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Biochemical composition of the cold-water coral *Dendrophyllia cornigera* under contrasting productivity regimes: Insights from lipid biomarkers and compound-specific isotopes

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ABSTRACT

The cold-water coral (CWC) *Dendrophyllia cornigera* is widely distributed in areas of both high and low productivity, suggesting a significant trophic plasticity of this coral depending on the food available in the environment. In this study, lipid biomarkers and their isotopic signature were compared in colonies of *D. cornigera* and sediment from the highly productive Cantabrian Sea (Northeast Atlantic Ocean) and the less productive Menorca Channel (Western Mediterranean Sea). Lipid content and composition in coral tissue clearly reflected the contrasting productivity in the two areas. Cantabrian corals presented higher content in fatty acids (FA), fatty alcohols and sterols than Menorca corals.

Energy storage (saturated + mono-unsaturated FA) to structural (poly-unsaturated FA) ratio was higher in Cantabrian than in Menorca corals. The high ΣC20:1 content as well as $PUFA_{(n-3)}/PUFA_{(n-6)}$ ratio suggest that Cantabrian corals mainly feed on phytoplankton and herbivorous grazers. This is also supported by the higher mono-unsaturated fatty alcohols (MUOH) and long chain mono-unsaturated fatty alcohols (LCMUOH) content in Cantabrian compared to Menorca corals. Conversely, higher $PUFA_{(n-6)}$ content in Menorca corals, with the dominance of $C22:4_{(n-6)}$ and $C20:4_{(n-6)}$, as well as the dominance of cholesterol and $norC_{27}\Delta^{5,22}$ among sterols, point to a higher trophic role of dinoflagellates and invertebrates. The observed geographical variability in trophic ecology supports a high trophic plasticity of D. *cornigera*, which may favour the wide distribution of this CWC in areas with highly contrasted food availability.

1. Introduction

Cold-water coral (CWC) distribution has been related to areas of high primary production (Frederiksen et al., 1992; Mortensen et al., 2001; Roberts et al., 2006; Davies et al., 2008) and hydrodynamic conditions that determine a direct transport of food from the surface to the seafloor (Thiem et al., 2006; Davies et al., 2009; Roberts et al., 2009; Moreno-Navas et al., 2014). Food availability significantly affects metabolism and growth rates in CWC (Naumann et al., 2011). Nevertheless, the increasing exploration of deep-sea ecosystems has revealed that some CWC species may also occur in areas of lower productivity (Taviani et al., 2015; Cau et al., 2017; Orejas et al., 2017). Areas of low surface productivity represent harsh nutritional conditions for deep-sea organisms, since the sinking flux of particulate organic matter to the deep sea has been estimated to be 10% of the surface production (Eppley and Peterson, 1979). The distribution of the CWC *Dendrophyllia cornigera* ranges from the highly productive areas of the Northeast Atlantic Ocean to the low productive waters of the Mediterranean Sea (Gori et al., 2014, and references herein). This distribution in areas with highly contrasted productivity hints at a geographical variability in the trophic ecology and the nutritional condition of this CWC species, according to the food availability in each area. CWC can feed on a wide range of particles, from bacteria (Mueller et al., 2014), to phytodetritus, phytoplankton and mesozooplankton (Duineveld et al., 2004, 2007,

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2012; Kiriakoulakis et al., 2005; Carlier et al., 2009; Dodds et al., 2009; Naumann et al., 2015), to cover their basic energy requirements for growth and the build of energy reserves in the form of lipid.

Lipids are important energetic (triglycerides and wax esters) and structural (phospholipids and sterols) components of coral tissue (Imbs et al., 2010; Imbs, 2013). Triglycerides and phospholipids are mainly composed of fatty acids (FA) (Pernet et al., 2002), which are obtained through feeding and endogenous biosynthesis (Dalsgaard et al., 2003; Imbs et al., 2007). Poly-unsaturated fatty acids (PUFA) play important roles in metabolic regulation, growth and formation of biomass (Müller-Navarra et al., 2000; Wacker, von Elert, 2001), whereas mono-unsaturated (MUFA) and saturated (SFA) fatty acids are mainly used as basic metabolic energy and stored for short and long-term energy demands (Sargent et al., 1999; Dalsgaard et al., 2003). FA are combined with alcohols to form wax esters, which are the main long-term energy reserves in coral tissue (Grottoli et al., 2004; Larsson et al., 2013), varying seasonally in coral species in relation to food availability (Oku et al., 2003; Yamashiro et al., 2005). Finally, sterols and phospholipids, which are main constituents of cell membranes, are directly related to the amount of coral tissue biomass (Nes, 1973; Boutry et al., 1979; Dalsgaard et al., 2003; Tchernov et al., 2004; Tolosa et al., 2011). Content of FA, fatty alcohol and sterol is consequently directly related to the nutritional condition of corals, both in terms of tissue biomass as well as amount of energetic reserves. Moreover, since lipid composition is often specific to particular groups of organisms (Volkman, 1986; Volkman et al., 1989), the analysis of FA, fatty alcohol and sterol composition has been widely used to identify the main food sources in marine organisms in general (e.g. Graeve et al., 1997; Dalsgaard et al., 2003; Budge et al., 2006; Jeffreys et al., 2009) including tropical (e.g. Treignier et al., 2008; Imbs, 2013) and CWC species (Table 1; Dodds et al., 2009; Duineveld et al., 2012; Larsson et al., 2013; Naumann et al., 2015). Compound-specific stable carbon isotope analysis (δ^{13}C-CSIA) can be used to further identify the origin of food sources utilised by corals (Tolosa et al., 2011; Naumann et al., 2015). δ^{13}C value of a specific FA compound reflects its synthetic pathway and hence its source (Teece et al., 1999; Hayes, 2001). For FA that cannot be directly synthesized by animals and have to be acquired through feeding, δ^{13}C values will be comparable to those of the prey, since little or no isotopic fractionation occurs (Villinski et al., 2004; Treignier et al., 2008). Conversely, for FA that can be synthesized de novo, δ^{13}C values will reflect the competing processes of assimilation and synthesis (Villinski et al., 2004).

This study aimed to characterize the composition in lipid biomarkers of the CWC *Dendrophyllia cornigera*, and to explore how its nutritional condition and main food sources vary in areas with contrasting primary productivity. Specifically, the highly productive Cantabrian Sea in the Northeast Atlantic Ocean (Chl *a* ranges from 0.36 to 1.36 mg m^{-3}), and the less productive Menorca Channel in the Western Mediterranean Sea (Chl *a* 0.13–0.43 mg m^{-3}) (Feldman and McClain; https://oceancolor.gsfc.nasa.gov/cms). Nutritional condition and main food sources were assessed by quantifying FA, fatty alcohol and sterol compounds in *D. cornigera* colonies as well as in sea bottom sediment samples collected from the two areas, together with the assessment of the δ^{13}C of individual lipid compounds.

2. Materials and methods

2.1. Study species

Dendrophyllia cornigera (Lamarck, 1816) is a scleractinian coral (Anthozoa, Scleractinia, Dendrophylliidae) with polyps 2–4 cm in diameter forming colonies larger than 50 cm in height (Zibrowius, 1980; Brito and Ocaña, 2004). Its known distribution is restricted to the Mediterranean Sea and the eastern Atlantic from the south of Ireland to the Cape Verde Islands, at seawater temperatures ranging from 11 to 17 °C (Gori et al., 2014 and references herein). A severe reduction in the metabolic rates at 8 °C (Gori et al., 2014) may explain the absence of this CWC from most of the Northeast Atlantic, where seawater temperatures range from 5 to 10 °C (Dullo et al., 2008). Conversely, its capability to maintain physiological functions between 12 and 16 °C (Naumann et al., 2013; Gori et al., 2014) probably contributes to the abundance of *D. cornigera* in deep-sea ecosystems of the Mediterranean Sea and Canary Islands (Brito and Ocaña, 2004; Freiwald et al., 2009; Orejas et al., 2009; Salomidi et al., 2010; Bo et al., 2011; Gori et al., 2013). This species locally forms dense mono-specific aggregations between 50 and 800 m depth (Le Danois, 1948; Álvarez-Claudio, 1994; Brito and Ocaña, 2004; Reveillaud et al., 2008; Sánchez et al., 2009; Bo et al., 2011), and occurs at shallower depths of 30 m in areas characterized by upwelling of cold waters (Castric-Fey, 1996). Experimental studies measured growth rates of 0.04 ± 0.02% d^{-1} (Orejas et al., 2011), efficient zooplankton capture under a larger range of flow velocities (2–10 cm s^{-1}) and seawater temperatures (Gori et al., 2015), and no reduction in calcification rate, skeletal microdensity and porosity under reduced pH (Movilla et al., 2014).

Table 1
Lipid biomarkers detected in the analyzed sediment samples and *Dendrophyllia cornigera* corals.

	Indicator	Reference
(a) Fatty Acids Biomarkers		
(SFA + MUFA)/PUFA	Storage (metabolic energy) vs structural (biomembrane functioning)	Dalsgaard et al. (2003); Treignier et al. (2008)
$PUFA_{(n-3)}/PUFA_{(n-6)}$	Hervirbory vs carnivory; diatoms vs dinoflagellates	Wilson et al. (2010); Dalsgaard et al. (2003)
LCSFA (> C22)	Terrestrial vascular material	Dalsgaard et al., 2003; Tolosa et al. (2004)
LCMUFA	Herbivorous grazers	Dalsgaard et al. (2003)
$C22:6_{(n-3)}$	Dinoflagellates	Harwood and Russell (1984)
$C20:5_{(n-3)}$	Diatoms	Harwood and Russell (1984)
$C22:6_{(n-3)}/C20:5_{(n-3)}$	Phytoplankton: dinoflagellates vs diatoms; carnivory degree	Harwood and Russell (1984); Dalsgaard et al. (2003)
$C20:4_{(n-6)}$	Dinoflagellates and invertebrates	Wilson et al. (2010)
C15, C17 and branched FA	Bacterial	Volkman and Johns (1977)
(b) Fatty Alcohols Biomarkers		
LCMUOH (C20:1 - C22:1)	Herbivorous grazers	Dalsgaard et al. (2003)
3,7,11,15-tetramethyl-2-hexadecen-1-ol (phytol)	Phytoplankton	Volkman et al. (1998)
(c) Sterols Biomarkers		
Phytosterols[a]	Eukaryotic phototrophic organisms	Volkman et al. (1998)
$C_{27}\Delta^5$ (cholesterol)	Zooplankton, invertebrates (phytoplankton)	Sun and Wakeham (1999); Volkman (1986)
$norC_{27}\Delta^{5,22}$	Marine invertebrates (dinoflagellates)	Goad and Withers (1982); Volkman et al. (1981)

[a] Include: cholesta-5,22(E)-dien-3β-ol ($C_{27}\Delta^{5,22}$); 24-methylcholesta-5,22(E)-dien-3β-ol (brassicasterol, $C_{28}\Delta^{5,22}$); ergosta-5,7,22-trien-3β-ol (ergosterol, $C_{28}\Delta^{5,7,22}$); 24-methylcholesta-5-en-3β-ol ($C_{28}\Delta^5$); 24-methylcholesta-5,24(28)-dien-3β-ol ($C_{28}\Delta^{5,24(28)}$); 24-ethylcholesta-5,22(E)-dien-3β-ol ($C_{29}\Delta^{5,22}$); 24-ethylcholest-5-en-3β-ol (sitosterol, $C_{29}\Delta^5$); 24-ethylcholesta-5,24(28)(Z)-dien-3β-ol (isofucosterol; $C_{29}\Delta^{5,24(28)}$); 4α-23,24-trimethylcholest-22(E)-en-3β-ol ($C_{30}\Delta^{22}$) and the 24-propylcholesta-5,24(28)-dien-3β-ol ($C_{30}\Delta^{5,24(28)}$).

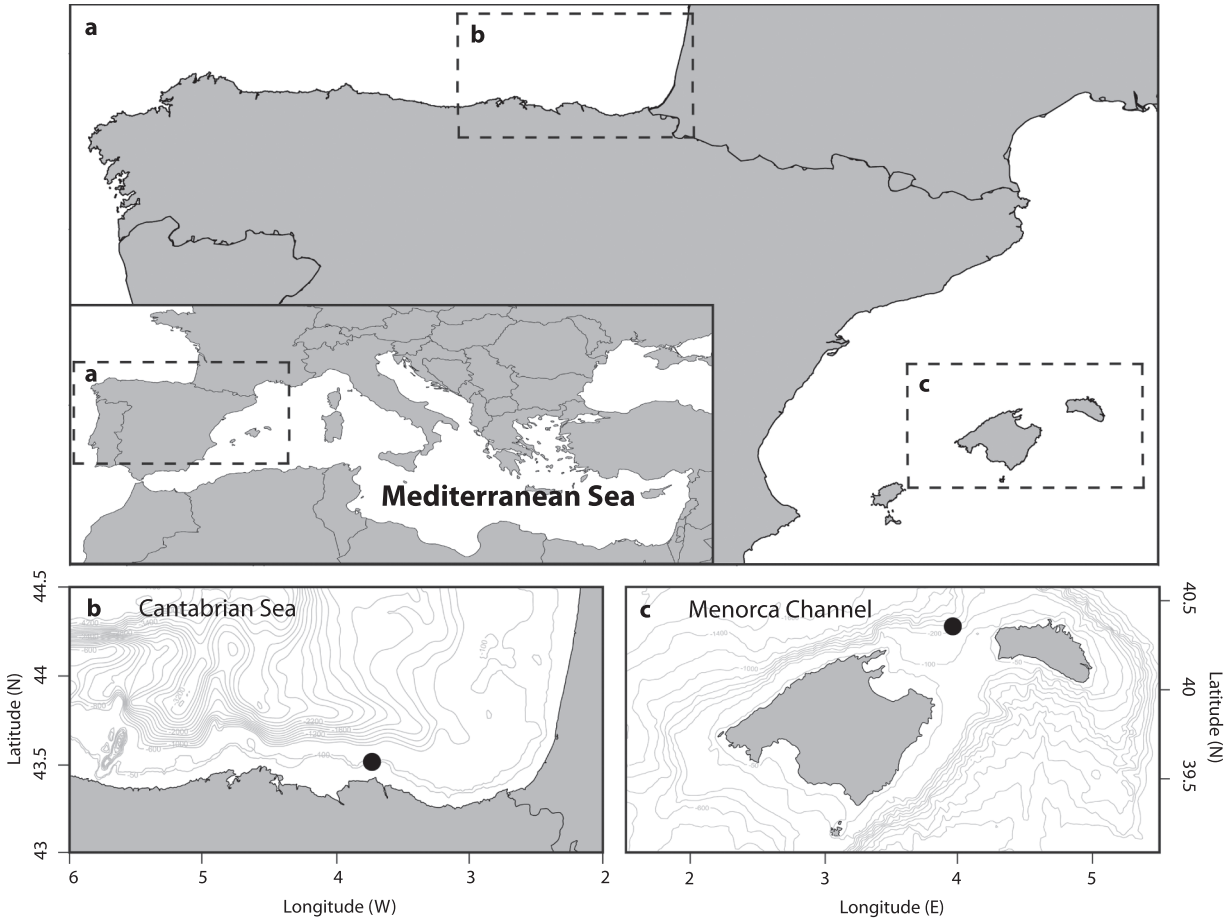

Fig. 1. Map of the (a) sampling area encompassing the south of the Bay of Biscay and the Western Mediterranean Sea. Black dots indicate the sampling location in the (b) Cantabrian Sea and the (c) Menorca Channel.

2.2. Study areas

Colonies of *D. cornigera* were collected in the Cantabrian Sea in the Northeast Atlantic Ocean, and in the Menorca Channel in the Western Mediterranean Sea (Fig. 1a). The Cantabrian Sea (Fig. 1b) embraces the southern part of the Bay of Biscay, where a narrow continental shelf is limited to the north by Cap Breton canyon. The origin of water masses in the area are predominantly North Atlantic and Mediterranean (outflow waters) (Pollard et al., 1996). Several rivers feed the sedimentary basin of the Cantabrian Sea (Jouanneau et al., 1998; Castaing et al., 1999), where surface chlorophyll *a* concentration during the year prior to sampling (summer 2010–spring 2011) ranged from 0.36 mg m^{-3} in summer to 1.36 mg m^{-3} in spring (mean of 0.72 mg m^{-3}, Fig. 2a, b; MODIS-Aqua sensor data from the NASA Goddard Space Flight Center, Ocean Biology Processing Group, Feldman and McClain; https://oceancolor.gsfc.nasa.gov/cms). The Menorca Channel is located between the islands of Mallorca and Menorca (Fig. 1c), which are part of a large shallow promontory with a regular relief and gentle slopes (Canals and Ballesteros, 1997; Acosta et al., 2002). This area is affected by strong northerly winds and offshore currents (Pinot et al., 1995, 2002), and is highly oligotrophic (i.e. poor nutrient content, especially nitrogen and phosphorus) due to low rainfall and limited runoff from rivers (Estrada, 1996; Segura-Noguera et al., 2011). Surface chlorophyll *a* concentration in the Menorca Channel during the year prior to sampling (summer 2010–spring 2011) ranged from 0.13 mg m^{-3} in summer to 0.43 mg m^{-3} in winter (mean of 0.21 mg m^{-3}, Fig. 2c, d; Feldman and McClain; https://oceancolor.gsfc.nasa.gov/cms).

2.3. Coral and sediment collection

Corals were collected near Cap Breton canyon in the Cantabrian Sea (43° 31′ 44″ N; 002° 45′ 36″ E, 216–221 m depth) by a TV-grab operated from the research vessel "Meteor" during the cruise M84/5 (June 2011). In the Menorca Channel (40°00′ 00″ N; 003° 32′ 20″ E, 180–330 m depth), corals were collected using the manned submersible JAGO (IFM-GEOMAR, Kiel, Germany) operated from the research vessel "García del Cid" during the cruise INDEMARES 4 (April 2011). These corals will be subsequently called Cantabrian and Menorca corals, respectively. Three coral colonies were sampled from each area (Table 2), each colony from a different location. Locations were separated by 0.1–0.9 km in the Cantabrian Sea, and by 1.2–3.6 km in the Menorca Channel. A sediment sample was also collected from the sea bottom of each area (from one of the locations where corals were collected) using a TV-grab (Cantabrian Sea, 200 m depth) and a Van-Veen grab (Menorca Channel, 225 m depth). Coral colonies and sediment samples were immediately frozen on board at − 80 °C, and stored at − 20 °C until freeze-dried for 16 h at − 110 °C and at 100 mbar pressure with a Christ Alpha 2–4 LD plus freeze-dryer.

2.4. Lipid biomarkers extraction and characterization

Lipids were extracted and characterized as described in Treignier et al. (2008), Tolosa et al. (2011) and Naumann et al. (2015). Thawed samples (i.e., bulk corals including skeleton, and sediment samples) were spiked with surrogate standards (cholanic acid and 5α-androstan-3β-ol), extracted in CH_2Cl_2:MeOH (2:1), stirred and sonicated for 10 min each. This procedure was repeated twice and the three extracts

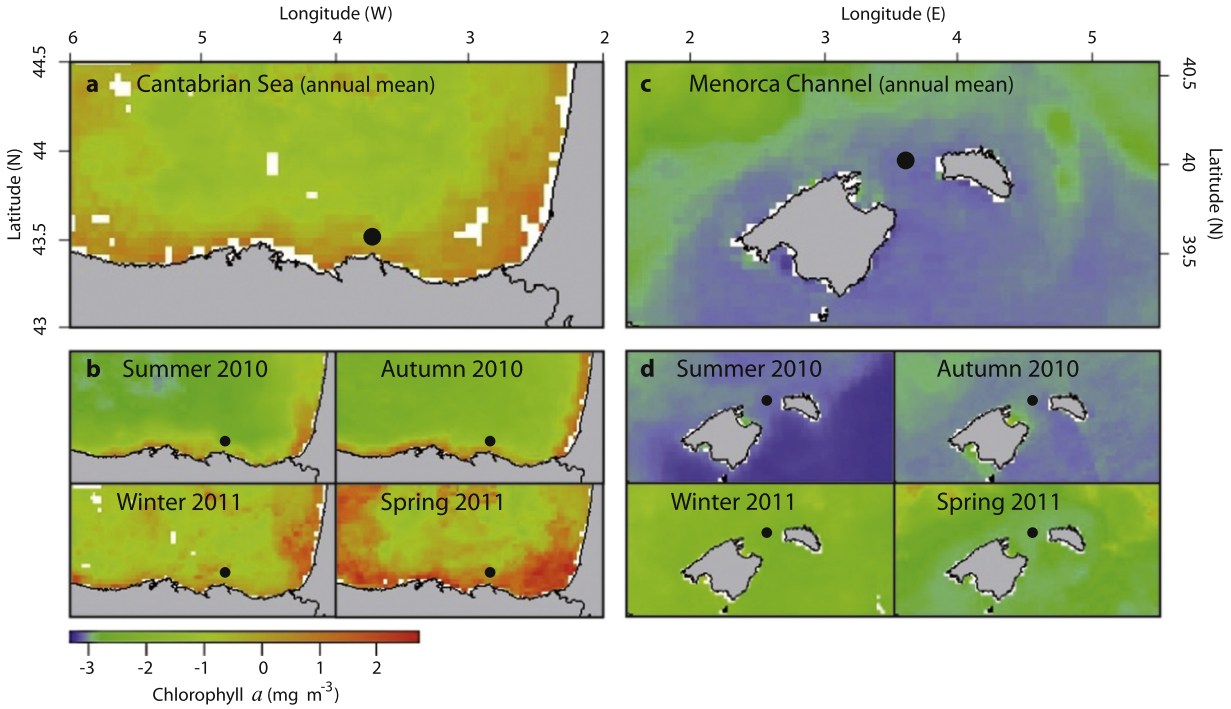

Fig. 2. Annual mean and seasonal variation of surface primary production (Chl *a*) during the year prior the sampling (summer 2010–spring 2011) in the (a, b) Cantabrian Sea and the (c, d) Menorca Channel (MODIS-Aqua sensor data from the NASA Goddard Space Flight Center, Ocean Biology Processing Group, Feldman and McClain; https://oceancolor.gsfc.nasa.gov/cms/). Black dots indicate the sampling location in the Cantabrian Sea and the Menorca Channel.

Table 2
Dry weight and surface of the *Dendrophyllia cornigera* colonies analyzed for each geographic area.

Location	Coral dry weight (g)	Coral surface (cm^2)
Cantabrian Sea	1.86	2.6
	2.20	2.8
	2.20	2.8
	2.09 ± 0.19	2.7 ± 0.1
Menorca Channel	2.86	3.1
	2.03	2.7
	1.53	2.4
	2.14 ± 0.67	2.7 ± 0.4

were pooled. MeOH (4 mL) was added before extracts were concentrated on a rotary evaporator, and saponified using 1 mL of KOH 6% + 1 mL MilliQ-water (1 h at 80 °C). Isolation of the neutral and acidic fractions was carried out after Tolosa and de Mora (2004). The neutral fraction was extracted with n-hexane and then, the remaining saponified solution was acidified with 1 mL of HCl 6N to pH 2, and the fatty acids were extracted with hexane:ethyl acetate (9:1).

2.4.1. Derivatization

The neutral fraction was treated with bis-trimethylsilyl-trifluoroacetanamide (BSTFA, 1 h at 70 °C) to convert the hydroxyl group of the fatty alcohols and sterols into their tri-methyl silyl homologues. Subsequently, the fraction was evaporated to dryness under N_2 and diluted in isooctane for gas chromatographic (GC) analysis. The acidic fraction was trans-esterified with BF_3:MeOH (20%, 1 h at 80 °C) to convert FA into their corresponding methyl esters.

2.4.2. Compound identification and quantification

Coupled gas chromatography/mass spectrometry (GC/MS) was used for compound identification on an Agilent 6890 N with MSD 5975 equipped with a DB-XLBMSD column (30 m length, 0.25 mm internal diameter, 0.25 µm thickness). Helium was used as carrier gas (1.6 mL min^{-1}). The oven temperature was programmed from 60 °C to 100 °C at 10 °C min^{-1} and from 100 °C to 285 °C at 4 °C min^{-1}. Identification of compounds was made according to their mass spectra and retention time of standards (see Appendix A for details). Quantification of neutral compounds was performed on a Hewlett-Packard HP 7890 A with a flame ionization detector (FID) and a split-less injector. The column was a HP-5 (30 m length, 0.25 mm internal diameter, 0.25 µm thickness). Injector and detector temperatures were 270 °C and 320 °C, respectively. The oven temperature was programmed at 4 °C min^{-1} from 60 °C to 310 °C, and maintained at 310 °C for 20 min. Quantification of the acidic compounds was carried out with a Hewlett Packard HP5890 series II equipped with a FID and on-column injector. The DB-23 (30 m length, 0.32 mm internal diameter, 0.25 µm thickness) column was pre-connected with a press-fit connector to a 0.32 mm internal diameter deactivated fused silica capillary. Helium was used as carrier gas (1.2 mL min^{-1}). The GC oven for the DB-23 column was programmed from 60 °C (0.5 min hold) to 250 °C at 6 °C min^{-1}.

2.4.3. Carbon stable isotope measurements

The $\delta^{13}C$ (‰) isotopic signature of the major lipid compounds was analyzed using a Thermo Trace GC coupled to a Delta V Advantage isotope-ratio mass spectrometer (GC-IRMS) through the GC-Isolink and the Conflo IV interface (GC-C-IRMS). The system was equipped with a DB-5 column (30 m length, 0.25 mm internal diameter, 0.25 µm thickness) pre-connected with a press-fit connector to a 0.53 mm internal diameter deactivated fused silica capillary retention gap of 2 m. The injection was on-column. The GC oven was programmed at 60 °C for 1 min, then to 290 °C at 4 °C min^{-1} and maintained at 290 °C for 30 min. Three CO_2 on/offs were run at the beginning of each chromatogram in backflush-on and at the end of each chromatogram in backflush-off, to control for any significant change on the carbon isotope composition due to coelution compounds from the capillary column. Certified isotope standards (n-alkanes mixture B4 from n-C16 to n-C30, nC36 alkane (− 29.62 $\delta^{13}C$ mean value in ‰ vs VPDB), 5 α-androstane (– 32.64‰), and C30 FAME (− 26.31‰)) were obtained from Dr. Schimmelmann (Indiana University; http://php.indiana.edu/~ aschimme/hc.html) and

were used to calibrate directly the GC-C-IRMS. The C18 FAME, C20:4 FAME standards and compounds/reagents involved in the derivatization (e.g., Cholesterol, 18:0 fatty acid, methanol_BF3 and BSTFA) were measured by elemental analyser coupled to IRMS and used to correct the isotopic change resulting from the introduction of additional methyl groups (Jones et al., 1991; Tolosa et al., 1999; Tolosa and de Mora, 2004). For example, for the stable isotope ratio of fatty acids, the effect of adding a methyl group from methanol during methylation was corrected as:

$$\delta^{13}CFA = [(n + 1) \times \delta^{13}CFAME - \delta^{13}CMeOH]/n$$

where δ^{13}CFAME is the measured value of FAME, and δ^{13}CMeOH is the δ^{13}C value of methanol that was measured by EA-IRMS (− 32.57 ± 0.10‰ in this study), δ^{13}CFA is the δ^{13}C value of fatty acid, which does not include the C from methanol; and n is the number of C atoms in the non-methylated fatty acid. The calibrated isotopic standards and the mixtures of FAME, sterol and alcohols were injected in between the samples to monitor any change in the δ^{13}C values. The precision of the C18 FAME, C30 FAME, C-18-OH and cholesterol IRMS standards injected through all the sequence of the samples ranged from 0.2‰ to 0.35‰ (n = 9). Three sample replicates per compound were analyzed to calculate the mean and standard deviation.

2.5. Statistical analyses

FA, fatty alcohol and sterol contents were normalized to the coral dry weight (bulk corals including skeleton; Table 2), and expressed as mean ± standard deviation. Normal distribution of the data was tested by means of Kolmogorov–Smirnov test performed with the R-language function ks.test of the R software platform (R Core Team, 2014). Homogeneity of variances was tested by means of the F test performed with the R-language function var.test. Differences in FA, fatty alcohol and sterol content and composition between Cantabrian (n = 3) and Menorca (n = 3) corals were tested by t-test performed with the R-language function t.test. Corals (n = 6) were ordinated based on their composition (relative percentages) in FA, fatty alcohols or sterols by means of a principal component analyses (PCA) performed with the R-language function prcomp, on data transformed with the R-language function logit (Warton and Hui, 2011).

3. Results

3.1. Lipid biomarkers in sediment

3.1.1. Fatty acid content and composition

In both Cantabrian and Menorca sediment samples, SFA and MUFA represented respectively ~ 50% and ~ 30–40% of total FA, whereas PUFA were present in a small proportion (< 10% of total FA in Cantabrian sediment, and < 5% of total FA in Menorca sediment; Table 3a). C16 and C22:1 were the main FA in Menorca sediment, followed by C18, C18:1$_{(n-9)}$, C14 and C16:1$_{(n-9)}$ (Fig. 3a). Conversely, C18:1$_{(n-9)}$ and C16 were the main FA in the Cantabrian sediment, followed by C16:1$_{(n-7)}$, C18:1$_{(n-7)}$, C18 and medium abundances of several long chain SFA (LCSFA) from C22 to C32 (Fig. 3a). The high concentration of C22:1 MUFA in Menorca sediment was responsible for the higher long chain MUFA (LCMUFA) concentration (Fig. 3a and Table 3a) compared to the Cantabrian sediment. Higher C16 SFA and C22:1 MUFA in Menorca compared to Cantabrian sediment resulted in higher (SFA + MUFA)/PUFA ratio (Fig. 4a). Total bacterial FA (iso- and anteiso- C13, C15 and C17, C12 $_{methyl}$, C13 $_{methyl,}$ C17 $_{cyclo}$, C19 $_{cyclo}$ and C13, C15, C17) were 10–12% of total FA (Table 3a).

3.1.2. Fatty alcohol content and composition

Sediment in Cantabria had lower concentration of fatty alcohols than in Menorca (Table 3b). Phytol and long chain fatty alcohols of even carbon number (C26-OH and C28-OH) were the main constituents of Cantabrian sediment (Fig. 5a). Conversely, short chain fatty alcohols of even carbon number (C14-OH, C16-OH and C18-OH) dominated Menorca sediment (Fig. 5a).

3.1.3. Sterol content and composition

Sterol content was much higher in the Cantabrian than in the Menorca sediment (Table 3c). Cholesterol ($C_{27}\Delta^5$) and sitosterol ($C_{29}\Delta^5$) were the main constituents of the Menorca sediment (Fig. 6a). Conversely, Cantabrian sediment had a more diversified composition dominated by cholesterol ($C_{27}\Delta^5$), brassicasterol ($C_{28}\Delta^{5,22}$), $C_{28}\Delta^{5,24(28)}$, sitosterol ($C_{29}\Delta^5$) and dinosterol ($C_{30}\Delta^{22}$) (Fig. 6a).

3.2. Lipid biomarkers in Dendrophyllia cornigera

3.2.1. Fatty acid content and composition

Total FA content per mg coral dry weight in Cantabrian corals was twice higher than in Menorca corals (t = − 4.044, *p*-value = 0.015; Tables 2 and 3a). A total of 42 FA was identified in corals from both areas (Fig. 3b). PUFAs were the dominant fatty acid class in all corals, representing more than 60% of FA (main compounds: C20:5$_{(n-3)}$, C20:4$_{(n-6)}$, C22:5$_{(n-3)}$ and C22:4$_{(n-6)}$), followed by SFAs (main compounds: C16 and C18) and MUFAs (main compounds: C18:1$_{(n-9)}$ and C20:1) (Fig. 3b and Table 3a). Total bacterial FA (iso- and anteiso- C13, C15 and C17, C12 $_{methyl}$, C13 $_{methyl}$, C17 $_{cyclo}$, C19 $_{cyclo}$ and C13, C15, C17) were minor components of coral lipids (~ 3% of total FA). There was no significant difference in the percentage of SFA respect to total FA between areas (t = 3.140, *p*-value = 0.035). Conversely, the percentage of MUFA respect to total FA was higher in Cantabrian corals (t = − 3.978, *p*-value = 0.016), whilst percentage of PUFA was higher in the Menorca ones (t = 4.394, *p*-value = 0.012). Percentage of LCSFA from C22 to C32 (t = − 0.815, *p*-value = 0.461), LCMUFA from C20 to C24 (t = − 2.233, *p*-value = 0.089), as well as bacterial FA (iso- and anteiso- C15 and C17, iso-C16, C17 $_{cyclo}$, and C13, C15, C17, C19) (t = 1.983, *p*-value = 0.118) were similar in both Cantabrian and Menorca corals (Table 3a). Cantabrian corals had significantly higher storage energy (SFA + MUFA)/structural (PUFA) lipids ratio (t = − 3.848, *p*-value = 0.018) and PUFA$_{(n-3)}$/PUFA$_{(n-6)}$ ratio (t = − 6.302, *p*-value = 0.003) compared to Menorca corals (Fig. 4b). Whereas, C22:6$_{(n-3)}$/C20:5$_{(n-3)}$ ratio was similar in Cantabrian and Menorca corals (t = 3.162, *p*-value = 0.034; Fig. 4b).

The first two principal components of the PCA explained 90.0% of the data variance; the first axis explained 78.8%. Corals from the two areas were clearly segregated along the first axis of the PCA (Fig. 7a), with a higher relative abundance of C18:1$_{(n-9)}$, C20:5$_{(n-3)}$, ΣC20:1 and C22:5$_{(n-3)}$ in Cantabrian corals, and a higher relative abundance of C22:4$_{(n-6)}$, C20:4$_{(n-6)}$, C18 and C19 in Menorca corals; the FA composition of these latter corals was more variable (see the scattered distribution of white squares in the PCA), due to different concentrations in C22:6$_{(n-3)}$ and C24.

3.2.2. Fatty alcohol content and composition

Fatty alcohol content per mg coral dry weight was four times higher in Cantabrian corals compared to Menorca ones (t = − 3.771, *p*-value = 0.019; Tables 2 and 3b). A total of 19 fatty alcohols were identified in corals from both areas, with a dominance of C16-OH, which represented ~ 60% of the total fatty alcohols (Fig. 5b). The proportions of mono unsaturated fatty alcohols (Σ MUOH) (t = − 5.442, *p*-value = 0.005) and long chain mono unsaturated fatty alcohols (LCMUOH) from C22 to C24 (t = − 4.934, *p*-value = 0.008) respect to total fatty alcohols were significantly higher in Cantabrian corals (Table 3b). This was mainly driven by the higher proportion of C20:1-OH and C22:1-OH in Cantabrian corals (Fig. 5b). Conversely, proportion of branched alcohols was higher in Menorca corals compared to Cantabrian ones (t = 6.401, *p*-value = 0.003; Table 3b).

The first two principal components of the PCA explained 94.9% of the variance; the first axis explained 83.0%. Corals from the two areas

Table 3
Concentration and percentage contribution of selected classes of (a) fatty acids, (b) fatty alcohols and (c) sterols in sediment samples (n = 1) and *Dendrophyllia cornigera* colonies (mean ± SD, n = 3) from the Cantabrian Sea and Menorca Channel. Significant differences in the concentration (Total fatty acids, fatty alcohols and sterols) and in the percentage contribution of the selected classes between the two areas are indicated by one (t-test, *p*-value < 0.02), two (*p*-value < 0.01), or three asterisks (*p*-value < 0.001).

	Sediment				*Dendrophyllia cornigera*				
	Cantabrian Sea		Menorca Channel		Cantabrian Sea		Menorca Channel		
	(μg g^{-1} DW)	(%)	(μg g^{-1} DW)	(%)	(μg g^{-1} DW)	(%)	(μg g^{-1} DW)	(%)	
(a) Fatty Acids									
Total FA	24.5		110.9		3103.6 ± 688.6		1436.4 ± 199.9		*
SFA	11.9	48.3	60.9	54.9	589.2 ± 138.8	18.9 ± 0.2	297.7 ± 34.8	20.8 ± 1.0	
MUFA	8.1	32.9	38.7	34.9	475.6 ± 124.1	15.2 ± 0.8	155.1 ± 44.7	10.7 ± 1.8	*
PUFA	2.1	8.6	4.3	3.9	1987.9 ± 416.3	64.2 ± 0.8	963.3 ± 124.3	67.1 ± 0.8	*
LCSFA	5.0	20.5	3.2	2.9	39.1 ± 13.0	1.2 ± 0.2	15.2 ± 2.9	1.1 ± 0.3	
LCMUFA	0.5	2.1	19.5	17.5	171.7 ± 34.0	5.6 ± 0.8	59.2 ± 21.1	4.0 ± 0.9	
Bacterial	3.1	12.4	11.2	10.1	101.1 ± 21.0	3.3 ± 0.2	51.7 ± 7.7	3.6 ± 0.2	
(b) Fatty Alcohols									
Total Alcohols	3.7		9.4		232.4 ± 71.5		52.6 ± 41.5		*
Σ MUOH	0.0	0.0	0.1	1.0	56.9 ± 20.1	24.2 ± 3.5	5.2 ± 2.9	11.0 ± 2.3	**
LCMUOH	0.0	0.0	0.1	1.0	45.0 ± 17.0	19.1 ± 3.6	2.5 ± 0.7	6.2 ± 2.7	**
Branched	0.1	2.2	0.4	3.8	5.3 ± 1.4	2.3 ± 0.2	1.7 ± 1.3	3.3 ± 0.2	**
(c) Sterols									
Total Sterols	5.3		1.8		1240.0 ± 94.1		813.2 ± 66.9		**

were clearly segregated along the first axis of the PCA (Fig. 7b), with a higher relative abundance of ΣC22:1-OH and ΣC20:1-OH in Cantabrian corals, and a more variable composition among Menorca corals (see the scattered distribution of white squares in the PCA) with a higher relative abundance of C18-OH, C17-OH, C16-OH and C14-OH.

3.2.3. Sterol content and composition

Cantabrian corals had significantly higher sterol content per mg coral dry weight than Menorca ones (t = − 6.401, *p*-value = 0.003; Tables 2 and 3c). A total of 21 sterols were identified in corals from both areas (Fig. 6b). Cholesterol ($C_{27}\Delta^5$) was the dominant sterol in corals from both areas, representing ~ 50% of total sterols (Fig. 6b).

The first two principal components of the PCA explained 78.6% of the data variance; the first axis explained 45.1%. Cantabrian corals were characterized by a higher relative abundance of $C_{29}\Delta^5$ + $C_{29}\Delta^{5,24(28)}$, $C_{30}\Delta^{5,24(28)}$ + $C_{29}\Delta^{5,7}$ and $C_{28}\Delta^5$. Conversely, sterol

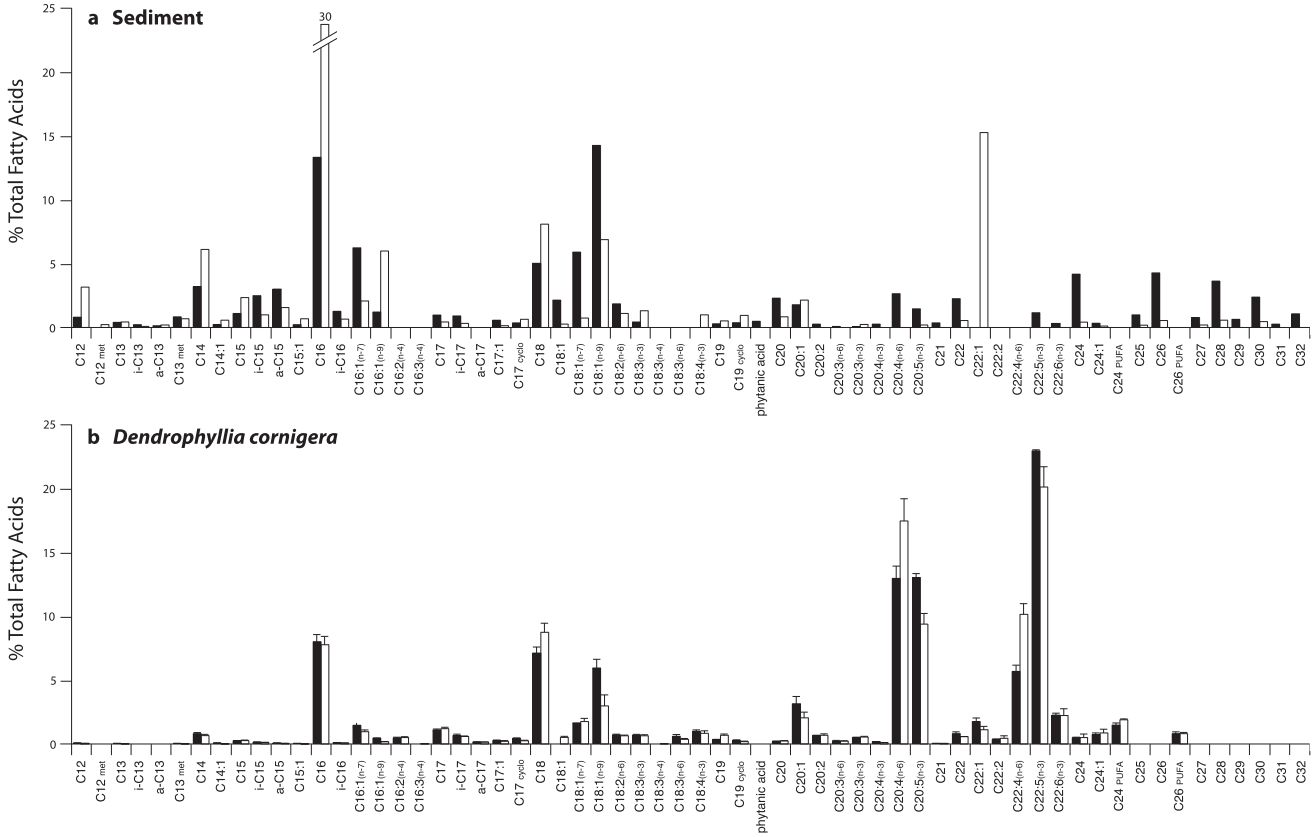

Fig. 3. Percentage contribution of the fatty acid compounds to total fatty acid content measured in (a) sediment samples (n = 1) and (b) *Dendrophyllia cornigera* colonies (mean ± SD, n = 3) from the Cantabrian Sea (black) and Menorca Channel (white).

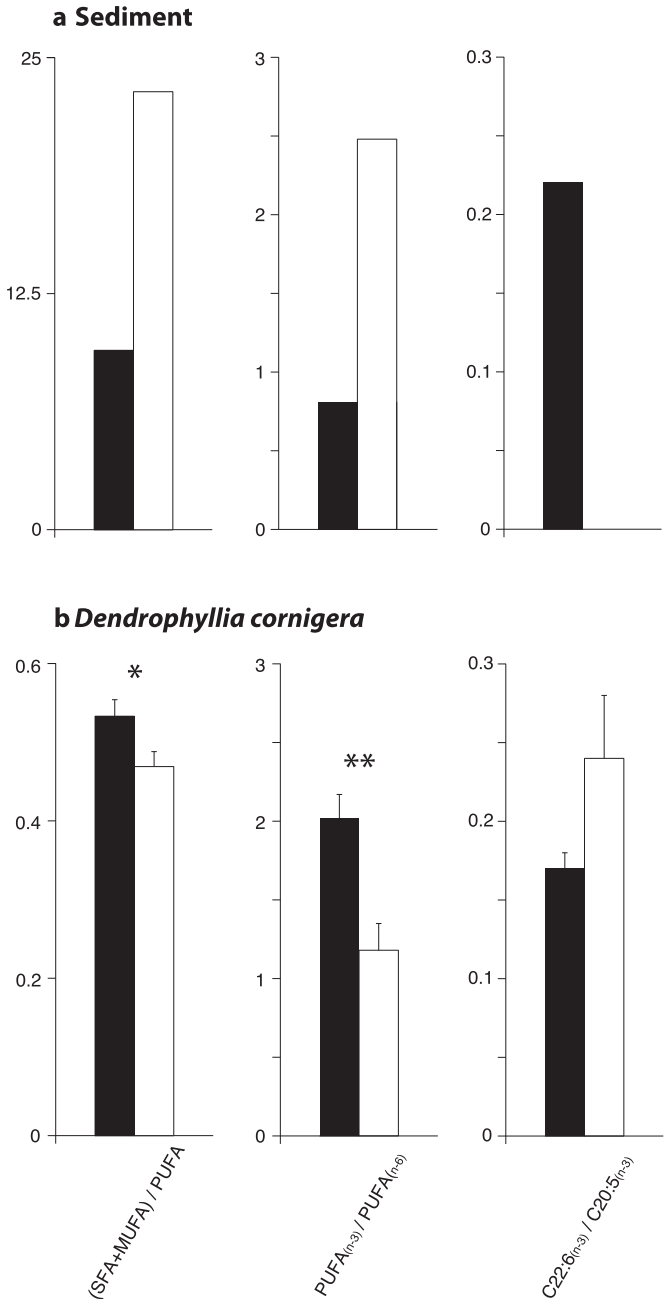

Fig. 4. (SFA + MUFA)/PUFA, $PUFA_{(n-3)}/PUFA_{(n-6)}$ and $C22:6_{(n-3)}/C20:5_{(n-3)}$ ratio in (a) sediment samples (n = 1) and (b) *Dendrophyllia cornigera* colonies (mean ± SD, n = 3) from the Cantabrian Sea (black) and Menorca Channel (white). Significant differences between the two areas are indicated by one (t-test, p-value < 0.02), two (p-value < 0.01), or three asterisks (p-value < 0.001).

composition was more variable among Menorca corals (see the scattered distribution of white squares in the PCA), with a higher relative abundance of $norC_{27}\Delta^{5,22}$, brassicasterol ($C_{28}\Delta^{5,22}$) and cholestanol ($C_{27}\Delta^{0}$), or cholesterol ($C_{27}\Delta^{5}$) and ergosterol ($C_{28}\Delta^{5,7,22}$), depending on the sample (Fig. 7c).

3.3. Carbon stable isotopes of lipid biomarkers

The $\delta^{13}C$ values of the major lipid biomarkers in corals ranged from − 24.0 to − 27.7‰ for FA, − 23.7 to − 26.8‰ for fatty alcohols and − 27.6 to − 33.8‰ for sterols (Table 4). The $\delta^{13}C$ signature of most FA and fatty alcohols was enriched by approximated 1‰ in Cantabrian

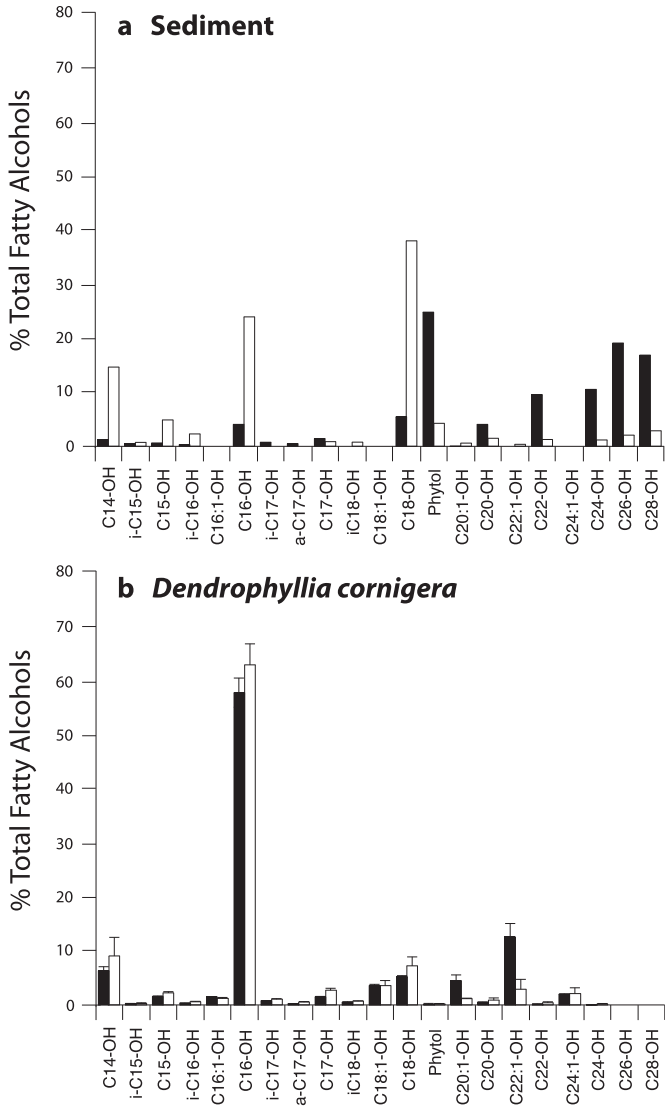

Fig. 5. Percentage contribution of the fatty alcohol compounds to total fatty alcohol content measured in (a) sediment samples (n = 1) and (b) *Dendrophyllia cornigera* colonies (mean ± SD, n = 3) from the Cantabrian Sea (black) and Menorca Channel (white).

compared to Menorca corals. The $\delta^{13}C$ signature of sterols was depleted by ~ 5‰ compared to FA and fatty alcohols in corals from Cantabrian as well as Menorca. $\delta^{13}C$ of long-chain SFA, long-chain alcohols and phytol in the Cantabrian sediment ranged from − 29.9 to − 37.3‰.

4. Discussion

The results of this study show that the content and composition of FA, fatty alcohols and sterols in the CWC *Dendrophyllia cornigera* clearly reflect the contrasted productivity in the Cantabrian Sea (high productivity) and the Menorca Channel (low productivity).

4.1. Geographical variability in the nutritional condition of Dendrophyllia cornigera

The higher lipid content of the Cantabrian compared to Menorca corals, in addition to the higher energy storage (SFA + MUFA) to structural (PUFA) FA ratio, reflects the thicker coral tissue (higher FA and sterol content) with greater lipid reserves in the form of triglycerides and wax esters (higher FA and alcohol content). These results suggest that Cantabrian corals received a higher amount of food

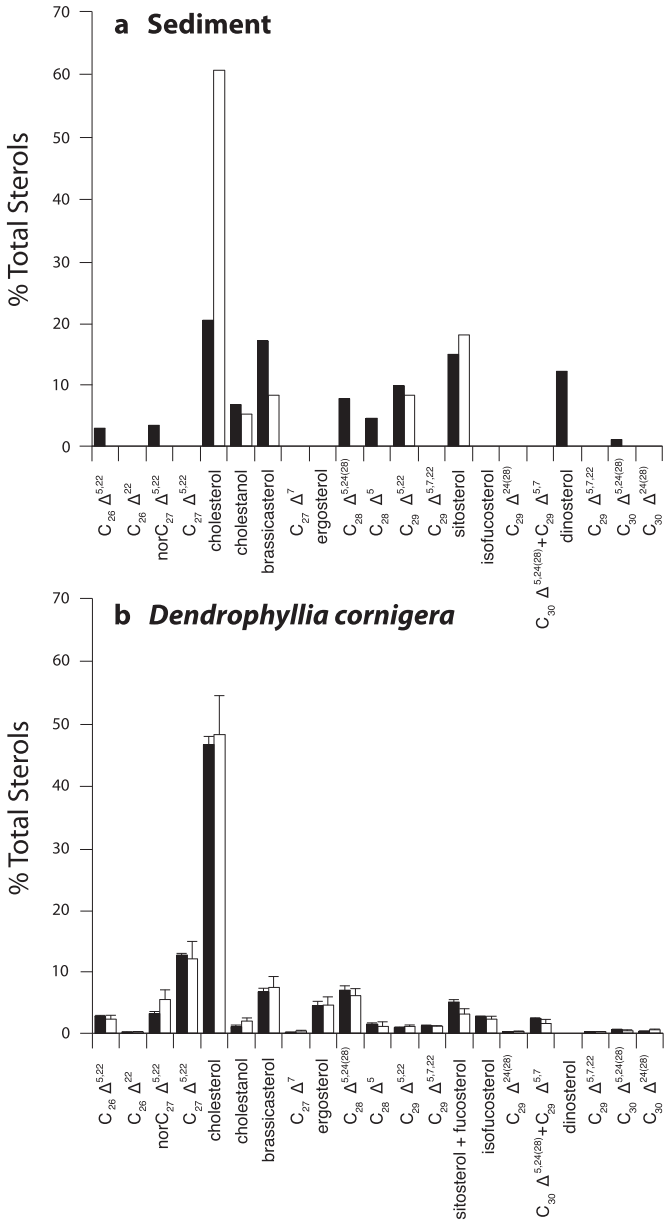

Fig. 6. Percentage contribution of the sterol compounds to total sterol content measured in (a) sediment samples (n = 1) and (b) *Dendrophyllia cornigera* colonies (mean ± SD, n = 3) from the Cantabrian Sea (black) and Menorca Channel (white).

compared to Menorca ones, consistent with previous studies that highlighted a direct relationship between lipid content and food supply in corals (Al-Moghrabi et al., 1995; Treignier et al., 2008). In the CWC *Lophelia pertusa*, FA content increased with food availability (Larsson et al., 2013), positively influencing coral fitness (Büscher et al., 2017). High content of reserve lipids (triglycerides and wax esters) in *L. pertusa* from the Mingulay Reef Complex (~ 130 m depth) was related to the higher primary productivity in this area compared to the deeper Rockall Bank (~ 900 m depth) and New England Seamount (~ 1200–1330 m depth) (Dodds et al., 2009; Duineveld et al., 2012). Similarly, the higher lipid content observed in Cantabrian *D. cornigera* reflects the higher primary productivity in this area compared to the Menorca Channel (Fig. 2). The enriched $\delta^{13}C$ values of FA in Cantabrian compared to Menorca corals, also supports this high productivity of the Cantabrian area, as higher growth rates of phytoplankton are generally associated to high $\delta^{13}C$ values in high productivity areas (Laws et al., 1995; Bidigare et al., 1999; Tolosa et al., 2004). Such high primary productivity of the Cantabrian Sea was also reflected by the high percentage of PUFA (especially $C20:5_{(n-3)}$ and $C22:6_{(n-3)}$) and the lower (SFA + MUFA)/PUFA ratio in Cantabrian sediment, indicating a significantly contribution of fresh organic matter (Harwood and Russell, 1984). The presence of phytol and the high diversity of phytosterols ($C_{28}\Delta^{5,22}$, $C_{28}\Delta^{5,24(28)}$, $C_{29}\Delta^{5}$, and $C_{30}\Delta^{22}$) in the Cantabrian sediment also suggest a high and diversified autotrophic activity in the surface waters (Volkman et al., 1998; Jeffreys et al., 2009). In addition to these marine sources, the presence of long-chain FA and fatty alcohols with depleted $\delta^{13}C$ signatures in the Cantabrian sediment is indicative of a significant amount of terrestrial material derived from C3 plants (Hedges et al., 1997; Meziane et al., 1997; Chikaraishi and Naraoka, 2003; Bi et al., 2005) from riverine inputs (Rumín-Caparrós et al., 2016). On the contrary, low productivity in the Menorca Channel is reflected in the higher proportion of PUFA (in particular $C20:4_{(n-6)}$) in corals from this area (Table 3). A retention of PUFA (especially $C20:4_{(n-6)}$ and $C22:6_{(n-3)}$) under periods of food shortage has been similarly observed in deep-sea organisms from the Mediterranean Sea compared to the Atlantic Ocean (Jeffreys et al., 2011). Moreover, experimental studies have also demonstrated that invertebrates preferentially use SFA and MUFA to fuel metabolism under stress conditions (such as starvation), preserving PUFA as long as possible (Mezek et al., 2010). Sediments from Menorca are dominated by the C16 SFA, C18:1 and C22:1 MUFAs, short-chain fatty alcohols and cholesterol (Figs. 3a, 5a, and 6a, respectively). This highlights the contribution of bacterial and plankton detritus (Volkman and Johns, 1977; Wakeham, 1995; Kiriakoulakis et al., 2001; Balzano et al., 2011) and reflects the lower productivity that is characteristic of the Menorca Channel.

4.2. Geographical variability in the main food sources for Dendrophyllia cornigera

Contrasted food composition in the Cantabrian Sea and the Menorca Channel is clearly reflected in the different lipid composition and $\delta^{13}C$ values of coral tissue.

Feeding on phytoplankton and herbivorous grazers by Cantabrian *D. cornigera* is supported by the high content in $C20:5_{(n-3)}$ (Harwood and Russell, 1984; Dunstan et al., 1994) and ΣC20:1 FA (Fig. 3b; Sargent and Henderson, 1986; Kattner and Hagen, 1995), as well as by the high $PUFA_{(n-3)}/PUFA_{(n-6)}$ ratio (Fig. 4b; Dalsgaard et al., 2003). Moreover, the lower $C22:6_{(n-3)}/C20:5_{(n-3)}$ ratio in Cantabrian compared to Menorca corals (Fig. 4b) suggests that diatoms prevailed over dinoflagellates in the diet (Sargent et al., 1987; Harwood and Russell, 1984; Volkman et al., 1989; Seeman et al., 2013). Herbivorous feeding of Cantabrian *D. cornigera* is also supported by the higher content of MUOH and LCMUOH (Table 3), specifically C20:1-OH and C22:1-OH, synthesized by herbivorous zooplankton such as calanoid copepods (Sargent and Falkpetersen, 1988; Dalsgaard et al., 2003). Conversely, the higher $PUFA_{(n-6)}$ content in Menorca corals, with the dominance of $C22:4_{(n-6)}$ and $C20:4_{(n-6)}$ (Fig. 3b), points to a main trophic role of dinoflagellates, invertebrates and bacteria (Desvilettes et al., 1997; Howell et al., 2003; Jeffreys et al., 2009; Wilson et al., 2010). High content of short chain saturated fatty alcohols in Menorca corals, with dominance of C16-OH and C14-OH (Fig. 5b), as well as the major contribution of cholesterol and $norC_{27}\Delta^{5,22}$ among sterols (Fig. 6b), also suggest a carnivorous trophic ecology and direct feeding on invertebrates and flagellates (Goad and Withers, 1982; Sun and Wakeham, 1999; Kattner et al., 2003; Jeffreys et al., 2009). Overall, the observed geographical variability in the trophic ecology of *D. cornigera* supports previous findings on the CWC *M. oculata* and *L. pertusa*. While Atlantic *M. oculata* mainly relied on herbivorous calanoid copepods (Kiriakoulakis et al., 2005), Mediterranean *M. oculata* from Santa Maria di Leuca rather fed on omnivorous and carnivorous zooplankton (Naumann et al., 2015). Similarly, FA and alcohol composition of *L. pertusa* significantly differed with location in Northeast Atlantic, with a

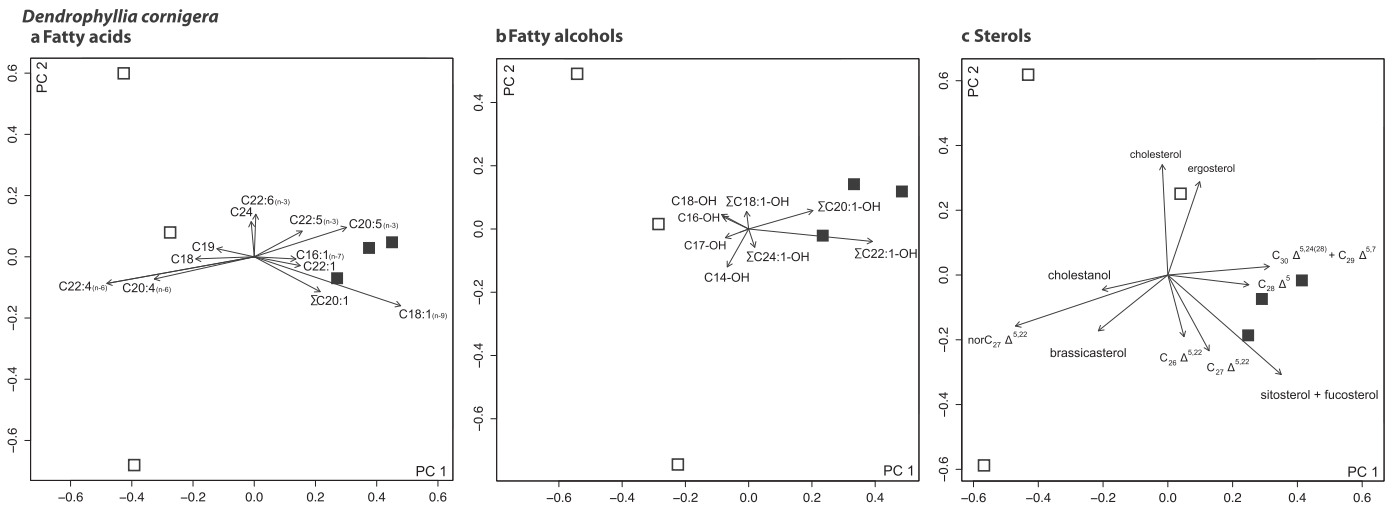

Fig. 7. Principal component analysis (PCA) biplot illustrating the ordination of the studied *Dendrophyllia cornigera* colonies from the Cantabrian Sea (black) and Menorca Channel (white) based on their (a) fatty acid, (b) fatty alcohol and (c) sterol composition. Arrows indicate the roles of the first compounds sorted according to the explained variance.

Table 4
Carbon stable isotopic signature ($\delta^{13}C$) of selected (a) fatty acids, (b) fatty alcohols and (c) sterols in sediment samples (n = 1) and *Dendrophyllia cornigera* colonies (mean ± SD, n = 3) from the Cantabrian Sea and Menorca Channel.

	Sediment		*Dendrophyllia cornigera*	
	Cantabrian Sea	Menorca Channel	Cantabrian Sea	Menorca Channel
	(‰)	(‰)	(‰)	(‰)
(a) Fatty Acids				
c14	− 25.4 ± 1.4	− 25.6 ± 1.8	− 25.4 ± 0.1	− 26.4 ± 0.3
i-C15	− 24.9 ± 0.6	− 23.6 ± 0.2		
a-C15	− 25.0 ± 0.7	− 26.9 ± 0.4		
C15	− 25.6 ± 0.5	− 25.3 ± 0.2		
C16	− 27.7 ± 0.4	− 29.5 ± 0.4	− 24.9 ± 0.9	− 26.5 ± 0.3
$C18:1_{(n-9)} + C18:1_{(n-7)} + C18:3_{(n-3)}$	− 28.5 ± 0.1		− 24.0 ± 0.7	− 25.6 ± 0.4
C18	− 28.5 ± 0.7	− 30.1 ± 0.8	− 24.8 ± 0.9	− 26.3 ± 0.9
C20	− 30.3 ± 0.4			
C20:1	− 29.4 ± 1.4	− 30.8 ± 0.5		
$C20:4_{(n-6)} + C20:5_{(n-3)}$	− 25.1 ± 1.3		− 26.6 ± 0.5	− 27.7 ± 0.3
C22	− 30.9 ± 0.7			
C22:1		− 30.6 ± 0.3		
$C22:5_{(n-3)} + C22:4_{(n-6)}$	− 25.1 ± 0.2		− 26.0 ± 0.3	− 27.0 ± 0.2
C24	− 29.9 ± 0.3			
C25	− 31.0 ± 0.5			
C26	− 30.6 ± 0.5	− 27.0 ± 0.8		
C28	− 32.2 ± 0.5			
C30	− 34.9 ± 1.7			
(b) Fatty Alcohols				
C14-OH			− 24.7 ± 0.6	
C16-OH	− 27.7 ± 0.4		− 25.9 ± 0.2	− 26.8 ± 0.0
C18-OH	− 29.4 ± 0.9	− 25.9 ± 0.6	− 25.0 ± 0.4	− 26.1 ± 1.0
C20:1-OH			− 24.8 ± 0.7	
C22:1-OH			− 23.7 ± 0.8	
C22-OH	− 34.5 ± 1.4			
C24-OH	− 33.9 ± 0.8			
C26-OH	− 36.4 ± 0.4			
C28-OH	− 37.3 ± 0.3			
phytol	− 35.8 ± 0.6			
(c) Sterols				
$C_{26}\Delta^{5,22}$	− 27.7 ± 0.7		− 29.4 ± 0.9	− 30.0 ± 0.4
$norC_{27}\Delta^{5,22}$			− 29.3 ± 1.8	− 27.6 ± 1.9
$C_{27}\Delta^{5,22}$			− 28.5 ± 0.3	− 29.0 ± 0.7
cholesterol + cholestanol	− 27.5 ± 0.2		− 29.3 ± 0.5	− 30.2 ± 0.5
brassicasterol	− 28.4 ± 0.6		− 30.4 ± 0.2	− 30.8 ± 0.8
ergosterol			− 31.4 ± 0.4	− 31.7 ± 1.7
$C_{28}\Delta^{5,24(28)} + C_{28}\Delta^{5}$	− 27.2 ± 0.9		− 30.4 ± 0.4	− 32.4 ± 1.2
sitosterol	− 26.8 ± 1.2		− 31.6 ± 0.2	− 32.1 ± 0.5
fucosterol			− 33.8 ± 0.4	− 30.6 ± 2.5
$C_{29}\Delta^{5,7,22}$			− 31.7 ± 0.1	
dinosterol	− 27.2 ± 0.9			

major role played by herbivorous calanoid copepods in the shallow Mingulay Reef Complex contrasting with dominance of omnivorous and carnivorous non-calanoid copepods in the deeper Rockall Bank and New England Seamount (Dodds et al., 2009).

Despite geographical differences in lipid content and composition, PUFA were the major FA class in both Menorca and Cantabrian *D. cornigera* (Table 3), as well as in the other CWC *L. pertusa* and *M. oculata* (Duineveld et al., 2012; Naumann et al., 2015). This dominance of PUFA is a major characteristic of marine lipids, even if the proportion varies among species (Yamashiro et al., 1999; Treignier et al., 2008) or with temperature (Meyers, 1979). In CWC species, high proportions of unsaturated FA may contribute to the maintenance of the fluidity of cellular membranes under the low temperatures and high pressures of deep-sea environments (Cossins and Prosser, 1978; Naumann et al., 2015). High concentrations of PUFA in coral tissue may also suggest that these FA are actively synthesized by *D. cornigera*, supporting the recent observation of endogenous biosynthesis of $PUFA_{(n-3)}$ (i.e. $20:5_{(n-3)}$ and $22:6_{(n-3)}$) by the CWC *L. pertusa* (Mueller et al., 2014) and the tropical coral *Acropora millepora* (i.e. $18:2_{(n-6)}$ and $18:3_{(n-3)}$; Kabeya et al., 2018). Several deep-sea organisms are also able to biosynthesize long chain PUFA (e.g. $C22:6_{(n-3)}$ and $C24:6_{(n-3)}$) required in cell membranes and for reproduction, through chain elongation of ingested fatty acids (i.e. $C20:4_{(n-6)}$ and $C20:5_{(n-3)}$) (Jeffreys et al., 2009).

The high cholesterol content in *D. cornigera* tissue, as also observed in *L. pertusa* and *M. oculata* tissue (Naumann et al., 2015), may derive from a carnivorous diet or feeding on suspended sediment (where cholesterol is abundant, especially in the Menorca Channel). Indeed, expensive pathways of sterols biosynthesis are not energetically suitable if compounds are readily available in the environment (Ginger et al., 2001). Finally, the presence of ergosterol and related sterols, suggests that *D. cornigera* may take up this sterol from chlorophytes (Chu et al., 2008), fungi and protozoans (Volkman, 2003), or actually be capable of its own biosynthesis, as also suggested for the CWC *L. pertusa* and *M. oculata* (Naumann et al., 2015).

4.3. Ecological consequences

The geographical variability observed in the trophic ecology of *D. cornigera* demonstrates its high trophic plasticity, which favours the wide distribution of this CWC in areas with contrasted food availability, from the Eastern Atlantic (from the south of Ireland to the Cape Verde Islands, Le Danois, 1948; Zibrowius, 1980; Álvarez-Claudio, 1994; Brito and Ocaña, 2004; Sánchez et al., 2009; Braga-Henriques et al., 2013) to the oligotrophic Western (Zibrowius, 1980; Freiwald et al., 2009; Orejas et al., 2009; Bo et al., 2011) and Eastern Mediterranean Sea (Zibrowius, 1980; Salomidi et al., 2010). Our results underline the opportunistic trophic behavior of *D. cornigera*, which is very efficient in taking advantage of the available food sources, as has been previously observed in *L. pertusa* (Mueller et al., 2014). This trophic behavior is particularly efficient in deep-sea habitats where food availability may be extremely heterogeneous in time and space (White et al., 2005; Mienis et al., 2009), allowing CWC to follow an optimal foraging pattern as observed in most sessile benthic suspension feeders (Coma et al., 2001). However, low productivity in the Menorca Channel clearly resulted in a significant lower lipid content in *D. cornigera* tissue (both structural and energy reserve lipids). Consequently, fundamental biological processes that require high-energy investments, such as coral growth and reproduction, may also significantly change geographically depending on the local availability in food sources.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr.2018.08.010.

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