

Volume 55    Number 10    October 2008    ISSN 0967-0637	
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## Deep-Sea Research I

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# Stable C and N isotopic composition of cold-water corals from the Newfoundland and Labrador continental slope: Examination of trophic, depth and spatial effects

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## ARTICLE INFO

### Article history:

Received 5 October 2007

Received in revised form

16 May 2008

Accepted 27 May 2008

Available online 6 June 2008

### Keywords:

$\delta^{13}\text{C}$

$\delta^{15}\text{N}$

Cold-water corals

Trophic level

Continental slope

Newfoundland and Labrador

## ABSTRACT

With the aim of understanding of the trophic ecology of cold-water corals, this paper explores the tissue  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of 11 'coral' species (8 alcyonacean, 1 antipatharian, 1 pennatulacean, 1 scleractinian) collected along the Newfoundland and Labrador continental slope. Isotopic results delimit species along continua of trophic level and food lability. With an isotopic signature similar to macrozooplankton, *Paragorgia arborea* occupies the lowest trophic level and most likely feeds on fresh phytodetritus. *Primnoa resedaeformis* occupies a slightly higher trophic level, likely supplementing its diet with microzooplankton. *Bathypathes arctica*, Pennatulacea and other alcyonaceans (*Acanella arbuscula*, *Acanthogorgia armata*, *Anthomastus grandiflorus*, *Duva florida*, *Keratoisis ornata*, *Paramuricea* sp.) had higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, suggesting these species feed at higher trophic levels and on a greater proportion of more degraded POM. *Flabellum alabastrum* had an isotopic signature similar to that of snow crab, indicating a primarily carnivorous diet. Isotopic composition did not vary significantly over a depth gradient of 50–1400 m. Coral  $\delta^{13}\text{C}$  increased slightly (<1‰) from the Hudson Strait to the southern Grand Banks, but  $\delta^{15}\text{N}$  did not. By modulating the availability and quality of suspended foods, substrate likely exerts a primary influence on the feeding habits of cold-water corals.

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## 1. Introduction

There has been increasing interest in cold-water coral ecosystems over the past decade. Cold-water corals may live for decades to hundreds or even thousands of years (Druffel et al., 1995; Roark et al., 2006; Sherwood et al., 2006) and create structurally complex habitat for invertebrates and fish (Henry and Roberts, 2007; Husebø et al.,

2002; Krieger and Wing, 2002; Costello et al., 2005; Edinger et al., 2007). Despite the great deal of recent interest in cold-water corals, relatively little is known about their trophic ecology (Roberts et al., 2006).

Previous research on the trophic ecology of cold-water corals has focused mainly on the scleractinian *Lophelia pertusa* reefs of the northeast Atlantic. Aquarium and field observations show that *L. pertusa* may capture live zooplankton up to 2 cm in length (Mortensen et al., 2001; Freiwald et al., 2002). Fatty acid and stable nitrogen isotope signatures suggest cold-water scleractinia may also feed on detrital particulate organic matter (POM; Duineveld et al., 2004, 2007; Kiriakoulakis et al., 2005).

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Suspension feeding cnidarians at the Porcupine Abyssal Plain occupy a wide trophic niche, feeding on resuspended material and swimmers to compensate for seasonal shortages in fresh phytodetritus (Iken et al., 2001). Shallower-water octocorals consume a wide range of prey items, from bacteria to zooplankton and detrital POM in proportion to availability (Fabricius et al., 1995; Ribes et al., 1999; Coma et al., 2001; Orejas et al., 2003; Tsounis et al., 2006).

Here, we use stable isotopes to examine the trophic ecology of cold-water 'corals' (Alcyonacea, Pennatulacea, Antipatharia, Scleractinia) collected off Newfoundland and Labrador, in the northwest Atlantic Ocean (Gass and Willison, 2005; Mortensen and Buhl-Mortensen, 2005a; Wareham and Edinger, 2007). We present new data on tissue carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotopic composition of 11 species collected over a depth range of 50–1400 m. The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of organisms are used to interpret food sources and trophic levels, respectively (Fry, 1988; Hobson et al., 1995; Vander-Zanden and Rasmussen, 2001). This is particularly useful when traditional methods of diet analysis, such as gut contents or incubations (Ribes et al., 1999), are impracticable.

A second objective of this study is to explore geographic patterns in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of coral tissues. Isotopic composition of primary consumers provides time-integrated data on processes operating near the base of the food web, such as eutrophication (Heikoop et al., 2000; Ward-Paige et al., 2005; Vander-Zanden et al., 2005) and nutrient dynamics across oceanographic gradients (Dunton et al., 1989; Schell et al., 1998; Sherwood et al., 2005a). A previous study from Newfoundland and Labrador reported higher  $\delta^{15}\text{N}$  in fish and invertebrates inhabiting the inner reaches of the continental shelf than in fish and invertebrates living near the shelf break (Sherwood and Rose, 2005). Here, we assess the strength of similar isotopic gradients along the main axis of the outer Labrador Current, from its origin near the Hudson Strait to the southern Grand Banks.

## 2. Materials and methods

### 2.1. Sampling

Since 2003, coral specimens caught as trawl by-catch during stock assessment surveys and fisheries operations have been collected and stored at the Northwest Atlantic Fisheries Center in St. John's, Newfoundland (Wareham and Edinger, 2007). The dataset consisted of 169 coral tissue samples, representing 11 species, three regions and a depth range of 47–1433 m (Table 1). The regions represented were Hudson Strait, Labrador Slope, and southern Grand Banks (Fig. 1). The Hudson Strait and Labrador Slope are located along the main axis of the cold and low salinity Labrador Current. The southern Grand Banks is located at the southern extent of the Labrador Current, and is also influenced by warmer and higher salinity Gulf Stream waters and Warm Slope Waters. Sampling depths (50–1400 m) were constrained by stock

assessment and fisheries protocols. Additional information relevant to potential feeding habits is included in Table 1.

### 2.2. Stable isotopic and C:N elemental analysis

To carry out the isotopic analysis, several polyps were removed from each coral to provide a composite sample. These were then freeze-dried and ground to a powder using an agate mortar and pestle. Samples for elemental (%N and %C) and carbon isotope analysis were treated with 5% (v/v) HCl to remove carbonates, triple rinsed in de-ionised water and dried at 60 °C. Samples for nitrogen isotope analysis were left untreated and analysed separately. Approximately 0.7 mg samples were weighed into 10 × 10 mm ultralight Sn capsules. The analyses were carried out using a Carlo Erba 1500 elemental analyser connected by a ConFlo-II interface to a Finnigan™ MAT 252 isotope ratio mass spectrometer in the Department of Earth Sciences, Memorial University. Analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were carried out separately. The carbon and nitrogen isotopic values are reported in the standard  $\delta$ -notation:

$$\delta X = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 10^3,$$

where X is  $^{13}\text{C}$  or  $^{15}\text{N}$  and R is  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ . Values are in per mill (‰) units with respect to Vienna Pee Dee Belemnite (VPDB) standard and the  $\text{N}_2$  in air, respectively. Calibration of the mass spectrometer data was carried out using external reference materials. For carbon, L-SVEC  $\text{Li}_2\text{CO}_3$  ( $-46.48 \pm 0.15\text{‰}$ ) and IAEA-CH-6 sucrose ( $+10.43 \pm 0.13\text{‰}$ ) were used as calibration standards. IAEA-N-1 ( $+0.43 \pm 0.07\text{‰}$ ) and USGS 26 ( $+53.62 \pm 0.25\text{‰}$ ) were used to calibrate the nitrogen data. Replicate measurements of additional standards were used to assess accuracy and precision of the isotope results. Over the course of the study, the measured  $\delta^{13}\text{C}$  value of the USGS 24 graphite standard ( $-15.99 \pm 0.11\text{‰}$ ) was  $-15.98 \pm 0.10\text{‰}$  ( $n = 21$ ). The  $\delta^{15}\text{N}$  value of IAEA-N-2 ( $(\text{NH}_4)_2\text{SO}_4$  ( $+20.34 \pm 0.47\text{‰}$ )) was measured as  $+20.36 \pm 0.13\text{‰}$  ( $n = 23$ ). An additional internal organic standard composed of homogenized cod muscle tissue ( $\delta^{13}\text{C} = -18.88 \pm 0.17$ ,  $n = 41$ ;  $\delta^{15}\text{N} = +14.80 \pm 0.16$ ,  $n = 37$ ) was also analysed over the course of the study; measured values of  $-18.76 \pm 0.13\text{‰}$  ( $n = 9$ ) and  $14.65 \pm 0.10\text{‰}$  ( $n = 7$ ) were obtained for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively. Replicate analyses were also carried out on selected coral samples. The average standard deviation between replicates was  $\pm 0.20\text{‰}$  for  $\delta^{13}\text{C}$  and  $0.24\text{‰}$  for  $\delta^{15}\text{N}$ .

Elemental concentrations (%C and %N) were analysed in conjunction with the isotopic analyses. The reference materials sulphanilamide ( $\text{C}_6\text{H}_8\text{N}_2\text{SO}_2$ ; 41.85%C) and BBOT ( $\text{C}_{26}\text{H}_{26}\text{N}_2\text{O}_2\text{S}$ ; 6.51%N) were used as calibration standards. Replicate analyses on selected coral samples had an average standard deviation of  $\pm 0.76$  for %C and  $\pm 0.30$  for %N.

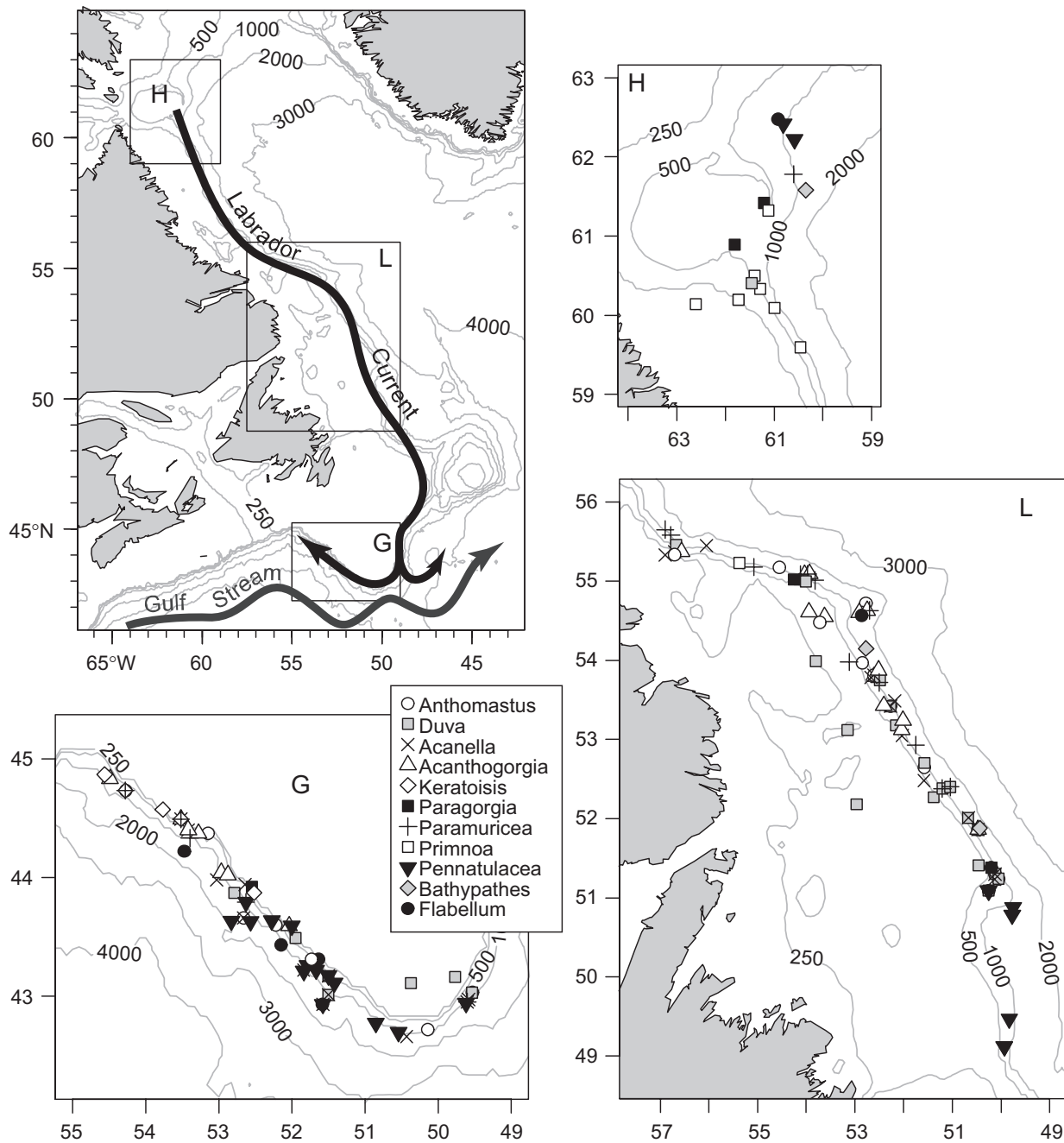
**Table 1**  
Taxonomy, C:N ratios, stable isotope values, and data relevant to potential feeding habits for coral species used in this study

Order	Common name	Species	n	C:N (mean ± S.D.)	$\delta^{13}\text{C}$ (‰) (mean ± S.D.)	$\delta^{13}\text{C}$ (‰) (mean ± S.D.)	$\delta^{15}\text{N}$ (‰) (mean ± S.D.)	Known depth range (m) <sup>a</sup>	Colony height (cm) <sup>a</sup>	Polyp diameter (mm) <sup>b</sup>	Preferred substrate <sup>a</sup>
Alcyonacea	Soft corals	<i>Anthomastus grandiflorus</i> (Verrill 1878)	21	3.96 ± 0.41	-19.33 ± 0.54	-18.73 ± 0.57	11.24 ± 0.84	170–1400	<30	3–5	Gravel on muddy seabeds
		<i>Duva florida</i> (Verrill 1869)	29	4.40 ± 0.62	-19.67 ± 0.92	-18.59 ± 0.54	11.46 ± 0.42	50–1400	<20	1–2	Gravel on muddy seabeds
	Sea fans	<i>Acanthogorgia armata</i> (Verrill 1878)	20	5.37 ± 0.70	-20.59 ± 1.13	-18.91 ± 0.44	11.27 ± 0.55	170–1400	<50	2–4	Gravel on sandy-mud seabeds
		<i>Acanella arbuscula</i> (Johnson 1862)	25	4.60 ± 0.42	-20.68 ± 0.70	-19.44 ± 0.49	10.52 ± 0.60	150–1400	<50	2–4	Gravel on sandy-mud seabeds
		<i>Keratoisis ornate</i> (Verrill 1878)	6	3.98 ± 0.18	-20.07 ± 0.68	-19.65 ± 0.45	11.25 ± 0.79	200–1100	<100	3–5	Gravel on muddy seabeds
		<i>Paragorgia arborea</i> (L. 1758)	5	5.70 ± 1.16	-22.18 ± 0.65	-19.85 ± 0.65	9.28 ± 0.69	370–1300	<300	5	Boulders, current-swept channels
		<i>Paramuricea</i> sp.	19	4.40 ± 0.67	-19.86 ± 1.08	-18.94 ± 0.45	11.72 ± 0.57	150–1400	<200	4–5	Boulders and cobbles on sand to mud seabeds
		<i>Primnoa resedaeformis</i> (Gunnerus 1763)	8	4.72 ± 0.61	-21.56 ± 0.75	-20.29 ± 0.27	10.27 ± 0.69	160–1100	<100	4	Boulders, current-swept channels
Pennatulacea	Sea pens	<i>Pennatula</i> sp.	26	4.01 ± 0.56	-19.60 ± 0.92	-18.95 ± 0.52	10.87 ± 0.47	100–1400	<70	1–5	Mud
Antipatharia	Black corals	<i>Halipterus finnarchia</i> (Sars, 1851)									
		<i>Bathypathes</i> sp. (Brooke, 1889) (?)	3	3.88 ± 0.32	-20.27 ± 0.58	-19.75 ± 0.27	10.76 ± 1.16	750–1300	<100	1–2	Boulders and cobbles on sand to mud seabeds
Scleractinia	Cup corals	<i>Flabellum alabastrum</i> (Moseley 1876)	7	7.07 ± 0.73	-20.81 ± 0.64	-17.18 ± 0.65	12.76 ± 0.68	220–1400	<10	20–35	Mud to sandy mud

$\delta^{13}\text{C}$  = lipid-corrected  $\delta^{13}\text{C}$  values.

<sup>a</sup> Wareham and Edinger (2007). Note: sampling effort limited to ≤ 1400 m; some species may live deeper.

<sup>b</sup> Mortensen and Buhl-Mortensen (2005a) and P. Mortensen, personal communication, September 2006.



**Fig. 1.** Map of the Newfoundland and Labrador area showing surface water currents and sampling regions (H = Hudson Strait, L = Labrador Slope, G = Grand Banks). Inset maps show locations of coral samples listed by species.

### 2.3. Correction of $\delta^{13}C$ values for lipid bias

Interpretation of  $\delta^{13}C$  data is potentially complicated by lipid content, because lipids are  $^{13}C$  depleted relative to proteins (DeNiro and Epstein, 1977). It is important to account for lipid-related bias in  $\delta^{13}C$  when comparing animals of different lipid composition, which is the case for cold-water corals (Hamoutene et al., 2008). Consequently,  $\delta^{13}C$  data were normalised for lipid content using C:N as a proxy for lipid content according to the following equation in Post et al. (2007):

$$\delta^{13}C' = \delta^{13}C - 3.32 + 0.99 \times C : N,$$

where  $\delta^{13}C'$  represents lipid-normalised  $\delta^{13}C$ . This equation is based on data primarily from fish collected from a range of different lake, river and coastal marine habitats. Recognizing that the correction may be slightly different for cold-water corals, we report below the results for both uncorrected and corrected  $\delta^{13}C$ .

### 2.4. Statistical analysis

The distribution of species with respect to regions and depths was unbalanced. For example, *Keratoisis* was collected only at the Grand Banks and *Bathypathes* was

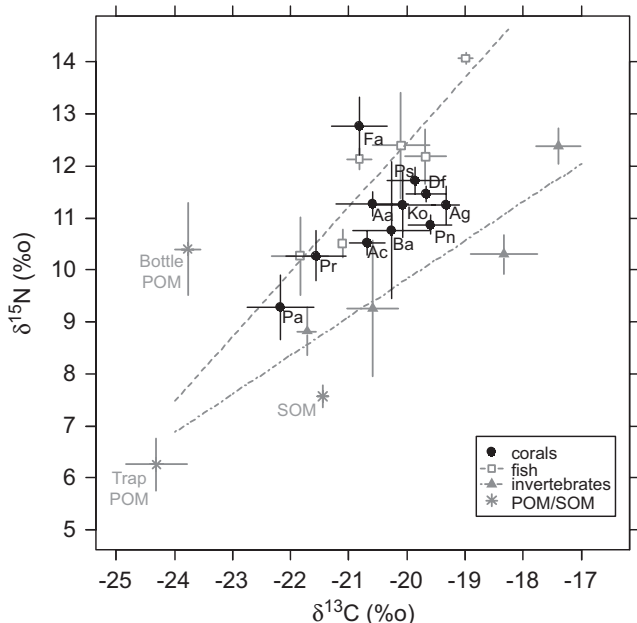
only collected from deeper than 1000 m. Data were therefore analysed in the following way. First, the effect of species on each of  $\delta^{13}\text{C}$ ,  $\delta^{13}\text{C}'$  and  $\delta^{15}\text{N}$  was tested over the entire dataset using one-way ANOVA. Then, the effects of region and depth were tested for each level of species using ANCOVA. Where necessary, non-significant interactions were eliminated and models were refit sequentially (Venables and Ripley, 1999). Model residuals were checked to verify assumptions of normality and homogeneity of variance; transformations were not required. Post-hoc comparisons were performed with Tukey's honestly significant differences (HSD) test. Statistical significance is reported at the  $p < 0.05$  level. Statistical analysis was performed in the R language and environment (<http://www.r-project.org>).

### 3. Results

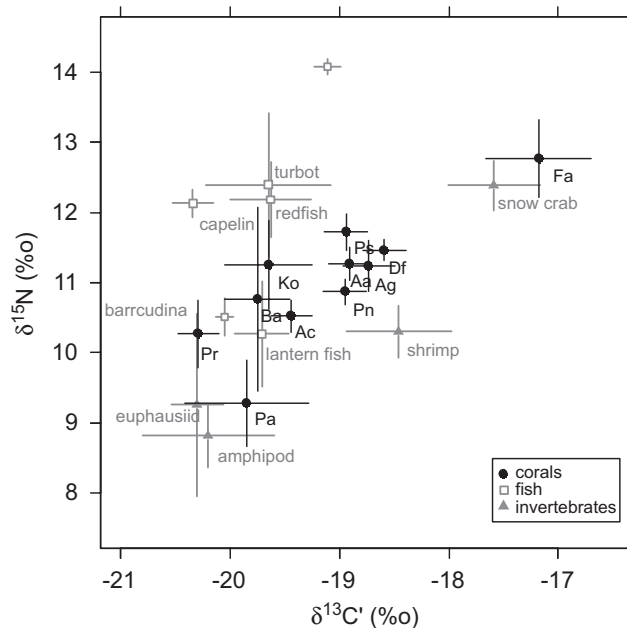
Within the pooled dataset, the effect of species was highly significant on  $\delta^{13}\text{C}$  (one-way ANOVA;  $F_{10,142} = 10.46, p < 0.001$ ),  $\delta^{13}\text{C}'$  ( $F_{10,138} = 20.18, p < 0.001$ ) and  $\delta^{15}\text{N}$  ( $F_{10,154} = 16.81, p < 0.001$ ). Fig. 2 shows the distribution of coral species in  $\delta^{15}\text{N}$  vs.  $\delta^{13}\text{C}$  (uncorrected for lipid effects) space compared with previously published values for other components of the Newfoundland and Labrador marine foodweb. As a proxy for resuspended POM, we used sedimentary organic matter (SOM) data from the Labrador Slope (340–2648 m water depth), as reported in Muzuka and Hillaire-Marcel (1999). Data for suspended (bottle-collected) and sinking (sediment trap-collected) POM were not available for the offshore region of New-

foundland and Labrador. Instead, we used data collected from the shelf waters of Conception Bay (approximately 47.9°N/52.8°W), as reported in Ostrom (1992) and Ostrom et al. (1997). These data were collected over an April–September seasonal cycle in 5–240 m deep water. To account for seasonal and depth-related variability in bottle-collected POM, we calculated respective POC and PON concentration weighted mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Ostrom et al., 1997). To correct for nearshore enrichment in  $\delta^{15}\text{N}$  (Sherwood and Rose, 2005), we subtracted 1‰ from POM  $\delta^{15}\text{N}$ , based on the difference in mean SOM  $\delta^{15}\text{N}$  between Conception Bay (Ostrom, 1992) and Labrador Slope (Muzuka and Hillaire-Marcel, 1999). Invertebrate (amphipod, euphausiid, shrimp (*Pandalus borealis* and *Pasiphaea multidentata*), snow crab (*Chionoecetes opilio*)) and fish (lantern fish (*Myctophum* sp.), white barracudina (*Notolepis rissoi*), capelin (*Mallotus villosus*), redfish (*Sebastes* sp.), turbot (*Reinhardtius hippoglossoides*), cod (*Gadus morhua*)) data from offshore Newfoundland and Labrador were reported in Sherwood and Rose (2005). In Fig. 2, fish and invertebrate data formed separate trendlines that converged around the value for sediment trap-collected POM and enveloped all of the coral data except *Flabellum*. Corals plotted 3–6.5‰ higher in  $\delta^{15}\text{N}$  than sediment trap-collected POM, and 1.7–5.2‰ higher than SOM. Bottle-collected POM overlapped with all of the corals in  $\delta^{15}\text{N}$ , except *Paramuricea* and *Flabellum*, which plotted 1.3–2.4‰ higher.

In Fig. 3, the coral, other invertebrates and fish data were re-plotted using  $\delta^{13}\text{C}'$  (corrected for lipid effects). Data for POM and SOM were omitted, because the lipid correction was developed for animal tissues (Post et al., 2007). Coral data plotted along a relatively tight trendline ( $r^2 = 0.71, p < 0.001, n = 11$ ) extending from *Paragorgia* to



**Fig. 2.** Distribution of deep-sea coral data in  $\delta^{15}\text{N}$  vs.  $\delta^{13}\text{C}$  space: *Anthomastus* (Ag), *Duva* (Df), *Acanella* (Ac), *Acanthogorgia* (Aa), *Keratois* (Ko), *Paragorgia* (Pa), *Paramuricea* (Ps), *Primnoa* (Pr), *Pennatulacea* (Pn), *Bathypathes* (Ba), *Flabellum* (Fa). Also shown, other invertebrates and fish (Sherwood and Rose, 2005; labels omitted for clarity), sinking (trap-collected) and suspended (bottle-collected) POM (Ostrom, 1992; Ostrom et al., 1997), and SOM (Muzuka and Hillaire-Marcel, 1999). Separate trendlines are shown for fish and invertebrates. Error bars are 95% confidence intervals.



**Fig. 3.** Same as Fig. 2, using lipid-corrected values of  $\delta^{13}\text{C}$  ( $\delta^{13}\text{C}'$ ). POM and SOM data were omitted because the lipid correction was developed for animal tissues (Post et al., 2007). Invertebrate and fish taxa (Sherwood and Rose, 2005) are labelled. Trendlines omitted for clarity. Error bars are 95% confidence intervals.

**Table 2**

ANCOVA table for the effects of region and depth on each of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , calculated separately for each species

Species	Source	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
		F	p	F	p
<i>Anthomastus</i>	Region	1.633	0.219	17.402	< <b>0.001</b>
	Depth	2.083	0.167	0.561	0.464
	Region $\times$ depth	–	–	12.907	<b>0.002</b>
	Residual d.f.	18		17	
<i>Duva</i>	Region	5.735	<b>0.009</b>	1.274	0.298
	Depth	6.904	0.015	2.408	0.134
	Region $\times$ depth	–	–	–	–
	Residual d.f.	24		24	
<i>Acanella</i>	Region	13.348	0.002	0.008	0.928
	Depth	4.614	0.046	0.511	0.482
	Region $\times$ depth	1	<b>0.006</b>	–	–
	Residual d.f.	17		22	
<i>Acanthogorgia</i>	Region	0.078	0.787	17.287	< <b>0.001</b>
	Depth	0.014	0.909	3.652	0.074
	Region $\times$ depth	–	–	10.692	<b>0.005</b>
	Residual d.f.	8		16	
<i>Keratois</i>	Region	–	–	–	–
	Depth	0.152	0.722	0.000	0.992
	Region $\times$ depth	–	–	–	–
	Residual d.f.	3		5	
<i>Paragorgia</i>	Region	2.112	0.438	0.946	0.588
	Depth	0.886	0.519	0.331	0.668
	Region $\times$ depth	–	–	–	–
	Residual d.f.	1		1	
<i>Paramuricea</i>	Region	0.420	0.665	1.713	0.214
	Depth	2.581	0.130	1.826	0.197
	Region $\times$ depth	–	–	–	–
	Residual d.f.	14		15	
<i>Primnoa</i>	Region	0.116	0.751	0.334	0.588
	Depth	4.033	0.115	0.572	0.483
	Region $\times$ depth	–	–	–	–
	Residual d.f.	4		5	
<i>Pennatulacea</i>	Region	<b>10.654</b>	< <b>0.001</b>	0.342	0.714
	Depth	0.151	0.702	0.194	0.664
	Region $\times$ depth	–	–	–	–
	Residual d.f.	20		22	
<i>Flabellum</i>	Region	4.925	0.113	3.301	0.233
	Depth	0.060	0.823	4.660	0.164
	Region $\times$ depth	–	–	–	–
	Residual d.f.	3		3	

Similar results obtained for both  $\delta^{13}\text{C}$  (not shown) and  $\delta^{15}\text{N}$ . Where the region  $\times$  depth interaction was insignificant at the  $p = 0.05$  level, the interaction was dropped and the model was re-run. Region effect not applicable for *Keratois* because it was collected from Grand Banks only. *Bathypathes* excluded because of insufficient sample numbers. Values in bold are significant at the  $p < 0.05$  level.

*Flabellum*. At the lower end of the trendline, *Paragorgia* plotted closer to both amphipods and euphausiids. At the higher end, *Flabellum* plotted around snow crab.

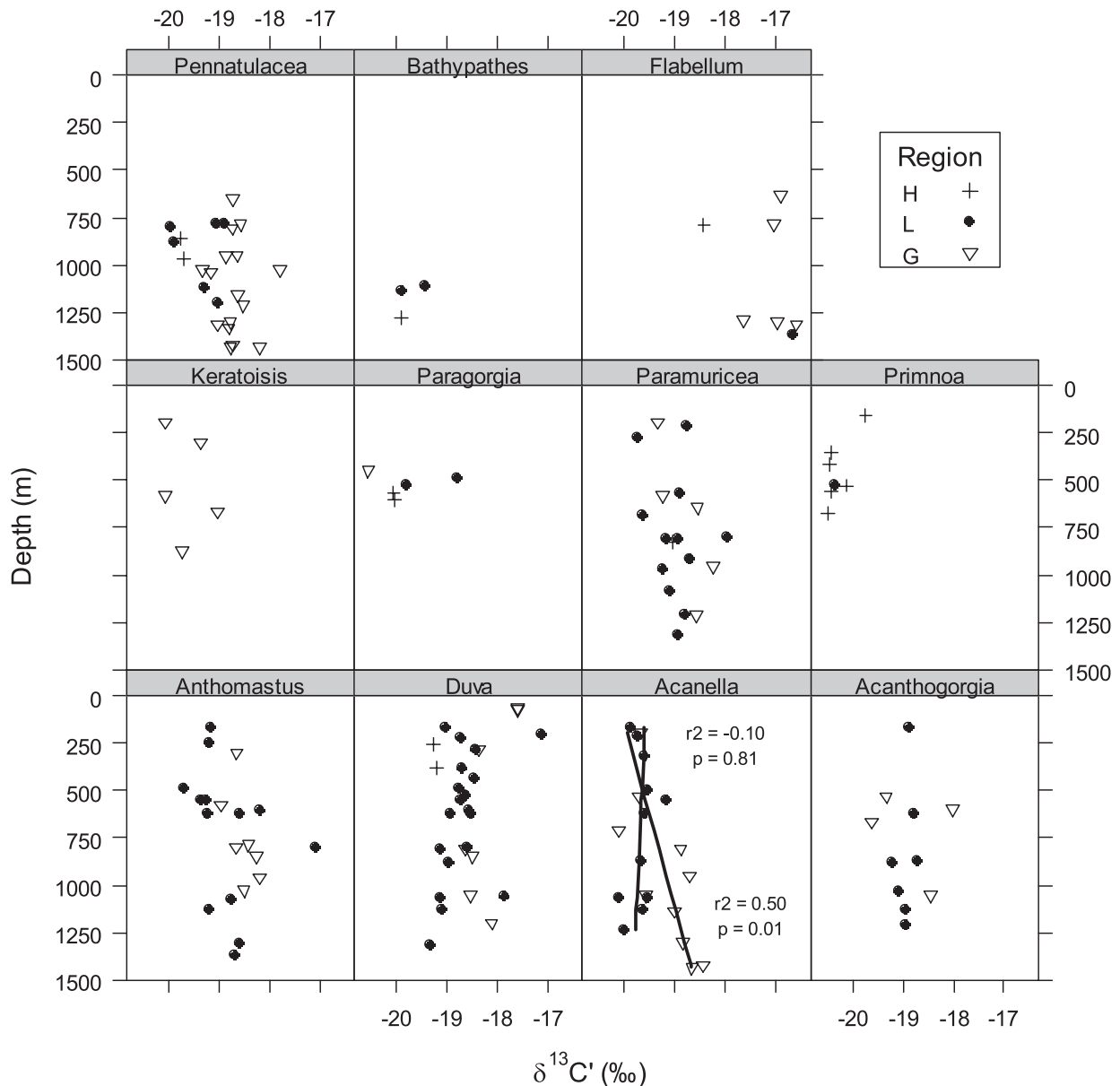
Within each level of species, the effects of region and depth on  $\delta^{13}\text{C}$  (both uncorrected and corrected for lipid effects) and  $\delta^{15}\text{N}$  were largely insignificant (Table 2). For  $\delta^{13}\text{C}$  (Fig. 4), the region  $\times$  depth interaction was significant for *Acanella*, with values increasing with depth at Grand Banks (G), but not at Labrador Slope (L). The region effect was also significant for *Duva* (Hudson Strait (H) < L = G) and *Pennatulacea* (H = L < G). All other main effects and interactions of region and depth on  $\delta^{13}\text{C}$  were not significant. For  $\delta^{15}\text{N}$  (Fig. 5), the region  $\times$  depth interaction was significant for *Anthomastus* and *Acanthogorgia*. In both species, values of  $\delta^{15}\text{N}$  increased with depth at Labrador Slope and decreased with depth at Grand Banks. All other main effects and interactions of region and depth on  $\delta^{15}\text{N}$  were not significant.

## 4. Discussion

### 4.1. Inter-specific variation in stable isotopic composition

Stable isotope values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  varied significantly among species, but showed weak and inconsistent patterns of variation in relation to depth or latitude. We hypothesise that differences in feeding habits account for the strong inter-specific variation, based on the wide range of habitats and colony morphologies, and the need to reduce inter-specific competition in food-limited, deep-sea environments (Iken et al., 2001). The distribution of data in Figs. 2 and 3 provide a convenient way to visualize trophic relationships among different taxa, with each  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  pair corresponding to a unique trophic niche. The vertical axes represent a continuum of trophic level, with  $\delta^{15}\text{N}$  increasing by about 3‰ per trophic level (Fry, 1988; Sherwood and Rose, 2005). The  $^{15}\text{N}$  enrichment per trophic level may be smaller in the deep sea where food is scarce (Iken et al., 2001). The horizontal axis is often interpreted as a continuum of feeding types, from pelagic (low  $\delta^{13}\text{C}$ ) to benthic (high  $\delta^{13}\text{C}$ ; McConnaughey and McRoy, 1979; Sherwood and Rose, 2005; Nadon and Himmelman, 2006). Among benthic organisms, detritivores have higher  $\delta^{13}\text{C}$  than suspensivores (Dunton et al., 1989; Rossi et al., 2004); therefore lighter (heavier)  $\delta^{13}\text{C}$  may be interpreted to reflect more labile (refractory) food sources (Fischer, 1991; Nyssen et al., 2002; Lovvorn et al., 2005). Coral species therefore occupy different positions along two continua: trophic level and food “freshness”.

At the lower end of the continua, isotopic composition of *Paragorgia* overlapped with pelagic amphipods and euphausiids (Fig. 3). In addition to the one trophic level offset ( $\Delta\delta^{15}\text{N} = 3\text{‰}$ ) from sediment trap-collected POM (Fig. 2), this suggests that fresh phytodetritus is the primary food source for this species. *Primnoa* had a similar  $\delta^{13}\text{C}$  value to that of *Paragorgia*, but was 1‰ heavier for  $\delta^{15}\text{N}$ . Its diet therefore is probably supplemented with microzooplankton, as previously inferred for *Primnoa* spp. living off Nova Scotia and in the Northeast Pacific (Sherwood et al., 2005a). With higher values of  $\delta^{13}\text{C}$ , *Bathypathes*, *Pennatulacea* and the remaining Alcyonacea probably rely on more degraded fractions of POM, because they plotted to the right of the fish trendline. Finally, with



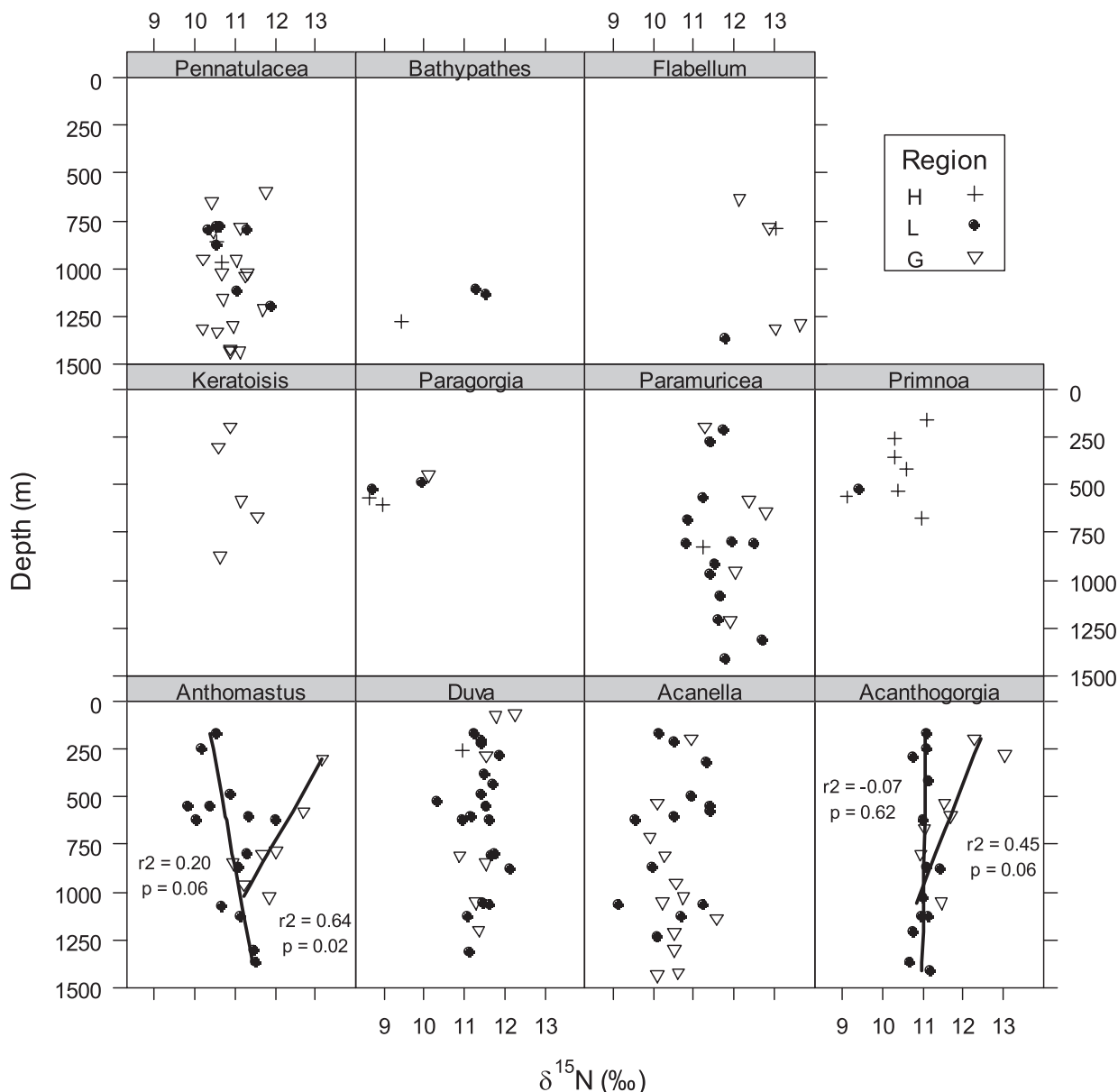
**Fig. 4.** Plots of  $\delta^{13}C'$  (lipid-corrected) vs. depth, grouped by region (H = Hudson Strait, L = Labrador Slope, G = Grand Banks). The region  $\times$  depth interaction was significant for *Acanella*; linear fits are shown separately for each region with adjusted  $r^2$  and  $p$  values. The region effect was also significant for *Duva* (H < L = G) and *Pennatulacea* (H = L < G). All other region and depth effects and interactions were not significant at the  $p = 0.05$  level.

an isotopic composition similar to that of snow crab, *Flabellum* most likely feeds carnivorously on benthic meiofauna and demersal zooplankton. This is consistent with aquarium observations showing that *Flabellum* can ingest swimmers up to 1.5 cm in length (Buhl-Mortensen et al., 2007).

In continental slope settings, lateral fluxes of POM may dominate over sinking fluxes (Thomsen and van Weering, 1998), particularly in areas with strong currents. Therefore, substrate type and resuspension processes likely play a far more important role in the trophic ecology of cold-water corals than other factors such as colony or polyp morphology or depth. For example, *Paragorgia* and *Primnoa* inhabit boulder fields and current-swept bedrock canyons along the upper slope of the northwest Atlantic (Mortensen and Buhl-Mortensen, 2004, 2005a). Focusing of tidal currents around these features may result in

higher rates of productivity at the surface and increased supply of fresh phytodetritus at depth (e.g., Kiriakoulakis et al., 2004; Thiem et al., 2006). The other species mainly inhabit lower current settings, often including a mix of hard and muddy substrates, where resuspended material is more readily available. As a result, more degraded fractions of POM must account for a greater share of diet. Our isotopic results are consistent with this hypothesis, with the lower  $\delta^{13}C$ – $\delta^{15}N$  species (*Paragorgia*, *Primnoa*) inhabiting boulder and bedrock substrates, intermediate  $\delta^{13}C$ – $\delta^{15}N$  species (*Bathypathes*, *Acanella*, *Keratoisis*) inhabiting mixed gravel-sand-mud substrates, and highest  $\delta^{13}C$ – $\delta^{15}N$  species (*Acanthogorgia*, *Anthomastus*, *Duva*, *Paramuricea*) inhabiting gravels on muddy sand to mud substrates. Only pennatulaceans and *Flabellum* grow directly on mud substrates. Substrate control over feeding habits, at least for the octocorals, is consistent with the





**Fig. 5.** Plots of  $\delta^{15}\text{N}$  vs. depth, grouped by region (H = Hudson Strait, L = Labrador Slope, G = Grand Banks). The region  $\times$  depth interaction was significant for *Anthomastus* and *Acanthogorgia*; linear fits are shown separately for each region with adjusted  $r^2$  and  $p$  values. All other region and depth effects and interactions were not significant at the  $p = 0.05$  level.

idea that diets vary in proportion to food availability (Ribes et al., 1999; Coma et al., 2001).

Colony morphology may influence feeding habits through adaptation to different flow regimes (Dai and Lin, 1993). For example, tall (> 1 m), concave gorgonians are better adapted to laminar, unidirectional currents supplying fresher material, while shorter, bushy gorgonians are better adapted to turbulent currents supplying resuspended material (Mortensen and Buhl-Mortensen, 2005b). With even shorter colonies (< 30 cm), soft corals and cup corals are more closely in contact with resuspension processes at the sediment surface. Soft corals may even deposit feed directly from the sea floor (Slattery et al., 1997). Unfortunately, because our samples were rarely recovered as intact colonies, we were unable to directly correlate colony heights with isotopic composition. Qualitatively, taller species (*Paragorgia*, *Primnoa*,

*Bathypathes*, *Keratoisis*, *Paramuricea*) seem mainly to occupy the lower trophic level/fresher food niches, while species with shorter colonies (*Acanella*, *Pennatulacea*, *Anthomastus*, *Duva*, *Flabellum*) occupy higher trophic level/more degraded food niches.

Polyp morphology may also influence feeding habits. For example, polyp size determines the size of particles the corals are able to ingest (Lewis, 1982). Corals with larger diameter polyps would be expected to have higher tissue  $\delta^{15}\text{N}$  because  $\delta^{15}\text{N}$  generally increases with particle size (e.g., Wu et al., 1999). The large, solitary polyps of *Flabellum*, ranging from 20 to 35 mm in diameter, allow it to capture large prey (Buhl-Mortensen et al., 2007), and this likely accounts for its high  $\delta^{15}\text{N}$  values. Among the other species, however, there was a narrow range of polyp diameters, which did not relate to isotopic composition (linear regression,  $p > 0.05$ ). In addition to polyp size,

tentacle diameter may also influence the type of particles the corals are able to capture. For example, many octocorals have pinnate tentacles which can be used to handle smaller and more delicate particles than scleractinians (Lewis, 1982). This may partly explain why the octocorals occupied lower trophic niches than the scleractinian *Flabellum*.

#### 4.2. Depth variation in stable isotopic composition

There was no significant effect of depth on isotopic composition overall. A companion study using many of the same species reported here also demonstrated no depth-related trends in total lipid composition, although depth trends were apparent for specific lipid classes (Hamoutene et al., 2008). Our results contrast with a recent study of Antarctic suspension feeders in which  $\delta^{15}\text{N}$  did increase with depth (Mintenbeck et al., 2007). This was explained by the well established fact that  $\delta^{15}\text{N}$  of suspended (bottle- and pump-collected) POM increases with depth (up to 15‰) in many different oceanographic settings (e.g., Saino and Hattori, 1987; Altabet, 1988; Wu et al., 1999), caused by preferential release of  $^{15}\text{N}$  depleted compounds during microbial degradation (Macko et al., 1986). In their analysis, Mintenbeck et al. (2007) excluded facultative predators of zooplankton such as octocorals. The ability of some octocorals (Lewis, 1982; Coma et al., 1994; Orejas et al., 2003) and *Flabellum* (Buhl-Mortensen et al., 2007) to consume zooplankton may partly explain the absence of depth-related trends in our study. On the other hand, Antarctic and northwest Atlantic waters differ in the type of POM available to suspension feeders. Antarctic waters are characterised by low productivity, flagellate dominated plankton communities (Hewes et al., 1985; Nöthig et al., 1991). The small particles produced by these communities remain in suspension for long periods of time, thus becoming  $^{15}\text{N}$  enriched with depth. Antarctic suspension feeders largely feed on these small particles (Gili et al., 2001; Orejas et al., 2003), so they too become  $^{15}\text{N}$  enriched with depth (Mintenbeck et al., 2007). Northwest Atlantic slope waters are characterised by blooms of large phytoplankton (Longhurst, 2001). Consequently, there is a larger flux of fast sinking and sedimenting particles which undergo negligible change in  $\delta^{15}\text{N}$  during vertical transport (Altabet, 1988; Wu et al., 1999). The situation here is probably similar to coral mound communities in the northeast Atlantic, where labile material consisting of intact phytoplankton remains and fecal pellets was sampled at ~1000 m depth (Kiriakoulakis et al., 2004). Feeding on recently exported, sinking and/or resuspended POM would explain the lack of depth trends in coral  $\delta^{15}\text{N}$ .

Radiocarbon measurements also support a diet of recently exported POM (Griffin and Druffel, 1989; Roark et al., 2006). Suspended POM below the mixed layer is typically thousands of radiocarbon years old (Bauer et al., 2002). In contrast, we have measured the presence of recent, nuclear bomb-produced (i.e., post-1958) radiocarbon in every gorgonian and antipatharian species studied to date (*Primnoa*, *Paragorgia*, *Paramuricea*,

*Keratoisis*, *Acanella*, and *Bathypathes*) (Sherwood et al., 2005b, 2007). This indicates that pulses of more labile, sinking POM, and subsequent resuspension, are more important to cold-water coral nutrition than the highly degraded and nutrient poor suspended POM found at depth.

#### 4.3. Inter-regional variation in stable isotope composition

Since the tissues of cold-water corals are derived ultimately from recently exported POM, stable isotope values have the potential to track surface water processes such as isotopic composition of primary producers across oceanographic gradients (Heikoop et al., 2002; Sherwood et al., 2005a). Values of  $\delta^{13}\text{C}$  increased slightly (<1‰) from Hudson Strait to Grand Banks, although the effect was statistically significant only for *Duva*, *Acanella* and Pennatulacea. This pattern is consistent with lower values of phytoplankton  $\delta^{13}\text{C}$  in colder, high latitude waters, relating to higher concentrations of dissolved  $\text{CO}_2$  (Rau et al., 1989). There were no significant differences in coral  $\delta^{15}\text{N}$  between the Hudson Strait, Labrador Slope or Grand Banks. All three regions lie along the main axis of the southward flowing Labrador Current, which extends to >1000 m water depth (Lazier and Wright, 1993). The Grand Banks is also partially influenced by Gulf Stream-derived waters at the surface. Primary production is more light-limited at Hudson Strait and Labrador Slope and more nutrient-limited at the southern Grand Banks (Afanasyev et al., 2001). For  $\delta^{15}\text{N}$ , we expected lower values at the northern sites, where  $\text{NO}_3$  is less limiting, because phytoplankton discriminate against  $^{15}\text{N}$  (Needoba et al., 2003). Conversely, we expected higher values at the southern Grand Banks, where  $\text{NO}_3$  is more limiting, with the  $\delta^{15}\text{N}$  of phytoplankton converging on that of  $\text{NO}_3$ . This system may be more complicated, possibly because of different phytoplankton assemblages at the northern and southern regions (Longhurst, 2001), perhaps with different isotopic fractionation effects (Needoba et al., 2003). Another confounding influence may arise from entrainment of Gulf Stream-derived  $\text{NO}_3$  at the southern Grand Banks, perhaps of a lower  $\delta^{15}\text{N}$  signature as observed in the Sargasso Sea (Knapp et al., 2005).

#### Acknowledgements

We gratefully acknowledge the fisheries observers and the officers and crews of the Canadian Coast Guard Ships *Teleost* and *Wilfred Templeman* for providing samples. We also thank Kent Gilkinson for logistical support, Alison Pye for assisting with stable isotope analysis, Graham Sherwood for sharing isotope data on Newfoundland and Labrador fish and invertebrates and for valuable discussions. The manuscript was improved by comments from two anonymous reviewers. This work was supported by the Fisheries and Oceans Canada IGP funds, an NSERC Discovery Grant to EE, and an NSERC postdoctoral fellowship to OAS.

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