Lipids and nitrogen isotopes of two deep-water corals from the North-East Atlantic: initial results and implications for their nutrition

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Abstract. The lipid and organic nitrogen isotopic ($\delta^{15}N$) compositions of two common deep-water corals (*Lophelia pertusa* and *Madrepora oculata*) collected from selected locations of the NE Atlantic are compared to the composition of suspended particulate organic matter, in order to determine their principle food source. Initial results suggest that they may feed primarily on zooplankton. This is based on the increased abundances of mono-unsaturated fatty acids and alcohols and the different ratios of the polyunsaturated fatty acids, 22:6/20:5 of the corals when compared to those of the suspended particulate organic matter. There is enrichment in *L. pertusa* of mono-unsaturated fatty acids and of $\delta^{15}N$ relative to *M. oculata*. It is unclear whether this reflects different feeding strategies or assimilation/storage efficiencies of zooplankton tissue or different metabolism in the two coral species.

Keywords. Deep-water corals, suspended particulate organic matter, nitrogen isotopes, lipids, fatty acids, PUFA, MUFA

Introduction

Cold-water azooxanthellate corals (most commonly *Lophelia pertusa* and *Madrepora oculata*) are widespread at the western European continental margin, where their framework and structure support diverse ecosystems (e.g., Freiwald et al. 2002). The deep-water corals (DWCs) often grow on carbonate mounds (e.g., Hovland et al. 1994; Henriet et al. 1998; Freiwald et al. 1999, 2002; De Mol et al. 2002; Huvenne et al. 2002 amongst others). They normally occur between 50 and

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2000 m depth, typically at temperatures of 4-12ºC (Wilson 1979; Kenyon et al. 1998, 2003; Rogers 1999; De Mol et al. 2002, 2005), although they can tolerate sub-zero water temperatures for short periods of time (Bett 2000). *L. pertusa*, the dominant DWC, sometimes forms extensive reefs (e.g., Sula Ridge - Norwegian Shelf; Freiwald et al. 1999, 2002), but more often occurs as small colonies of a few centimetres to a few metres across (e.g., Darwin Mounds - Northern Rockall Trough; Masson et al. 2003).

Despite their widespread distribution, very little is known regarding the nutrition of DWCs and their role in the biogeochemistry of carbon and nitrogen. Observations of corals in aquaria and *in situ* provide evidence that *L. pertusa* can selectively feed on live zooplankton of up to 2 cm, although it also ingests sediment particles (Mortensen 2001; Freiwald 2002). It has also been suggested that DWCs may acquire their nutrients from bacteria associated with seafloor hydrocarbon seeps, which in turn promote carbonate mound formation (Hovland and Thomsen 1997; Henriet et al. 1998). However, coral-colonised mounds occur in areas where such seeps are absent and it seems that ambient current strength, the availability of hard substrata and elevated locations are key factors influencing the distributions of DWCs (Rogers 1999; Masson et al. 2003; van Rooij et al. 2003; Kiriakoulakis et al. 2004).

The principal objective of this study was to assess the preferred food source of the DWCs. Our approach was to investigate the biochemical (lipid) and isotopic ($\delta^{15}N$) compositions of the two most common species in the NW European margin, *L. pertusa* and *M. oculata* and to compare these with suspended particulate organic matter (sPOM) in overlying waters. Lipids are essential in the storage and mobilisation of energy, in reproduction and metabolism and are key components in cell membranes (e.g., Brassell and Eglinton 1986). The distributions of fatty acids can be used to determine the diet of biogenic material of marine organisms (e.g., Parrish et al. 2000). To date, there have been few studies of lipids in DWCs (e.g., Mancini et al. 1999), in contrast to their shallow-water counterparts (e.g., Meyers 1979; Latyshev et al. 1991; Harland et al. 1993; Yamashiro et al. 1999 amongst others).

The stable isotopes of nitrogen ($^{15}N/^{14}N$) also have value in ecosystem studies (Owens 1987; Peterson and Fry 1987; Hesslein et al. 1991; Kling et al. 1992; Kidd et al. 1995), although their application to deep-water settings has been limited (e.g., Iken et al. 2001; Heikoop et al. 2002a, b).

Sampling

Lophelia pertusa and *Madrepora oculata* samples were obtained from selected sites along the western European margin (n = 11, 3 respectively Fig. 1) between the years 1998-2000 (Table 1). Samples were collected from a wide range of depths (Table 1) using a variety of gear (boxcores, grabs, dredges, trawls and remotely operated vehicle (ROV)). When possible, sPOM was collected by *in situ* filtration of large volume (~1000 l) water samples from the same locations (Darwin, Logachev,

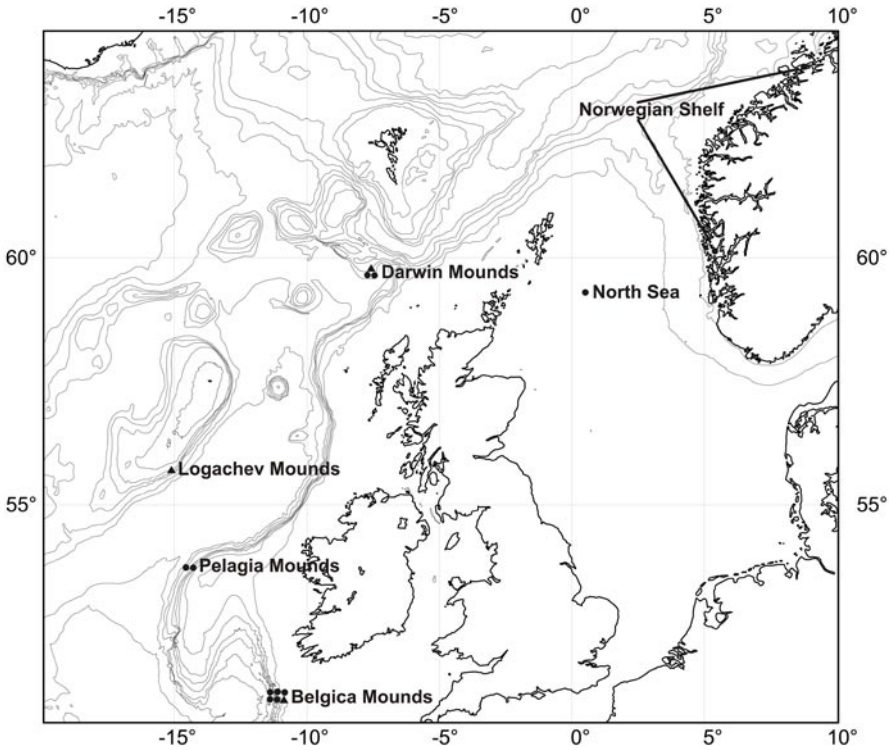

Fig. 1 Bathymetric map of the locations sampled for corals. Contours are every 200 m down to 1000 m, every 500 m down to 2000 m and every 1000 m down to 4000 m. Black circles denote *Lophelia pertusa* and triangles *Madrepora oculata*

Hovland and Belgica Mounds only; Table 2; 293 mm GF/F; stand alone pumping system - Challenger Oceanic; Kiriakoulakis et al. 2004). In all cases the coral and filter samples were immediately frozen (-20°C) and then freeze-dried before analysis.

Methodology

Methods for analysis of lipids have been described in detail elsewhere (Kiriakoulakis et al. 2001). No separation of lipid classes (e.g., phospholipids, glycolipids, etc.) was attempted.

Briefly, separate aliquots of freeze-dried filter and coral tissue material (0.5-1 g) were spiked with internal standard (cholestane), Soxhlet extracted (24 h; dichloromethane:methanol 9:1) and methylated (methanolic acetyl chloride; Christie 1982). GC-MS analyses were carried out on the silylated (bis-trimethyl silyltrifluoroacetamide; BSFTA, 1 % TMS; 30-50 µl; 40°C; 0.5-1 h), methylated total extracts using a Trace 2000 Series gas chromatograph (on-column injector; fused silica high temperature column, 60 m × 0.25 mm i.d.; 0.1 μm film thickness,

Table 1 Sampling and $\delta^{15}N$ values of DWCs collected from the Rockall Trough, Porcupine Bank, North Sea and offshore Norway. WTR is Wyville Thomson Ridge

Station	Coordinates	Gear	Depth	Location	Date	$\delta^{15}N$
Lophelia pertusa						
Dredge 4	63° 36.55N 09° 23.13E	Triangular dredge	200 m	Norwegian shelf	01 May 99	11.01
Osterfjord	60° 39.26N 05° 43.95E	Video-assisted grab	80 m	Norwegian fjord	01 Oct 98	11.72
13831#1	59° 48.88N 07° 17.99W	Trawl	989 m	Darwin Mounds	17 July 00	8.38
S98-467	59° 38.00N 07° 50.00W	Scraper trawl	870 m	South of WTR	01 Oct 98	8.32
Beryl Alpha	59° 32.78N 01° 32.23E	ROV	100 m	North Sea	01 Oct 99	9.58
M2000 BX11#3	53° 46.87N 13° 56.76W	Box core	655 m	Pelagia Mounds	30 July 00	8.16
M2000 BX13#34	53° 46.84N 13° 56.63W	Box core	646	Pelagia Mounds	30 July 00	8.40
13874#2	51° 25.68N 11° 46.40W	Box core	865 m	Belgica Mounds	06 Aug 00	7.37
13881#3	51° 25.66N 11° 46.32W	Box core	859 m	Belgica Mounds	08 Aug 00	7.97
M2000 BX02#50	51° 25.75N 11° 46.29W	Box core	~900 m	Belgica Mounds	28 July 00	7.80
M2000 BX 01#32	51° 25.48N 11° 46.05W	Box core	963 m	Belgica Mounds	28 July 00	7.59
Mean						**8.75**
sd						**1.42**
Madrepora oculata						
13831#1	59° 48.88N 07° 17.99W	Trawl	989 m	Darwin Mounds	17 July 00	7.72
M2000 BX21#51	55° 32.07N 15° 40.12W	Box core	733 m	Logachev Mounds	02 Aug 00	8.62
13874#2	51° 25.68N 11° 46.40W	Box core	865 m	Belgica Mounds	06 Aug 00	6.79
Mean						**7.71**
sd						**0.91**

Table 2 Sampling and $\delta^{15}N$ values for sPOM collected from the Rockall Trough and Porcupine Bank. In most cases sPOM was collected from 10-30 m above bottom, i.e., at or close to the benthic boundary layer (BBL). *Water collected at 150 m above bottom (mab)

Station	Location	Date	Depth	$\delta^{15}N$
13823#12*	Darwin Mounds	14-Jul-00	943 m	5.37
13825#1*	Darwin Mounds	15-Jul-00	948 m	5.09
13828#1*	Darwin Mounds	16-Jul-00	938 m	3.03
13832#2*	Darwin Mounds	17-Jul-00	938 m	5.02
13841#1*	Darwin Mounds	19-Jul-00	948 m	6.27
13823#8	Darwin Mounds	14-Jul-00		5.98
13823#12	Darwin Mounds	14-Jul-00	943 m	5.78
13825#1	Darwin Mounds	15-Jul-00	948 m	4.75
13828#1	Darwin Mounds	16-Jul-00	938 m	5.53
13832#2	Darwin Mounds	17-Jul-00	938 m	5.73
13841#1	Darwin Mounds	19-Jul-00	948 m	4.91
SAPS4	Logachev Mounds	12-Aug-01	666 m	
GeoB 8029/1	Logachev Mounds	23-Jul-02	700 m	
GeoB 8036/1	Logachev Mounds	24-Jul-02	700-730m	
SAPS3	Pelagia Mounds	9-Aug-01	635 m	
GeoB 8050/1	Porcupine Bank	27-Jul-02	153 m	
GeoB 6710	Hovland Mounds	17-Sep-00	691 m	
GeoB 6713	Hovland Mounds	18-Sep-00	670 m	
GeoB 6732/1	Hovland Mounds	24-Sep-00	700 m	
GeoB 8042/1	Hovland Mounds	25-Jul-02	710 m	
GeoB 8076/1	Hovland Mounds	29-Jul-02	850 m	
GeoB 8048/1	Hovland Mounds	26-Jul-02	875 m	
GeoB 8068/1	Hovland Mounds	29-Jul-02	655-700m	5.08
GeoB 8044/1	Hovland Mounds	26-Jul-02	805 m	
GeoB 8078/1	Hovland Mounds	30-Jul-02	735-740m	4.67
SAPS2	Hovland Mounds	6-Aug-01	605 m	
GeoB 8081/1	Belgica Mounds	31-Jul-02	916 m	4.48
GeoB 8103/1	Belgica Mounds	2-Aug-02	680 m	4.25
GeoB 8106/1	Belgica Mounds	2-Aug-02	880 m	4.31
GeoB 6742/1	Belgica Mounds	26-Sep-00	830 m	
SAPS1	Belgica Mounds	1-Aug-01	865 m	7.33
GeoB 8107/1	Belgica Mounds	3-Aug-02	785-800m	4.16

5 % phenyl/95 % methyl polysiloxane equivalent phase, DB5-HT, J&W; carrier gas helium at 1.6 ml min^{-1}), coupled with a Thermoquest Finnigan TSQ7000 mass spectrometer (ionisation potential 70 eV; source temperature 215°C; trap current 300 μA) and processed using Xcalibur software. Compounds were identified using authentic standards or relative retention indices, and quantified using cholestane as an internal standard (Kiriakoulakis et al. 2004).

Nitrogen isotopic analyses were carried out on aliquots of sPOM using a PDZ Europa Scientific Geo 20/20 running in continuous flow mode coupled to a Carlo-

Erba Instruments EA1108 elemental analyser. Data were calibrated to atmospheric nitrogen by replicate analyses of the international standards NBS18, NBS19 and IAEACO1 as well as in-house nylon and alanine standards.

Results

Suspended POM

$\delta^{15}N$ of particulate organic nitrogen in selected samples collected at three sites (Darwin, Hovland and Belgica Mounds) ranged from +3.03 to +7.33 ‰ (mean 5.01 ± 0.92 ‰) and were not significantly different between sites and/or depths (Table 2). One sample from the Belgica Mounds collected in summer 2001 (SAPS1) was heavier (+7.33 ‰) than those collected a year later (+4.16 to +4.68 ‰; Table 2). There are no sPOM data from the North Sea and Norwegian fjord and shelf. Detailed lipid results for sPOM are presented elsewhere (Kiriakoulakis et al. 2004, submitted), but to allow easy comparison with the coral lipids, the lipid compositions of POM from four sites (i.e., Darwin, Logachev, Hovland and Belgica Mounds) are presented in Table 3. They show significant regional differences in their distributions, but fatty acids and sterols dominate (mean for all sites 67.6 ± 19.5 % and 24.3 ± 16.6 %, respectively; see Table 3), whereas alcohols are less abundant constituents of the POM (mean of all sites 6.5 % ±3.9 %). Polyunsaturated fatty acids (PUFAs) comprise ~20 % (±13.7 %) of fatty acids and are dominated by $C_{20:4}$, $C_{20:5}$ and $C_{22:6}$ compounds with lesser amounts of $C_{18:4}$ at all sites. Bacterial fatty acids which include C_{15}, C_{17}, all branched and $C_{18:1}$ Δ-7 fatty acids are also abundant (mean ~14 ± 4.14 %), while the mono-unsaturated fatty acids (MUFAs), $C_{20:1}$ and $C_{22:1}$ fatty acids comprise 3 ±3.8 % of fatty acids.

Corals

The $\delta^{15}N$ composition of *L. pertusa* tissue is variable, but this seems to be site-related. Corals from the Belgica Mounds (4) have rather constant composition (mean 7.68 ±0.3 ‰) and this is also true for the two samples from the Pelagia Mounds site (mean 8.28 ‰) and the Northern Rockall Trough (i.e., Darwin Mounds and south of the Wyville Thomson Ridge, see Table 1). There are no seasonal or interannual data for the Pelagia and Belgica Mounds, but samples from the Northern Rockall Trough that were collected in 1998 and 2000 (Table 1) have similar isotopic values. The sample of *L. pertusa* from the North Sea is ~1.3-1.8 ‰ heavier, whereas samples from Norwegian waters are significantly heavier than all other samples (Table 1).

The $\delta^{15}N$ composition of *M. oculata* tissue from three sites is also variable (up to ~2 ‰, Table 1). When comparing the isotopic composition of species collected from the same site *L. pertusa* seems consistently enriched in ^{15}N (up to 1.2 ‰ at Belgica Mounds, Table 1) relative to *M. oculata*.

Lipids in *L. pertusa* are dominated by fatty acids (mean of all sites 67 ±7.8 %) and alcohols (mean of all sites 28.8 ±9.1 %). Sterol abundances are much lower (4.2 ±4.3 %). Fatty acids and alcohols also dominate the lipids of *M. oculata*, with lower proportions of sterols (Table 4). The two species have significantly different PUFA/

Table 3 Lipid composition of sPOM at selected sites. *Water was collected 150 m above bottom (mab). [1]relative to total lipids, [2]relative to total fatty acids. FA is fatty acids, PUFAs, MUFAs and BactFA are poly-unsaturated, mono-unsaturated and bacterial fatty acids respectively. 22:6/20:5 is the ratio of the concentration of $C_{22:6}$ *vs.* $C_{20:5}$ PUFAs

Station	FA	alcohols	sterols	PUFAs	MUFAs	bactFA	22:6/20:5	PUFAs/ MUFAs
	[1] %	[1] %	[1] %	[2] %	[2] %	[2] %		
13823#12*	88.99	1.98	8.97	22.37	0.00	19.20	1.03	
13825#1*	77.75	10.03	11.55	46.38	13.87	10.52	6.49	68.10
13828#1*	21.40	12.81	65.70	11.23	2.06	9.51	0.55	5.46
13832#2*	85.97	4.74	9.10	37.70	14.11	12.24	1.33	16.60
13841#1*	92.49	1.21	5.63	41.63	13.66	13.35	1.18	23.00
13823#8	70.65	2.99	26.01	28.19	1.69	11.27	1.14	16.73
13823#12	86.88	10.02	3.07	29.60	2.93	11.29	0.69	10.11
13825#1	92.00	2.39	5.49	29.94	1.12	19.47	1.11	60.13
13828#1	90.75	2.90	6.11	41.51	2.17	11.24	1.37	19.14
13832#2	90.72	2.28	6.85	22.70	1.50	20.27	0.80	15.11
13841#1	86.43	9.10	4.40	37.56	3.03	17.40	1.16	162.23
mean Darwin	**89.36**	**5.34**	**5.18**	**32.26**	**2.15**	**15.93**	**1.03**	**53.34**
sd (±)	**2.52**	**3.88**	**1.48**	**7.37**	**0.84**	**4.39**	**0.28**	**64.03**
SAPS4	30.69	16.43	46.56	16.32	0.00	5.40		
GeoB8029/1	64.43	2.19	27.00	23.80	0.00	10.52	1.32	
GeoB8036/1	75.71	6.40	17.59	7.39	0.32	12.44	1.41	23.36
mean Logachev	**56.94**	**8.34**	**30.38**	**15.84**	**0.11**	**9.45**	**0.91**	**23.36**
sd (±)	**23.43**	**7.31**	**14.78**	**8.22**	**0.18**	**3.64**	**0.79**	
GeoB 6710	53.38	4.54	41.07	7.85	0.73	19.11	3.40	10.75
GeoB 6713	56.09	5.79	31.14	0.00	0.00	12.89		
GeoB 6732/1	52.59	4.96	38.65	4.42	1.18	16.72		3.75
GeoB 8042/1	71.32	4.05	23.85	22.22	1.01	13.66		0.64
GeoB 8076/1	79.32	3.19	17.49	25.49	4.37	15.04	1.50	5.83
GeoB 8048/1	65.43	5.37	29.20	18.79	2.99	14.06	1.10	6.28
GeoB 8068/1	73.87	12.11	14.02	38.21	2.34	9.74	1.90	16.30
GeoB 8044/1	80.07	10.48	9.36	3.15	1.65	18.75	0.61	1.90
GeoB 8078/1	67.65	7.49	23.69	3.42	1.20	20.50		2.85
SAPS2	31.89	7.50	60.61	0.00	0.00	22.68		
mean Hovland	**63.16**	**6.55**	**28.91**	**12.35**	**1.55**	**16.32**	**1.70**	**6.04**
sd (±)	**14.87**	**2.87**	**15.06**	**13.05**	**1.36**	**3.95**	**1.06**	**5.20**
GeoB 8081/1	59.64	4.47	35.89	31.58	2.50	9.98	1.46	
GeoB 8103/1	52.42	9.22	37.60	21.70	1.92	8.25	1.39	11.30
GeoB 8106/1	64.05	5.84	28.70	17.78	1.97	15.97	1.45	9.04
GeoB 6742/1	52.26	4.05	27.89	2.45	4.12	18.26		0.59
SAPS1	31.86	14.78	51.13	4.41	1.24	16.09		3.56
GeoB 8107/1	61.83	8.31	29.86	7.19	0.00	15.07	0.18	
Mean Belgica	**53.68**	**7.78**	**35.18**	**14.19**	**1.96**	**13.94**	**1.12**	**6.12**
sd (±)	**11.74**	**4.00**	**8.76**	**11.44**	**1.37**	**3.92**	**0.63**	**4.91**
mean total	**67.60**	**6.50**	**24.28**	**20.10**	**2.70**	**14.22**	**1.46**	**20.86**

MUFA ratios (ANOVA; $p<0.05$); in *M. oculata* this ratio is three times higher than in *L. pertusa*. The proportions of bacterial fatty acids and the 22:6/20:5 ratio are similar in both species (Table 4). $C_{20:1}$ and $C_{22:1}$ alcohols constitute >90 % of total alcohols in both species.

Mean lipid compositions of both coral species are also significantly different (ANOVA; $p<0.05$) to those of the sPOM at all sites (Tables 3 and 4). In particular, mean fatty alcohol and MUFA proportions are significantly higher in the DWCs (26.1 ±10.2 % and 19.7 ±10.4 %, respectively) than in the sPOM (6.5 ±3.9 % and 2.7 ±3.8 %, respectively), whereas the reverse is true for sterols (4.5 ±4 % for the corals and 24.3 ±16.6 % for sPOM) and bacterial fatty acids (5.6 ±1.5 % for the corals and 14.2 ±4.1 % for sPOM). On the other hand, total fatty acids and PUFAs are not significantly different between the corals (69.5 ±8.7 % and 25.8 ±11.1 % respectively) and sPOM (67.6 ±19.5 % and 20.1 ±13.7 % respectively). Mean 22:6/20:5 ratios do however differ between the corals (0.6 ±0.1) and sPOM (1.5 ±1.2).

Table 4 Lipid composition of collected coral samples. [1]relative to lipids, [2]relative to total fatty acids. FA is fatty acids, PUFAs, MUFAs and BactFA are poly-unsaturated, mono-unsaturated and bacterial fatty acids respectively. 22:6/20:5 is the ratio of the concentration of $C_{22:6}$ *vs.* $C_{20:5}$ PUFAs

Station	**FA**	**alcohols**	**sterols**	**PUFAs**	**MUFAs**	**bactFA %**	**22:6/20:5**	**PUFA/ MUFA**
	[1] %	**[1] %**	**[1] %**	**[2] %**	**[2] %**	**[2] %**		
Lophelia pertusa								
Dredge 4	64.07	35.30	0.63	21.56	38.44	4.95	0.61	0.56
Osterfjord	69.61	28.19	2.20	23.37	12.18	5.92	0.67	1.92
13831#1	62.41	31.41	6.18	24.60	28.32	5.95	0.30	0.87
S98-467	77.56	21.32	1.11	24.80	28.10	5.59	0.52	0.88
Beryl Alpha	63.07	36.62	0.31	27.78	31.46	4.03	0.68	0.88
M2000 BX11#3	64.48	23.08	12.44	9.63	12.27	8.02	0.44	0.78
13874#2	53.72	45.06	1.22	10.17	9.34	5.45	0.76	1.09
13881#3	78.47	16.61	4.91	16.33	28.47	6.81	0.69	0.57
M2000 BX02#50	69.07	21.89	9.04	31.49	12.23	5.26	0.74	2.57
Mean *Lophelia*	**66.94**	**28.83**	**4.23**	**21.08**	**22.31**	**5.77**	**0.60**	**1.13**
sd (±)	**7.76**	**9.08**	**4.27**	**7.56**	**10.75**	**1.13**	**0.15**	**0.68**
Madrepora oculata								
13831#1	68.33	27.12	4.55	27.28	16.40	7.31	0.46	1.66
M2000 BX21#51	84.19	6.79	9.01	45.97	8.53	5.63	0.61	5.39
13874#2	78.69	19.41	1.90	42.69	11.10	2.41	0.66	3.85
Mean *Madrepora*	**77.07**	**17.78**	**5.15**	**38.65**	**12.01**	**5.12**	**0.58**	**3.63**
sd (±)	**8.05**	**10.26**	**3.60**	**9.98**	**4.01**	**2.49**	**0.10**	**1.87**
Mean both species	**69.47**	**26.07**	**4.46**	**25.47**	**19.74**	**5.61**	**0.60**	**1.75**
sd (±)	**8.75**	**10.21**	**3.98**	**11.08**	**10.43**	**1.47**	**0.14**	**1.50**

Discussion

Nitrogen isotopes

Nitrogen isotopes can provide information on food webs, based on the stepwise enrichment of $^{15}N/^{14}N$ ratios with increasing trophic level. This is caused by the preferential elimination of ^{14}N in urine and excretion products and the resulting enrichment of ^{15}N in tissues and faeces (Miyake and Wada 1967; Steele and Daniel 1978; Checkley and Entzeroth 1985). The absolute values ultimately depend on the isotopic composition of the trophic base of the ecosystem. Here, we assume that this is sPOM, since no evidence has been found for hydrocarbon seepage at the sampled sites (Masson et al. 2003; Kiriakoulakis et al. 2004 submitted). $\delta^{15}N$ of sPOM from the three deep-water sites studied here (Darwin, Hovland and Belgica Mounds) shows some variability, but the sites are not significantly different. Interannual variability at the Belgica Mounds area (see Table 2) probably reflects differing nitrogen fractionation during phytoplankton production in the overlying waters (see below). The mean isotopic composition of nitrogen in both coral species studied here is about 2.5-3.5 ‰ heavier than that in sPOM. Many studies have shown that higher trophic levels of an ecosystem show a nitrogen isotopic enrichment of about 3-3.5 ‰, (e.g., DeNiro and Epstein 1981; Miniwaga and Wada 1984; Schoeninger and DeNiro 1984; Toda and Wada 1990; Cabana and Rasmussen 1994). Thus a simplistic view would be that the DWCs feed on sPOM. However, in deep-sea benthic ecosystems, which are usually food limited, the paucity of nitrogen is likely to lead to rather limited isotopic fractionation through benthic respiration. Indeed, Iken et al. (2001) showed that in a deep-sea benthic setting in the NE Atlantic Ocean (Porcupine Abyssal Plain), there is significant overlap in nitrogen isotopic values between trophic levels, reducing the "typical" 3 ‰ stepwise enrichment and indicating overlap in food sources. Therefore, additional information is needed for more secure conclusions regarding the trophic position of the corals (see below).

$\delta^{15}N$ values in *L. pertusa* showed variability between the sites, being heavier in the Norwegian fjord and shelf (see Table 1). Between-reef isotopic variability in $\delta^{15}N$ and $\delta^{13}C$ has been shown before in shallow-water coral tissue (Heikoop et al. 2000a) and this was attributed to varying environmental factors such as temperature, light intensity, eutrophication, and terrestrial inputs, which affect nitrogen fractionation during photosynthesis. Subsequent incorporation of photosynthetic nitrogen into the coral tissue, either *via* autotrophy or heterotrophy, could then reflect or even enhance this variability. Similar "coupling" of regional variation in $\delta^{15}N$ values of phytoplankton with that in DWCs may also occur, if phytoplankton detritus, which forms an important part of sPOM (Kiriakoulakis et al. 2004), stays relatively unaltered (i.e., "fresh") during transport to the sea bed. The regional variation in $\delta^{15}N$ values of the corals may therefore ultimately reflect the nitrogen dynamics of the surface waters. Anthropogenic inputs have also been shown to shift the nitrogen isotopic values of shallow-water coral reefs towards heavier values (Heikoop et al. 2000b; Risk and Erdmann 2000). This could also be a plausible explanation of heavier values in Norwegian corals in this study because they are located very close to land (Fig. 1) and in relatively shallow waters (Table 1).

$\delta^{15}N$ values in *M. oculata* also show some variability (see Table 1), but they are lighter than those of *L. pertusa* by about 0.6-0.8 ‰ at the Darwin and Belgica Mounds. These results are preliminary, but could indicate an overlap in feeding, perhaps with a different degree of selection. Iken et al. (2001) showed that suspension feeders (cnidarians) at the Porcupine Abyssal Plain exhibited a wide trophic spectrum, feeding both on particulate material and live prey.

Total lipids

A recent study of sPOM at the benthic boundary layer (BBL) of British and Irish waters revealed that there is fresh (i.e., lipid-rich) sPOM supply at all sites considered here. Nevertheless, there is some variability which may be related to the distinct oceanographic regime of each site (Kiriakoulakis et al. submitted).

The total lipid composition in both coral species is dominated by fatty acids, of which PUFAs and MUFAs comprise significant, although different and variable, proportions (see Table 4). PUFAs in the marine environment are usually thought to derive mainly from phytoplankton (e.g., Parrish et al. 2000), although they are often found in other marine organisms, including herbivorous zooplankton (Corner et al. 1986 and references therein) and deep-sea bacteria (DeLong and Yayanos 1985; Jøstensen and Landfald 1997; Fang et al. 2000). The main source of PUFAs in the phytoplankton are diatoms which biosynthesise mostly $C_{20:5}$ (Volkman et al. 1989), and dinoflagellates which produce more $C_{22:6}$ (Sargent et al. 1987; Harvey et al. 1988).

The 22:6/20:5 PUFA ratios of both coral species are similar, but significantly different to those of the sPOM samples. This implies that coral PUFAs may have a similar source and that this may not be sPOM. Zooplankton are a potential food source for the corals (see also below), but were not collected at the study sites.

Differences in the biochemistry of the two species may also be important. Recently, Mancini et al. (1999) isolated novel 10-hydroxydocosapolyenoic acids in *M. oculata* and *L. pertusa* from Galicia Bank and the Indian Ocean (*M. oculata* only). These authors pointed out that these fatty acids are considered to be intermediates of the $C_{20:4}$ fatty acid cascade in mammals, but rarely are found in marine invertebrates and little is known about their biosynthetic pathways in the marine environment. Such fatty acids were not detected in this study, but the variability in proportions of PUFAs (and MUFAs) of both corals may also be related to environmental, physiological and/or biochemical factors. For example, Oku et al. (2002) showed that the polyps of the shallow-water branching coral *Montipora digitata* have different lipid distributions according to their position in the branch. Clearly much more detailed work is required (see also Mancini et al. 1999).

Herbivorous and omnivorous mesozooplankton feeding predominantly on phytoplankton contain elevated amounts of MUFAs within the wax ester lipid fraction (Ratnayake and Ackman 1979; Graeve et al. 1994; Albers et al. 1996). Moreover, calanoid copepods, which overwinter at depth and constitute a large proportion of the mesozooplankton community in the N.E. Atlantic (e.g., Heath and Jónasdóttir 1999; Planque and Batten 2000), are currently the only organisms

known to biosynthesize de novo $C_{20:1}$ and $C_{22:1}$ fatty acids (MUFAs identified in this study) and alcohols (for a review see Dalsgaard et al. 2003). Thus, MUFAs and their corresponding alcohols are commonly used as mesozooplankton markers. It should be noted that the mean proportion of MUFAs and alcohols (of which $C_{20:1}$ and $C_{22:1}$ alcohols are dominant) in both DWCs are significantly higher than that in sPOM. This suggests that the corals may acquire these fatty acids from mesozooplankton, supporting the indication from 22:6/20:5 ratio. Similarly, enrichment of MUFAs in *L. pertusa* (indicated by the lower PUFA/MUFA ratio), relative to *M. oculata* could be attributed to strategies that assimilate more zooplankton tissue, consistent with the heavier $\delta^{15}N$ values of *L. pertusa*. Alternatively, metabolism of these compound classes could be different in the two species.

Proportions of microbial fatty acids were similar in both coral species but lower than those in sPOM. Microbial biomarkers are commonly found in sPOM (e.g., Kiriakoulakis et al. 2001), therefore their presence in the coral tissue is unsurprising, although it is not clear from whether they are dietary or symbiotic. Even so, their usefulness as biomarkers is currently disputed (see discussion in Parrish et al. 2000) and they should be used with caution and in a qualitative rather than quantitative sense in estimating microbial contributions.

Conclusions

1. Increased abundances of MUFAs and alcohols and different ratios of 22:6/20:5 in DWCs when compared with sPOM implies that they may largely feed on mesozooplankton.
2. The enrichment of MUFAs and ^{15}N in *L. pertusa* relative to *M. oculata* could be attributed to different feeding and/or assimilation/storage strategies of mesozooplankton tissue or to different metabolism in the two coral species.

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