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Chapter 1

COLD-WATER CORAL REEFS ALONG THE EUROPEAN CONTINENTAL MARGIN: THE ROLE OF FORAMINIFERA

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INTRODUCTION

To understand the role of foraminifera in cold-water coral ecosystems it is essential to have an overview on their functioning, although these mechanisms are not yet fully understood. Presently, the full extent of cold-water coral reef's geographical distribution is still unknown (Freiwald and others, 2004). They have been documented in Fjords and on the continental shelf off Norway (Fosså and others, 2002; Freiwald and others, 2002), along the upper continental slope from the Faroe-Shetland Channel southwards to central Africa, in the northwest Atlantic from Canada, Florida, the Gulf of Mexico down to Brazil and Argentina, but also in the Indian and Pacific Oceans (Stetson and Squires, 1962; Freiwald and others, 1999; Paull and others, 2000; Heifetz, 2002; Reed, 2002; Freiwald and others, 2004; Gass and Willison, 2005; Mortensen and Buhl-Mortensen, 2005; Schroeder and others, 2005; Reyes and others, 2005; Muñoz and others, 2012). On deep-sea banks cold-water corals have been documented on the Rockall and Porcupine Bank in the northeast Atlantic, on Galicia Bank close to Spain, the Chatman Rise and Campbell Plateau near New Zealand, on several seamounts in the Atlantic and Pacific Oceans (Grigg, 1984; Wilson and Kaufman, 1987; Richer de Forges, 1990, 1993; Grigg, 1993; Probert and others, 1997; Koslow and others, 2001; Andrews and others, 2002; Gubbay, 2003; Baco and Shank, 2005), and on mud volcanoes and ridges in the Gulf of Cadiz and in the Mediterranean (Van Rensbergen and others, 2005; Foubert and others, 2008; Freiwald and others, 2009; Wienberg and others, 2009; Margreth and others, 2011). Peculiar and spectacular cold-water coral settings are the scleractinian coral reef build-ups and carbonate mounds along the European margin from northern Norway to the Mediterranean. The shallowest occurrence has been recorded at 39 m depth in the Trondheimsfjord, the deepest from the New England Seamount chain in the North Atlantic, at 3383 m, and off Morocco, at 2775 m (Zibrowius, 1980). The largest reef complexes of up to 40 km in length have been described along the Norwegian margin (Freiwald and others, 2002; Fosså and others, 2005).

Herebelow, we mainly refer to the cold-water coral reef build-ups of *Lophelia pertusa,* which is the main reef forming scleractinian cold-water coral along the European margin with minor contribution of *Madrepora oculata* and *Desmophyllum* spp. (Freiwald and others, 2004). All these corals are suspension feeders (Messing and others, 1990; Jensen and Frederiksen, 1992) and need to be supplied by a diverse range of food from live zooplankton to particle aggregates of marine snow and resuspended material (Mortensen and others, 2001; Freiwald, 2002; Kiriakoulakis and others, 2004; 2005; Duineveld and others, 2007). In regions where *L. pertusa* is abundant, high primary productivity by surface phytoplankton is observed (Duineveld and others, 2004). This is important to trigger the zooplankton blooms. Strong bottom currents provide the cold-water corals with food, remove the waste products and limit sediment smothering (Klitgaard-Kristensen and others, 1997; Duineveld and others, 2004; Freiwald and others, 2004; White and others, 2007; Thiem and others, 2006).

The biogenic reef frameworks built by the cold-water corals are similar in morphology to their warm-water counterparts, controlled by a complex interaction between biological and geological processes under suitable hydrodynamic conditions. *Lophelia pertusa* may form white, orange or pink bush-like colonies often of several meters in height. A typical cold-water coral reef starts with the settlement of coral larvae on suitable hard substrate such as pre-existing heights, moraine ridges, iceberg plough mark levees (Freiwald and others, 1999; Mortensen and others, 2001), mud breccia extruded from mud volcanoes, or skeletal debris (Roberts and others, 2005; Margreth and others, 2011). Under favourable environmental conditions like permanently or episodically strong currents and food supply, small coral colonies are able to grow (Dons, 1944; Frederiksen and others, 1992). Under stable physical oceanographic conditions in terms of temperature, salinity, food supply and currents, the colonies may continue their growth, colonize larger areas to form coral thickets (Dons, 1944; Freiwald, 2002). These thickets provide support and protection for other organisms, which form together a complex reef biocoenosis (Dons, 1944; Burdon-Jones and Tambs-Lyche, 1960; Jensen and Frederiksen, 1992, Fosså and Mortensen, 1998; Rogers, 1999; Fosså and others, 2000; Freiwald and others, 2004). The continuous growth of the reef results in a separation between the live reef and the dead framework providing different habitats resulting in distinct faunal zonation. Bioeroders, dominantly sponges and fungi, attack the dead corals (Beuck and Freiwald, 2005). This process leads to the formation of extended fields of coral rubble, which provide additional different habitats for distinct fauna but also the substrates for renewed coral settlement supporting horizontal reef growth. The bottom water circulation pattern may produce a facies zonation, which can be identified by the presence of abundant exposed glacial dropstones in the northern regions. This facies harbours distinct communities, different from the more sheltered areas (Mullins and others, 1981; Messing and others, 1990).

The most significant environmental factors controlling cold-water coral distribution and growth, next to the hard substrate required for initial attachment of the coral larvae, are temperature, salinity, and the nutrient supply. *Lophelia pertusa* tolerates a temperature range between 4 and 14 °C (Freiwald and others, 1997; Freiwald and others, 2002) and a salinity range between 32 psu and 38.8 psu (Strømgren, 1971; Taviani and others, 2005). A combination of these two parameters is expressed in the seawater density sigma-theta (σ_θ). Recent studies show that thriving *L. pertusa* coral reefs occur within a density range of sigma-theta (σ_θ) = 27.35 to 27.65 kg m^{-3} in the NE Atlantic Ocean (Dullo and others, 2008; Rüggeberg and others, 2011). However, the Mediterranean occurrences show a special and very narrow sigma-theta (σ_θ) range of 29.1 ± 0.03 kg m^{-3} (Freiwald and others, 2009).

COLD-WATER CORAL CARBONATE MOUNDS

Providing stable environmental conditions over longer periods (100's of kyr), cold-water coral reefs are able to form several 100-m high carbonate mounds. The known occurrences of cold-water coral carbonate mounds in the North Atlantic are generally confined to the upper and mid-slope of continental margins like the Rockall Bank, the Porcupine Seabight, the Gulf of Cadiz, the Moroccan and Mauritanian margins, the Florida-Hatteras Straight, the Blake Plateau (Florida), the eastern USA and the Gulf of Mexico (e.g., Newton and others, 1987; Colman and others, 2005; De Mol and others, 2005; Grasmueck and others, 2006, Foubert and Henriet, 2009). The growth rate of coral carbonate mounds is relatively high ~0.05–0.1 mm yr^{-1} (= 5–10 cm kyr^{-1}) and up to 5 mm yr^{-1} (~500 cm kyr^{-1}) under favourable conditions compared to off-mound sedimentation rates (Freiwald and others, 1999; Lindberg and others, 2007; Kano and others, 2007; López Correa and others, 2012). For this reason cold-water coral carbonate mounds can be also called 'carbonate factories' (Tucker and Wright 1990; James and Bourque 1992) although most of them occur in mixed carbonate–siliciclastic domains.

During the past decades intensive studies on cold-water coral carbonate mounds were conducted within the Porcupine Seabight and east and west of the Strait of Gibraltar (Gulf of Cadiz, Alboran Sea). These mounds are interpreted to be formed by cyclic development of cold-water corals, which includes a number of processes acting in different ranges of temporal and spatial scales as described in several models (De Mol and others, 2002; Kenyon and others, 2003; De Mol and others, 2005; Dorschel and others, 2005; Huvenne and others, 2005; Kozachenko, 2005; Roberts and others, 2006; Rüggeberg and others, 2007; Huvenne and others, 2009). All these models have a common point, which is the widely accepted mechanism of cold-water coral mound initiation from a cold-water coral reef (Roberts and others, 2009). According to this theory, mounds develop from extended cold-water coral reefs (Williams and others, 2006; Kano and others, 2007) by vertical coral growth on accumulated coral rubble, sediment accumulation of biogenic and authigenic carbonate and sediment baffled in the coral framework. The majority of these models shows also that climatic cycles from interglacial to glacial cause fundamental changes in environmental conditions and sedimentation rates, thus in the coral's development.

Rüggeberg and others (2007) showed that the decrease in temperature, nutrient supply, current speed and increase in sediment input during glacial times produces unfavourable conditions for cold-water coral growth. They show that the return to interglacial/interstadial conditions is marked by the return to relatively warmer temperatures and by the re-establishment of a stronger hydrodynamic regime with consequent removal of the glacio-marine deposits, thus producing again the favourable conditions for cold-water coral growth. In the northern hemisphere glacial/interglacial cycles occurred many times over the last 2.7 Ma (Bartoli and others, 2005). Consequences of this cyclicity are the typical mound sequences with fine-grained sediments accumulated during glacial times and coarser deposits accumulated during interglacials/interstadials (Dorschel and others, 2005; Rüggeberg and others, 2007; Huvenne and others, 2009). Cyclic sedimentation is also responsible for the accumulation of thick mound deposits. When mounds reach a certain size, their top may become isolated from bedload transport, thus they cannot longer expand and they may result embedded within sediment drifts whose accumulation rate is higher than the mound growth rate (Van Rooji and others, 2003, 2007a, b). Sometimes large mounds can create their own hydrodynamic regime influencing the accumulation and erosion (Wheeler and others, 2005, 2007; White and others, 2005; Dorschel and others, 2007; Huvenne and others, 2003, 2007; Van Rooij and others, 2008).

AIM OF THIS ATLAS

As the field of cold-water coral research has developed during the past decades, an increasing number of publication and unpublished reports identify, describe and analyse these ecosystems with respect to their biology, geology, sedimentology, and habitat characterisation from different settings around the world. Only recently, scientists have started to understand the complex interaction of ecological variables controlling the development of cold-water coral ecosystems.

Further investigations are still needed to obtain a complete picture of cold-water coral reefs and their ecology. It is known that these ecosystems are 'hot-spots' for marine life and host thousands of species of sponges, hydrozoans, mollusks, bryozoans, echinoderms, polychaetes, crustaceans, and fishes with a comparable biodiversity as observed for their warm-water analogues (Dons, 1944; Burdon-Jones and Tambs-Lyche, 1960; Jensen and Frederiksen, 1992, Fosså and Mortensen, 1998; Rogers, 1999; Fosså and others, 2000; Freiwald and others, 2004). Until now, studies on cold-water coral associated faunas mainly focused on the mega- and macrofauna (e.g., Jensen and Frederiksen, 1992; Costello and others, 2005; Henry and Roberts, 2007) or microfauna (e.g., Penn and others, 2006; Neulinger and others, 2009; Schöttner and others, 2009).

The study on benthic foraminifera associated to cold-water coral reefs has just started and publications related to these organisms are only a few (Table 1.1, Figure 1.1). Cedhagen (1994), Freiwald and Schönfeld (1996), and Beuck and others (2008) focused on the single parasitic foraminifera *Hyrrokkin sarcophaga* living attached to corals. Jensen and Frederiksen (1992) described foraminiferal fauna attached to *L. pertusa*; Hawkes and Scott (2005) investigated benthic foraminifera associated to an 'octocoral garden' at the east coast of Canada. Wisshak and Rüggeberg (2006) performed a colonization experiment on artificial substrates next to a *Lophelia* reef and Rüggeberg and others (2007) focused on fossil benthic foraminiferal assemblages in sediment cores on a carbonate mound in the Porcupine Seabight. Successively Margreth and others (2009; 2011), Schönfeld and others (2011), Morigi and others (2012), and Spezzaferri and others (2013) studied Recent benthic foraminiferal assemblages from different *Lophelia* reef sites (Porcupine Basin and Rockall region, Alboran Basin). Remia and Taviani (2005), Rüggeberg and others (2007), Rosso and others (2010), Margreth and others (2011), Raddatz and others (2011), Smeulders and others (2014), and Stalder and others (2014) focused on fossil species or assemblages from this ecosystem.

The aim of this Atlas is:

1) To summarize our results acquired over ~12 years of research on Recent, sub-Recent and Holocene benthic foraminifera associated to scleractinian

Table 1.1. List of published studies on benthic foraminifers associated to cold-water coral reefs.

Study	Area	Comments
1. Burdon-Jones and Tambs-Lyche (1960)	Norway	Recent assemblages
2. Jensen and Frederiksen (1992)	Faroe	Foraminifera attached to *Lophelia*
3. Cedhagen (1994)	Norway	*Hyrrokkin sarcophaga*
4. Freiwald and Schönfeld (1996)	Norway	*Hyrrokkin sarcophaga* on live *Lophelia*
5. Hawkes and Scott (2005)	Nova Scotia	Foraminifera attached to *Primnoa*
6. Remia and Taviani (2005)	Tuscan Archipelago	Single foraminiferal species, 11 kyr BP
7. Wisshak and Rüggeberg (2006)	Skagerrak	Colonization experiment at *Lophelia* reefs
8. Rüggeberg and others (2007)	Porcupine	Fossil assemblages, 0–300 kyr BP
9. Beuck and others (2008)	Norway, Porc., Med.	*Hyrrokkin sarcophaga*
10. Margreth and others (2009)	Rockall, Porcupine	Recent assemblages
11. Rosso and others (2010)	Ionian Sea	Recent, dead assemblages
12. Margreth and others (2011)	Alboran Sea	Fossil assemblages, 3–15 kyr BP
13. Raddatz and others (2011)	Porcupine	Single foraminiferal species, ~2.5 Myr BP
14. Schönfeld and others (2011)	Porcupine, Biscay	Recent assemblages
15. Morigi and others (2011)	Rockall Bank	Recent assemblages
16. Spezzaferri and others (2013)	Norway	Recent assemblages
17. Smeulders and others (2014)	Rockall, Porcupine	Fossil assemblages, sub-Recent
18. Stalder and others (2014)	Norway	Fossil assemblages, 2–15 kyr BP

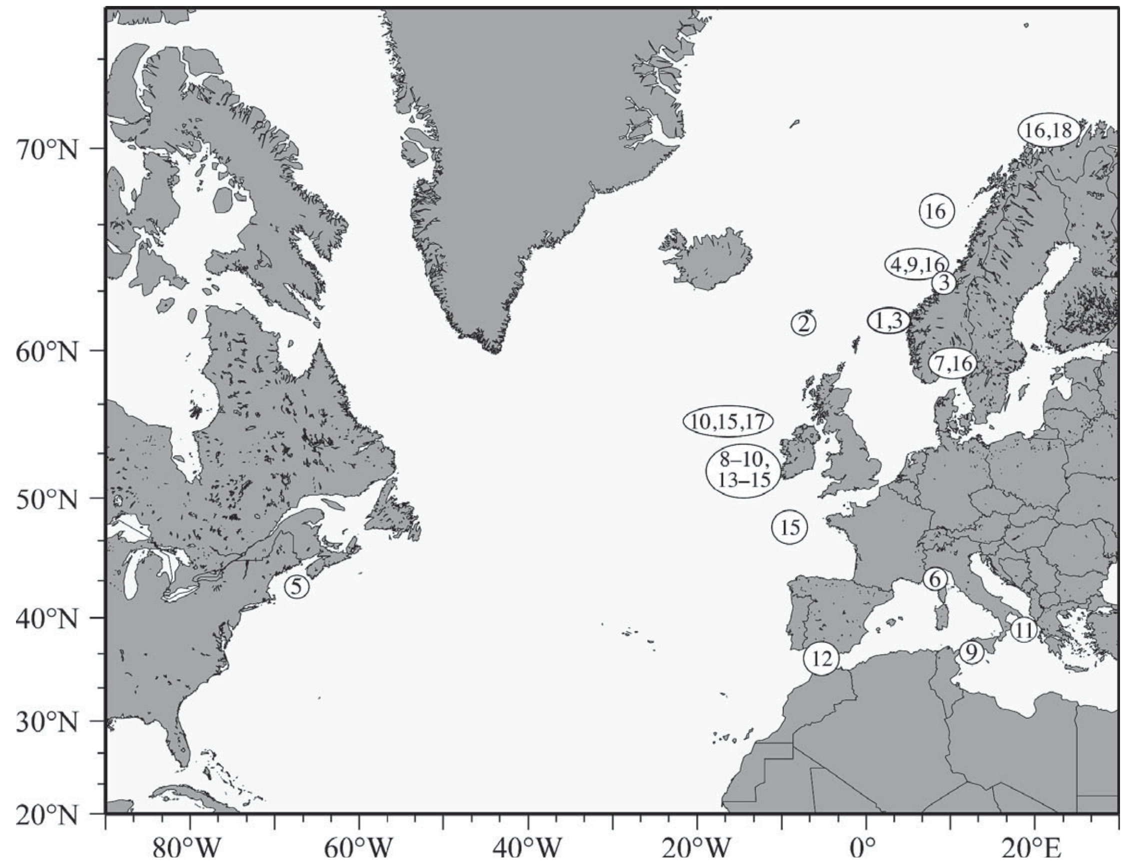

Figure 1.1. Studies on benthic foraminifera related to cold-water coral reefs. Numbers indicate studies: 1. Burdon-Jones and Tambs-Lyche (1960), 2. Jensen and Frederiksen (1992), 3. Cedhagen (1994), 4. Freiwald and Schönfeld (1996), 5. Hawkes and Scott (2005), 6. Remia and Taviani (2005), 7. Wisshak and Rüggeberg (2006), 8. Rüggeberg and others (2007), 9. Beuck and others (2008), 10. Margreth and others (2009), 11. Rosso and others (2010), 12. Margreth and others (2011), 13. Raddatz and others (2011), 14. Schönfeld and others (2011); 15. Morigi and others (2012); 16. Spezzaferri and others (2013), 17. Smeulders and others (2014), 18. Stalder and others (2014).

cold-water coral reef ecosystems along the European continental margin.

2) To illustrate sub-Recent benthic foraminiferal distribution patterns and abundances along the Norwegian margin, the Porcupine Seabight and the Rockall Bank.
3) To compare two fossil examples, (a) the buried cold-water coral reef developed in the Holocene on mud-volcanoes in the Alboran Sea, Western Mediterranean, and (b) the Holocene cold-water coral reef record from the Lopphavet (Northern Norway) to show their eventual similarities and differences in space and time.
4) To give an overview of their ecological preferences in cold-water coral reefs in relation to sedimentary facies and oceanographic parameters.
5) To highlight the potential of these organisms to serve as a tool for identifying these ecosystems in the geologic record, when the corals may be dissolved.

Three hundred ~~seventy three~~ species of benthic foraminifers including some species poorly documented in the literature have been selected to represent different sedimentary facies associated to cold-water coral reefs. They are documented in 37 plates, which will serve as a basis for integration in further studies on the subject.

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REFERENCES

Andrews, A. H., Cordes, E. E., Mahoney, M. M., Munk, K., Coale, K. H., Cailliet, G. M., and Heifetz, J., 2002, Age, growth and radiometric age validation of a deep-sea, habitat-forming gorgonian (*Primnoa resedaeformis*) from the Gulf of Alaska: Hydrobiologia, v. 471, p. 101–110.

Baco, A. R., and Shank, T. M., 2005, Population genetic structure of Hawaiian precious *Corallium lauuense* (Octocorallia: Coralliidae) using microsatellites, *in*: Freiwald, A., Roberts, J. M. (eds.) Cold-water Corals and Ecosystems: Springer Verlag, Berlin, Heidelberg, p. 663–678.

Bartoli, G., Sarnthein, M., Weinelt, M., Erlenkeuser, H., Garbe-Schönberg, D., and Lea, D. W., 2005, Final closure of Panama and the onset of northern hemisphere glaciation: Earth and Planetary Science Letters, v. 237, p. 33–44.

Beuck, L., and Freiwald, A., 2005, Bioerosion patterns in a deep-water *Lophelia pertusa* (Scleractinia) thicket (Propeller Mound, northern Porcupine Seabight), *in*: Freiwald, A., Roberts, J. M. (eds.) Cold-water Corals and Ecosystems: Springer-Verlag, Berlin Heidelberg, p. 915–936.

———, López Correa, M., and Freiwald, A. 2008, Biogeographical distribution of *Hyrrokkin* (Rosalinidae, Foraminifera) and its host-specific morphological and textural trace variability, in: Wisshak, M., and Tapanila, L. (eds.) Current Developments in Bioerosion: Springer-Verlag, Berlin Heidelberg, p. 329–360.

Burdon-Jones, C., and Tambs-Lyche H., 1960, Observations on the fauna of the North Brattholmen stone-coral reef near Bergen: Årbok for Universitetet i Bergen, Matematisk-naturvitenskaplig Serie, v. 4, p. 1–24.

Cedhagen, T., 1994, Taxonomy and biology of *Hyrrokkin sarcophaga* gen. et sp. n., a parasitic foraminiferan (Rosalinidae): Sarsia, v. 79, p. 65–82.

Colman, J. G., Gordon, D. M., Lane, A. P., Forde, M. J., and Fitzpatrick, J. J., 2005, Carbonate mounds off Mauritania, Northwest Africa: status of deep-water corals and implications for management of fishing and oil exploration activities, *in*: Freiwald, A., Roberts, J. M. (eds.) Cold-water Corals and Ecosystems: Springer-Verlag, Berlin Heidelberg, p. 417–441.

Costello, M. J., McCrea, M., Freiwald, A., Lundälv, T., Jonsson, L., Bett, B. J., van Weering, T. C. E., de Haas, H., Roberts, J. M., and Allen, D., 2005, Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic, *in*: Freiwald, A., Roberts, J. M. (eds.) Cold-water Corals and Ecosystems: Springer-Verlag, Berlin Heidelberg, p. 771–805.

De Mol, B., Henriet, J.-P., and Canals, M., 2005, Development of coral banks in Porcupine Seabight: do they have Mediterranean ancestors? *in*: Freiwald, A., Roberts, J. M. (eds.) Cold-water Corals and Ecosystems: Springer-Verlag, Berlin Heidelberg, p. 515–533.

———, Van Rensbergen, P., Pillen, S., Van Herreweghe, K., Van Rooij, D., McDonnell, A., Huvenne, V., Ivanov, M., Swennen, R., and Henriet, J. P., 2002, Large deep-water coral banks in the Porcupine Basin, southwest of Ireland: Marine Geology, v. 188, p. 193–231.

Dons, C., 1944, Norges korallrev: Det Kongelige Norske Videnskabers selskab, Forhandlinger, v. 16, p. 37–82.

Dorschel, B., Hebbeln, D., Rüggeberg, A., and Dullo, C., 2007, Carbonate budget of a deep water coral mound: Propeller Mound, Porcupine Seabight: International Journal of Earth Sciences, v. 96, p. 73–83.

———, ———, ———, ———, and Freiwald, A., 2005, Growth and erosion of a cold-water coral covered carbonate mound in the Northeast Atlantic during the Late Pleistocene and Holocene: Earth and Planetary Science Letters, v. 233, p. 33–44.

Duineveld, G. C. A., Lavaleye, M. S. S., and Berghuis, E. M., 2004, Particle flux and food supply to a seamount cold-water coral community (Galicia Bank, NW Spain): Marine Ecology Progress Series, v. 277, p. 13–23.

———, ———, Bergman, M. J. N., De Stigter, H. C., and Mienis, F., 2007, Trophic structure of a cold-water coral mound community (Rockall Bank, NE Atlantic) in relation to the near-bottom particle supply and current regime: Bulletin of Marine Science, v. 81, p. 449–467.

Dullo, W.-C., Flögel, S., and Rüggeberg, A., 2008, Cold-water coral growth in relation to the hydrography of the Celtic and Nordic European continental margin: Marine Ecology Progress Series, v. 371, p. 165–176.

Fosså, J. H., and Mortensen, P. B., 1998, Artsmangfoldet på Lopheliakorallrev og metoder for kartlegging og overvåkning (Diversity of species associated with *Lophelia* coral reefs and methods for mapping and monitoring) (in Norwegian with abstract and legends to tables and figures in English): Fisken og Havet, v. 17, 95 p.

———, ———, and Furevik, D. M., 2000, Lopheliakorallrev langs norskekysten. Forekomst og tilstand (*Lophelia coral* reefs in Norway. Distribution and effects of fishing) (in Norwegian with abstract and legends to tables and figures in English): Fisken og Havet, v. 2, 94 p.

———, ———, ———, 2002, The deep-water *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts: Hydrobiologia, v. 471, p. 1–12.

———, Lindberg, B., Christensen, O., Lundalv, T., Svellingen, I., Mortensen, P. B., and Alsvag, J., 2005, Mapping of *Lophelia* Reefs in Norway: experiences and survey methods, *in*: Freiwald, A., and Roberts, J. M. (eds.) Cold-Water Corals and Ecosystems: Springer-Verlag, Berlin Heidelberg, p. 359–391.

Foubert, A., Depreiter, D., Beck, T., Maignien, L., Pannemans, B., Frank, N., Blamart, D., and Henriet, J.-P., 2008, Carbonate mounds in a mud volcano province off northwest Morocco: Key to processes and controls: Marine Geology, v. 248, p. 74–96.

———, and Henriet, J.-P., 2009, Nature and Significance of the Recent Carbonate Mound Record: Lecture Notes in Earth Sciences, Springer-Verlag, Berlin-Heidelberg, v. 126, 298 p.

Frederiksen, R., Jensen, A., and Westerberg, H., 1992, The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe islands and the relation to internal tidal mixing: Sarsia, v. 77, p. 157–171.

Freiwald, A., 2002, Reef-Forming Cold-Water Corals, *in*: Wefer, G., Billett, D., Hebbeln, D., Jørgensen, B. B., Schlüter, M., van Weering, T. (eds.) Ocean Margin Systems: Springer Verlag, Berlin, Heidelberg, New York, p. 365–385.

———, Beuck, L., Rüggeberg, A., Taviani, M., Hebbeln, D., and R/V METEOR cruise M70-1 Participants, 2009, The white coral community in the Central Mediterranean Sea revealed by ROV surveys: Oceanography, v. 22, p. 58–74.

———, Fosså, J. H., Grehan, A., Koslow, T., and Roberts, J. M., 2004, Cold-water Coral Reefs: UNEP-WCMC, Cambridge, UK, 84 p.

———, Hühnerbach, V., Lindberg, B., Wilson, J.B., and Campbell, J., 2002, The Sula Reef Complex, Norwegian Shelf: Facies, v. 47, p. 179–200.

———, Wilson, J. B., and Henrich, R., 1999, Grounding Pleistocene icebergs shape recent deep-water coral reefs: Sedimentary Geology, v. 125, p. 1–8.

———, Henrich, R., and Pätzold, J., 1997, Anatomy of a deep-water coral reef mound from Stjernsund, West Finnmark, Northern Norway, *in:* James, N. P., and Clarke, J. A. D. (eds.) Cool-Water Carbonates: SEPM Special Publication, v. 56, p. 141–162.

———, and Schönfeld, J., 1996, Substrate pitting and boring pattern of *Hyrrokkin sarcophaga* Cedhagen, 1994 (Foraminifera) in a modern deep-water coral reef mound: Marine Micropaleontology, v. 28, p. 199–207.

Gass, S. E., and Willison, J. H. M., 2005, An assessment of the distribution of deep-sea corals in Atlantic Canada by using both scientific and local forms of knowledge, *in*: Freiwald, A., Roberts, J. M. (eds.) Cold-water Corals and Ecosystems. Springer-Verlag, Berlin, Heidelberg, New York, p. 223–245.

Grasmueck, M., Eberli, G. P., Viggiano, D. A., Correa, T., Rathwell, G., and Luo, J., 2006, Autonomous underwater vehicle (AUV) mapping reveals coral mound distribution, morphology, and oceanography in deep water of the Straits of Florida: Geophysical Research Letters, v. 33, L23616, doi:10.1029/2006GL027734.

Grigg, R.W., 1984, Resource management of precious corals: a review and application to shallow water reef building corals: Marine Ecology, v. 5, p. 57–74.

———, 1993, Precious coral fisheries of Hawaii and the U.S. Pacific Islands - Fisheries of Hawaii and U.S: Associated Pacific Islands: Marine Fisheries Review, v. 55, p. 50–60.

Gubbay, S., 2003. Seamounts of the North-East Atlantic: World Wildlife Fund, OASIS Reports, 40 p.

Hawkes, A. D., and Scott, D. B., 2005, Attached benthic Foraminifera as indicators of past and present distribution of the coral *Primnoa resedaeformis* on the Scotian Margin, *in*: Freiwald, A., Roberts, J. M. (eds.) Cold-water Corals and Ecosystems: Springer-Verlag, Berlin, Heidelberg, New York, p. 881–894.

Heifetz, J., 2002, Coral in Alaska: distribution, abundance, and species associations: Hydrobiologia, v. 471, p. 19–28.

Henry, L.-A., and Roberts, J. M., 2007, Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic: Deep-Sea Research I, v. 54, p. 654–672.

Huvenne, V. A. I., De Mol, B., and Henriet, J.-P., 2003, A 3D seismic study of the morphology and spatial distribution of buried coral banks in the Porcupine Basin, SW of Ireland: Marine Geology, v. 198, p. 5–25.

———, Bailey, W. R., Shannon, P. M., Naeth, J., di Primio, R., Henriet, J.-P., Horsfield, B., de Haas, H., Wheeler, A., and Olu-Le Roy, K., 2007, The Magellan mound province in the Porcupine Basin: International Journal of Earth Sciences, v. 96, p. 85–101.

———, Beyer, A., de Haas, H., Dekindt, K., Henriet, J. P., Kozachenko, M., Olu-Le Roy, K., Wheeler, A. J., and the TOBI/Pelagia 197 and CARACOLE cruise Participants, 2005, The seabed appearance of different coral bank provinces in the Porcupine Seabight, NE Atlantic: results from sidescan sonar and ROV sea-bed mapping, *in*: Freiwald, A., Roberts, J. M. (eds.) Cold-water Corals and Ecosystems: Springer-Verlag, Berlin Heidelberg, p. 535–569.

———, Masson, D. G., and Wheeler, A. J., 2009, Sediment dynamics of a sandy contourite: the sedimentary context of the Darwin cold-water coral mounds, Northern Rockall Trough: International Journal of Earth Sciences, v. 98, p. 865–884.

James, N. P., and Bourque, P.-A., 1992, Reefs and Mounds, *in*: Walker, R. G., and James, N. P. (eds.) Facies Models: St. John's, Geological Association of Canada, p. 13–34.

Jensen, A., and Frederiksen, R., 1992, The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (Scleractinaria) on the Faroe shelf: Sarsia, v. 77, p. 53–69.

Kano, A., Ferdelman, T. G., Williams, T., Henriet, J.-P., Ishikawa, T., Kawagoe, N., Takashima, C., Kakizaki, Y., Abe, K., Sakai, S., Browning, E. L., Li, X., and Integrated Ocean Drilling Program Expedition 307 Scientists, 2007, Age constraints on the origin and growth history of a deep-water coral mound in the northeast Atlantic drilled during Integrated Ocean Drilling Program Expedition 307: Geology, v. 35, p. 1051–1054.

Kenyon, N. H., Akhmetzhanov, A. M., Wheeler, A. J., van Weering, T. C. E., de Hass, H., and Ivanov, M. K., 2003, Giant carbonate mud mounds in the southern Rockall Trough: Marine Geology, v. 195, p. 5–30.

Kiriakoulakis, K., Fischer, E., Wolff, G. A., Freiwald, A., Grehan, A., and Roberts, J. M., 2005, Lipids and nitrogen isotopes of two deep-water corals from the North-East Atlantic: initial results and implications for their nutrition, *in*: Freiwald, A., Roberts, J. M. (eds.) Cold-water Corals and Ecosystems: Springer-Verlag, Berlin, Heidelberg, New York, p. 715–729.

———, White, M., Bett, B. J., and Wolff, G. A., 2004, Organic biogeochemistry of the Darwin Mounds, a deep-water coral ecosystem, of the NE Atlantic: Deep-Sea Research I, v. 51, p. 1937–1954.

Klitgaard, A.B., Tendal, O.S., and Westerberg, H., 1997, Mass occurrences of large sponges (Porifera) in Faroe Island (NE Atlantic) shelf and slope areas: characteristics, distribution and possible causes, *in* Hawkins, L.E. Hutchinson, S. (eds.), The responses of marine organisms to their environments: Proceedings of the 30th European Marine Biology Symposium, Southampton, p. 129-142.

Koslow J. A., Gowlett-Holmes K., Lowry J. K., O'Hara T., Poore G. C. B., and Williams A., 2001. Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling: Marine Ecology Progress Series, v. 213, p. 111-125.

Kozachenko, M., 2005, Present and past environments of the Belgica mounds (deep-water coral carbonate mounds), Eastern Porcupine Seabight, NE Atlantic: PhD Thesis, Departement of Geology and Environmental Research Institute Cork, Ireland, 550 p.

Lindberg, B., Berndt, C., and Mienert, J., 2007, The Fugløy Reef at 70°N; acoustic signature, geologic, geomorphologic and oceanographic setting: International Journal of Earth Sciences, v. 96, p. 201–213.

López Correa, M., Montagna, P., Joseph, N., Rüggeberg, A., Fietzke, J., Flögel, S., Dorschel, B., Goldstein, S. L., Wheeler, A., and Freiwald, A., 2012, Preboral onset of cold-water coral growth beond the Arctic Circle revealed by coupled radiocarbon and U-series dating and neodymium isotoes: Quarternary Science Reviews, v. 34, p. 34–43.

Margreth, S., Gennari, G., Rüggeberg, A., Comas, M. C., Pinheiro, L. M., and Spezzaferri, S., 2011, Growth and demise of cold-water coral ecosystems on mud volcanoes in the West Alboran Sea: The messages from the planktonic and benthic foraminifera: Marine Geology, v. 282, p. 26–39.

———, Rüggeberg, A., and Spezzaferri, S., 2009, Benthic foraminifera as bioindicator for cold-water coral reef ecosystems along the Irish margin: Deep-Sea Research I, v. 56, p. 2216–2234.

Messing C.G., Neumann A.C., and Lang J.C., 1990, Biozonation of deep-water lithoherms and associated hardgrounds in the Northeastern Straits of Florida: Palaios, v. 5, p. 15–33.

Morigi, C., Sabbatini, A., Vitale, G., Pancotti, I., Gooday, A. J., Duineveld, G. C. A, De Stigter, H. C., Danovaro, R., and Negri, A., 2012, Foraminiferal biodiversity associated with cold-water coral carbonate mounds and open slope of SE Rockall Bank (Irish continental margin—NE Atlantic): Deep-Sea Research I, v. 59, p. 54–71.

Mortensen, P. B., 2001, Aquarium observations on the deep-water coral *Lophelia pertusa* (L., 1758) (scleractinia) and selected associated invertebrates: Ophelia, v. 54, p. 83–104.

———, and Buhl-Mortensen, L., 2005, Deep-water corals and their habitats in The Gully, a submarine canyon off Atlantic Canada, *in*: Freiwald, A., Roberts, J. M. (eds.) Cold-water Corals and Ecosystems: Springer-Verlag, Berlin Heidelberg, p. 247–277.

———, Hovland, M., Fosså, J. H. and Furevik, D.M., 2001, Distribution, abundance and size of *Lophelia pertusa* coral reefs in mid-Norway in relation to seabed characteristics: Journal of the Marine Biological Association of the United Kingdom, v. 81, p. 581–597.

Muñoz, A., Cristobo, J., Rios, P., Druet, M., Polonio, V., Uchupi, E., Acosta, J., and the Atlantis Group, 2012, Sediment drifts and cold-water coral reefs in the Patagonian upper and middle continental slope: Marine and Petroleum Geology, v. 36, p. 70–82.

Mullins, H.T., Newton, C.R., Heath, K., and Vanburen, H.M., 1981, Modern deep-water coral mounds north of Little Bahama Bank: criteria for recognition of deep-water coral bioherms in the rock record: Journal of Sedimentary Petrology, v. 51, p. 999–1013.

Neulinger, S. C., Gärtner, A., Järnegren, J., Ludvigsen, M., Lochte, K., and Dullo, W.-Chr., 2009, Tissue-Associated "Candidatus Mycoplasma corallicola" and Filamentous Bacteria on the Cold-Water Coral *Lophelia pertusa* (Scleractinia): Applied and Environmental Microbiology, v. 75(5), p. 1437–1444.

Newton, C.R., Mullins, H.T., Gardulski, A.F., Hine, A.C., and Dix, G.R., 1987, Coral mounds on the western Florida Slope: unanswered questions regarding the development of deep-water banks: Palaios, v. 2, p. 359–367.

Paull, C.K., Neimann, A.C., Ende, B.A.A. Ussler, W., and Rodriguez, N.M., 2000, Lithiherms on the Florida-Hatteras slope: Marine Geology, v. 166, p. 83–101.

PENN, K., WU, D.Y., EISEN, J. A., and WARD, N., 2006, Characterization of bacterial communities associated with deep-sea corals on Gulf of Alaska Seamounts: Applied Environmental Microbiology, v. 72, p. 1680–1683.

PROBERT P. K., MCKNIGHT D. G., and GROVE S. L., 1997, Benthic invertebrate bycatch from a deep-water trawl fishery, Chatham Rise, New Zealand: Aquatic Conservation, Marine Freshwater Ecosystems, v. 7, p. 27–40.

RADDATZ, J., RÜGGEBERG, A., MARGRETH, S., DULLO, W.-C., and IODP EXP. 307 INTERNATIONAL SCIENTIFIC PARTY, 2011, Paleoenvironmental reconstruction of Challenger Mound initiation in the Porcupine Seabight, NE Atlantic: Marine Geology, v. 282, p. 79–90.

REED, J. K., 2000, Comparison of deep-water coral reefs and lithoherms off southeastern USA: Hydrobiologia, v. 471, p. 57–69.

REMIA, A., and TAVIANI, M., 2005, Shallow-buried Pleistocene Madrepora-dominated coral mounds on a muddy continental slope, Tuscan Archipelago, NE Tyrrhenian Sea: Facies, v. 50, p. 419–425.

REYES, J., SANTODOMINGO, N., GRACIA, A., BORRERO-PÉREZ, G., NAVAS, G., MEJÍA-LADINO, L. M., BERMÚDEZ, A., and BENAVIDES, M., 2005, Southern Caribbean azooxanthellate coral communities off Colombia, *in*: Freiwald, A., Roberts, J. M. (eds.) Cold-water Corals and Ecosystems. Springer-Verlag, Berlin, Heidelberg, New York, p. 309–330.

RICHER DE FORGES B., 1990, Les campagnes d'exploration de la faune bathyale dans la zone économique de la Nouvelle-Calédonie, *in*: Crosner, A. (ed.), Résultats des Campagnes MUSORSTOM: Mémoires Museum Histoire Naturelle, Paris, Part A, v. 6, n. 145, p. 9–54.

———, 1993, Deep-sea crabs of the Tasman Seamounts (Crustacea: Decapoda: Brachyura): Records of the South Australian Museum, v. 45, p. 11–24.

ROBERTS, J. M., PEPPE, O. C., DODDS, L. A., MERCER, D. J., THOMSON, W. T., GAGE, J. D., and MELDRUM, D. T., 2005, Monitoring environmental variability around cold-water coral reefs: the use of a benthic photolander and the potential of seafloor observatories, *in*: Freiwald, A., Roberts, J. M. (eds.) Cold-water Corals and Ecosystems. Springer-Verlag, Berlin, Heidelberg, New York, p. 483–502.

———, WHEELER, A. J., and FREIWALD, A., 2006, Reefs of the Deep: The Biology and Geology of Cold-Water Coral Ecosystem: Science, v. 312, p. 543–547.

———, ———, ———, and CAIRNS, S., 2009, Cold-Water Corals: The Biology and Geology of Deep-Sea Coral Habitats: Cambridge University Press, Cambridge, 334 p.

ROGERS, A. D., 1999, The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef forming corals and impact from human activities: International Reviews of Hydrobiology, v. 84, p. 315–406.

ROSSO, A., VERTINO, A., DI GERONIMO, I., SANFILIPPO, R., SCIUTO, F., DI GERONIMO, R., VIOLANTI, D., CORSELLI, C., TAVIANI, M., MASTROTOTARO, F., and TURSI, A., 2010, Hard- and soft-bottom thanatofacies from the Santa Maria di Leuca deep-water coral province, Mediterranean: Deep-Sea Research II, v. 57, p. 360–379.

RÜGGEBERG, A., DULLO, C., DORSCHEL, B., and HEBBELN, D., 2007, Environmental changes and growth history of Propeller Mound, Porcupine Seabight: Evidence from benthic foraminiferal assemblages: International Journal of Earth Sciences, v. 96, p. 57–72.

———, FLÖGEL, S., DULLO, W.-C., HISSMANN, K., and FREIWALD, A., 2011, Water mass characteristics and sill dynamics in a subpolar cold-water coral reef setting at Stjernsund, northern Norway: Marine Geology, v. 282, p. 5–12.

SCHÖNFELD, J., DULLO, W.-C., PFANNKUCHE, O., FREIWALD, A., RÜGGEBERG, A., SCHMIDT, S., and WESTON, J., 2011, Recent benthic foraminiferal assemblages from cold-water coral mounds in the Porcupine Seabight: Facies, v. 57, p. 187–213.

SCHÖTTNER, S., HOFFMANN, F., WILD, C., RAPP, H. T., BOETIUS, A., and RAMETTE, A., 2009, Inter- and intra- habitat bacterial diversity associated with cold-water corals: The ISME Journal, v. 3, 756–759.

SCHROEDER, W. W., BROOKE, S. D., OLSON, J. B., PHANEUF, B., MCDONOUGH III, J. J. M., and ETNOYER, P., 2005, Occurrence of deep-water *Lophelia pertusa* and *Madrepora oculata* in the Gulf of Mexico, *in*: Freiwald, A., Roberts, J.M. (eds.) Cold-water Corals and Ecosystems. Springer-Verlag, Berlin Heidelberg, p. 297–307.

SMEULDERS, G. G. B., KOHO, K. A., DE STIGTER, H. C., MIENIS, F., DE HAAS, H., and VAN WEERING, T.C.E., 2014, Cold-water coral habitats of Rockall and Porcupine Bank, NE Atlantic Ocean: Sedimentary facies and benthic foraminiferal assemblages: Deep-Sea Research II, v. 99, p. 270–285.

SPEZZAFERRI, S., RÜGGEBERG, A., STALDER, C., and MARGRETH, S., 2013, Benthic foraminifera assemblages from the Norwegian cold-water coral reefs: Journal of Foraminiferal Research, v. 43, p. 21–39.

STALDER, C., SPEZZAFERRI, S., RÜGGEBERG, A., PIRKENSEER, C., and GENNARI, G., 2014, Late Weichselian deglaciation and early Holocene development of a cold-water coral reef along the Lopphavet shelf (Northern Norway) recorded by benthic foraminifera and ostracoda: Deep-Sea Research II, v. 99, p. 249–269.

STETSON, T. R., and SQUIRES, D. F., 1962, Coral banks occurring in deep water on the Blake Plateau: American Museum Novitatem, v. 2114, p. 1–39.

STRØMGREN, T., 1971, Vertical and horizontal distribution of *Lophelia pertusa* (Linné) in Trondheimsfjorden on the west coast of Norway: Det Kongelige Norske Videnskabers Selskabs Skrifter, v. 6, p. 1–9,

TAVIANI, M., FREIWALD, A., and ZIBROWIUS, H., 2005, Deep coral growth in the Mediterranean Sea: an overview, *in*: Freiwald, A., Roberts, J. M. (eds.) Cold-water Corals and Ecosystems: Springer-Verlag, Berlin Heidelberg, p. 137–156.

THIEM, Ø., RAVAGNAN, E., FOSSÅ, J. H., and BERNTSEN, J., 2006, Food supply mechanisms for cold-water corals along a continental shelf edge: Journal of Marine Systems, v. 60, p. 207–219.

TUCKER, M. E., and WRIGHT, V. P., 1990, Carbonate Sedimentology. Blackwell Science, Oxford, 482 p.

VAN RENSBERGEN, P., DEPREITER, D, PANNEMANS, B., MOERKERKE, G., VAN ROOIJ, D., MARSSET, B., AKHMANOV, G., BLINOVA, V., IVANOV, M., RACHIDI, M., MAGALHAES, V., PINHEIRO, L., CUNHA, M., and HENRIET, J.-P., 2005, The El Arraiche mud volcano field at the Moroccan Atlantic slope, Gulf of Cadiz: Marine Geology, v. 219, p. 1–17.

Van Rooij, D., Blamart, D., Kozachenko, M., and Henriet, J. P., 2007a, Small mounded contourite drifts associated with deep-water coral banks, Porcupine Seabight, NE Atlantic Ocean, *in*: Viana, A., Rebesco, M. (eds.) Economic and palaeoceanographic importance of contourite deposits: Geological Society Special Publication, v. 276, p. 225–244.

———, ———, Richter, T., Wheeler, A., Kozachenko, M., and Henriet, J.-P., 2007b, Quaternary sediment dynamics in the Belgica mound province, Porcupine Seabight: ice-rafting events and contour current processes: International Journal of Earth Sciences, v. 96, p. 121–140.

———, De Mol, B., Huvenne, V., Ivanov, M., and Henriet, J.-P., 2003, Seismic evidence of current-controlled sedimentation in the Belgica mound province, upper Porcupine slope, southwest of Ireland: Marine Geology, v. 195, p. 31–53.

———, Huvenne, V. A. I, Blamart, D., Henriet, J.-P., Wheeler, A., and de Haas, H., 2008, The Enya mounds: a lost mound-drift competition: International Journal of Earth Sciences, v. 96, p. 121–140.

Wheeler, A. J., Beck, T., Thiede, J., Klages, M., Grehan, A., Monteys, F. X., and the Polarstern ARK XIX/3a Shipboard Party, 2005, Deep-water coral mounds on the Porcupine Bank, Irish Margin: preliminary results from the Polarstern ARK-XIX/3a ROV cruise, *in*: Freiwald, A., and Roberts, J. M. (eds.) Cold-water Corals and Ecosystems: Springer-Verlag, Berlin Heidelberg, p. 393–402.

———, Beyer, A., Freiwald, A., de Haas, H., Huvenne, V. A. I., Kozachenko, M., and Olu-Le Roy, K., 2007, Morphology and Environment of Deep-water Coral Mounds on the NW European Margin: International Journal of Earth Sciences, v. 96, p. 37–56.

White, M., 2007, Benthic dynamics at the carbonate mound regions of the Porcupine Sea Bight continental margin: International Journal of Earth Sciences, v. 96, p. 1–9.

———, Mohn, C., de Stigter, H., and Mottram, G., 2005, Deep-water coral development as a function of hydrodynamics and surface productivity around the submarine banks of the Rockall Trough, NE Atlantic, *in*: Freiwald, A., Roberts, J.M. (eds.) Cold-water Corals and Ecosystems: Springer-Verlag, Berlin Heidelberg, p. 503–514.

Wienberg, C., Hebbeln, D., Fink, H. G., Mienis, F., Dorschel, B., Vertino, A., López Correa, M., and Freiwald, A., 2009, Scleractinian cold-water corals in the Gulf of Cádiz — First clues about their spatial and temporal distribution: Deep-Sea Research I, v. 56, p. 1873–1893.

Williams, T., Kano, A., Ferdelmann, T., Henriet, J.-P., Abe, K., Andres, M. S., Bjerager, M., Browning, E. L., Cragg, B. A., De Mol, B., Dorschel, B., Foubert, A., Frank, T. D., Fuwa, F., Gaillot, P., Gharib, J. J., Gregg, J. M., Huvenne, V. A. I., Léonide, P., Li, X., Mangelsdorf, K., Tanaka, A., Monteys, X., Novosel, I., Sakai, S., Samarkin, V.A., Sasaki, K., Spivack, A. J., Takashima, C., and Titschack, J., 2006, Cold-Water Coral Mounds Revealed: EOS, v. 87, p. 525–536.

Wilson R. R., and Kaufman R. S., 1987, Seamount biota and biogeography. *in:* Keating, B. H., Fryer, P., Batiza, R., Backland, G. W. (eds.) Seamounts, Islands and Atolls: Geophysical Monographs, Washington, v. 43, p. 355–377.

Wisshak, M., and Rüggeberg, A., 2006, Colonisation and bioerosion of experimental substrates by benthic foraminiferans from euphotic to aphotic depths (Kosterfjord, SW Sweden): Facies, v. 52, p. 1–17.

Zibrowius, H., 1980, Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental: Memoires de l'Institut Oceanographique, Fondation Albert Ier, Prince de Monaco, v. 11, p. 1–227.