

Cold-water coral growth in relation to the hydrography of the Celtic and Nordic European continental margin

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ABSTRACT: Along the Atlantic European continental margin, living cold-water coral reefs occur over a wide bathymetric and hydrographical range. Focusing on 2 regions, the Celtic and the Norwegian shelves, we found that cold-water coral reefs are limited to different intermediate water masses. Measurements of the physical and geological properties showed that parameters such as temperature, salinity, dissolved oxygen content, current intensities, and different substrates vary widely without specifically impacting the distribution of living cold-water coral reefs. The habitat of living reefs within the NE Atlantic comprises a temperature-salinity field, with its lower boundary equivalent to the Intermediate Salinity Maximum (ISM). The ISM on the Celtic margin is represented by Mediterranean Outflow Water (MOW), but is replaced by Atlantic Water (AW) on the Norwegian margin. The upper limit corresponds to water mass boundaries of Eastern North Atlantic Water/MOW on the Celtic margin and Norwegian Coastal Water/AW on the Norwegian margin. Our study shows that cold-water corals in the North Atlantic tolerate a wide range of environmental conditions. However, our data indicate that living cold-water coral reefs occur within the density envelope of sigma-theta (σ_θ) = 27.35 to 27.65 kg m⁻³, thus highlighting the importance of physical boundary conditions for cold-water coral growth and distribution.

KEY WORDS: Cold-water corals · NE Atlantic · Oceanography · Environmental parameters · Density dependence · Habitat

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INTRODUCTION

The environmental control of scleractinian coral reef growth is characterized by physical parameters such as temperature, salinity, and the deduced density as a function of temperature, salinity, and pressure, as well as oxygen availability and currents. These physical factors have been predominantly reported for tropical shallow-water zooxanthellate coral reefs (e.g. Veron 1993, Dullo 2005). Since the discovery of cold-water non-zooxanthellate coral reefs along the NW European continental margin (Dons 1944, Le Danois 1948, Henriot et al. 1998), it has also been discovered that similar dynamics seem to control reef and coral growth on deeper continental margin settings (Dorschel et al. 2007, White 2007). In this paper, we present for the first time detailed hydrographic measurements of water

masses on seasonal time scales from cold-water coral reefs on the Celtic and Norwegian margin (see Fig. 1).

Cold-water coral reefs are widespread along the European continental margin (Freiwald et al. 2004, Roberts et al. 2006). They create large carbonate mounds along the shelves of the Porcupine and Rockall Banks, and form dense reef ecosystems on morphological highs off Norway, the Faroe Islands, and in Scottish waters (Freiwald et al. 1999, Roberts et al. 2005). In the present study we focused on dense living *Lophelia pertusa* coral reefs identified by ground truthing and video surveys from remotely operated vehicles and manned submersibles.

Carbonate mounds occur in distinct regions on the Celtic continental margin (Wheeler et al. 2007). The largest mounds have diameters of up to 5 km and elevations up to 350 m above the surrounding seafloor. Liv-

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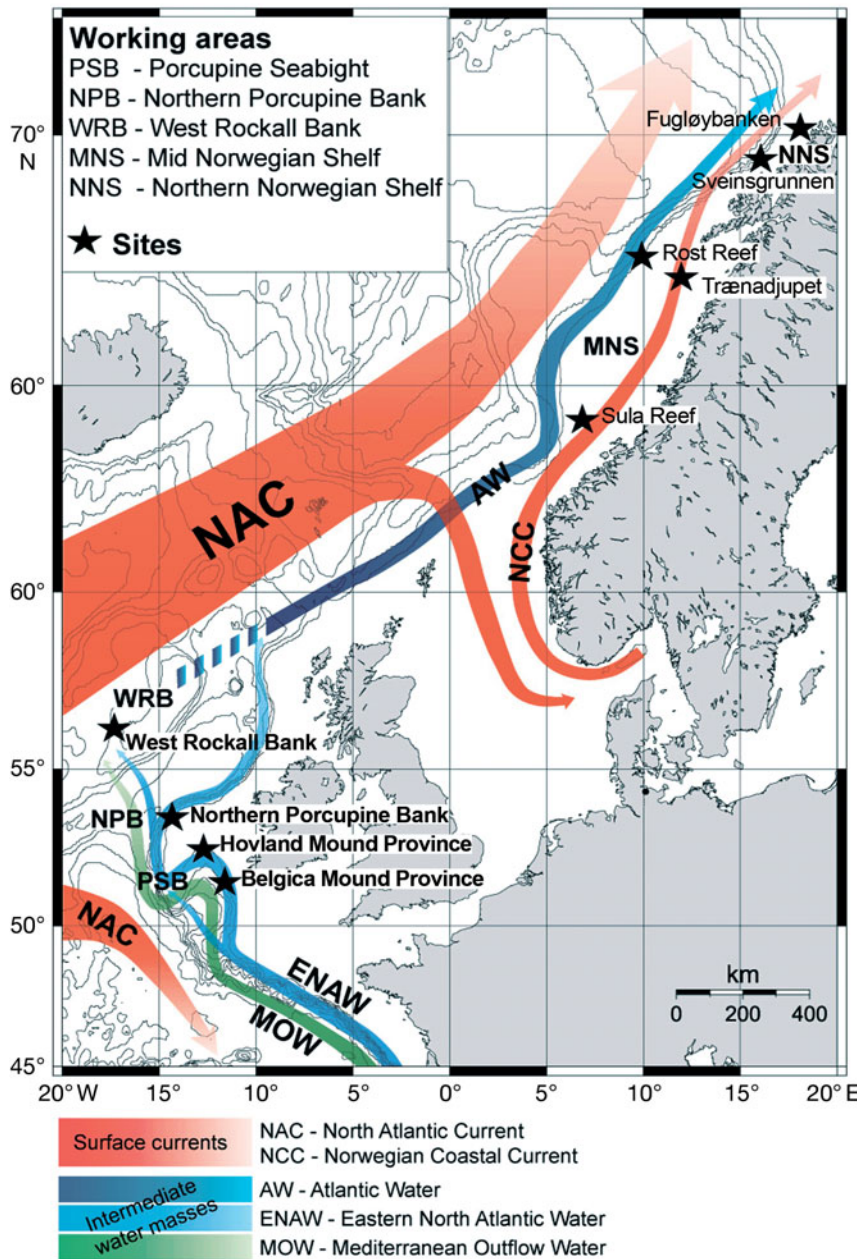


Fig. 1. Investigated locations of cold-water reefs along the Celtic and Norwegian Margin and prevailing current regimes. Red arrows indicate surface currents of the North Atlantic Current (NAC) and the Norwegian Coastal Current (NCC), blue and green arrows indicate intermediate water mass circulation of Mediterranean Outflow Water (MOW), the overlying Eastern North Atlantic Water (ENAW) and Atlantic Water (AW)

ing cold-water coral reefs thrive in depths of about 700 to 850 m. The Porcupine Seabight hosts 3 carbonate mound provinces, the Belgica, Hovland, and Magellan Mound Provinces. Each mound province is defined by distinct mound characteristics (Henriet et al. 1998, De Mol et al. 2002). The Belgica Mound Province is located in the eastern Porcupine Seabight and is characterized by dense coral reefs on the top and upper western

flanks of the mounds. The Hovland Mound Province shows similar mound morphologies. However, the crops of living corals are restricted to isolated patches. Present-day coral reef and mound growth is very poor and limited to the upper flanks (Dorschel et al. 2005, Rüggeberg et al. 2007). The Magellan Mound Province north of the Hovland Mounds consists mainly of buried mounds (Huvenne et al. 2007). Carbonate mounds on the western Rockall Bank and the northern Porcupine Bank occur in water depths between 550 and 1200 m. Living cold-water corals are found at depths of 600 to 800 m (Kenyon et al. 2003, van Weering et al. 2003, Wienberg et al. 2008). They form a complex arrangement of mound clusters that are aligned up- and downslope (Mienis et al. 2006). The mounds have diameters of hundreds of meters to several kilometers.

The living cold-water coral reefs along the Norwegian margin are post-glacial in age (Freiwald et al. 1999, Lindberg et al. 2007) and do not form carbonate mounds such as those seen on the Celtic margin. The corals build elongated reef-like structures up to 40 m in height and several kilometers in length (Freiwald et al. 1999, Freiwald 2002). They mainly occupy water depths between 150 and 400 m with shallower occurrences in fjord settings. Their distribution is controlled by bottom topography of glacial origin, e.g. plough marks, moraines, and ridges (Fosså et al. 2005). In some parts, they form a small veneer over the existing topography mimicking coral mounds, as seen in the classic locality of Stjærnsund Sound (Dons 1944, Freiwald et al. 1997).

The general surface hydrography in the NE Atlantic and the Norwegian-Greenland Sea is characterized by the northward transport of warm subtropical water to high latitudes, the North Atlantic Current (NAC). The NAC splits into 2 branches, the northern branch entering the Norwegian-Greenland Sea through the Faroe-Shetland Channel, and the southern branch flowing into the Bay of Biscay moving south to join the subtropical gyre (Pingree 1993).

Waters bathing cold-water coral reefs and mound structures along the Celtic margin belong to 2 major components of the NE-Atlantic circulation. The upper-layer water mass, described as Eastern North Atlantic Water (ENAW), is part of the NAC being formed mainly during the winter months in the Bay of Biscay. Seasonally, a surface layer of up to 50 to 100 m thickness develops and is modified by atmospheric interaction. It is characterized by increased surface temperatures ($\Delta T = 4$ to 6°C , Ellet et al. 1986). The other important component of the NE Atlantic circulation on the Celtic Margin is the Mediterranean Outflow Water (MOW) which forms the major intermediate water mass. The MOW is characterized by an increase of salinity and potential temperature in comparison to over- and underlying water masses. In the Porcupine Seabight, this water mass has its core at around 1000 m water depth, exhibiting a thickness of ~ 600 m. MOW can be differentiated in the Gulf of Cadiz into a higher density lower core (~ 1250 m) and a lower density upper core around 750 m (Zenk & Armi 1990). The upper core of the MOW flows farther north along the European continental margin underlying ENAW. Upper portions of this MOW mix with ENAW in the eastern North Atlantic and with Subarctic Intermediate Water (SAIW) in the western North Atlantic, while lower portions mix with Labrador Sea Water (LSW) (Harvey 1982, Ellet et al. 1986, Pollard et al. 1996, van Aken 2000, White et al. 2005, White 2007).

Within the Porcupine Seabight, warm, saline water fills the upper layer down to about 600 m depth. This water mass is of ENAW origin, carried northwards adjacent to the NE Atlantic margin (Pollard et al. 1996). A high salinity level marks MOW, which occupies the whole basin between 800 and 1000 m depth. The upper level of MOW is associated with the permanent thermocline. The thermocline matches the mean water depth where carbonate mounds are found. MOW is also present west of the Porcupine Bank, but its signal rapidly diminishes north of 53°N because it re-circulates west of the bank (e.g. New et al. 2001).

Surface water masses around Rockall Bank derive from a northwestern branch of ENAW and North Atlantic Waters as well as from fresher, modified North Atlantic Water, the SAIW from the north and west (Lankhorst & Zenk 2006). Detached pockets of MOW reach the western Rockall Bank at water depths between 800 and 1100 m (Harvey 1982). Beneath these pockets lies intermediate water still showing ENAW characteristics. In contrast to the Porcupine Seabight where ENAW and MOW dominate the intermediate hydrography, the southwestern Rockall Bank shows the influence of SAIW at the surface to ~ 300 m water depth and of LSW, which is found at greater depths (Harvey 1982, Bower et al. 2002).

The hydrography along the Norwegian margin is characterized by the Norwegian Atlantic Current (NwAC) under which Arctic Intermediate Water constitutes a salinity minimum at depths of ~ 600 m (Blindheim 1990). This intermediate water mass has no influence on the distribution of living corals. Their depth habitat is much shallower (300 to 380 m in Røst Reef, 140 to 250 m in Fugløybanken, 300 to 380 m in Sula Reef; Fig. 1) and the water masses involved belong to the surface water regime of the NAC, which is overlain by less saline freshwater discharge from the Norwegian landmass (Freiwald 2002). The Norwegian Coastal Current (NCC), which originates primarily from the freshwater outflow from the Baltic and freshwater runoff from Norway, flows northwards parallel to the coast and dominates the large-scale surface water circulation (Mork 1981). The distribution of this water mass within the Norwegian Sea is governed by a density-induced flow generally towards the north (Heaps 1980), which has a north-eastward component along the Norwegian slope through the study area (Blindheim 1990).

Recent studies have demonstrated that the ocean is changing both chemically and physically as a result of the uptake of anthropogenic CO_2 (e.g. Orr et al. 2005), which may affect deep-water coral distribution and growth (Guinotte et al. 2006, Turley et al. 2007). Although this is a major future concern, it is beyond the scope of this study, since we focused exclusively on the present situation of living cold-water coral reef distribution.

MATERIALS AND METHODS

The major objective of Conductivity-Temperature-Depth (CTD) measurements during RV 'Meteor' cruises M61-1 (April 2004) and M61-3 (June 2004), RV 'Poseidon' cruises P316 (August 2004) and P325 (July 2005), and RV 'Polarstern' cruise ARK XXII/1a (June 2007) was to determine the variability of water masses around the carbonate mounds and cold-water coral reefs in the provinces shown in Fig. 1. This study is based on a total of 157 CTD casts (Table 1).

During all cruises, CTD measurements of the water column were conducted using a Seabird 'SBE 9 plus' underwater unit and a Seabird 'SBE 11 plus' deck unit. Pre-cruise laboratory calibrations of the conductivity, temperature, and pressure sensors were performed, yielding coefficients for a linear fit. For the analysis and interpretation of the measurements, the downcast raw data were used. Further processing of the data, including standard statistics, was performed using the software SBE Data Processing, Version 5.30a (www.seabird.com or <ftp://ftp.halcyon.com/pub/seabird/OUT>)

Table 1. Investigated sites and number of CTD casts. PSB: Porcupine Seabight; NPB: Northern Porcupine Bank; WRB: Western Rockall Bank; MNS: Mid-Norwegian Shelf; NNS: Northern Norwegian Shelf

Area	Site	Latitude	Longitude	Depth (m)	No. of casts
PSB	Poseidon Mound	51°27.44'N	11°42.00'W	691	11
PSB	Galway Mound	51°27.11'N	11°45.17'W	784	39
PSB	Thérèse Mound	51°25.70'N	11°46.27'W	850	8
PSB	Propeller Mound	52°09.00'N	12°46.50'W	670	3
NPB	Connacht Mound	53°31.00'N	14°21.00'W	680	6
WRB	Kiel Mount	56°41.85'N	17°31.26'E	842	19
WRB	Franken Mound	56°30.02'N	17°18.10'E	652	20
MNS	Sula Reef	64°08.20'N	08°11.40'E	300–380	1
MNS	Røst Reef	67°31.74'N	09°30.14'E	300–380	28
MNS	Trænadjupet Reefs	66°53.50'N	11°07.47'E	300–380	16
NNS	Sveinsgrunnen	69°43.00'N	16°21.00'E	150–250	5
NNS	Fugløybanken	70°07.74'N	18°07.98'E	140–190	1

and Ocean Data View mp-Version 2.0 (<http://odv.awi.de>) for visualization.

Additionally, the CTD was equipped with a dissolved oxygen sensor and a Seabird bottle release unit including a rosette water sampler with 10 l Niskin bottles. At each site, bottom water and water from selected depth levels were sampled and analyzed to validate CTD oxygen data. Samples were then analyzed on-board by iodometric oxygen titration according to the Winkler method (Grasshoff 1983). Immediately after the collection, the water samples were filled into volume-calibrated, 100 ml Winkler bottles, and the oxygen was fixed with 0.5 cm³ manganese-II-chloride and 0.5 cm³ alkaline iodide. The bottles were shaken and stored cooled for several hours.

Prior to titration, 1 cm³ H₂SO₄ (9 M) was added, the bottles were shaken to dissolve the Mn-hydroxides, and the sample was poured into a 400 ml beaker. We titrated with sodium thiosulfate (0.02 M), which was calibrated prior to analyses, until a light yellowish color appeared. At this point, 1 cm³ zinc iodide solution was added and titration was continued until the blue color disappeared. The oxygen content was calculated from the thiosulfate consumption using the standard formula:

$$O_2 \text{ [ml/l]} = (a \times f \times 112) / (b - 1) \quad (1)$$

where a = consumption of thiosulfate solution (cm³), b = volume of the sample bottle (cm³), and f = calibration factor of the thiosulfate solution. The offset between measured and titrated samples never exceeded 2%.

The density of seawater is important to describe and understand ocean-mixing processes because it is easier to mix water along a surface of constant density (an 'isopycnal') than across it. Density is a nonlinear function of pressure, temperature, and salinity resulting in e.g. 1028.106 kg m⁻³ when pressure = 0 db, tempera-

ture = 0°C and salinity = 35. To properly compare seawater samples, one should refer their densities to the same isobar (e.g. at the sea surface = 0, Dietrich et al. 1992). Conductivity and temperature are first used to compute salinity, which is then combined with potential temperature to compute the potential density anomaly (σ_θ = sigma-theta) defined as

$$\sigma_\theta \text{ (sigma-theta)} = 1 / V_{(S, \theta, p)} - 1000 \text{ kg m}^{-3} \quad (2)$$

where V = specific volume, S = salinity, θ = potential temperature, and p = pressure at the sea surface. To compare cold-water corals and the surrounding water masses at the investigated sites, we used potential temperature and

sigma-theta to describe these settings of the different coral sites along the European continental margin. Living cold-water coral reefs are nevertheless limited to the water masses defined by sigma-theta and experience the characteristics of this environment.

RESULTS

During this study, CTD measurements were used to identify the distribution of water masses in the NE Atlantic and the Norwegian-Greenland Sea and relate these to the distribution of living cold-water coral reefs (Fig. 1). Temperature-Salinity (TS) plots were used to determine the water mass structure and stratification (Fig. 2) in the study area. The CTD data for the Porcupine Seabight, the West Rockall Bank, and the Norwegian margin (no seasonal cover) were collected throughout the water column.

At the Celtic sites, the emphasis was on the depth interval of living corals between 640 and 1150 m water depth (Fig. 3a,b), while Norwegian margin data were investigated in detail between 188 and 1040 m water depth (Fig. 3c). All data displayed the typical water mass characteristics of the NE Atlantic. Within the Porcupine Seabight, warm surface waters overlay the ENAW (Fig. 2a). With increasing water depth, potential temperature and salinity decreased to a minimum at ~600 m (Fig. 3a). Increasing salinity values indicate the occurrence of MOW below ~700 m, with coherent decreasing oxygen content. Here, bottom waters also showed a seasonal signal indicating seasonal variation of MOW outflow. Individual CTD casts from the Hovland Mound Province in the northern Porcupine Seabight showed that the signature of MOW seemed to be bathymetrically shallower compared to the Eastern margin (Belgica Mound Province), resulting from

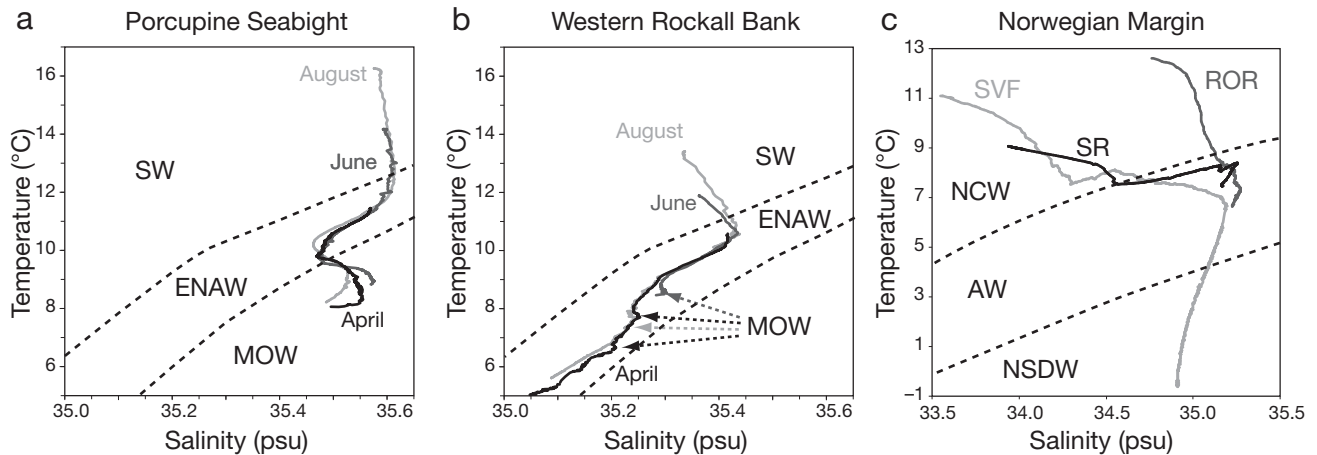


Fig. 2. Temperature-Salinity (TS) plots indicating different water masses of (a) Porcupine Seabight, (b) Western Rockall Bank, and (c) Røst Reef/Trænadjupet (ROR), Sveinsgrunnen/Fugløy (SVF), and Sula Reef (SR). Black, dark gray and light gray lines represent April, June and August respectively in (a) and (b), and SR, ROR and SVF respectively in (c). MOW in (b) shows seasonal variation in water depth (black arrows: April; dark gray arrow: June; light gray arrow: August at the Western Rockall Bank). AW: Atlantic water; ENAW: Eastern North Atlantic Water; MOW: Mediterranean Outflow Water; NACW: North Atlantic Central Water; NCW: Norwegian Coastal Water; NSDW: Norwegian Sea Deep Water; SW: Surface Water. ENAW envelope in (a) and (b) after Harvey (1982)

the northward and up-slope flow of water masses. A previous study indicated that the current intensity weakens in the northern Porcupine Seabight and the general flow turns to the southwest (White 2007).

Compared to the Porcupine Seabight, the TS-plot for the West Rockall Bank (Fig. 2b) showed colder and less saline surface waters, which can be attributed to SAIW, which has an influence down to ~300 m water depth (Harvey 1982). Below the surface water, the linear TS-relation indicates the occurrence of a colder and less saline water mass, which we interpret as ENAW. It plotted within the ENAW envelope of Harvey (1982). Detached pockets of increased salinity show contributions of MOW (Harvey 1982) or at least traces, since MOW diminishes north of 53°N (Bower et al. 2002, White 2007). Additionally, the hydrographic data from this region showed the influence of seasonal variations of MOW outflow and transport to the West Rockall Bank. Three distinct spikes marked the variable influence of MOW (arrows in Fig. 2b) between April, June, and August.

The Norwegian sites were clustered in 2 larger regions. Sula Reef and Røst Reef/Trænadjupet belong to the Mid-Norwegian Shelf, while Sveinsgrunnen/Fugløy belongs to the Northern Norwegian Shelf (NNS). All 3 Norwegian sites (Fig. 2c) showed a TS relation of surface waters belonging to the Norwegian Coastal Water (NCW). The observed difference of less saline surface water at the northern Sveinsgrunnen/Fugløy and southern Sula Reef sites originates from a stronger influence of continental river discharge and fjord waters (Fig. 3c). Below the coastal water, the dominance

of Atlantic Water (AW) was clearly marked by a sharp increase in salinity to values >35 and a simultaneous decrease in potential temperature to values of <8.5°C. While the AW was detected at all 3 sites, the Norwegian Sea Deep Water (NSDW) was only observed in the northernmost locality below 800 m water depths.

The analysis of the single parameters T, S, density, and dissolved oxygen was used to determine possible envelopes favoring the distribution of living cold-water corals. In the bathymetric window of living cold-water coral reefs along the European continental margin, the investigated environmental parameters mentioned above lay in the range of described values for *Lophelia pertusa* (Freiwald et al. 2004). Following the latitudinal gradient from south to north, temperature and salinity decreased from ~10°C and 35.55 in the Porcupine Seabight to ~6.5°C and ~35.51 at the NNS, while dissolved oxygen increased from ~4 ml l⁻¹ in the Porcupine Seabight to ~6.6 ml l⁻¹ at the NNS. Density values remained constant with $\sigma_{\theta} = 27.3 \text{ kg m}^{-3}$ at the upper limit (UL) and $\sigma_{\theta} = 27.5 \text{ kg m}^{-3}$ at the lower limit (LL) of living cold-water coral reefs at the Celtic sites (Fig. 3a,b). Norwegian localities had similar density values of 27.4 to 27.6 kg m⁻³.

Within the bathymetric window of living corals, potential temperatures in the Porcupine Seabight ranged from 9.24°C at the lower depth limit to 9.89°C at the UL (Fig. 3a). Farther north, the same window had a potential temperature range from 8.57 to 9.28°C at West Rockall Bank (Fig. 3b) while the Norwegian sites plotted between 6.5 and 7.6°C (Fig. 3c,d). Although the habitat of living corals becomes shallower

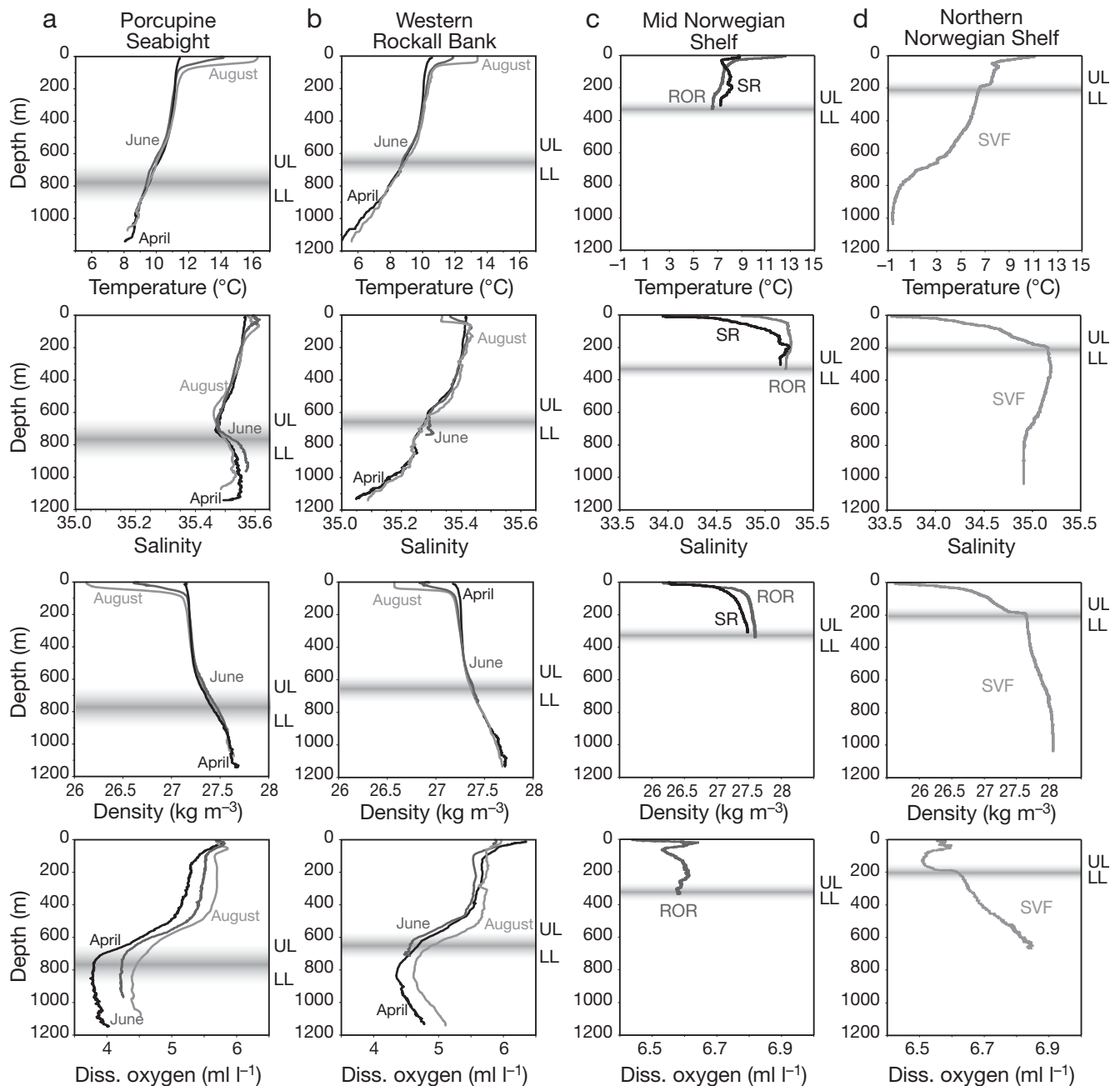


Fig. 3. Seasonal (April, June, and August) physical parameters of salinity, potential temperature, density, and dissolved (diss.) oxygen in (a) the Porcupine Seabight and (b) the Western Rockall Bank. The same physical parameters in June/July in (c) the Røst Reef/Trænadjupet (ROR) and Sula Reef (SR) areas along the Mid-Norwegian Shelf and (d) the Sveinsgrunnen/Fugløy area of the Northern Norwegian Shelf. Black, dark gray and light gray lines represent April, June and August respectively in (a) and (b) and SR, ROR and SVF respectively in (c) and (d). The blurred, grey horizontal bar represents the depth habitat of living cold-water coral reefs with its lower (LL) and upper limits (UL)

in a northward direction, the potential temperatures decrease and do not play a significant role in coral distributions. Even on a seasonal scale, potential temperature changes only very little ($\Delta T = 0.05^{\circ}\text{C}$) at the Celtic sites but has a greater variability farther north ($\Delta T = 1$ to 2°C , Mortensen & Rapp 1998).

Within the Porcupine Seabight, the LL of the relevant depth interval showed salinities between 35.52 and 35.57, while the UL was almost constant at 35.48 (Fig. 3). The shallower coral habitat on the West Rockall Bank plotted between 35.27 (LL) and 35.29 (UL). Less saline waters exhibited values of 35.25 for the

LL and UL at Røst Reef/Trænadjupet. A wider range was recorded for Sveinsgrunnen/Fugløy (between 35.2 [LL] and 34.9 [UL]). In contrast to the potential temperature readings, the salinity data showed an observable temporal variability in the Porcupine Seabight. While the UL was almost constant, the LL varied between 35.52 (August), 35.53 (April), and 35.57 (June).

Oxygen measurements showed a different pattern with respect to the habitat range of living corals (Fig. 3). The latitudinal variability ranged from 3.76–4.39 ml l⁻¹ (LL) to 3.94–4.60 ml l⁻¹ (UL) in the Porcupine Seabight, from 4.57–4.73 ml l⁻¹ (LL) to 4.84–5.18 ml l⁻¹ (UL) at the West Rockall Bank, and from 6.57 ml l⁻¹ (LL) to 6.61 ml l⁻¹ (UL) at the mid-Norwegian shelf, to 6.52 ml l⁻¹ (LL) to 6.64 ml l⁻¹ (UL) at the northernmost site.

Strong seasonality in our Celtic data was observed in the surface layer (<100 m) with increasing summer values of potential temperature and density and decreasing salinity values. Only dissolved oxygen showed a seasonal variability through the entire water column. At the depth of living cold-water coral reefs, values ranged from 3.8 ml l⁻¹ in April to 4.6 ml l⁻¹ in August for the Porcupine Seabight and from 4.5 to 4.9 ml l⁻¹ on the West Rockall Bank, respectively. It is interesting to note that the bathymetric range where living corals occur (Fig. 3a,b) is not influenced by any seasonal variation in potential temperature and density during spring and summer. A potential temperature difference of 0.05°C in bottom waters (spring and summer) was measured in the Porcupine Seabight, while density plotted between 27.3 and 27.5 kg m⁻³. The West Rockall Bank showed a similar pattern with a ΔT of 0.2°C and constant σ_θ of ~ 27.4 kg m⁻³. However, our data indicate variability in salinity between the months of April and June, with an increase of 0.03 to 0.04, while no offset was observed between April and August.

DISCUSSION

Hydrographic measurements on the Celtic and Norwegian margin revealed that different water masses influence cold-water coral ecosystems. The question arises whether a single or a set of environmental factors controls their distribution. Previous studies have shown that cold-water corals tolerate a wide range of environmental factors (Rogers 1999, De Mol et al. 2002, Freiwald 2002). However, along a transect stretching from 51 to 70°N (~ 3000 km), our study indicates that corals are not randomly distributed but rather follow a narrow density (σ_θ) envelope of $\sigma_\theta = 27.35$ to 27.65 kg m⁻³, independent from the surrounding water masses.

Physical/oceanographic parameters

Our measured data show that cold-water corals tolerate a wide range of potential temperatures. In the Porcupine Seabight, temperatures ranged from 9.24°C at the lower depth limit to 9.89°C at the UL, and from 8.57 to 9.28°C at West Rockall Bank. The Norwegian sites plotted between 6.5 and 7.6°C. Thus, our data illustrate that potential temperature is not the decisive factor controlling growth and distribution of corals. However, our temperature data correspond to the findings of Bryan & Metaxas (2006), who indicated that gorgonian corals can survive in a wide temperature range but are most abundant primarily between 5 and 9°C.

In contrast to the potential temperature readings, the salinity data showed an observable temporal variability in the Porcupine Seabight. This small-scale variability is related either to differences in seasonal vertical mixing processes also displayed in the dissolved oxygen content at Galway Mound (Belgica Mound Province) or to variable MOW content (Bower et al. 2002). Within the Porcupine Seabight, the LL of cold-water coral habitats had salinities from 35.52 to 35.57, while the UL varied around 35.48. A wider range of 35.2 to 34.9 was measured for the northern Norwegian sites. The increasing influence of less saline waters to the north indicates the presence of NCW, which forms a freshwater wedge under the influence of brackish Baltic outflow water and continental discharge. This wedge is thickest at the coastal sites (Sveinsgrunnen/Fugløy), covering the upper 200 m, and thins out westwards to the continental margin (Røst Reef/Trænadjupet) where it decreases to about 50 m. Due to the large range of tolerated salinity values, we suggest that this parameter is important but is not the limiting factor for cold-water coral growth.

Oxygen measurements showed a different pattern with respect to the habitat range of living corals. The oxygen content exhibits a large latitudinal variability with strongly increasing values from the south to the north. In the southernmost location (Porcupine Seabight) dissolved oxygen ranged from 3.76–4.39 ml l⁻¹ for the LL to 3.94–4.60 ml l⁻¹ for the UL, while the northernmost site (Sveinsgrunnen/Fugløy) exhibited values of 6.52 ml l⁻¹ (LL) to 6.64 ml l⁻¹ (UL). This is most likely associated with the simultaneous decrease in water depths and bottom temperatures and the increasing solubility product. In addition, the Celtic sites experience the influence of O₂-depleted MOW. Although the measured values of dissolved oxygen were almost twice as high at the Norwegian sites, the internal reef structure of the cold-water coral habitats is not considerably different (Mortensen et al. 1995, Freiwald 2002, Foubert et al. 2005), suggesting that cold-water corals live within a wide range of dissolved oxygen. This is in

agreement with a study by Dodds et al. (2007), who demonstrated a wide tolerance of *Lophelia* with respect to oxygen values in an experimental setup. In contrast to potential temperature and salinity, the annual variability of dissolved oxygen is well pronounced at each site. We ascribe these differences to the annually changing nutrient supply, which in turn controls oxygen availability and consumption (Kenyon et al. 2003, pers. obs. with the manned submersible JAGO and IFM-GEOMAR's Ocean Floor Observatory System

[OFOS]). Furthermore, these seasonal nutrient variations are also recorded in the distinct isotope signal of *L. pertusa* skeletons (Mortensen & Rapp 1998, Freiwald 2002). Thus, we consider that—like potential temperature and salinity—dissolved oxygen is not a limiting parameter controlling the distribution of living cold-water corals along the NW European continental margin.

Irrespective of depth and location, each site showed similar potential densities ($\sigma_\theta = \text{sigma-theta}$) of bottom water masses bathing living cold-water coral reefs. All

investigated sites had maximum values of 27.45 to 27.65 kg m^{-3} characterizing the LL of living coral occurrences, while values slightly decreased to 27.35 kg m^{-3} at the UL (Fig. 3). No seasonal variation was observed at least for the southern provinces on the Celtic margin, for which we have a seasonal data set. It is striking that the corals are bound to water masses with a very specific sigma-theta value. Fig. 4 displays major TS-signatures of the Celtic and Norwegian sites within the framework of regional hydrography. The habitat of living cold-water corals comprises a field in the TS-diagram with its lower boundary equivalent to the upper boundary of the Intermediate Salinity Maximum (ISM; Ellett et al. 1986). The ISM along the Celtic margin is represented by MOW, whereas the ISM along the Norwegian margin is characterized by AW. The upper boundary of this field corresponds to the lower boundary of ENAW along the Celtic margin, while it is confined by NCW on the Norwegian margin. We argue that water masses with a sigma-theta of $27.5 \pm 0.15 \text{ kg m}^{-3}$ are a crucial prerequisite for cold-water coral growth and distribution at the investigated sites. This raises the question of 'What is unique about the described density interval and its relation to living cold-water coral reefs?'

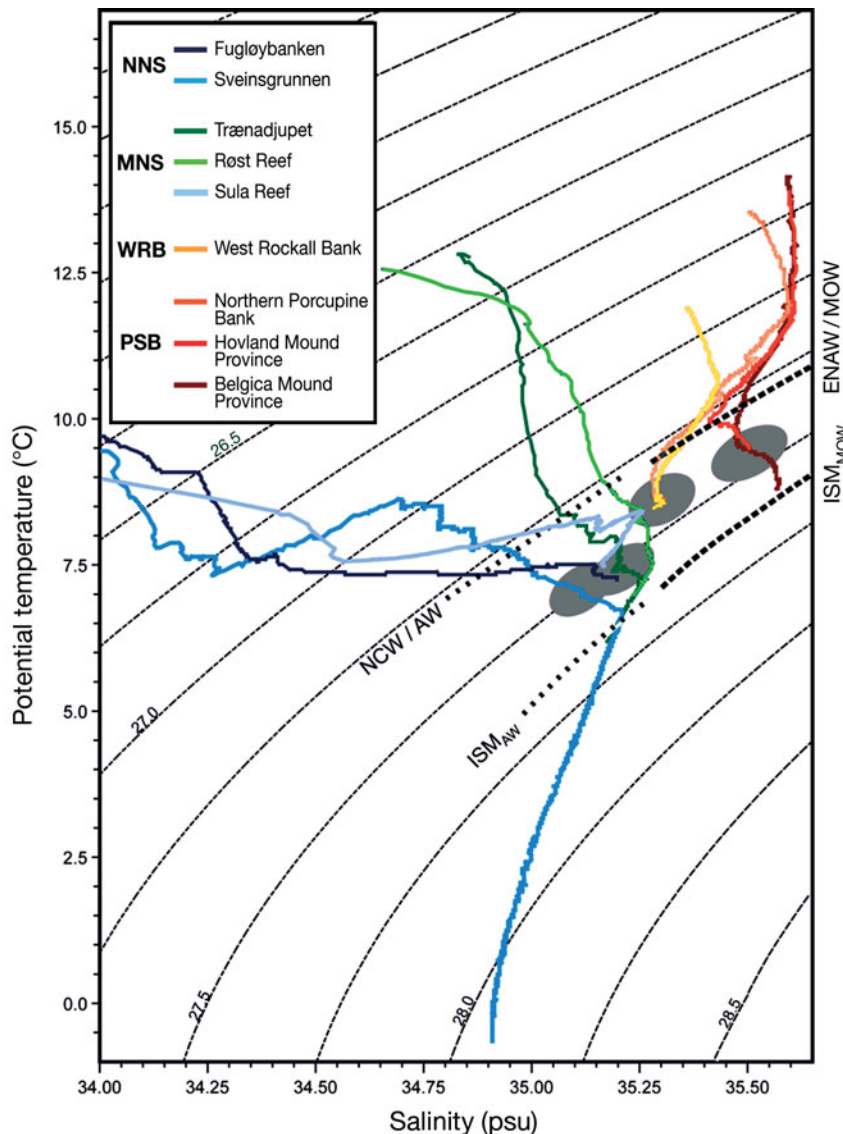


Fig. 4. TS-plot of all investigated sites. Thin dashed lines indicate levels of isodensity (σ_θ) in kg m^{-3} . Grey patches show habitats of living cold-water coral reefs. The lower limit is confined by the Intermediate Salinity Maximum (ISM) corresponding to Mediterranean Outflow Water (ISM_{MOW}) on the Celtic margin and to Atlantic Water (ISM_{AW}) on the Norwegian margin. The upper limit is characterized by the water mass boundaries of Eastern North Atlantic Water (ENAW)/MOW (Celtic sites) and Norwegian Coastal Water (NCW)/AW (Norwegian sites). MNS: Mid-Norwegian Shelf; NNS: Northern Norwegian Shelf; PSB: Porcupine Seabight; WRB: Western Rockall Bank

Geological and biological factors

Previous studies have shown that cold-water corals occur mainly in areas with a high current regime where exposed hard ground serves as a substrate on which filter-feeding organisms can settle (Rogers 1999, De Mol et al. 2002, Freiwald 2002). Bryan & Metaxas

(2006) reported that bottom topography can be used as a proxy for locations with hard substrates, since areas of pronounced topographic relief will exhibit low sedimentation rates (Freiwald et al. 1999, Herring 2002). For example, seamounts and canyons are areas with pronounced vertical relief with hard substrata providing ideal settling sites for corals, often associated with a strong current regime and therefore low sediment deposition (Herring 2002). The scleractinian *Lophelia pertusa* has been recorded on morainic ridges, lithified sediments, and vertical cliffs (Freiwald et al. 1999, Noé et al. 2006), but also in coarse sand habitats (Foubert et al. 2005, Huvenne et al. 2005, Wheeler et al. 2005). It is assumed that the coral initially settles on a hard substrate such as a pebble or a shell (e.g. Mortensen et al. 2001), but only in areas where environmental conditions are favorable for coral growth. These are associated with an adequate nutrient supply and removal of resuspended sediment. In a numerical simulation, Thiem et al. (2006) demonstrated that *Lophelia* reefs form in areas where the encounter rate of food is sufficiently high and stable over long periods of time. This condition is favored particularly on outer shelves and shelf breaks.

Irrespective of depth and location, each site showed living cold-water coral reefs in the well-defined density envelope of 27.35 to 27.65 kg m⁻³. This horizon shallows towards the north but correlates well with the occurrence of intermediate nepheloid layers (INLs), an important mechanism for nutrient supply to deeper shelf environments (White et al. 2005). Azooxanthellate corals depend mainly on particulate organic matter (POM), as was shown for *Lophelia* and *Madrepora* (Kiriakoulakis et al. 2005, 2007), although some exceptions of dissolved organic matter (DOM) do exist (Yakovovitch et al. 2003). Based on isotopic studies, Duineveld et al. (2004) report on a mixed diet (animals and algae) of the corals, but excluded bacteria as a possible food source. The physical boundary conditions for such POM enrichment are given at the described density contrasts, independently of the water masses involved. Well-developed INLs are reported on both margins of the Rockall Trough in a depth zone between 450 and 700 m (Dickson & McCave 1986, Kenyon et al. 2003). An INL has also been encountered in the Porcupine Seabight between 700 and 1400 m, and a strong autumn INL between 700 and 970 m (McCave et al. 2001). Rumohr et al. (2001) mapped the distribution of water masses and particle load by applying CTD plus a transmissiometer on a hydrographic transect at Røst Reef. Particle-rich bottom water detached from the seafloor formed an INL at ~400 m water depth, the depth where the water mass boundary of NCW and AW occurred. Similar processes have also been reported for the outer Trænadjupet

area (Rumohr et al. 2001), suggesting that these processes are a common episodic feature along the Norwegian margin, fuelling the living coral reefs.

In both areas, INLs correlate with the depth range of living coral reef occurrences and are important as a source of detrital organic particles, increasing the food availability for bottom fauna (Frederiksen et al. 1992), and their presence may be crucial for the formation of mature *Lophelia* reefs (Kenyon et al. 2003). The question arises as to whether the density envelope of $\sigma_{\theta} = 27.35$ to 27.65 kg m⁻³ supports the formation of INL at mid-depth shelf areas. INLs are an important mechanism for nutrient supply to cold-water coral reefs, but also form where no coral reefs occur and other factors dominate. Therefore, INLs are also a second-order control mechanism and not a prerequisite for the occurrence of cold-water coral reefs.

Beyond this, we speculate that the distribution of associated coral larvae may be controlled by the density surface/envelope as well, although spawning, subsequent external fertilization, and larval development have not yet been documented (T. Lundälv pers. comm.). Cold-water coral larvae have been documented, but no information on the densities of larvae is available. As an example, a seasonal phytoplankton bloom in July has been reported for the Porcupine Seabight (Lampitt et al. 2001). The surface primary production sinks rapidly to the seafloor (Billett et al. 1983, Lampitt 1985, Thiel et al. 1989) where it initiates gametogenesis in corals (e.g. Waller & Tyler 2005) due to a substantial increase in the availability of POM. This coincides with the energetically expensive onset of production of gametes in *Lophelia pertusa*. This gamete growth continues in *L. pertusa* until the gametogenic cycle is completed and, according to Waller & Tyler (2005), spawning takes place in January/February. No studies have reported the collection of *Lophelia* or *Madrepora* larvae. Therefore, models from shallow-water reefs have been used so far. There are basically 3 types of larvae: buoyant larvae that rise to the sea surface upon ejection, neutral larvae that drift with the current staying submerged, or negatively buoyant or crawling larvae. We speculate that gametes could have densities that limit their concentration and lateral transport to the described density envelope of 27.35 to 27.65 kg m⁻³, since above and below these levels all coral mounds are dead.

Potential density – a tool to locate cold-water corals

During cruise ARK XXII-1a with RV 'Polarstern,' we used the following approach to locate cold-water coral reefs along the Norwegian margin. First, we used CTD measurements to identify bottom water characteristics

with respect to sigma-theta. Next, we checked if bottom water densities were within the described envelope of 27.35 to 27.65 kg m⁻³ and within the T-S-O₂ range tolerated by the corals. Next, we used bottom topography data to identify localities with a pronounced relief and a suitable current regime, which favors low sedimentation rates, high nutrient influx, and hard ground formation, which are necessary for initial growth. In a final step, we successfully used the manned submersible JAGO to ground-truth living cold-water coral reefs.

Leverette & Metaxas (2005) have shown that the ecological niche factor analysis is a potential tool for determining suitable habitats for deep-water corals (gorgonians) which requires a complex data set of different environmental parameters; our approach, however, is simpler. The applicability of our method has been successfully confirmed by literature data for the Strait of Florida (Wang & Mooers 1998, Grasmueck et al. 2006), the Scotian Shelf off Nova Scotia and Newfoundland (Han & Loder 2003, Mortensen & Buhl-Mortensen 2005), and the Brazilian shelf (Kitahara 2006). These studies have further confirmed that potential density is an important prerequisite for cold-water coral distribution in the North Atlantic. Grasmueck et al. (2006) showed that living cold-water corals (*Lophelia pertusa*, *Enallopsammia profunda*, and *Madrepora oculata*) in the Florida Strait occur in water depths of ~600 m where potential density is ~27.5 kg m⁻³ (Wang & Mooers 1997). Scleractinian cold-water corals on the Scotian Shelf occupy water depths between 340 and 540 m (Mortensen & Buhl-Mortensen 2005). A potential density of 27.5 kg m⁻³ has been found at 450 m water depth (Han & Loder 2003). Data from all the above localities raise our confidence regarding sigma-theta as a controlling factor in the North Atlantic. Moreover, our method can also be used as an approach to exclude areas where corals do not occur.

CONCLUSIONS

The study of hydrographic parameters in the NE Atlantic and their relation to cold-water coral reefs along the NW European margin reveals that a potential density envelope of $\sigma_{\theta} = 27.35$ to 27.65 kg m⁻³ is a basic prerequisite for coral development, growth, and distribution. Other oceanographic and environmental parameters such as temperature, salinity, dissolved oxygen, currents, sedimentation rates, bathymetry, sea-floor morphology, substrate, and nutrient supply show variations on different scales in space and time.

Our study indicates that a density surface supports the formation of INLs, which increase food availability for bottom biota. We further speculate that this density

surface could be important for lateral transport of coral larvae and is therefore an important mechanism for their distribution.

Contrary to previous studies, which have shown that cold-water corals tolerate a wide range of environmental factors, our study indicates for the first time that corals are not randomly distributed but rather follow a density envelope.

Furthermore, we have shown that our method has the potential to be used as a tool to locate living cold-water coral reefs along continental margin settings of the North Atlantic. Nevertheless, further research must be carried out to assess related processes, e.g. nutrient inventories, larval dispersal, and carbonate chemistry.

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