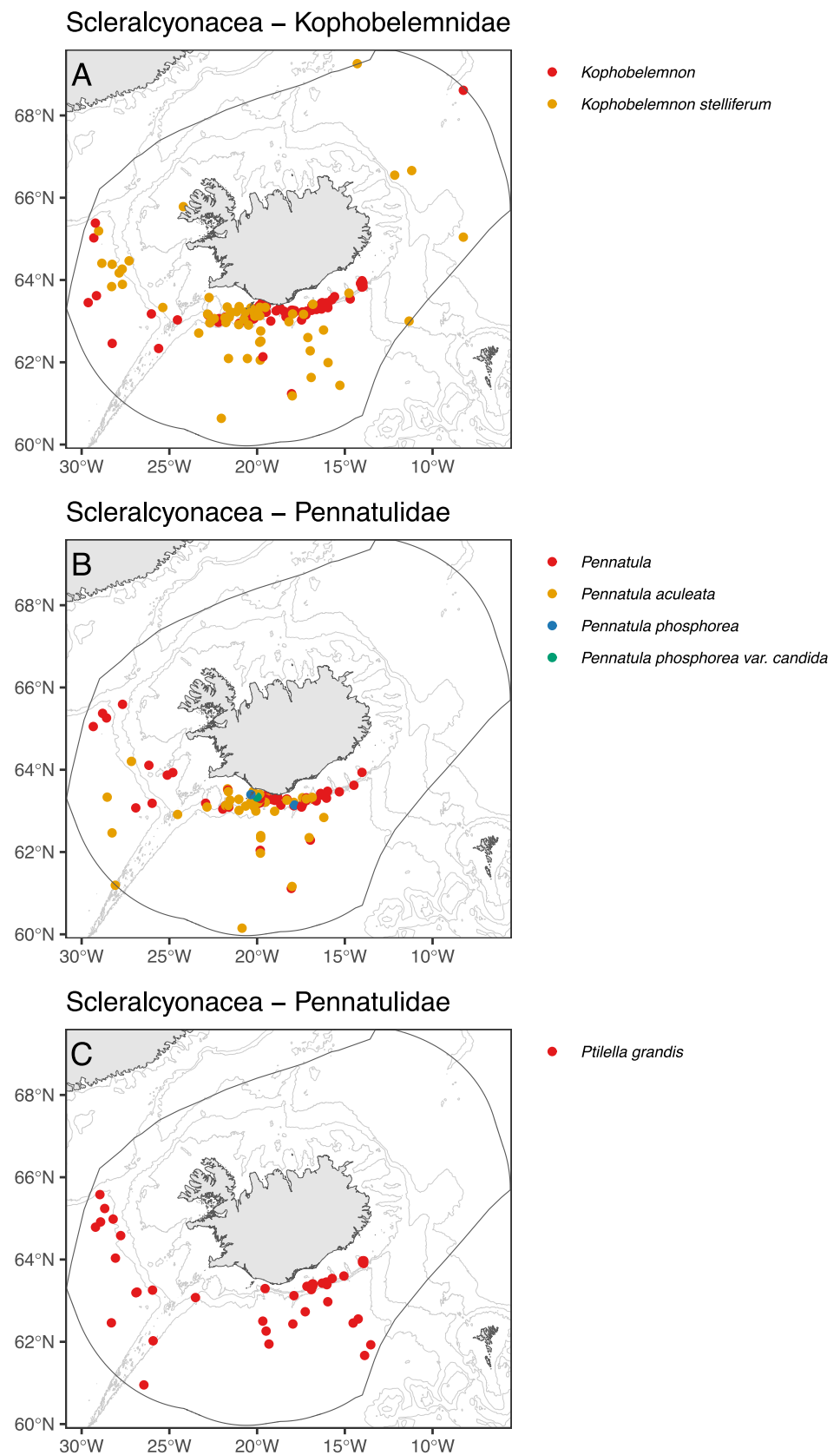


Fig. 10 Observations of species in the families Protoptilidae; (A), Pseudumbellulidae; (B), and Sarcodictyonidae; (C) in the order Scleralcyonacea

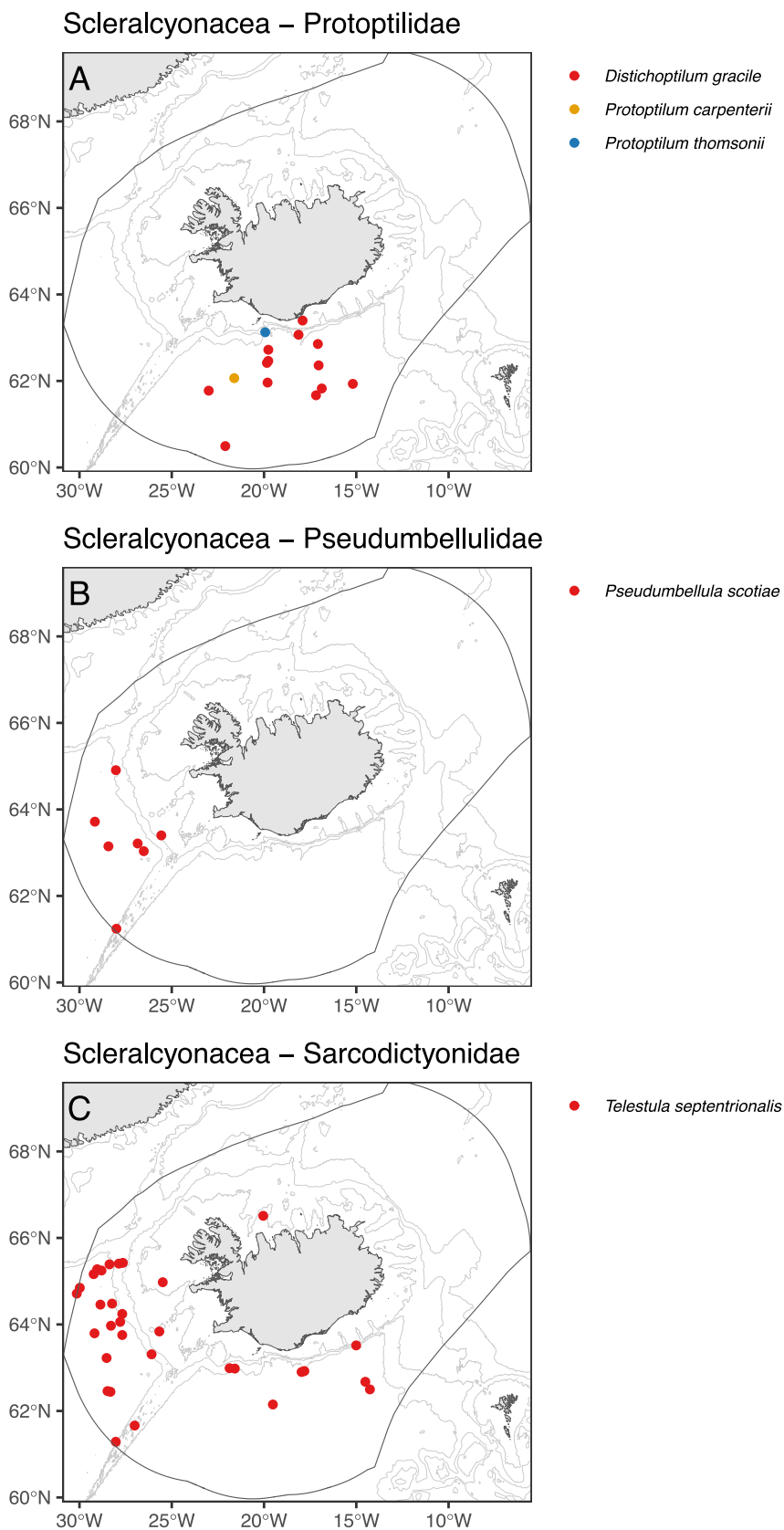
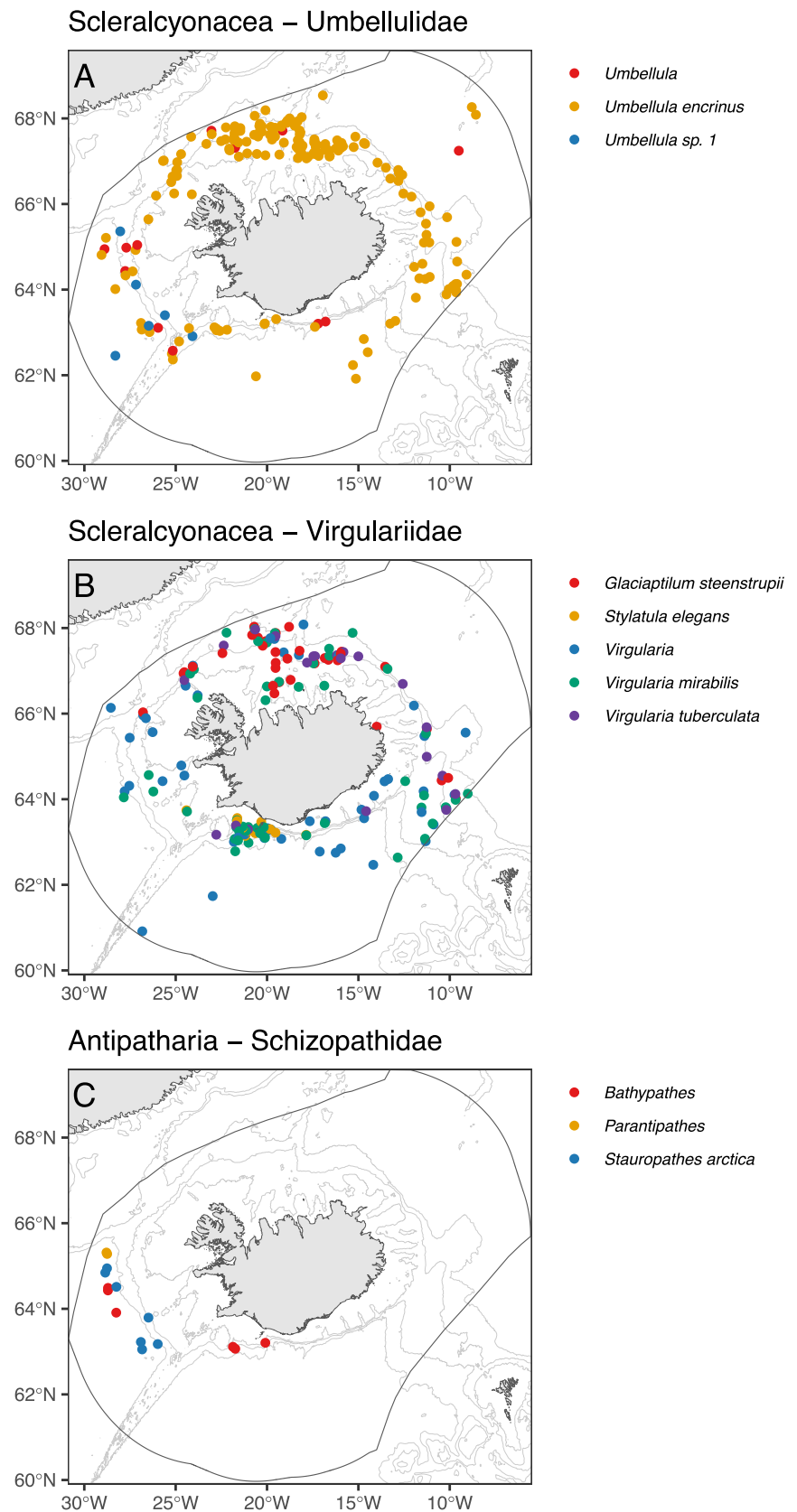


Fig. 11 Observations of species in the families Umbellulidae; (A) and Virgulariidae; (B) in the order Scleralcyonacea, and in the family Schizopathidae; (C) in the order Antipatharia



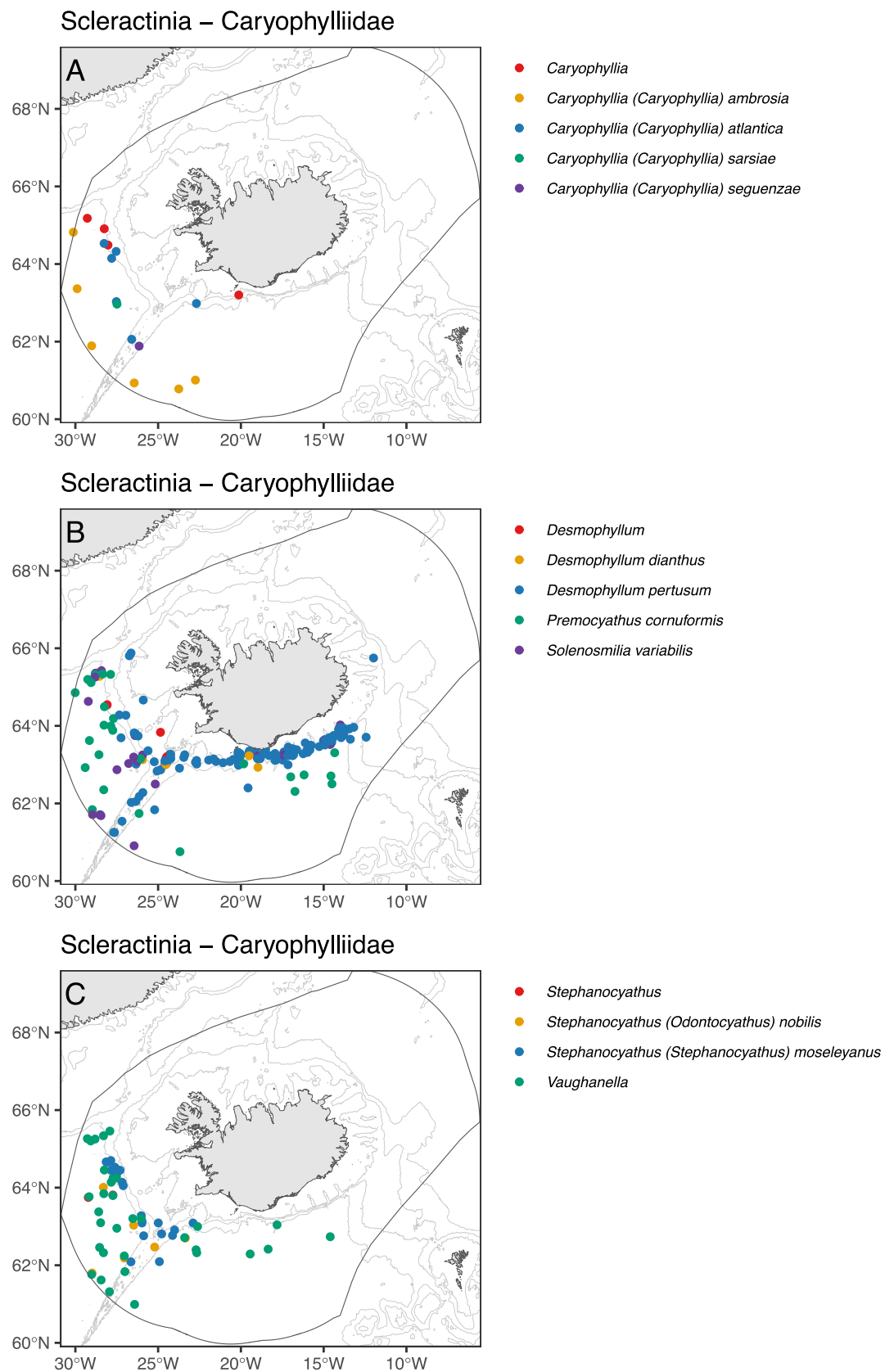


Fig. 12 Observations of species in the family Caryophylliidae (**A**, **B** and **C**) in the order Scleractinia

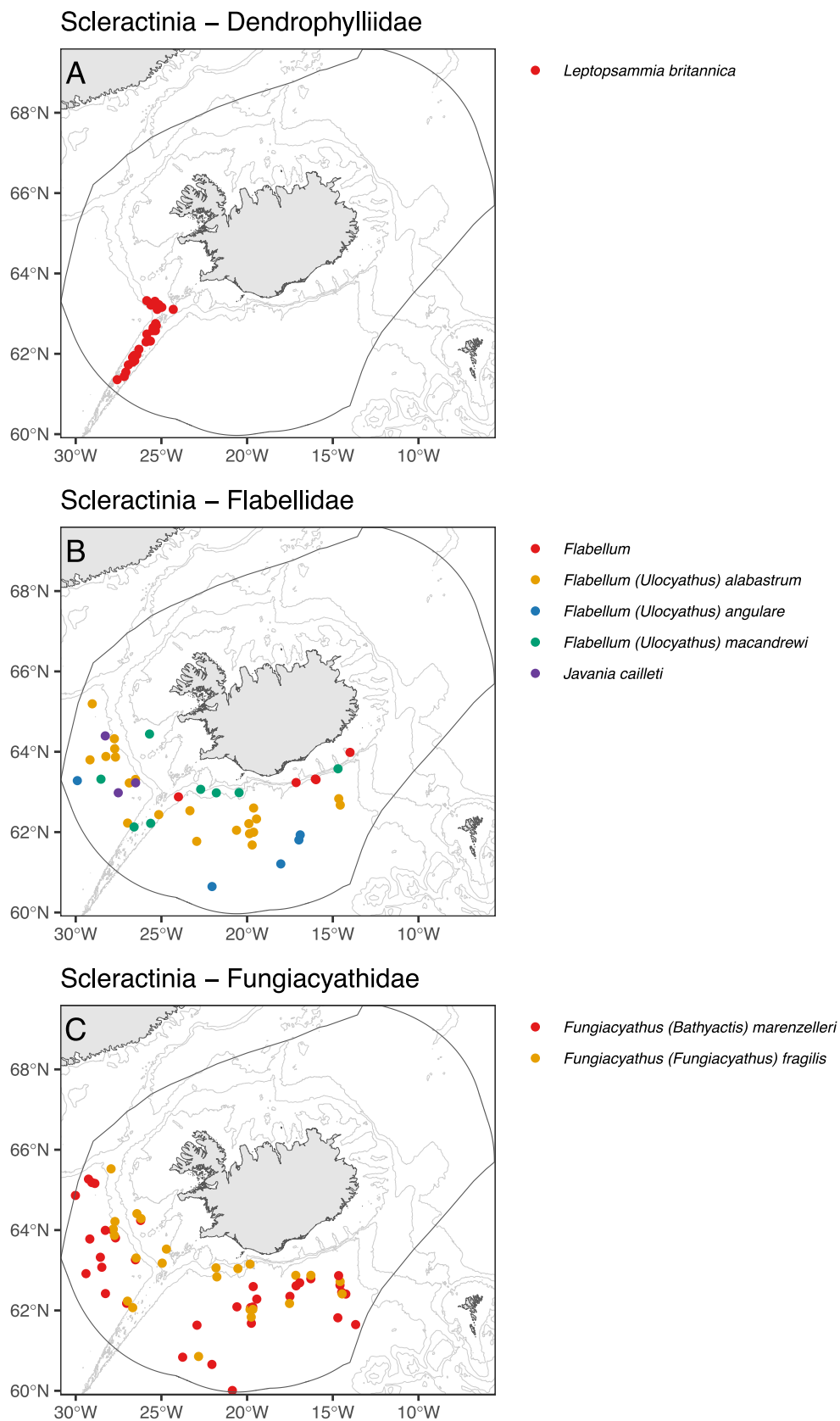


Fig. 13 Observations of species in the families Dendrophylliidae; (A), Flabellidae; (B), and Fungiacyathidae; (C) in the order Scleractinia

Scleractinia – Oculinidae

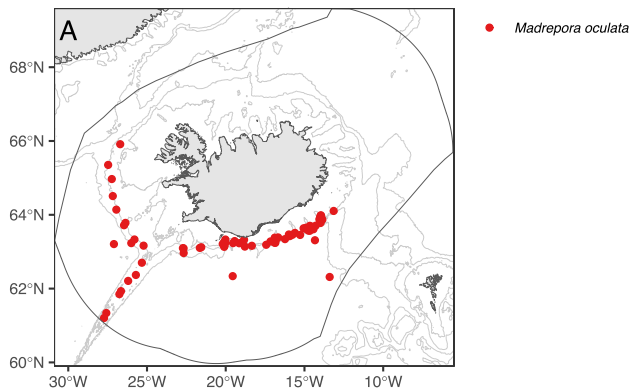


Fig. 14 Observations of species in the family Oculinidae (A) in the order Scleractinia

Order Scleractinia

Twenty species from five Scleractinia families have been recorded, all found exclusively south and west of Iceland.

Family Caryophylliidae

Genera: *Caryophyllia* (5 species), *Desmophyllum* (2 species), *Premocyathus* (1 species), *Solenosmilia* (1 species), *Stephanocyathus* (2 species), *Vaughanella* (1 species). Twelve species of six genera belonging to the family Caryophylliidae are distributed south of the GIFR (Table 1, Fig. 12A–C).

Family Dendrophylliidae

Genus: *Leptosammia* (1 species).

A single species belonging to the family Dendrophylliidae is distributed along the Reykjanes Ridge (Table 1, Fig. 13A).

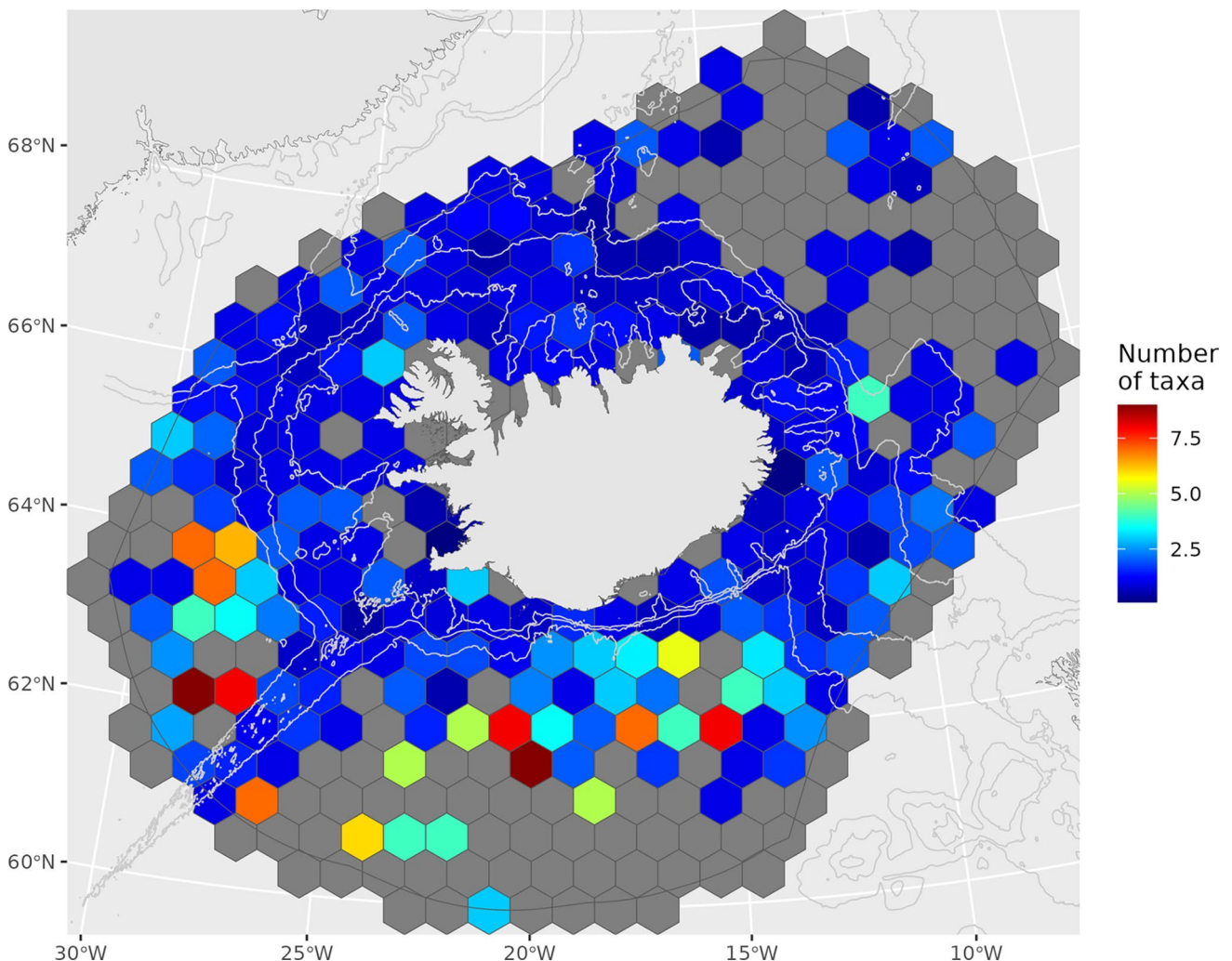


Fig. 15 Species richness of cold-water corals in Icelandic waters. Species richness was computed as the number of taxa recorded standardized by the number of samples

Family Flabellidae

Genera: *Flabellum* (3 species), *Javania* (1 species). The four species belonging to the family Flabellidae are distributed mostly in deep waters south of the GIFR (Table 1, Fig. 13B).

Family Fungiacyathidae

Genus: *Fungiacyathus* (2 species).

Two species belonging to the family Fungiacyathidae are mainly distributed in the deep waters south of the GIFR (Table 1, Fig. 13C).

Family Oculinidae (Fig. 14A):

Genus: *Madrepora* (1 species).

A single species belonging to the family Oculinidae is distributed along the continental slope off the west and south coasts of Iceland, as well as along Reykjanes Ridge.

Depth and temperature distribution of CWC

Cold-water coral species richness ranged from 0.1 to 9 taxa per sample (Fig. 15). Richness was highest in the temperate waters south and southwest of Iceland, where over 90% of the species are distributed. Notably, 30% of these species, including all Scleractinia and Antipatharia, are found exclusively in these temperate regions (Figs. 11, 12, 13, 14). Nine species (10%) are distributed in cooler waters northeast and east of Iceland.

CWC records span depths from 15 to 2709 m and temperatures from -1.0 to 9.0 °C. The depth and temperature ranges for each species are listed in Table 1. To examine the distribution pattern in detail, the depth range was divided into four zones: (1) neritic/eutrophic zone (low-tide level to 200 m); (2) upper bathyal (200–600 m); (3) middle bathyal (600–1000 m); and (4) lower bathyal (1000–3000). The majority of species occur in the middle bathyal zone (80%) and lower bathyal zone (78%), while 29% and 61% were present in the neritic/eutrophic and upper bathyal zones, respectively (Table 2).

The temperature range was divided into five zones: -1 to 0 °C; 0 to 2.5 °C; 2.5 to 5 °C; 5 to 7.5 °C, and 7.5 to 11 °C. Most species (80%) were found within the 2.5 – 5 °C range, with over 28% occurring in waters below 0 °C (Table 3).

The relationship between temperature and depth was analyzed for the coral species across the orders Scleractinia, Malacalcyonacea, Anthipatharia and Scleractinia. Most Scleractinia species occur within 3 – 8 °C, and at depth down to 2000 m (Fig. 16). Malacalcyonacea exhibited a temperature range of 0 – 8 °C, with most species present at 400–600 m depth (Fig. 17). The Anthipatharia and Scleractinia showed an occurrence gradient related to temperatures of 4 – 8 °C and depths of 115–2709 m (Fig. 18).

Species assemblages

Three distinct species assemblages were identified (Fig. 19):

Assemblage A: Circum-Iceland and Northern species This group contains twelve species (26%), including the cauliflower corals *Duva florida*, and *Drifa glomerata*, and the sea pens *Umbellula encrinus*, and *Gersemia fruticosa*, which are prevalent in northern waters but also extend southward. It also includes exclusively northern species such as *Ceratocaulon wandeli*, *Virgularia tuberculata* and *Glaciaptilum steenstrupii* (syn: *Virgularia glacialis*), primarily associated with waters cooler than 2 °C.

Assemblage B: Deep south and western species This group contains 18 species (39%) occurring mostly in the deep Iceland Basin south of Iceland and Irminger Basin to the west, typically within temperature range of 2 – 5 °C and at depths exceeding 1000 m.

Assemblage C: Shallow south and western species The two reef-forming coral species *D. pertusa* and *M. oculata*, along with *Paramuricea*, frequently co-occurred in video observations along a narrow strip confined to the southern and western insular shelf break and along the Reykjanes Ridge, at depths less than 600 m and temperatures above 5 °C (Fig. 4).

Biogeographical comparison of Scleractinia and Alcyonacea

Cairns and Chapman (2001) identified nine Scleractinia species in Icelandic waters, though their analysis did not encompass the Arctic region. The present study contributes an additional 15 species to their list, providing a foundation for assessing biogeographic similarities with neighbouring areas. The Scleractinia fauna from Iceland exhibited the greatest resemblance to the outlier region SHE (Shetland, Faroe, Orkney, New Hebrides, Rockall Bank) at 84.2% (Table 4). High similarity (70%) was observed between the Icelandic fauna and the western North Atlantic region IIA (Atlantic Canada to the Gulf of Maine). Compared to the broader IIIA group, extending from the Bay of Biscay to the southern coast of Africa, similarity was 33.9%. However, when focusing solely on the GB sub-region (North Sea and coasts of Great Britain, Ireland and France, Bay of Biscay to 45° N), similarity increased to 66.7%.

For Octocorallia, we incorporated 17 new species records not previously listed for region IIB in Watling et al. (2011) and updated accepted names of species,

Table 2 Number of species belonging to each family within the orders Malacalcyonacea, Scleralcyonacea, Antipatharia and Scleractinia recorded within four depth ranges

Taxon group	Neritic/eutrophic zone (m)	Bathyal zone (m)		
		Upper	Middle	Lower
	0–200	200–600	600–1000	1000–3000
MALACALCYONACEA				
Alcyoniidae	3	6	4	4
Capnellidae	3	4	4	3
Clavulariidae	1	2	4	2
Paramuriceidae		5	5	3
Plexauridae	1	1	1	1
Tubiporidae		1	1	1
SCLERALCYONACEA				
Chrysogorgiidae			1	5
Keratosidae		2	3	2
Primnoidae	1	1	1	1
Coralliidae	1	3	5	5
Anthoptilidae		2	2	2
Balticinidae			2	1
Funiculinidae		1	1	1
Kophobelemnidae	1	1	1	1
Pennatulidae	3	2	3	2
Protoptilidae			1	3
Umbellulidae	1	2	2	2
Virgulariidae	5	5	5	3
Sarcodictyonidae	1		1	1
ANTIPATHARIA				
Schizopathidae			2	3
SCLERACTINIA				
Caryophylliidae	1	4	8	9
Dendrophylliidae	1	1	1	
Flabellidae		2	2	3
Fungiacyathidae		2	2	2
Oculinidae		1	1	1
Total number of species pr. depth range (%)	23 (29.5%)	48 (61.5%)	63 (80.8%)	61 (78.2%)

families, and orders (Table 5). Analysis of the updated list indicates that the faunal composition in Icelandic waters closely resembles (75%) that of region IIB, which includes the coast of Norway, Iceland, and the Reykjanes Ridge, and exhibits 50% similarity with the western North Atlantic fauna from east Canada to Cape Hatteras (IIA) (Table 5).

An overview of the bathymetric distribution of sea pens (Pennatuloidea) by Williams (2011) indicates that the families identified in Icelandic waters (Table 1) fall within the categories of mid-depth range taxa (*Stylatula*, *Ptilella* and *Virgularia*) and deep-water taxa (*Balicina*, *Funiculina*, *Pennatula*, *Anthoptilum*, *Protoptilum*, *Distichoptilum*, *Kophobelemnion* and *Umbellula*).

Discussion

The cold-water coral fauna of Iceland is remarkably diverse, comprising 77 identified species across 27 families, with wide distribution across varying depths and temperatures. Diversity is highest in the temperate waters south and southwest off Iceland, where over 90% of species are found. Thirty percent of species (all Scleractinia and Antipatharia species) occur exclusively in these temperate waters.

Most specimens were preserved in formalin, limiting identification to morphological characteristics; only a few samples were preserved in ethanol for molecular analysis (García-Cárdenas et al. 2019; Korfhage 2022). Identification from underwater images carries considerable uncertainty,

Table 3 Number of species belonging to each family within the orders Malacalcyonacea, Scleralcyonacea, Antipatharia and Scleractinia recorded within five temperature ranges

Taxon group	Temperature °C				
	−1.0–0.0	0.0–2.5	2.5–5.0	5.0–7.5	7.5–9.0
MALACALCYONACEA					
Alcyoniidae	3	3	4	4	4
Capnellidae	4	4	4	4	2
Clavulariidae	2	2	2	3	
Paramuriceidae		2	6	3	2
Plexauridae			1	1	
Tubiporidae	1	1			
SCLERALCYONACEA					
Chrysogorgiidae			4	1	
Keratosidae	2	2	3	3	1
Primnoidae			2	2	1
Coralliidae		5	5	5	3
Anthoplitidae		1	2	2	1
Balticinidae	2	2	2	2	
Funiculinidae		1	1	1	1
Kophobelemnidae	1	1	1	1	1
Pennatulidae			2	4	2
Protoplitidae	1	1	3	1	
Umbellulidae	2	2	2	2	
Virgulariidae	3	3	3	3	2
Sarcodictyonidae			1	1	
ANTIPATHARIA					
Schizopathidae			1	2	
SCLERACTINIA					
Caryophylliidae		2	10	7	3
Dendrophylliidae				1	
Flabellidae	1	2	3	2	1
Fungiacyathidae		1	2	2	
Oculinidae			1	1	1
Total number of species pr. temp. range	22 (28.2%)	35 (44.8%)	65 (83.3%)	58 (74.3%)	25 (32%)

often confining it to the genus or family level. Building on known species from the area, learning from other publications using underwater images, and drawing on experience, we strive for consistency. This is challenging, however. For example, video-imaged specimens categorized as belonging to the family Nephtheidea encompass at least three genera (*Drifa*, *Duva* and *Gersemia*), and recent classifications have divided Nephtheidea into the families Capnellidae and Alcyoniidae (McFadden et al. 2022). This calls for revision of the annotations. Specimens identified to the family Anthotheliidae (now accepted as Alcyoniidae) include *Anthothela grandiflora* and *Lateothela grandiflora*, which exhibit very similar morphologies and cannot be distinguished from photographs. Prior to the revisionary systematic published in 2022, species of the genera *Paramuricea*, *Placogorgia*, *Acanthogorgia*, *Swiftia*, and *Muriceides* were all assigned to the family Plexauridae. The morphology of these species

is relatively similar making their identification challenging, particularly when based solely on underwater imagery. To address this uncertainty, specimens that could not be confidently identified to genus level were assigned to “Plexauridae”. Following the 2022 taxonomic revision, most species formerly placed in Plexauridae were transferred to the family Acanthogorgiidae. Consequently, the majority of these previously unresolved records can be assigned to Acanthogorgiidae. However, the genus *Swiftia*, remains within Plexauridae. This presents a caveat, as *Swiftia* species cannot be reliably distinguished from similar morphotypes within Acanthogorgiidae based solely on external morphology in underwater images. The diverse hydrographical systems and bathymetry in Icelandic waters create various habitat types for corals. de Marez et al. (2024) suggested that the main bottom current flowing south of Iceland generates a 200 m deep mixed layer as it interacts with the rough topography,

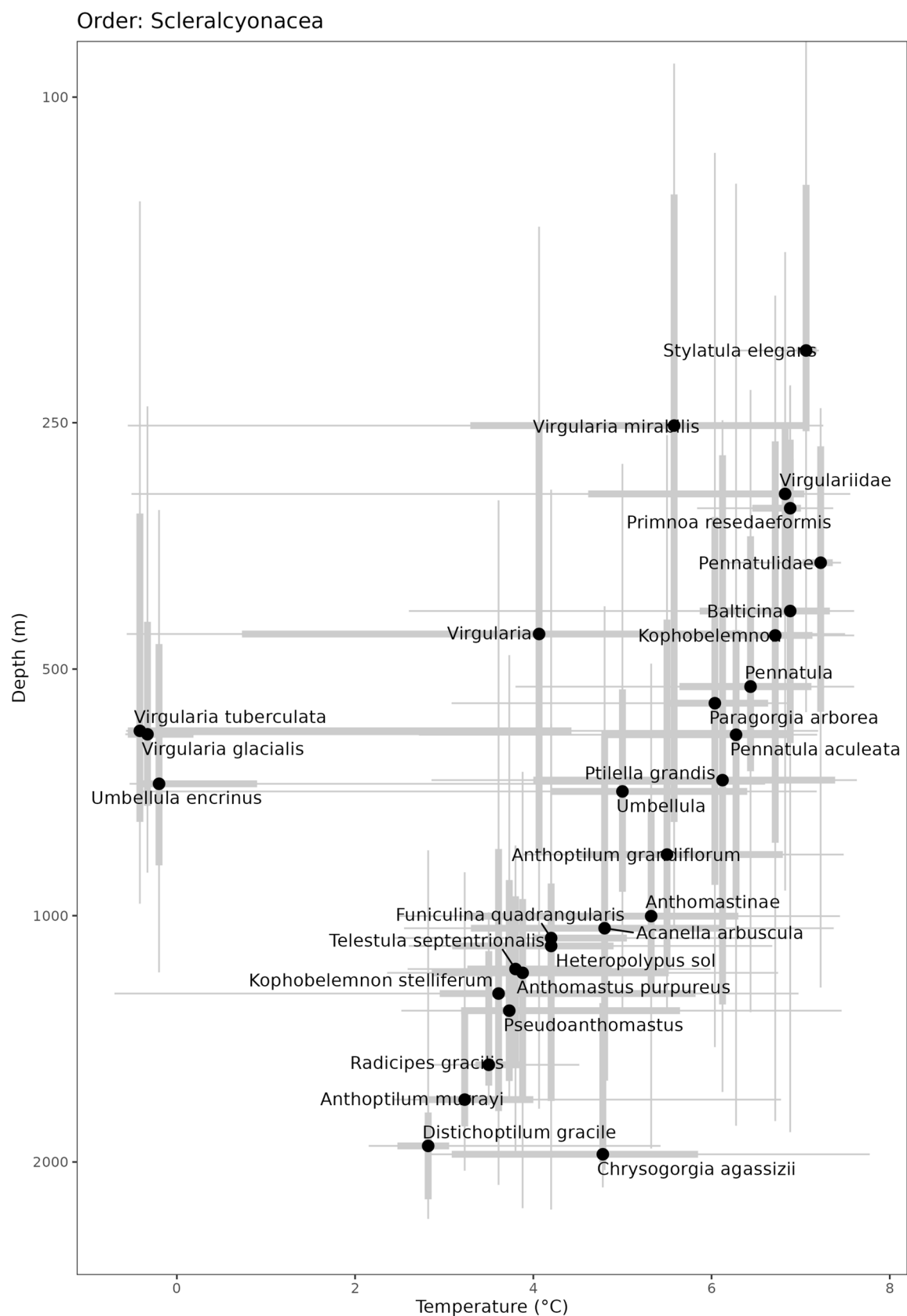


Fig. 16 Two-dimensional boxplots showing temperature and depth for the order Scleralcyonacea. Circles indicate median values. Thick lines mark the interval between the 25th and 75th percentile values. Thin lines mark the range between minimum and maximum values

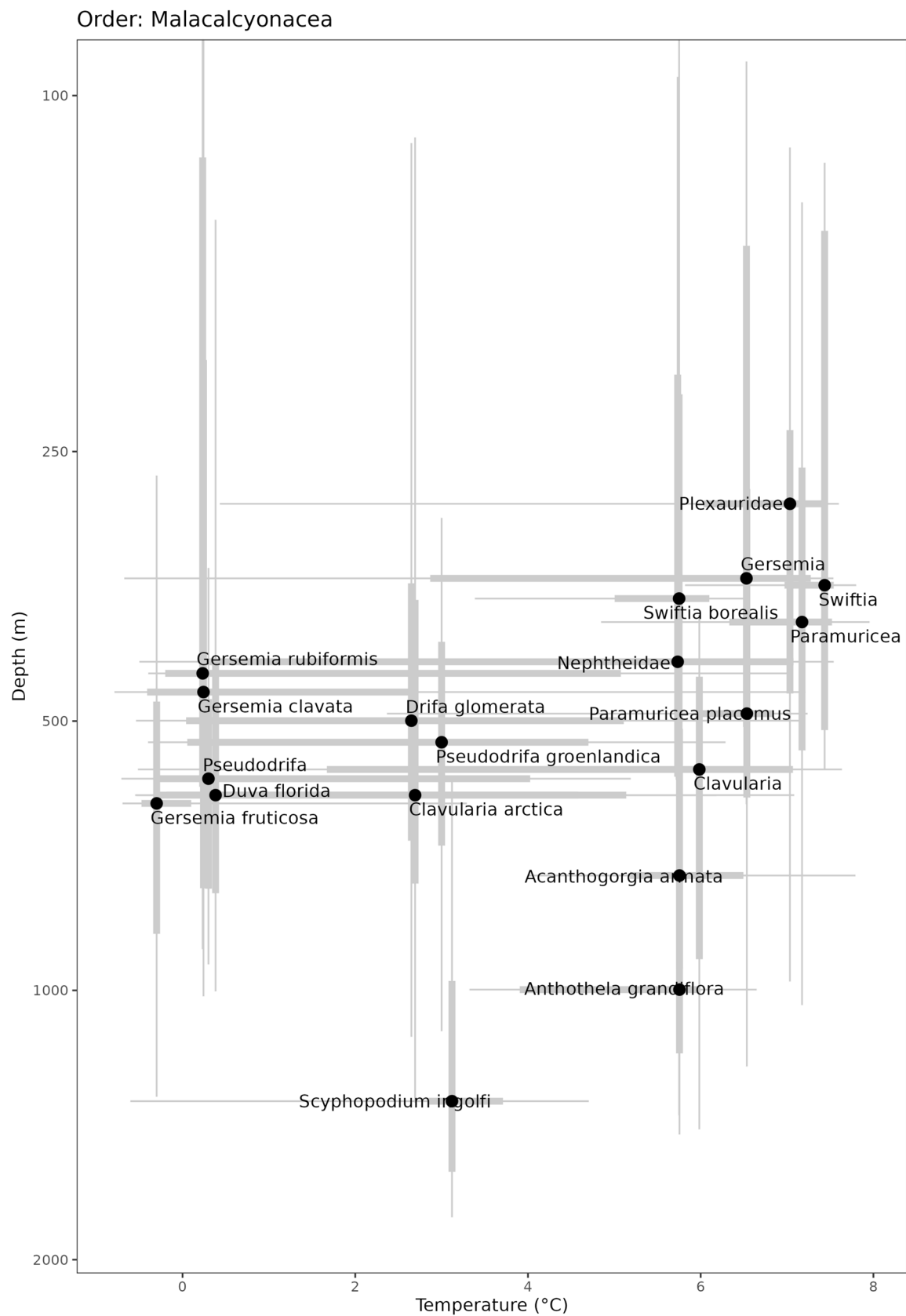


Fig. 17 Two-dimensional boxplots showing temperature and depth for the order Malacalcyonacea. Circles indicate median values. Thick lines mark the interval between the 25th and 75th percentile values. Thin lines mark the range between minimum and maximum values

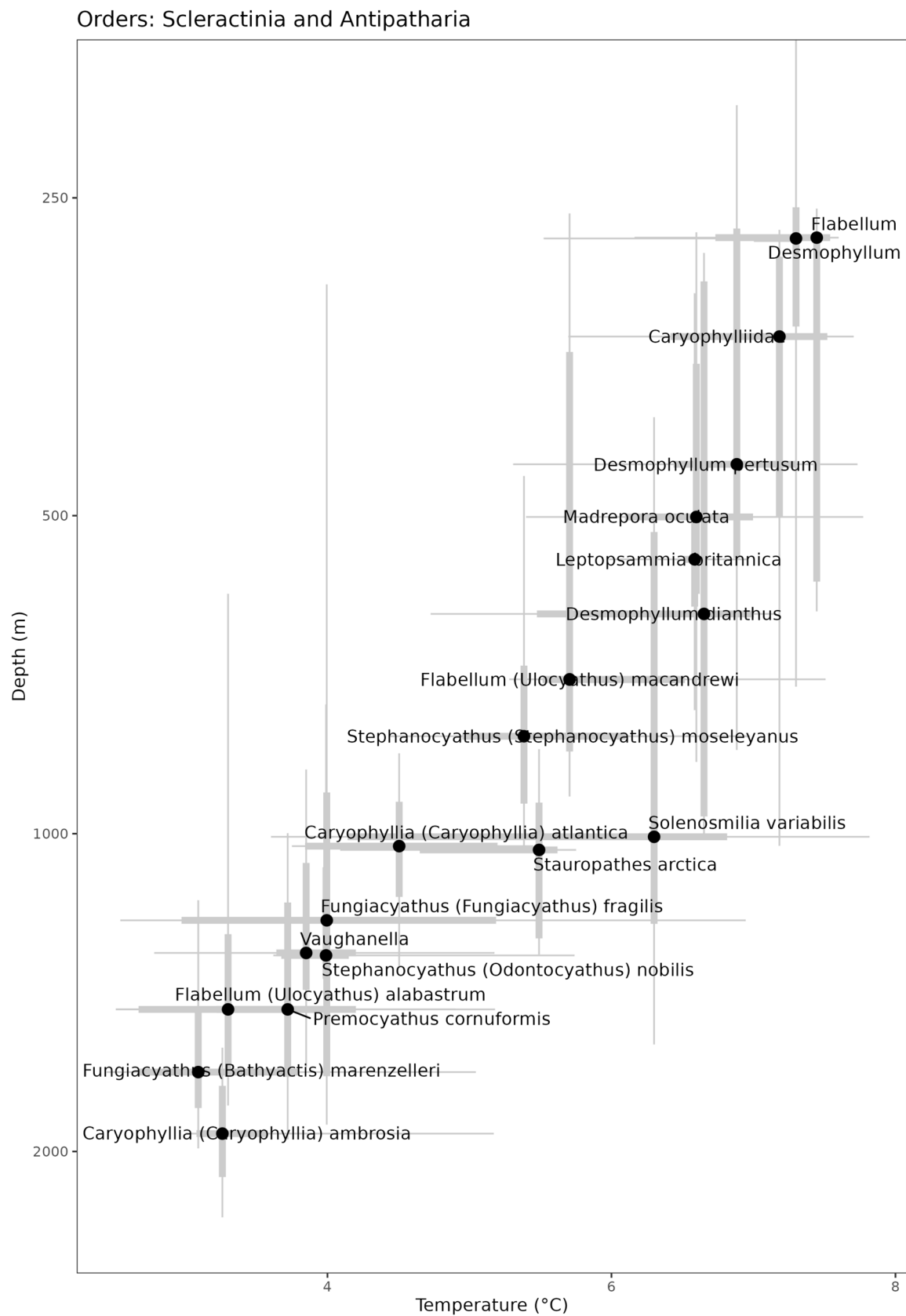


Fig. 18 Two-dimensional boxplots showing temperature and depth for species of the order Scleractinia. Circles indicate median values. Thick lines mark the interval between the 25th and 75th percentile values. Thin lines mark the range between minimum and maximum values

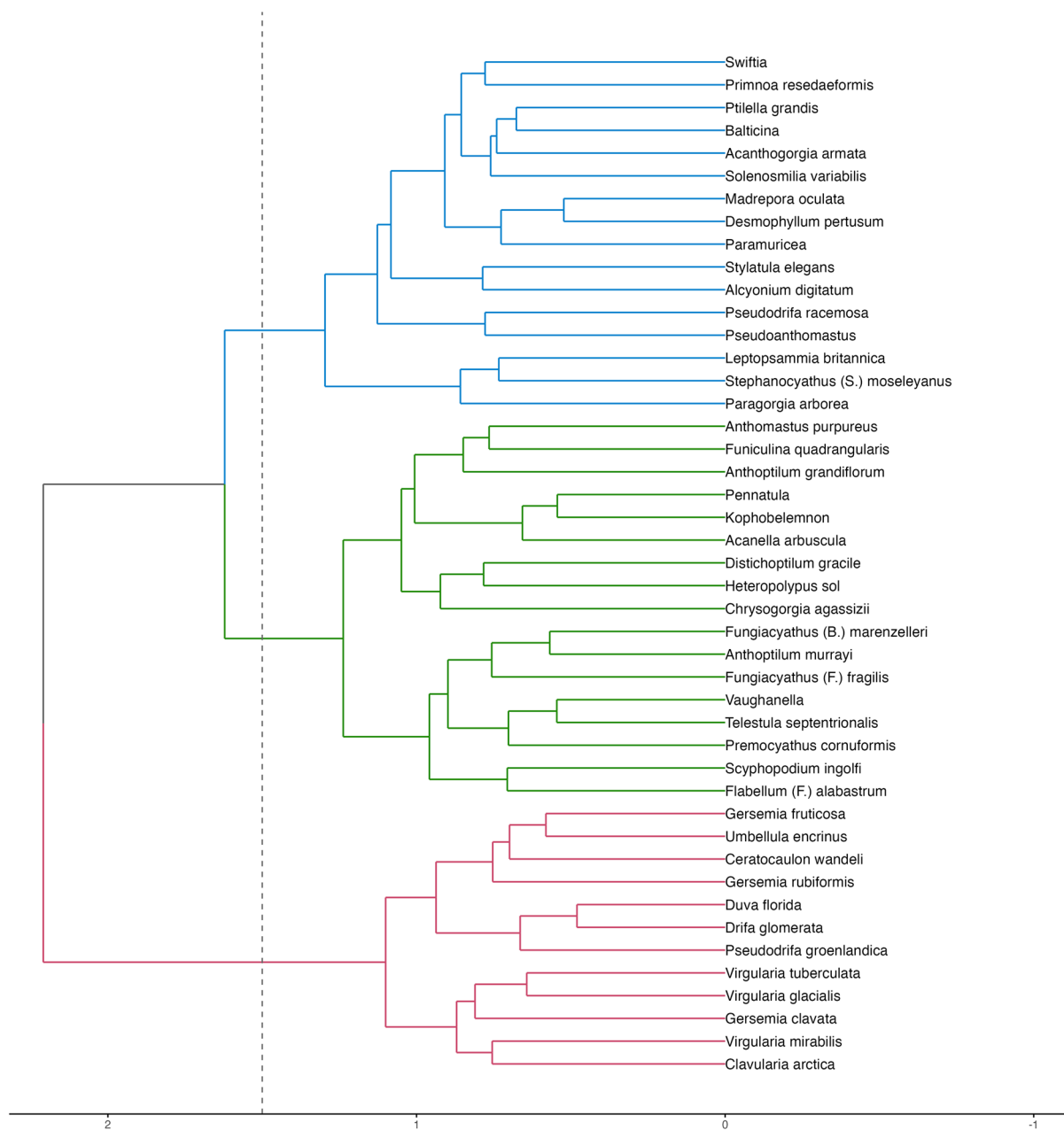


Fig. 19 Dendrogram showing the identified cold-water coral assemblages in Icelandic waters. Groups A, B and C are indicated by colors. A is red, B is green and C is blue

Table 4 Number of species belonging to the order Scleractinia within the Hexacorallia based on Cairns and Chapman (2001). ICE-2001 shows the resemblance of the species listed in Iceland to the other

regions expressed with number of species in common and as percentiles based on Cairns and Chapman (2001). ICE_new represent the updated list of species based on this paper.

Hexacorallia Taxonomic group	Western North Atlantic	North Atlantic			Eastern North Atlantic		
		IIA	IIB	IIC	IIIA	SHE	GB
Scleractinia	60	16	11		62	19	27
ICE_2001	5 (8.3)	5 (29.4)	9 (81.8)		9 (14.5)	7 (36.8)	7 (25.9)
ICE_new	12 (20)	12 (70.5)	24		21 (33.9)	16 (84.2)	18 (66.7)

Table 5 Number of species belonging to each family within the Octocorallia, based on Watling et al. 2011 and aligned with the 2022 revision of the Octocorallia taxonomic groups. The first number represents the updated number of species within each family, and the number after the slash represents the number of species shared with Icelandic waters, based on this paper

OCTOCORALLIA Taxonomic group	Western North Atlantic		North Atlantic		New England and Corner, Sea-mounts, Bermuda		Eastern North Atlantic	
	IA	IIB	IIA	IIB	IIC	IIB	IIIA	IIIA
SCLERALCYONACEA								
Chrysogorgiidae	8/1		3/2		10/1			8/2
Ellisellidae	1/0							3/0
Keratosidae	3/0		3/1	3/1	2/1			8/1
Primnoidae	26/0		3/1	3/2	11/1			9/1
Coralliidae	4/1		3/3	2/2	5/1			8/2
Chelidonomidae	1/0							1/0
Sarcodictyonidae		1/1						1/1
Spongiodermidae	1/0							
Total:								
Watling et al. 2011 revised	44		13	9	28			38
Icelandic waters	1		8	4	4			7
% of common species	2.3		61.5	44.4	14.3			18.4
MALACALCYONACEA								
Alcyoniidae			3/3	3/3	1/1			5/2
Capnellidae			2/2	2/2				1/1
Clavulariidae			3/1	3/3				3/2
Paramuriceidae	3/1		3/2	2/2	5/2			21/5
Plexauridae	2/0							1/0
Tubiporidae	1/1			1/1				1/1
Eunicellidae								4/0
Gorgoniidae				1/0				2/0
Paralcyoniidae								1/0
Pterogorgiidae	2/0		1/0		1/0			0/0
Victorgorgiidae			1/0		1/0			1/0
Malacalcyonacea incertae sedis								1/0
Total:								
Watling et al. 2011 revised	8		13	12	8			41
Icelandic waters	2		8	11	3			11
% of common species	25		61.5	91.7	37.5			26.8
Octocorallia incertae sedis	1/0			1/0				3/2
Total number of species 2011/ number of species 2022*	57/53		28/26	24/22	40/36			86/82

*Updates from Watling et al. 2011: Eight taxa were not possible to assign to any family. Four species were merged with other species as they are now considered the same species. Thirty-eight species have changed family, four species are considered incertae sedis.

which may influence the transport and distribution of benthic species, including *Desmopyllum pertusum*, along the Icelandic shelf. The Greenland-Iceland-Faroe Island Ridge (GIFR) acts as a barrier, separating the cold Arctic waters from the warmer North Atlantic waters, and generates marked differences in near-bottom temperatures north and south of Iceland at depths below 500 m (Jochumsen et al. 2016). This temperature gradient affects species distributions, making the GIFR a well-known barrier for benthos, including several isopod and amphipod species or families (Weisshappel 2000; Brix and Svavarsson 2010; Dauvin et al. 2012; Omarsdottir et al. 2013). A similar pattern is seen in some species of the genus *Kolga* (Holothuroidea) (Rogacheva 2012). The GIFR poses a distributional barrier to some coral species, due to steep temperature gradients, or by restricting of larval dispersal between the deep basins on either side of the ridge. Buhl-Mortensen et al. (2015) suggested that the absence of the deep-water *Acanella arbuscula* from the Nordic Seas could attributed to limited larval transport over the GIFR.

Our results suggest the presence of three distinct cold-water coral assemblages in waters surrounding Iceland. The first assemblage (A) includes species with a circum-Icelandic distribution over the shelf area (< 500 m), and with a stronger preference for the northern region of Iceland. These species exhibit broad temperature and depth ranges and are seemingly unaffected by the temperature differences at the GIFR. It is also associated with colder waters mainly found north of Iceland. The second (B) and third (C) assemblages are associated with the deep basins in the south and west of Iceland and the more shallow following the ridge and the south shelf break. These basins are well connected to adjacent areas through three main current systems: the warm water of the North-East Atlantic Drift in the upper layer; a branch of the Labrador and Irminger Seas crossing the Mid-Atlantic or Reykjanes Ridge; and near the bottom, cold water from the north (the Iceland and Norwegian basins), which flows across submarine ridges between Greenland, Iceland, the Faroe Islands, and Scotland as overflow water (Malmgren 2004). Notable faunal similarity exists between Icelandic waters and Canada's Atlantic coast and Davis Strait, exemplified by many shared species in these areas (Gass and Willison 2005; Mortensen et al. 2006; Wareham and Edinger 2007; Murillo et al. 2011). Similarly, some faunal connection can be observed with the eastern North Atlantic, as currents in upper layer of North Atlantic water flow from the Iceland basin towards Norway. Similar species compositions are found in waters off Iceland and Norway (Mortensen et al. 1995; Freiwald and Mortensen 2000; Mortensen and Fosså 2006), whereas few species are shared with cold-water corals off the Azores (Sampaio et al. 2019).

Dauvin et al. (2012) identified three primary distributional groups of ampeliscid amphipods: Northern species,

Circum-Iceland species, and Southern species with a tendency to cross the Ridge (GIFR) northwards. They found three distinct bathymetric distribution groups: one found on the shelf and the upper slope around Iceland, a second with a broad bathymetric range, and the third consisting of deep-water species only below 500 m. These bathymetric groups exhibit patterns that closely resemble the cold-water coral assemblages described here.

Cairns and Chapman (2001) categorized 134 cold-water species of Scleractinia (found below 200 m) into 38 biogeographic zones within the North Atlantic, utilizing species composition to determine biogeographic affinities and relationships among localities. Similarity is noted between the Icelandic Scleractinia fauna and those in the eastern Atlantic, extending from Norway to the Bay of Biscay, as well as in the western Atlantic, from Canada to the cold temperate waters off the U.S. coast.

Watling et al. (2011) assigned Alcyonacea species into biogeographic zones based on Cairns & Chapman (2001). These species are now classified within the orders Scleractinia and Malacalcyonacea, excluding those in the Superfamily Pennatulioidea. Icelandic waters fall under biographic zone IIB (boreal eastern Atlantic and northern Mid Atlantic Ridge), although the specific contribution of Icelandic species to this group is unclear. The Icelandic Octocorallia (previously part of the Alcyonacea group) show a greater similarity to the western North Atlantic region (IIA) compared to the eastern Atlantic region (IIIA). While a similar comparison has yet to be conducted for sea pens, Williams (2011) noted that the Pennatulioidea superfamily in Icelandic waters primarily consists of deep-water taxa (8 genera) and some mid- to deep-water taxa (2 genera).

Following a revision of the Anthomastinae by Moldostova (2013), species of *Pseudanthomastus* (Tixier-Durivault & d'Hondt, 1974) and *Heteropolypus sol* (Molodtsova, 2013) were incorrectly identified as *Anthomastus* species. A revision for *Clavularia* specimens collected in Icelandic waters is needed, as *C. arctica* (Sars, 1860) was recorded at 55 BIOICE stations, mainly on the northern side of the GIFR. However, Madsen (1944) recorded *C. alba* (Grieg, 1888), *C. borealis* Koren & Danielssen, 1883 and *C. griegii* Madsen 1944 from only five stations in the Ingolf expedition; none of these species were reported by the BIOICE project. Primnoidae were recorded in three video transects south of Iceland, with two specimens resembling *Callogorgia* Gray, 1858, and one specimen resembling *Narella* Gray, 1870. Neither genus has been previously identified in Icelandic waters, leaving their identification uncertain due to the lack of collected samples.

The diversity of Antipatharia diminishes at high latitudes. According to Molodtsova (2006), only four species have been recorded north of 52°N. *Bathypathes patula* Brook 1889, *Stauropathes arctica* (Lütken, 1871) and *Stichopathes*

dissimilis Roule, 1902 were recorded on the Reykjanes Ridge (Molodtsova 2006), albeit south of Iceland's 200-mile EEZ. Here, we confirm the presence of *S. arctica* in Icelandic waters, along with a species of *Bathypathes* Brook 1889. Specimens of both species were collected during the BIOICE project and as bycatch in annual groundfish surveys by MFRI. A specimen of *Parantipathes* sp. was collected in the Denmark Strait in 2021. These records represent the northernmost occurrences of Antipatharia species in the NE-Atlantic.

Further taxonomic analyses of available samples that remain identified only to genus and family level are likely to unveil additional species. Considering that nineteen of the known and putative octocoral species are represented with only one or two records (Table 1) suggests that further sampling is likely to reveal several undetected species, as suggested by nonparametric estimation of species richness (Chao et al. 2009; Gotelli and Chao 2013) for incidence data (Chao2).

Iceland, as a signatory to the Kunming-Montreal Global Biodiversity Framework, is committed to establish a system of protected areas that will include at least 30% of marine areas. According to Target 3 of this agreement, the system of protected areas should include rare or threatened species and habitats, areas of high biodiversity, as well as representative examples of widely distributed species and habitats. The information on the distribution of cold-water corals compiled in this study will contribute to the design of a system of protected areas that will fulfil this objective by including (a) a high proportion of locations where cold-water corals with limited distribution are found, (b) areas with high species richness, and (c) representative areas with widely distributed taxa. In addition, the compiled data will be used to fit distribution models (e.g. Burgos et al. 2020) to provide a more complete view of the distribution of these taxa, an improved understanding of the environmental factors driving their distribution, and potential shifts in species ranges as result of climate change.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval No animal testing was performed during this study.

Data Availability Data will be available in public repositories in the near future.

Author contribution SHO and GG compiled and cleaned the data and added missing data to the database. SHO and JMB analyzed the data. All authors wrote the manuscript. All authors read and approved the manuscript.

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