

The distribution of scleractinian corals in the Bay of Biscay, NE Atlantic

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Abstract Studies on the distribution of scleractinian corals in the Bay of Biscay were relatively numerous during the nineteenth and the first half of the twentieth century. Yet, recent reports are scattered, sometimes unpublished, and therefore knowledge about the current coral occurrence in the area is limited. This study aims at compiling the available historical and more recently collected information on the occurrence of scleractinian corals in the Bay of Biscay. Data from two recent cruises are included and compared with previous explored coral sites from as early as 1830 up to 1995. A database of 347 records including 34

described species of scleractinians highlights that the slope of the Bay of Biscay is an important habitat for scleractinians. This could be expected due to the high topographic relief providing the necessary hard substrate and accelerated bottom current flow that corals require. Further exploration of the occurrence and ecology of corals in the area is recommended to support the conservation of cold-water coral reefs along the European margin.

Keywords Cold-water corals · Scleractinia · Slope · Bay of Biscay · Biodiversity

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Introduction

Cold-water coral distributions in both shallow and deep, bathyal settings are well studied along the European margins in the NE Atlantic Ocean, in the Mediterranean Sea, and recently in the Strait of Gibraltar (Zibrowius 1980, 1983, 1985; Rogers 1999; Roberts et al. 2003; Álvarez-Pérez et al. 2005; Taviani et al. 2005; Hall-Spencer et al. 2007). In this way, it is shown that cold-water coral assemblages have been recorded from the continental margin of the NE Atlantic more frequently than from any other place in the world (Roberts et al. 2006). Yet, the NE Atlantic margin consists of many different marine environments and scientific documentation about the distribution of corals in each segment varies considerably. Intensive exploration and investigation on the Norwegian margins (Mortensen et al. 1995; Hovland et al. 1998; Freiwald et al. 2002; Lindberg and Mienert 2005; Fosså et al. 2005) was certainly facilitated through the relative shallow coral occurrences in some fjords and on various shelf banks, often <400 m deep (Fosså et al. 2005). This has shed some light on the distribution, the biology and the geological settings

of these coral ecosystems. The continental margin off Ireland and the UK with its hundreds of coral banks in water depths between 650 and 1,000 m recently emerged as a hot-spot of integrated multidisciplinary research in Europe (Van Weering et al. 2003; Weaver et al. 2004; Huvenne et al. 2003, 2005; Foubert et al. 2005; De Mol et al. 2002, 2005; Wheeler et al. 2005, 2007; Roberts et al. 2006). Further south, the Bay of Biscay was already an authentic hotspot for oceanographic exploration since the end of the nineteenth century until the 1950s. In the first decades of the twentieth century, this wide area was regularly visited by French biologists who made detailed investigations of the distribution and associated biodiversity of large coral reefs present in this area: the so-called “massifs coralliens” (Joubin 1922a, b, 1923; Le Danois 1948). However, it is not known to which extent the available historical information represents the actual distribution of corals in the area, since the status of previously recorded coral locations may have completely changed (Hall-Spencer et al. 2007). Zibrowius et al. (1975) and Zibrowius (1980, 1985) already pointed to the presence of isolated patches of corals in the area with new observations of scleractinians from the French BIOGAS and INCAL expeditions to the Bay of Biscay. The latest species compilation of Cnidaria, including a list of Scleractinia, was published by Altuna (2006). Yet, information is scattered through various reports, while many scientific results remain unpublished resulting in a paucity of updated documentation for the Bay of Biscay (ICES 2003, 2004).

It is generally accepted that the Biscay region represents a suitable habitat for corals (Hall-Spencer et al. 2007). The presence of hard substrates has been observed to be essential for coral reef formation both in shallow water and the deep sea (Dodge and Vaisnys 1977; Rogers 1990). Also a high bottom current flow, necessary for the delivery of food and larvae, as well as for the removal of waste and the excess of sediments (Grigg 1984) has been considered critical for reef development. Many observations indicate that scleractinians indeed occur in areas where the interaction between currents and topography can generate accelerated flow (Rogers 1999; De Mol et al. 2002; Freiwald et al. 2004; Mienis et al. 2006). Further, it is likely that periodic oscillations in the vertical stratification of water density (internal waves) are important for corals. They indeed result in increased vertical and bottom mixing within the vicinity of the shelf break when interacting with the seabed. In this way, the influence of internal waves in controlling the particulate food supply by increasing resuspension of organic matter, has been described by Frederiksen et al. (1992). Finally, the presence of nutrient-rich waters that stimulate high phyto- and zooplankton productivity, are providing a major food source for the corals (Freiwald et al. 2004). Given the notorious current-swept steep slope of the

Bay of Biscay, cut by numerous canyons (Le Suavé et al. 2000; Bourillet et al. 2003, 2006; Zaragosi et al. 2006), it is expected that the water mixing over the slope may result in enhanced suspended material and indeed favours high concentrations of planktonic biomass which can sustain the coral growth.

This paper provides an overview of observations on scleractinian reef framework-forming species (stony corals) along the slope of the Bay of Biscay based upon historical and recent reports. Coral reports from the last two centuries collected in the Bay of Biscay are assembled in a database and mapped in a geographical information system (GIS) environment. The historical context of the successive exploratory surveys conducted along the slope of the Bay of Biscay, as well as the evolution of our knowledge on scleractinians is briefly addressed. The data from two recent research cruises—along the Banc de la Chapelle (BC) and in the Penmarc’h Bank area (PB) in the North, and the Cantabrian margin in the South—are also included. The disparity of the size and species assemblage of the reefs observed in the past compared to present-day reports and the wide occurrence of dead cold-water coral fragments are reported.

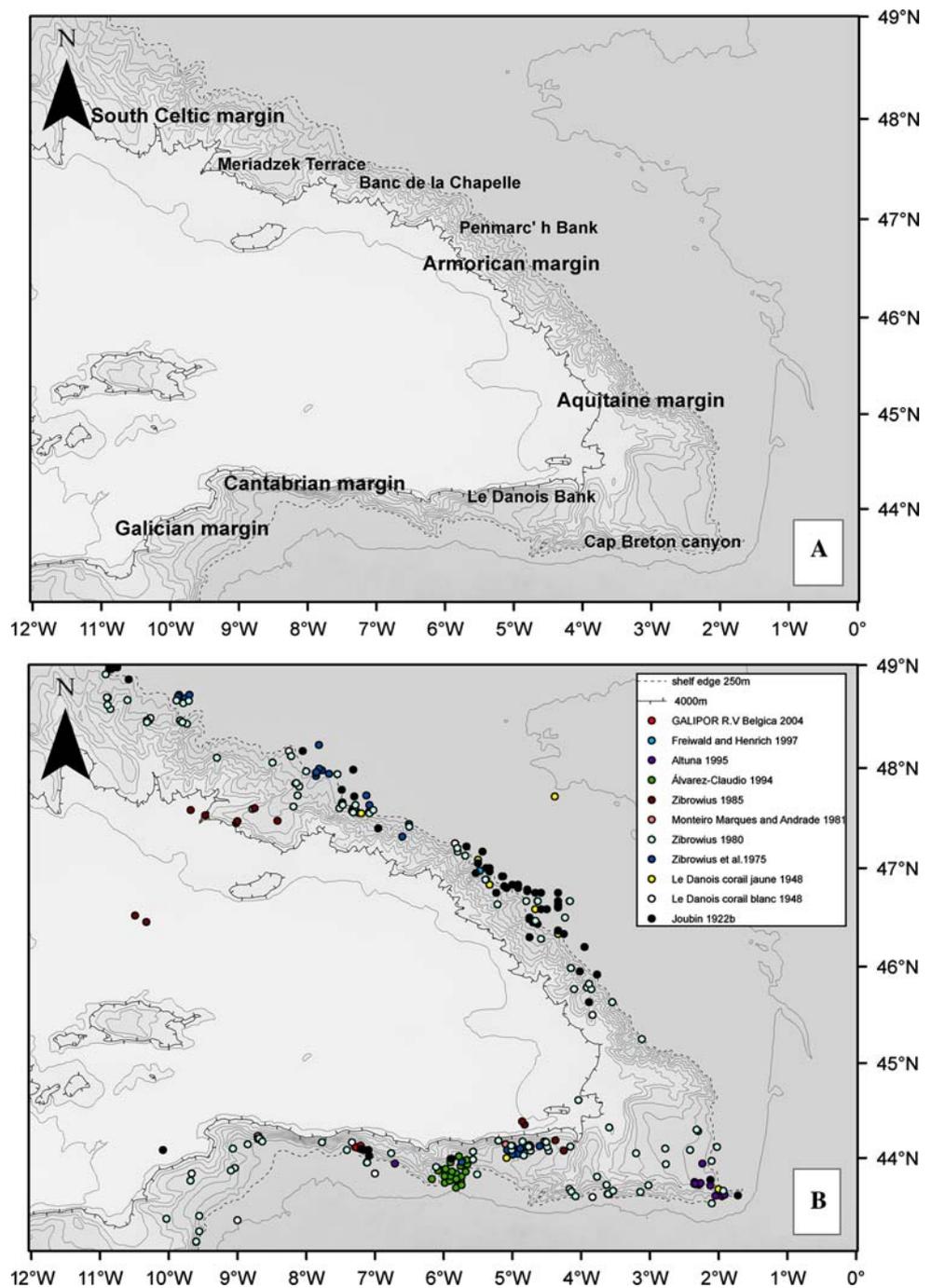
The main objective is to identify the recent past and present-day distribution and the diversity of scleractinians in the Bay of Biscay. This is of particular concern considering the low genetic differentiation of deep-water corals subpopulations along the NE Atlantic continental margin (Le Goff-Vitry et al. 2004; Le Goff-Vitry and Rogers 2005), suggesting a sporadic gene flow through larval dispersal over long periods of time. At a time where bottom fishing damage continues partly because coral-rich areas remain poorly mapped, it is essential to identify the potential and the importance of this region for the long-term protection of the European continental slopes.

Materials and methods

Study area

The present study area covers the continental shelf, the shelf break, bathyal and abyssal zone of the Bay of Biscay (from 90 to 4,830 m), stretching from 43 to 49°N and from 0 to 11°W (Fig. 1a). The Atlantic margin in the Bay of Biscay can be subdivided into five geographic regions (Fig. 1a)—with in the North the French Celtic and the Armorican margins, and in the South the French Aquitaine margin and the Iberian Cantabrian and Galician margins. The Celtic and Armorican margin display a relatively broad shelf from the coast to the shelf break (wider than 200 km) and a steep slope with an average gradient about 2.86–5.15° (Le Suavé et al. 2000; Lallemand and Sibuet 1986) which extends from a depth of about 200–4,000 m towards the

Fig. 1 **a** The continental margin of the Bay of Biscay with the geographic names used in the text. The shelf edge is on average at 250 m (*dashed line*) and the foot of the continental margin is at 4,000 m water depth (*crossed line*). Spacing of contour lines is 500 m. **b** Findings of cold-water scleractinians cluster along the continental margin in the Bay of Biscay. The map is modified from Sibuet et al. (2004)



abyssal plain. The Cantabrian margin has a narrow shelf (5–40 km wide) with a very steep continental slope (17°) between 500 and 4,500 m. A few marginal shelves (with a steep 10–12° slope) have been identified (Álvarez-Marrón et al. 1995). The most renowned of these Cantabrian marginal shelves, in relation to stony corals, is the “Le Danois Bank” (Le Danois 1948). From the Norwegian margin to the Portuguese margin, the overall steep European continental slope is characterized by the presence of a multitude of canyons (Weaver et al. 2000). More than 80 canyons cut

the 810 km of the Biscay slope (Le Suavé et al. 2000; Zaragosi et al. 2000; Canals et al. 2004). The hydrography of the Bay of Biscay is characterized by the presence of four main water masses: the North East Atlantic Central Water (NEACW) occupies the top 800 m of the water column; the large salinity maximum at 800–1,200 m depth corresponds to the Mediterranean Outflow Water (MOW); between approximately 1,200 and 3,000 m, lies the North East Atlantic Deep Water (NEADW), including the Labrador Sea Water (LSW) and the Iceland–Scotland Overflow

Water (ISOW; McCartney 1992). The LSW is recognized by a small salinity minimum at 1,800–2,000 m, and a small salinity maximum identifies the ISOW at ~2,600 m. The deepest water mass is the lower deep water (LDW; McCartney 1992). By definition, the different water masses should tend to mix very slowly; however, hydrological measurements of the salinity, temperature and turbidity at the Celtic Margin along the Meriadzek Slope from 2,120 to 4,700 m depth (Vangriesheim 1985), pointed to overall water mixing at the seafloor in association with a layer of resuspended particulate material of the same thickness. The Celtic–Armorican margin has a wide continental plateau with little terrestrial input and intensive vertical mixing at the shelf break providing enhanced primary production. In contrast, the Cantabrian–Galician margin is characterized by a narrow shelf with strong continental input and by seasonal upwelling with high primary production. An important feature of the Northeast Atlantic is the slope current that flows along the continental slope from the Bay of Biscay to the Norwegian Sea (Pingree and Le Cann 1990; Ellett 1995). The MOW also flows poleward (Dickson et al. 1985).

Data origin

Historical records were extracted from the following sources: Joubin (1922a, b, 1923), Le Danois (1948), Zibrowius et al. (1975), Zibrowius (1980, 1985), Monteiro Marques and Andrade (1981), Álvarez-Claudio (1994) and Altuna (1995). Taxon, latitude, longitude, depth range and station identification were entered into a separate Microsoft Access database for each author, research vessel (R/V) and cruise. Arc Map 9.2 GIS was used to plot each dataset in a map to illustrate the distribution of cold-water corals in the area (Fig. 1b). Records are given in chronological order. Joubin (1922b) and Le Danois (1948), when reporting “white coral sites”, did not make the distinction between the generally associated species *Madrepora oculata* (Linnaeus 1758) and *Lophelia pertusa* (Linnaeus 1758). The station list extracted from these sources (including *Lophelia pertusa* and/or *Madrepora oculata*) do not make a distinction between the two species and hence are not described in detail.

The Banc de la Chapelle (BC) and the Cantabrian margin were revisited during respectively the R/V Victor Hensen VH-97 cruise in 1997 and the R/V Belgica GALIPOR cruise in 2004. During the VH-97 cruise (Freiwald and Henrich 1997), several Van Veen grab samples and dredges were collected in order to explore canyon heads near the BC and in the Penmarc’h Bank (PB) areas in water depths between 167 and 790 m (Fig. 2). The sample locations were based on the report of Le Danois (1948) in the area between 47°32′30″–47°51′50″N and 7°12′30″–7°25′W (BC) and in

the area between 46°58′20″–46°58′30″N and 5°27′80″–5°28′W (PB). A 30 and 18 kHz single-beam echosounder was used for depth and morphologic control within the upper canyon heads and thalwegs. The R/V Belgica 2004 GALIPOR cruise near the Cantabrian margin focused on an area between 44°05′00″–44°10′00″N and 7°10′–7°20′00″W, a sector highlighted by Le Danois (1948) and by Álvarez-Claudio (1994), as being rich in coral banks (see Fig. 1b). The area was surveyed with Simrad E1002 multibeam echosounder and sampled with box cores (Foubert et al. 2004). Box cores were taken with a type NIOZ boxcorer, 30 cm diameter. These box cores allowed detailed biological sub-sampling faunal analysis (cold-water corals and associated fauna) and the records were added to the general database and coral distribution map.

Results

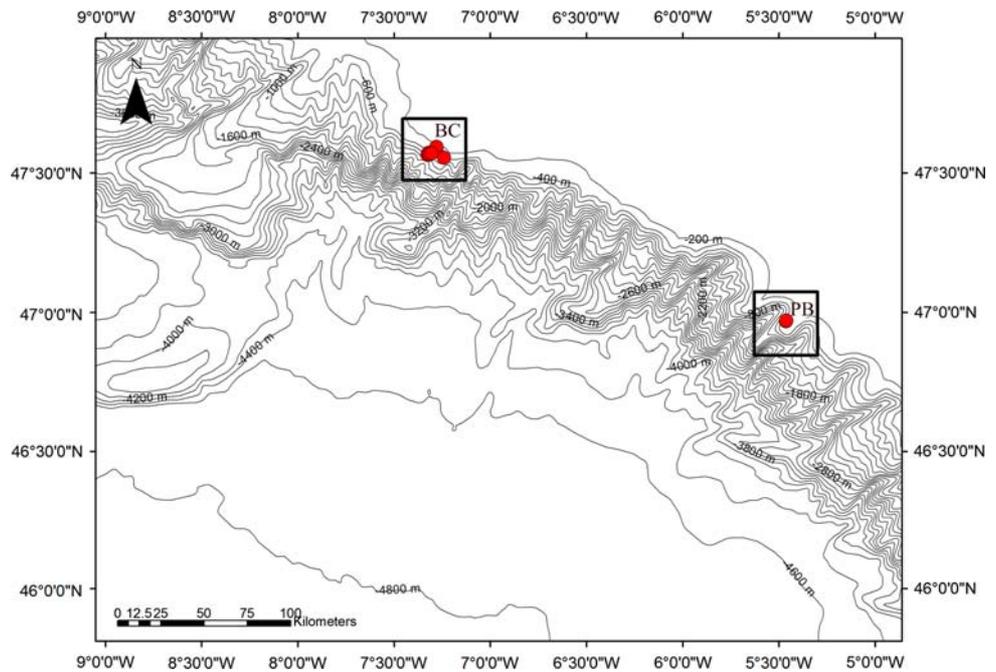
Historical data on scleractinian corals in the Bay of Biscay

In this section, an overview is given on the oceanographic campaigns realized in the Bay of Biscay from 1830 to 1995 as well as on the evolution of our knowledge on scleractinians from this area during this period. Cold-water coral research published up to now is presented in Table 1 and Fig. 1b, indicating depth and reported species. The authors provide a more detailed compilation of species, geographic coordinates, depth and their station codes in the FACIES web site (see [Electronic supplementary material](#)). Although the list is not exhaustive, it clearly demonstrates the wealth of data on the distribution of corals in the Bay of Biscay, as well as the extent of the research activities taken in this area. Special attention will be given to major biogeographic areas where cold-water corals were repeatedly reported in the Bay of Biscay.

Historical overview of campaigns in the Bay of Biscay

During the end of the nineteenth century and the first half of the twentieth century the Bay of Biscay was explored by the most eminent oceanographers. Audouin and Milne Edwards conducted in 1830 the first oceanographic dredge surveys along the French coasts at different water depths (Le Danois 1948). The first deep-sea research campaigns in the Bay of Biscay began in 1870 with the British expeditions of the H.M.S. Porcupine (Duncan 1870, 1873, 1878) followed from 1890 to 1896 by the expeditions of the H.M.S. Research in the North of the Bay of Biscay and in 1906 of the H.M.S. Huxley (Hickson 1907) on the Little Sole and the BC (Le Danois 1948). The French government provided the R/V le Travailleur (1880–1882; De Folin 1887), the R/V le Talisman (1883) and then the R/V

Fig. 2 Deep-water coral samples in the Banc de la Chapelle (BC) and Penmarc'h Bank area (PB), collected during the R/V Victor Hensen cruise VH-97



Caudan (1896) to the scientific community represented by Milne-Edwards (1881a, b), Roule (1896), Marion (1906) and Gourret (1906).

In 1885, the Prince of Monaco Albert I began a series of expeditions in the Atlantic. His first oceanographic campaign took place on board of the R/V l'Hirondelle (1886–1887) along the French coasts and in the Bay of Biscay (Jourdan 1895). On board of the R/V Princesse-Alice (1891–1896), he explored the entrance of the English Channel and returned in the Bay of Biscay. It is onboard of the R/V La Princesse-Alice II (1903 and 1904) that he sampled in total 150 stations in the Bay of Biscay and then the waters around Belle-Isle (1910). He explored for the last time the Bay of Biscay on board of the R/V Hirondelle II (1912–1914). The deep-sea corals collected during a series of campaigns between 1893 and 1913 were studied by Gravier (1915, 1920). Finally, in 1910, the Norwegian R/V Michaël-Sars, with John Murray carried out a small expedition in the Bay of Biscay.

With the aim to produce a map of cold-water coral reef occurrences in the NE Atlantic, Joubin (1922a, b, 1923) enlisted fishermen from the ports of Lorient, La Rochelle and Arcachon in France to report on the sites where they encountered coral fragments in their nets. The zoologist Le Danois, first in collaboration with Charcot on board of the R/V Pourquoi-Pas? (1912–1914), then on board of the R/V Perche in 1920, the R/V Tanche from 1921 to 1928, and finally the R/V President-Theodore-Tissier from 1934 to 1939, sampled hundreds of stations along the French and Spanish coasts. During these investigations, he discovered the bank now bearing his name, Le Danois Bank.

During the following 30 years, the Bay of Biscay only received occasional attention. Samples and collections obtained from the expeditions on board of R/V Job ha Zélian (1963–1972), R/V Thalassa (1967–1973), R/V Jean Charcot “Gestlante 2” 1967, R/V Jean Charcot “Noratlante” 1969, R/V Jean Charcot “Hespérides” 1976, R/V Walther Herwig 1974–1975 and R/V Sarsia 1954–1976 were studied by Zibrowius et al. (1975) and Zibrowius (1980). Zibrowius et al. (1975) reported and described numerous stations with scleractinians in the NE Atlantic, including the Bay of Biscay. Stations from the Hespérides 1976 cruise off the Atlantic coast of the Iberian Peninsula were additionally reported from Monteiro Marques and Andrade (1981).

More intensive bathyal and abyssal research was resumed in the area in the framework of the French BIO-GAS (Biology Gascogne) program, running from 1972 to 1981 (Laubier and Monniot 1985). Several selected stations within the northern and southern Bay of Biscay were visited during a total of 12 cruises on a variety of vessels including La Perle, Jean Charcot, Cryos, le Noroit and Capricorne (Zibrowius 1985). From 1987 to 1990, a French–Spanish project was conducted in the Cap Breton canyon (SE Biscay margin) on board of the Côte d’Aquitaine (CNRS; Sorbe 1990). Two bathymetric zones were selected at, respectively, 70–400 and 500–1,000 m in order to follow up the investigations of Le Danois (1948). Altuna (1994, 1995) studied the bathyal Scleractinia from this campaign and summarized the state of knowledge on this taxon in the area. Finally, 25 stations were sampled during the 1987 COCASE cruise (Central Cantabric

Table 1 Scleractinian species reported from the Bay of Biscay outer shelves, canyons and slopes based on Cairns and Chapman (2001) and few other sources cited in the text with depth ranges, numbers of samples and information on coloniality (C colonial, S solitary)

Species	Depth (m)	n	Coloniality
<i>Anomocora fecunda</i> (Pourtalès, 1871)	1,000	1	C
<i>Balanophyllia cellulosa</i> (Duncan, 1873)	137–463	5	S
<i>Balanophyllia thalassae</i> (Zibrowius, 1980)	380–1,150	12	S
<i>Caryophyllia abyssorum</i> (Duncan, 1873)	600–1,340	13	S
<i>Caryophyllia ambrosia</i> (Alcock, 1898)	1,520–2,940	8	S
<i>Caryophyllia atlantica</i> (Duncan, 1873)	1,107–1,470	6	S
<i>Caryophyllia calveri</i> (Duncan, 1873)	200–1,050	7	S
<i>Caryophyllia cyathus</i> (Ellis and Solander, 1786)	695–760	1	S
<i>Caryophyllia sarsiae</i> (Zibrowius, 1974)	500–1,100	7	S
<i>Caryophyllia seguenzae</i> (Duncan, 1873)	910–2,100	24	S
<i>Caryophyllia smithii</i> (Stokes and Broderip, 1828)	118–468	28	S
<i>Deltocyathus conicus</i> (Zibrowius, 1980)	1,100–2,430	4	S
<i>Deltocyathus moseleyi</i> (Cairns, 1979)	532–1,372	9	S
<i>Dendrophyllia alternata</i> (Pourtalès, 1880)	450–688	2	C
<i>Dendrophyllia cornigera</i> (Lamarck, 1816)	50–620	36	C
<i>Desmophyllum dianthus</i> (Esper, 1794)	310–2,350	25	S
<i>Eguchipsammia cornucopia</i> (Pourtalès, 1871)	330–960	7	C
<i>Enallopsammia rostrata</i> (Pourtalès, 1878)	915–2,430	10	C
<i>Flabellum alabastrum</i> (Moseley, 1873)	800–2,430	7	S
<i>Flabellum angulare</i> (Moseley, 1876)	1,884–3,800	8	S
<i>Flabellum macandrewi</i> (Gray, 1849)	790–930	3	S
<i>Fungiacyathus fragilis</i> (Sars, 1872)	910–1,810	3	S
<i>Fungiacyathus marenzelleri</i> (Vaughan, 1906)	1,884–4,825	8	S
<i>Javania cailleti</i> (Duchassaing and Michelotti, 1864)	1,200–2,430	4	S
<i>Lophelia pertusa</i> (Linnaeus, 1758)	150–2,000	102	C
<i>Madrepora oculata</i> (Linnaeus, 1758)	150–2,000	86	C
<i>Paracyathus pulchellus</i> (Philippi, 1842)	121	1	S
<i>Premocyathus cornuformis</i> (Pourtalès, 1868)	700–2,350	5	S
<i>Solenosmilia variabilis</i> (Duncan, 1873)	676–2,430	10	C
<i>Stenocyathus vermiformis</i> (Pourtalès, 1868)	450–960	9	S
<i>Stephanocyathus crassus</i> (Jourdan, 1895)	476	1	S
<i>Stephanocyathus moseleyanus</i> (Sclater, 1886)	910–1,570	14	S
<i>Stephanocyathus nobilis</i> (Moseley, 1873)	1,430–2,430	11	S
<i>Vaughanella concinna</i> (Gravier, 1915)	1,175–2,430	7	S

Oceanographic Cruise) in a small area of the Cantabrian margin, studied by Álvarez-Claudio (1994).

Evolution of the knowledge on scleractinians in the Bay of Biscay

The majority of knowledge on corals reported from 1870 to 1920 (Duncan 1870, 1873, 1878; Milne-Edwards 1881a, b; De Folin 1887; Jourdan 1895; Roule 1896; Marion 1906; Gourret 1906; Hickson 1907; Gravier 1915, 1920) is reviewed in Zibrowius (1980). Joubin (1922a, b, 1923) mainly investigated the distribution of the two white coral species *Lophelia pertusa*, which was at that time still called *Lophohelia prolifera*, and *Madrepora oculata* called

Amphihelia oculata. Also information on the coral species *Dendrophyllia cornigera* (Lamarck 1816) and *Dendrophyllia ramea* (Linnaeus 1758) were provided. He reviewed a total of 70 cold-water coral reef reports in the Bay of Biscay and described massive cold-water coral reefs so large and dense that fishermen fishing in these waters were afraid to damage their nets.

Le Danois (1948) also described the distribution of *Lophelia pertusa* and *Madrepora oculata*, while he recognized them as the two main reef forming species. Also *Desmophyllum dianthus* (Esper 1794), *Caryophyllia smithii* (Stokes and Broderip 1828) and *Flabellum alabastrum* Moseley, 1873 are often found associated with these framework-builder species (Le Danois 1948). Furthermore, the

yellow coral *Dendrophyllia cornigera* was mentioned in this work as well. Usually forming low patches with a mean size of about 30 cm, this species occurred in large quantities within large patches of white corals. Among some isolated patches, Le Danois further identified five sites where the density of these species was high enough to form coral reefs along the margins of the Bay of Biscay: the “Massif du Banc de la Chapelle” (a surface of about 3,500 km²), the much smaller “Massif de la Grande Vasière” (south of Armorican Margin, with a length of 180 km), the “yellow coral” “Le Danois Bank” or “Massif Cantabrique”, the “Massif Galicien de l’Est” (situated about 7°W) and the “Massif Galicien de l’Ouest” (stretching from 9°00′ to 9°40′).

Zibrowius et al. (1975) reported eight scleractinian species associated with the polychaete *Lumbriconereis flabellicola* (Fage 1937). In 1980, he reported 34 coral species from the Bay of Biscay including shallow-water species; in 1985, he reviewed the collections from the more recent cruises conducted in the Bay of Biscay (Programmes BIOGAS and POLYGAS, INCAL) and reported 11 species of scleractinians (Zibrowius 1985). The coral fauna from station 1 BIOGAS (1,920–2,350 m, northern Biscay margin) was characterized by a very high abundance of *Caryophyllia ambrosia* Alcock 1898 (2,000–3,000 individuals collected in one trawl) and *Premocyathus cornuformis* (Pourtalès 1868) and by the lower abundance of *Stephanocyathus nobilis* (Moseley 1873), *Flabellum alabastrum* Moseley 1873 (about 200 living individuals) and *Flabellum angulare* Moseley 1876. Zibrowius (1985) identified this coral assemblage as typical for soft bottoms. He described BIOGAS station 6 (1,894–2,430 m, southern Biscay margin) as a site of harder substrates where typical hard-bottom species were collected. Grasshoff (1981a, b) already concluded the same through the study of other groups of Anthozoa, mainly Octocorallia. At the deepest stations (>4,000 m), a single species was collected, *Fungiacyathus marenzelleri* (Vaughan 1906).

Álvarez-Claudio (1994) reported 1,100 cold-water coral specimens in a depth range from 50 to 1,347 m, belonging to 15 scleractinian species and 5 families. The analysis of the scleractinian species richness in the small sampling area of Cantabrian margin showed that only a few scleractinian species, such as *C. smithii*, settled on soft sandy shelf-bottom substrates. On the contrary, in deeper areas where the slope was less steep and bottoms were composed of very fine sand and mud, the scleractinian fauna was more diverse, comprising five to seven species within *Lophelia pertusa* and *Madrepora oculata* banks. Álvarez-Claudio (1994) reported *C. smithii* (depth 146–468 m), *C. abyssorum* Duncan 1873 (depth 702–1,189 m) and *Lophelia pertusa* (depth 702–1,347 m) as the most commonly represented species along the Cantabrian margin and *Dendrophyllia cornigera* as the most shallow occurring species (50 m).

Altuna (1995) found seven species in total. He reported *Fungiacyathus fragilis* Sars 1872 for the first time in the Bay of Biscay. Numerous colonies and fragments of *Lophelia pertusa* and *Madrepora oculata* were obtained at 948 m water depth. *C. seguenzae* Duncan 1873 was also very frequently present in some stations.

According to the biogeographic analysis of Cairns and Chapman (2001), who compiled all data available at that time, a third of the scleractinian species that are known to occur in the two deep-water coral provinces embracing the Bay of Biscay—province 1 from North Sea to northern Bay of Biscay; and province 2 from the southern Bay of Biscay—are endemic to the eastern Atlantic, while the others are amphi-Atlantic. Table 1 lists 34 scleractinian species collected from the Bay of Biscay in about 350 stations (see Fig. 1b). Eight species are colonial (23.6%) and were present on most sampling sites. *Lophelia pertusa* was encountered on 102 (29.1%) stations, followed by *Madrepora oculata* on 86 (24.6%) and *Dendrophyllia cornigera* on 36 (10.3%). Amongst the solitary corals, *C. smithii* (28 stations, 8%), *Desmophyllum dianthus* (25 stations, 7.1%) and *C. seguenzae* Duncan 1873 (24 stations, 6.9%) represent the most commonly found species (Table 1). A detailed account on species, depth ranges and stations is provided species-wise and can be downloaded from the journal’s online documentary website (see [Electronic supplementary material](#)).

New data The grab samples (Fig. 2) on the shallow sand-bank dominated top of the BC area, yield quartz sands rich in the solitary scleractinian *C. smithii*. In the deeper canyon heads, grab sampling often failed due to rough seabed morphology. Dead colonies of *Lophelia pertusa*, *Madrepora oculata* and *Desmophyllum dianthus* occurred from 340 (few) to 790 m (abundant). No living scleractinians were encountered. Further south, the outer Penmarc’h Bank was also explored (Fig. 2); but here, only Late Pleistocene *C. smithii* specimens were found which yielded calibrated U–Th ages of 13,960±120, 13,060±240 and 11,170±180 years BP (Schröder-Ritzrau et al. 2005) at 240 m. The only live coral in this area were colonies of *Dendrophyllia cornigera* (“coral jaune”; Fig. 3). Along the Cantabrian margin, 3 out of 32 boxcores were filled with dead coral fragments. *Madrepora oculata*, numerous small pieces of *Lophelia* and one fragment of *Desmophyllum dianthus* were observed.

Discussion

Worldwide, the aim is to have a better understanding of coral distributions and the factors that regulate them in order to manage these ecosystems more effectively (Cairns



Fig. 3 *Dendrophyllia cornigera* collected alive from outer Penmarc'h Bank (VH-97, Station 320, 290 m depth)

and Chapman 2001; Hall-Spencer et al. 2007; Bryan and Metaxas 2006, 2007; Davies et al. 2007). The NE Atlantic is the focus of the most extended historical literature available on deep-water corals. Out of 347 historical and new records, this study reports in total 34 species of scleractinians in the Bay of Biscay (see Table 1). The extraction of bathymetric information from these records shows a characteristic “shallow-water” coral assemblage which is found on the shelf and incised upper canyon heads. From 10 to 500 m water depth, *Balanophyllia cellulosa*, *C. smithii*, *Dendrophyllia cornigera* and *Paracyathus pulchellus* form a characteristic neritic community (Fig. 4). A transitional group of corals exists on the outer shelf edge canyon heads at around 200 m and upper slope down to 2,000 m water depth. This group consists of *Balanophyllia thalassae*, *C. calveri*, *Deltocyathus moseleyi*, *Desmophyllum dianthus*, *Dendrophyllia alternata*, *Eguchipsammia cornucopia*, *Stenocyathus vermiformis*, *Stephanocyathus crassus*, *Lophelia pertusa* and *Madrepora oculata* (Fig. 4). The latter two framework-building species show a wide depth range from 200 down to 2,000 m; however, the majority of findings are in the shallow canyon heads (200–400 m depth interval). Corals confined to the upper slope from 500 to 3,000 m are *Anomocora fecunda* (1,000 m), *C. abyssorum*

(600–1,400 m), *C. Ambrosia* (1,600–3,000), *C. atlantica* (1,200–1,500), *C. cyathus* (700–800), *C. sarsiae* (500–1,100 m), *C. seguenzae* (1,000–2,100 m), *Deltocyathus conicus* (1,100–2,500 m), *Enallopsammia rostrata* (1,000–2,500 m), *Flabellum alabastrum* (800–2,500 m), *Flabellum macandrewi* (800–1,000 m), *Fungiacyathus fragilis* (1,000–1,900 m), *J. cailletii* (1,200–2,500 m), *Premocyathus cornuformis* (700–2,400 m), *Solenosmilia variabilis* (700–2,500 m), *Stephanocyathus moseleyanus* (1,000–1,700 m), *Stephanocyathus nobilis* (1,500–2,500 m) and *V. concinna* (1,200–2,500 m). True deep bathyal corals are *Flabellum angulare* (1,900–3,900 m) and *Fungiacyathus marenzelleri* (1,900–4,900 m; Fig. 4).

Based on the reports of Joubin (1922a, b, 1923), Le Danois (1948), Zibrowius et al. (1975), Zibrowius (1980, 1985), Monteiro Marques and Andrade (1981), Álvarez-Claudio (1994) and Altuna (1995), scleractinian corals appear to cluster in several key regions: the Meriadzek Terrace (MT), the BC, the Aquitaine margin, the Cap Breton Canyon, Le Danois Bank and the Cantabrian–Galician margin (Fig. 1b). The boxcore samples acquired both from the BC area in 1997 and from the Cantabrian–Galician margin in 2004 contained a large amount of dead fragments and coral rubble rather than pieces of living corals. Yet, the

sediments in the NE Atlantic continental margin (Thomsen and Gust 2002). Ripple marks were also observed on the MT indicating the presence of strong bottom currents (Laubier and Sibuet 1977). These bottom currents, strong enough to resuspend the sediment may be related to internal tides (internal waves of tidal frequency) mainly occurring along the canyon axis (Gardner 1989). Indeed strong, localized internal tides in the Bay of Biscay (New 1988) result from a combination of a favourable stratification, a steep topography and strong barotropic tidal currents directed cross-isobath (Cartwright et al. 1980; Baines 1982; Pingree et al. 1986; Le Cann 1990; Pingree and New 1991). At the bottom within the canyons such as the Shamrock Canyon (north of MT), water mixing is responsible for resuspension of organic matter (Vangriesheim 1985). The canyons, mostly erosive and thus not filled with sediments (Le Suavé et al. 2000), probably induce locally strong currents and mixing which is essential for the corals to flourish. On the Nova Scotia margin, fishermen identified canyons as sites where dense gorgonian coral assemblages were thriving (Breeze et al. 1997). The significance of submarine canyons as coral habitats (Mortensen and Buhl-Mortensen 2005) may be due to their capacity to accumulate organic debris (Vetter and Dayton 1998), which may directly benefit suspension feeders. Submarine canyons are known to support high densities and diversity of megafaunal organisms (Hecker et al. 1980; Tyler and Zibrowius 1992) in greater abundance than in nearby slope areas (Hecker et al. 1980; Harrison and Fenton 1998; Vetter and Dayton 1998). Valuable reports are provided on higher fish occurrences in canyons and in relation to micro topography (Lorance et al. 2002).

Other examples document rich populations of stalked crinoids, *Diplocrinus whyvillethomsoni* (Conan et al. 1981) and pectinid bivalves (Schein 1989) on the bathyal slope of the Bay of Biscay. It is likely that this water mixing above the seabed results in enhanced levels of suspended material and favours higher concentrations of filter/suspension feeders. Indeed, high faunal biomass occurs especially where internal waves result in an increase in suspended material (Rex 1981). Additionally, there appears to be a direct link between higher coral densities and high productivity levels in the overlying surface waters (White et al. 2005; White 2007). The rapidly sinking seasonal blooms of surface primary production have been observed to have an effect on the reproductive biology of benthic invertebrates (Billett et al. 1983; Rice et al. 1991; Waller and Tyler 2005). A mass seasonal deposition of aggregated phytodetritus to the ocean floor was revealed for the first time at the Porcupine Seabight (Rice et al. 1991). It was also observed at a variety of other continental margin sites in the NE Atlantic, including the carbonate mounds in UK waters (Rockall Trough; Kenyon et al. 2003) and on the Galicia Bank (Duineveld

et al. 1994). Each year from May to September, the Celtic–Armorican shelf break exhibits a summer surface cooling of 0.5–1.5°C (Dickson et al. 1980; Pingree et al. 1982), coupled to high chlorophyll levels (Pingree et al. 1986) and to an augmentation of new production. A seasonal recurring upwelling of cold waters is thought to be mainly due to the propagation of exceptionally large internal waves, generated by the interaction of strong barotropic tidal currents with the steep shelf break topography (Dickson et al. 1980; Pingree et al. 1986). On the Cantabrian margin, the surface currents generally flow eastwards during winter and spring and change westwards in the summer. These changes in the direction of currents produce seasonal coastal upwelling. A combination of (1) a high production in the surface waters (Dickson et al. 1980; Pingree et al. 1982), (2) the availability of suitable seabed surfaces for reef formation, and (3) favourable hydrodynamic conditions (New 1988; Le Cann 1990) to produce enhanced bottom currents and to promote the transport of organic material to the seafloor is probably responsible for the occurrence of a dominant fauna of filter and suspension-feeders in the Bay of Biscay.

Besides cold-water corals, also a high diversity and abundance of associated species assemblages were found in the Cantabrian–Galician region. Dead shells of the bivalves *Spondylus gussoni* (Costa, 1829) and *Lima marioni* (Fischer, 1882) were identified in large quantities. Echiurids (*Bonellia viridis* Rolando, 1821), polychaetes (*Eunice* spp.), molluscs (*Limopsis aurita* Brocchi, 1814), *Delectopecten vitreus* (Gmelin, 1791), crustaceans (*Munida sarsi* Huus, 1935), and many commercial fish are reported in a high quantity along the Cantabrian–Galician margin. Although no species is actually stated as being restricted to cold-water corals, these species are frequently found associated with cold-water corals (Jonsson et al. 2004; Freiwald et al. 2004; López Correa et al. 2005; Henry and Roberts 2007). A unique highly diverse and abundant suprabenthic community was also observed on Le Danois Bank; also, a species of crustacean new to science was reported (Guerra-García et al. 2008). Finally, sponges are reported with high abundance (Le Danois 1948; Sánchez et al. 2002; Guerra-García et al. 2008). As major filter feeders, they may benefit from the same topographic and hydrological conditions required by stony corals; some are used to discriminate on- and off-mound habitats in the NE Atlantic (Henry and Roberts 2007).

The presence of probably larger amounts of coral rubble beds in the area is yet a critical issue on, i.e., Le Danois Bank. Live corals indeed attract a huge international attention (Roberts et al. 2006); yet, dead and live coral reefs are inevitably associated with each other. Both are co-occurring on carbonate mounds along the continental margin of the NE Atlantic (Van Weering et al. 2003; Huvenne et al. 2005; Foubert et al. 2005; De Mol et al. 2002, 2005) and both participate to the reproductive cycle of coral reefs

(Wilson 1979). Hard substrate on which to attach such as coral rubble and dead fragments is fundamental for any putative recolonization (Freiwald and Wilson 1998). The numerous dead cold-water corals may hence play a critical role for colonization by larvae from neighbouring isolated coral reefs in the Bay of Biscay (Roberts et al. 2006). Besides, there where live cold-water corals mainly provide protection and even nurseries for some mobile species (Rogers 1999), dead stony corals have been observed to provide a substrate for an associated fauna which is even more diverse (Mortensen et al. 1995; Freiwald 2002). It is likely that coral skeleton, found in high quantity in the area, provide additional hard substratum for attachment of epifaunal organisms. Conversely, disturbance of coral remnants prevents the maintenance of an area free of resuspended sediment and may even provoke polyp suffocation. In shallow water, Dodge and Vaisnys (1977) have shown that extended dredging operations have had a destructive effect on coral communities. Damage in cold-water coral areas inflicted by significant coral by-catch when trawling is well documented in the Porcupine Seabight (Hall-Spencer et al. 2002; Grehan et al. 2005). Genetic analysis of populations in the Darwin mound province, NE Rockall Trough (Masson et al. 2003) revealed the least genetic diversity of any of the sites in the NE Atlantic (Le Goff-Vitry et al. 2004).

Reproductive analysis studies also showed that no reproductively active polyps in *Lophelia pertusa* taken from the Darwin mounds were here observed (Waller and Tyler 2005). Intense trawling areas were actually observed in this area (Hall-Spencer et al. 2002). It was hypothesized that the damage from these operations may impede *Lophelia pertusa* to reach the size necessary for gametogenesis (Waller and Tyler 2005). Many scleractinian colonies indeed have to reach a certain size before acquiring reproductive maturity (Szmant 1986), while stress may reduce reproductive output, and even cause death in some cases (Brown and Howard 1985). A small, but non-permanent deep-sea fishery (e.g. *Hoplostethus atlanticus* Collett 1889, commonly named orange roughy) is established off France in the Bay of Biscay (Koslow et al. 2000). Fishermen, principally looking for orange roughy, mainly within the vicinity of canyon heads in the northern part of the Bay of Biscay (47°N/49°N), report living *Lophelia pertusa* by-catch up to 1,100 m (Le Guilloux personal observation).

Anthropogenic impact on this area, e.g. in terms of fishery has not yet been addressed so far. The consequences may be of a great extent because the fishing activity occurs within a narrow continental margin. Yet the steep topography could partially protect the coral communities by their inaccessibility for benthic trawling. However, it is also possible that many of the reefs of the Bay of Biscay may have been, like in other areas, obliterated by slumping and

erosion (Gage and Tyler 1991). There has actually recently been an increase in evidence that deep-water reefs are fragmented (Rogers 1999; Waller and Tyler 2005). Yet localized regions of high coral abundance exist that may support cold-water coral recolonization. Genetic and phylogeographic analysis of deep-water corals in the NE Atlantic (Le Goff-Vitry et al. 2004; Le Goff-Vitry and Rogers 2005) suggest that *Lophelia pertusa* does not form a panmictic population. Instead, there is a high genetic differentiation between subpopulations in fjords and those offshore. Along the NE Atlantic continental margin, the genetic differentiation can be regarded as moderate suggesting sporadic, but not continuous, gene flow through larval dispersal over long periods of time.

These last genetic analyses actually suggest that a certain genetic cohesion is maintained through larval dispersal over the slope of the Bay of Biscay. Consequently, the Biscay margin presumably acts as a semi-continuous habitat for larval dispersal of stony corals. The species distribution analysis of Cairns and Chapman (2001) also highlights that the Bay of Biscay nicely fits into the NE Atlantic biogeographic cluster. The wide Bay of Biscay canyons and slopes may hence represent a stepping-stone for dispersal. Indeed, due to its central position within the European margins and in a scenario of a possible recolonization, the relative importance of the Bay of Biscay for the global distribution of cold-water coral reefs in the NE Atlantic is highlighted. The Bay of Biscay is a crucial and obligate transit route for cold-water coral colonization from or to the Mediterranean Sea and to the NE Atlantic. During interglacial periods, deep and intermediate-water flow is directed poleward along the NE Atlantic continental margins (Kenyon 1986), thus supporting a northward migration of deep-water corals.

Conversely, a southern retreat of corals and other shelly benthic invertebrate assemblages from northern to southern latitudes occurred during the transition from warm to cold climatic conditions. This phenomenon is evidenced by the immigration of a boreal fauna into the Mediterranean Sea, both in shallow and deep-water environments (Taviani et al. 1991; Schröder-Ritzrau et al. 2005). In this sense, the “boreal guests” in the Mediterranean Sea found a refugium to survive and to expand distribution back into the Atlantic when climatic conditions switched back to an interglacial mode. It is tempting to suggest, that Mediterranean deep-water coral dispersal into the NE Atlantic was supported by the oceanographic circulation that carried the genetic information from Gibraltar as far north as to the Barents Sea (De Mol et al. 2005). Establishment of water masses of different properties might have introduced larvae of the cold-water corals to the NE Atlantic and initiated the carbonate coral mounds in the Porcupine Seabight (De Mol et al. 2002, 2005). After the Last Glacial Maximum between 14

and 10 ka BP, corals began to recolonize the Bay of Biscay canyons and open slopes and settled on the pre-existing mounds in the Porcupine Seabight and Rockall Trough (Frank et al. 2005; Schröder-Ritzrau et al. 2005). Late Pleistocene scleractinians, 14–11 ka BP (Schröder-Ritzrau et al. 2005), as well as primnoid octocorals about 11 ka BP (Noé et al. 2007) recovered in the BC and the Cantabrian–Galician margin, offer new data to get a better insight into the migration pattern in space and time and the relation between the Atlantic and Mediterranean coral communities.

Conclusions

The compilation of historical information on deep-water habitats provided a wealth of information about scleractinian distribution in the Bay of Biscay. Considering the several cold-water coral rich areas as potential stepping-stones for larval dispersal, it highlights the need for additional visual surveying and mapping for cold-water corals in the area. Indeed at a time where more advanced seabed mapping and sampling tools are now more accessible than ever before, it is highly recommended to get deeper insight into the current state of cold-water corals over the whole Bay of Biscay. The Bay of Biscay is an integral sector of the European Margin, therefore better knowledge about corals in the area will help to make decisions on the management and the conservation of the deep-water coral environment along the European continental margins.

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