Volume 56 Number 3 March 2009 ISSN 0967-0637

ELSEVIER

DEEP-SEA RESEARCH
PART I
Oceanographic Research Papers

Editor:
Michael P. Bacon
Woods Hole, MA, USA

www.elsevier.com/locate/dsri

Deep-Sea Research I 56 (2009) 408–424

Contents lists available at ScienceDirect

Deep-Sea Research I

journal homepage: www.elsevier.com/locate/dsri

Trophic relationships along a bathymetric gradient at the deep-sea observatory HAUSGARTEN

Melanie Bergmann *, Jennifer Dannheim [1], Eduard Bauerfeind, Michael Klages

Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, D-27570 Bremerhaven, Germany

ARTICLE INFO

Article history:
Received 16 April 2008
Received in revised form
16 October 2008
Accepted 21 October 2008
Available online 5 November 2008

Keywords:
Arctic
Deep sea
Trophic level
Food web
Megafauna
Nitrogen stable isotope
Deposit feeder
Suspension feeder

ABSTRACT

Deep-seafloor communities, especially those from the ice-covered Arctic, are subject to severe food limitation as the amount of particulate organic matter (POM) from the surface is attenuated with increasing depth. Here, we use naturally occurring stable isotope tracers (δ^{15}N) to broaden our rudimentary knowledge of food web structure and the response of benthic organisms to decreasing food supplies along the bathymetric transect (~1300–5600 m water depth) of the deep-sea observatory HAUSGARTEN. Encompassing five trophic levels, the HAUSGARTEN food web is among the longest indicating continuous recycling of organic material typical of food-limited deep-sea ecosystems. The δ^{15}N signatures ranged from 3.0‰ for Foraminifera to 21.4‰ (±0.4) for starfish (*Poraniomorpha tumida*). The majority of organisms occupied the second and third trophic level. Demersal fish fed at the third trophic level, consistent with results from stomach contents analysis. There were significant differences in the δ^{15}N signatures of different functional groups with highest δ^{15}N values in predators/scavengers (13.2±0.2‰) followed by suspension feeders (11.2±0.2‰) and deposit feeders (10.2±0.3‰). Depth (= increasing food limitation) affected functional groups in different ways. While the isotopic signatures of predators/scavengers did not change, those of suspension feeders increased with depth, and the reverse was found for deposit feeders. In contrast to the results of other studies, the δ^{15}N signatures in POM samples obtained below 800 m did not vary significantly with depth indicating that changes in δ^{15}N values are unlikely to be responsible for the depth-related δ^{15}N signature changes observed for benthic consumers. However, the δ^{15}N signatures of sediments decreased with increasing depth, which also explains the decrease found for deposit feeders. Suspension feeders may rely increasingly on particles trickling down the HAUSGARTEN slope and carrying higher δ^{15}N signatures than the decreasing POM supplies, which elevates the δ^{15}N value of their tissues. Our results imply that a depth-stratified approach should be taken to avoid a misinterpretation of data obtained at different depths.

1. Introduction

Most deep-sea ecosystems rely on the vertical particle flux from the euphotic zone to the seafloor, and on particles that are transported along the slope (Klages et al., 2003). Large food particles ('food falls') such as mammal carcasses, fish, and large invertebrates may also play a significant role in the vertical carbon flux to the seafloor (Smith, 1985; Jones et al., 1998; Klages et al.,

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* Corresponding author. Tel.: +49 471 4831 1739; fax: +49 471 4831 1776.

E-mail address: Melanie.Bergmann@awi.de (M. Bergmann).

[1] Present address: Institute of Marine Research, PO Box 6404, 9294 Tromsø, Norway.

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doi:10.1016/j.dsr.2008.10.004

2001; Soltwedel et al., 2003). Although the deep seafloor is considered the world's largest sink for biogenic carbon, only 1–10% of the material produced at the surface reaches the bottom (Klages et al., 2003; De La Rocha and Passow, 2007), as particles are exposed to biodegradation during sedimentation. Biodegradation also affects the biochemical properties of POM (particulate organic matter) reaching the sea bed (Rau et al., 1990; Mintenbeck et al., 2007). Deep-seafloor communities are thus subject to severe energy limitation (Gage and Tyler, 1991). It is still poorly understood how the deep-sea community is sustained despite the restricted energy input from the water column (Smith, 1987; Bailey et al., 2007). In general, most deep-sea organisms are deposit feeders (Jumars and Wheatcroft, 1989; Iken et al., 2001). Although our knowledge about the feeding ecology of benthic deep-sea species has expanded, few studies have explored the overall structure of deep-sea food webs (Iken et al., 2001; Polunin et al., 2001; Sahling et al., 2003).

Still less is known about deep-sea environments from polar regions which are frequently covered by ice and are thus even less accessible (Iken et al., 2005; Mintenbeck et al., 2007). Along with phytoplankton, which is the main source of production in open oceanic waters, ice algae also contribute to the net primary production in the Arctic (McMahon et al., 2006; Søreide et al., 2006; Tamelander et al., 2006), but we currently do not know what quantities reach the deep seafloor and to what extent they subsidise the fauna. Productivity is low because the annual sunlight cycle and sea ice limit the light available to primary producers. In addition, the deep Arctic is—like other regions of the ocean—characterised by a great retention of carbon in the twilight zone (Wassmann et al., 2003; Buesseler et al., 2007) further reducing food availability compared to open ocean waters (Klages et al., 2003; Sakshaug, 2003).

Climate change is the prominent global environmental threat of the 21st Century (IPCC, 2007) and will have severe impacts on the carbon flux to the deep seafloor (Smith et al., 2008), especially in the Arctic (Grebmeier et al., 2006). However, current predictions carry high levels of uncertainty as even crucial baseline information is scarce. It was in this context that the first and by now only long-term deep-sea observatory at high latitude, 'HAUSGARTEN', was established in the eastern Fram Strait (Soltwedel et al., 2005). Previous research along the bathymetric transect of HAUSGARTEN (1200–5600 m) has shown a decrease of organic carbon content, phytodetrital matter (Soltwedel et al., 2005) and bacterial abundance and viability (Quéric et al., 2004) with increasing water depth. Likewise, there was a stepwise decrease in meiofaunal densities and a decrease in macro- and megafaunal densities at nearby HAUSGARTEN stations as a function of depth (Jaeckisch, 2004; Włodarska-Kowalczuk et al., 2004; Hoste et al., 2007).

The main objective of this study was to assess deep-sea food web structure along a bathymetric gradient at a high northern latitude location using the stable isotope approach. This enables us to assess how decreasing food availability affects food web structure, as the food supply at HAUSGARTEN decreases with increasing depth. In the long run, this may allow us to fathom how changes at one level may impinge on other compartments of the ecosystem.

2. Material and methods

2.1. Study area

All samples were taken at 'HAUSGARTEN', a deep-sea observatory at high latitude established in the eastern Fram Strait, west of Svalbard at 79°N in 1999 (Fig. 1). HAUSGARTEN consists of nine stations along a bathymetric gradient from the upper slope of the Svalbard Margin (1200 m) to the Molloy Deep (5600 m) and of a latitudinal transect of seven stations along the 2500 m isobath starting at the margin of the sea ice zone (Soltwedel et al., 2005). While the shallower stations (1200–3000 m) are located along a gentle slope, those beneath are found on a steep slope (Hoste et al., 2007). Samples taken along these transects annually since 2000 have been used to determine a variety of faunal and environmental parameters.

The HAUSGARTEN area is affected by warm Atlantic waters transported by the West Spitsbergen Current in the upper 500 m, which is fed by the North Atlantic Current (Schauer et al., 2008) such that the area is ice-free most of the year. Part of the HAUSGARTEN region is covered by ice during winter, but ice can also be present during summer (Bauerfeind et al., in revision). Below the warm Atlantic water layer, there are low-temperature waters modified by polar water masses (Schlichtholz and Houssais, 2002).

2.2. Stable isotope analysis

The utility of the stable isotope approach lies in the fact that stable isotope ratios in the proteins of consumers reflect those of the proteins in their diet in a predictable manner. Conventionally expressed as $\delta^{15}N$ (‰), the ratio of the nitrogen isotopes ^{15}N to ^{14}N generally exhibits a stepwise enrichment between 2.5 and 5‰ per trophic step (Bearhop et al., 2004). The ratio of ^{13}C to ^{12}C ($\delta^{13}C$) indicates the distance to the primary carbon source. Among other things, it is affected by an organism's lipid content (Mintenbeck et al., 2008). Stable isotope ratios can thus be used to reconstruct food webs and determine the trophic level of consumers. As we did not extract lipids prior to analyses we focus on $\delta^{15}N$.

2.3. Sampling procedure

Most samples were taken by the research ice breaker *Polarstern* (Table 1). To assess the $\delta^{15}N$ of primary producers, we took water samples in August 2005 at HAUSGARTEN station IV (Table 1) by a CTD/rosette system from 10, 20, 30 and 50 m water depth. A volume of 0.5–2 l seawater was filtered onto pre-combusted (500 °C/12 h) glass-fibre filters (Whatman GF/F, ∅25 mm) which were stored at −20 °C. Prior to analysis, the filters were dried (60 °C/12 h), pelletised and stored in an exsiccator.

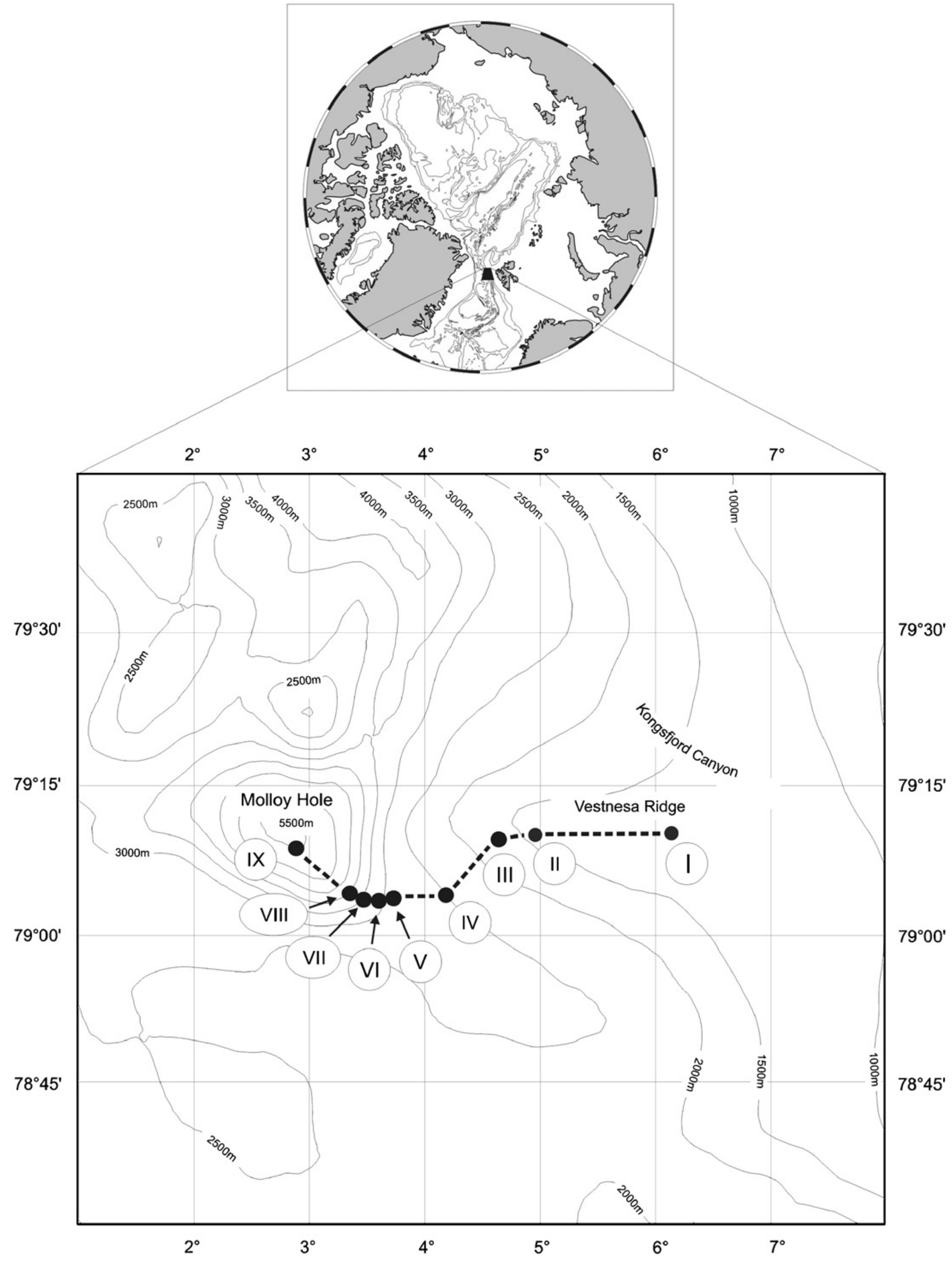

Fig. 1. Location of HAUSGARTEN and map of sampling stations HG I-IX distributed along the bathymetric transect (1200–5600 m).

Deep-sea fauna rely chiefly on particles sinking from the productive surface waters to the sea floor as their main source of carbon. To determine a δ^{15}N reference for benthic species, analyses of δ^{15}N were performed on POM collected by two year-round moored time-series sediment traps (800 m water depth and 200 m above bottom) in 2002–2003 and a sediment trap attached to a benthic lander (2.5 m above bottom) at HAUSGARTEN IV in 2004/2005. The samples were poisoned *in situ* with mercury chloride (0.14%). After retrieval of the traps, the samples were refrigerated and divided by a wet-splitting procedure with a rotating splitter after removal of the swimmers under a dissecting microscope (Bodungen et al., 1991). Sub-samples were then filtered

Table 1
List of stations sampled for food-web analysis in chronological order. (Lat) latitude, (Lon) longitude.

Expedition	Station No	Station	Position Lat (N)	Position Lon (E)	Depth (m)	Date (dd/mm/yy)	Sampling gear
ARKXVIII/1b	PS62/179-2	HG IV	79°1.04′	4°19.77′	2593	07/08/02–22/07/03	Sediment trap mooring
ARKXX/1a	PS66/103-1	HG I	79°8.97′	5°56.35′	1323	07/07/04	Agassiz trawl
ARKXX/1a	PS66/118-1	HG IV	79°9.75′	3°52.21′	2377	09/07/04	Agassiz trawl
ARKXXI/1b	PS68/240-1	HG IV	79°0.81′	4°20.51′	2590	12/07/04–19/08/05	Sediment trap mooring
ARKXXI/1b	PS68/238-4	HG IV	79°4.55′	4°6.52′	2504	19/08/05	Bottom lander
ARKXXI/1b	PS68/245-1	HG IV	79°3.79′	4°10.63′	2471	20/08/05	CTD/rosette
ARKXXI/1b	PS68/247-1	HG V	79°5.67′	3°38.68′	3072	20/08/05	Agassiz trawl
ARKXXI/1b	PS68/247-2	HG V	79°5.67′	3°38.68′	3072	20/08/05	Agassiz trawl
ARKXXI/1b	PS68/256-1	HG VII	79°4.10′	3°29.41′	3870	22/08/05	Agassiz trawl
ARKXXI/1b	PS68/260-1	HG VI	79°5.81′	3°33.27′	3576	22/08/05	Agassiz trawl
ARKXXI/1b	PS68/270-1	HG VI	79°5.19′	3°34.82′	3430	24/08/05	Bottom lander
ARKXXI/1b	PS68/272-2	HG III	79°5.31′	4°46.36′	1913	24/08/05	Agassiz trawl
ARKXXI/1b	PS68/276-1	HG II	79°7.24′	4°58.30′	1546	25/08/05	Agassiz trawl
ARKXXI/1b	PS68/278-1	HG IV	79°4.84′	4°25.05′	2293	26/08/05	Bottom lander
AWI-ROV2005	Victor-255	HG IX	79°06.08	3°06.71′	5375	20/09/05	ROV slurp gun
AWI-ROV2005	Victor-256	HG IV	79°04.7′	4°08.1′	2467	24/09/05	ROV slurp gun
ARKXXII/1c	PS70/ 200-1	HGIV	79°44.19′	4°25.66′	2644	17/07/07	Multiple corer
ARKXXII/1c	PS70/159-1	HGII	79°7.82′	4°53.65′	1565	11/07/07	Multiple corer
ARKXXII/1c	PS70/163-1	HGI	79°8.07′	5°59.45′	1304	12/07/07	Multiple corer
ARKXXII/1c	PS70/169-1	HGIV	79°4.42′	4°14.35′	2414	12/07/07	Bottom water sampler
ARKXXII/1c	PS70/174-1	HGIV	78°36.54′	5°3.82′	2354	13/07/07	Multiple corer
ARKXXII/1c	PS70/175-1	HGIV	78°46.85′	5°19.98′	2477	14/07/07	Multiple corer
ARKXXII/1c	PS70/183-1	HGV	79°3.92′	3°41.86′	2990	15/07/07	Multiple corer
ARKXXII/1c	PS70/184-1	HGVI	79°3.60′	3°34.81′	3548	15/07/07	Multiple corer
ARKXXII/1c	PS70/191-2	HGI	79°7.98′	6°5.73′	1292	18/07/07	Chamber lander
ARKXXII/1c	PS70/206-1	HGIV	79°5.77′	4°10.45′	2400	20/07/07	Chamber lander
ARKXXII/1c	PS70/211-1	HGVII	79°3.59′	3°28.50′	4065	19/07/07	Multiple corer
ARKXXII/1c	PS70/212-1	HGVIII	79°3.79′	3°18.80′	5140	19/07/07	Multiple corer
ARKXXII/1c	PS70/219-1	HGIX	79°7.89′	2°50.23′	5586	22/07/07	Chamber lander

onto pre-combusted Whatman GF/F filters and treated in the same way as above.

To obtain the δ^{15}N of deposit feeders' food source (sediments, organic matter and associated organisms) bulk sediment samples from the uppermost 5 cm were collected with a multiple corer, the benthic chambers of a lander and a bottom water sampler at different depths in summer 2007 (Table 1). Sediment samples and biota were stored at $-80\,^{\circ}$C until they were freeze-dried ($\geqslant$4 h) and thereafter stored in an exsiccator. The ground samples were treated with 1 mol l^{-1} hydrochloric acid to remove carbonates (Jacob et al., 2005), re-dried at 60 °C and ground to a fine powder by mortar and pestle.

To obtain megafaunal samples a 30-min tow was made at a speed of 1–1.5 knots with an Agassiz trawl (315 cm beam width, 110 cm beam height, 10 kg weight attached to cod-end of 20 mm mesh size) at HAUSGARTEN I-VII in 2004 and 2005 (Table 1). During sorting of the catch, all fish and megafauna were stored on ice. Where possible, muscle tissue of $\geqslant$5 megafaunal individuals per taxon caught were sampled with care taken to avoid bones, intestines and gonads. However, small macrofaunal organisms had to be sampled whole and sometimes pooled to obtain sufficient biomass for isotopic analysis (Table 2). A reference sample was preserved in a 4% formaldehyde solution for identification by different taxonomic experts (see acknowledgements).

Furthermore, two fish traps fitted to the tripod of an autonomous benthic lander were deployed for ~48 h. A baited funnel trap was deployed within each fish trap to prevent the fish from feeding on fish bait and to separate them from trapped amphipods. All fish and amphipods were sampled as described above. More samples were collected from *RV L'Atalante* in September 2005 with the hydraulic slurp gun of the remotely operated vehicle '*Victor 6000*' at HAUSGARTEN IV and IX (Table 1).

Stable isotope analysis was done by isotope-ratio mass spectrometry (Thermo/Finnigan Delta Plus at GeoBioCenterLMU, University of Munich). Gaseous standards (N_2 and CO_2, respectively) were calibrated against atmospheric nitrogen (AIR) and a PeeDee Belemite standard (PDB) for carbon. Analytical error was $\pm$0.15‰ based on the standard deviation of replicates of a peptone standard.

2.4. Data analysis

Stable isotope ratios are expressed in the conventional δ notation as parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{\mathrm{sample}}/R_{\mathrm{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio ^{13}C/^{12}C or ^{15}N/^{14}N. We used a δ^{15}N enrichment factor of 3.8‰ per trophic level to keep our results comparable with those from previous Arctic food web studies (Hobson and Welch, 1992; Adlandsvik et al., 2004; Iken et al., 2005):

$$\mathrm{TL}_i = (\delta^{15}\mathrm{N}_i - \delta^{15}\mathrm{N}_{\mathrm{ref}})/3.8$$

where TL_i is the trophic level of species i, $\delta^{15}\mathrm{N}_i$ is the mean species δ^{15}N and $\delta^{15}\mathrm{N}_{\mathrm{ref}}$ is the mean δ^{15}N of the food web baseline (POM).

Table 2
Mean stable isotope signatures of taxa from different depths..

Taxonomic group	Taxon	Station No.	Depth (m)	Sampling	Feeding type	*n*	$\delta^{13}C$ (‰)	SEM	$\delta^{15}N$ (‰)	SEM
Foraminifera	Foraminifera	PS68/276-1	1500	7 whole ind.	n.d.	2	−26.66	1.93	4.1	1.1
Porifera										
Hexactinellida	*Caulophacus arcticus*	PS66/118-1	2400	Section	SF	5	−0.25	0.43	10.6	1.7
Hexactinellida	*Caulophacus arcticus*	PS68/260-1	3600	Section	SF	3	−21.22	0.88	12.2	1.8
Demospongiae	Axinellidae	PS68/240-1	2400	Section	SF	2	−23.02	0.12	7.84	0
Demospongiae	*Cladorhiza gelida*	PS68/272-2	1900	Section	SF	3	−19.5	0.37	9.12	0.6
Demospongiae	*Cladorhiza gelida*	PS66/118-1	2400	Section	SF	5	−18.16	0.17	9.55	0.1
Demospongiae	*Cladorhiza gelida*	PS68/247-1	3100	Section	SF	3	−21.16	1.01	11.2	0.1
Demospongiae	*Cladorhiza gelida*	Victor-255	5400	Section	SF	2	−0.33	0.67	8.57	0.5
Demospongiae	*Esperiopsis* sp.	PS68/276-1	1500	Section	SF	1	−21.32		11.3	
Demospongiae	*Esperiopsis* sp.	PS68/272-2	1900	Section	SF	2	−19.46	1.96	16.6	0.4
Demospongiae	*Lissodendoryx complicata*	PS68/247-1	3100	Section	SF	3	−0.48	0.23	13.7	0.4
Demospongiae	*Radiella sol*	PS68/247-1	3100	Section	SF	3	−0.51	0.58	12.4	1.2
Demospongiae	*Tentorium semisuberites*	PS68/272-2	1900	1 whole ind.	SF	4	−21.8	0.52	13	0.9
Demospongiae	*Thenea abyssorum*	PS68/247-1	3100	1 whole ind.	SF	5	−0.32	0.15	12.1	0.8
Cnidaria										
Hydrozoa	Thecate hydroid	PS68/240-1	2400	Section	SF	1	−23.1		7.62	
Hydrozoa	Turbulariidae cf. *Bouillonia cornucopia*	PS68/238-4	2400	1 whole ind.	SF	4	−22.68	0.11	6.25	0.4
Alcyonacea	*Gersemia rubiformis*	PS68/276-1	1500	Section	SF	2	−21.71	0.93	8.88	1.8
Alcyonacea	*Gersemia rubiformis*	PS68/272-2	1900	Section	SF	5	−21.88	0.16	11.2	0.3
Actiniaria	Acontiaria gen. et sp. nov.	PS66/118-1	2400	Septum	SF	5	−21.55	0.85	10.8	0.6
Actiniaria	Hormathiidae cf. *Amphianthus* sp.	PS68/256-1	3900	1 whole ind.	SF	3	−21.97	0.29	12.2	0.3
Actiniaria	*Kadosactis rosea*	PS68/260-1	3600	Septum	SF	3	−19.1	0.23	15.3	0.4
Actiniaria	*Amphianthus* sp. 1	PS68/260-1	3600	Septum	SF	1	−21.82		11.4	
Actiniaria	*Amphianthus* sp. 2	PS68/260-1	3600	Septum	SF	5	−22.09	0.35	11.3	0.3
Actiniaria	*Amphianthus* sp. 4, Isophelliidae gen.1	PS68/272-2	1900	4 pooled	SF	2	−22.61	0.29	9.77	1.8
Actiniaria	*Amphianthus* spp., *Bathyphellia margaritacea*	PS68/247-1	3100	Septum	SF	4	−0.69	0.26	12.7	0.5
Actiniaria	*Bathyphellia margaritacea*	PS68/260-1	3600	Septum	SF	9	−21.44	0.16	11.2	0.2
Actiniaria	*Bathyphellia margaritacea*	PS68/256-1	3900	2 whole ind.	SF	7	−21.92	0.25	11.9	0.2
Actiniaria	*Bathyphellia margaritacea*	Victor-255	5400	Septum	SF	5	−19.61	0.26	16.6	0.2
Actiniaria	Isophelliidae gen. 1	PS68/272-2	1900	Septum	SF	2	−0.83	0.03	12.8	0.1
Errect biota	Hydroid or sponge	PS68/260-1	3600	Section	SF	1	−21.61		8.5	
Nemertea	Nemertea	PS68/276-1	1500	Posterior part	P/S	4	−19.01	0.67	12.4	2
Priapulidae	*Priapulus caudatus*	PS68/276-1	1500	Section	DF	1	−17.17		13.8	

Mollusca										
Gastropoda	*Cryptonatica affinis*	PS68/276-1	1500	1 whole ind.	DF	2	−19.06	0.65	9.7	0.3
Gastropoda	*Mohnia mohni, Tacita danielsseni*	PS66/103-1	1300	Section of foot	P/S	2	−18.22	0.02	13.4	0.5
Gastropoda	*Mohnia mohni, Tacita danielsseni*	PS68/276-1	1500	Section of foot	P/S	2	−18.95	0.12	10.9	0.2
Gastropoda	*Mohnia mohni, Tacita danielsseni*	PS68/272-2	1900	Section of foot	P/S	6	−0.02	0.11	10.7	0.2
Gastropoda	*Mohnia mohni, Tacita danielsseni*	PS66/118-1	2400	Section of foot	P/S	5	−17.99	0.33	13.2	0.1
Gastropoda	*Mohnia mohni, Tacita danielsseni*	PS68/247-1	3100	Section of foot	P/S	5	−19.69	0.33	10.6	0.7
Bivalvia	*Bathyarca frielei*	PS68/276-1	1500	2 whole ind.	SF	3	−0.08	0.7	10.9	1.3
Bivalvia	*Katadesmia kolthoffi*	PS68/260-1	3600	1 whole ind.	DF	8	−0.4	0.16	8.29	0.5
Bivalvia	*Katadesmia kolthoffi*	PS68/256-1	3900	1 whole ind.	DF	2	−19.7	0.03	10.5	0.1
Scaphopoda	*Siphonodentalium laubieri*	PS68/276-1	1500	3–4 whole ind.	DF	5	−0.64	0.08	10.8	0.1
Annelida										
Polychaeta	*Bylgides* cf. *groenlandica*	PS68/272-2	1900	Posterior part	P/S	2	−19.76	0.21	11.8	0.5
Polychaeta	*Lumbrineris* sp.	PS68/276-1	1500	Posterior part	n.d.	1	−19.81		12.5	
Polychaeta	*Nereis* cf. *gracilis*	PS68/272-2	1900	Posterior part	P/S	1	−17.97		15.8	
Polychaeta	*Praxillura longissima*	PS68/276-1	1500	1 whole ind.	DF	1	−21.3		15.1	
Polychaeta	Polychaeta sp. 1	PS68/247-1	3100	1 whole ind.	n.d.	1	−16.98		14.4	
Polychaeta	Polychaeta sp. 2	PS68/260-1	3600	1 whole ind.	n.d.	1	−18.57		15.2	
Polychaeta	Polychaeta sp. 3	PS68/272-2	1900	1 whole ind.	n.d.	1	−22.69		7.74	
Polychaeta	Polychaeta sp. 4	PS68/276-1	1500	Posterior part	n.d.	1	−20.54		9.74	
Polychaeta	Polychaeta sp. 5	PS68/272-2	1900	3 whole ind.	n.d.	8	−19.53	0.18	10.8	0.1
Polychaeta	Polychaeta sp. 6	PS68/276-1	1500	1 whole ind.	n.d.	2	−20.78	0.04	11.1	0
Echiurida	*Hamingia arctica*	PS66/103-1	1300	Body wall of 1	DF	5	−18.01	1.07	12.9	0.8
Echiurida	*Hamingia arctica*	PS68/276-1	1500	Body wall of 1	DF	2	−16.04	0.58	14.7	0.1
Arthropoda										
Pantopoda	*Ascorhynchus abyssi*	PS68/260-1	3600	1 whole ind.	DF	1	−21.55		9.65	
Pantopoda	*Colossendeis proboscidea*	PS66/103-1	1300	4 legs of various ind.	DF	3	−18.04	0.03	12.2	0.1
Pantopoda	*Colossendeis proboscidea*	PS68/276-1	1500	4 legs of various ind.	DF	2	−19.71	1.83	9.52	2.7
Copepoda	Calanoida	Victor-256	2400	1 whole ind.	HBPF	2	−0.09	0.74	10.7	1.6
Cirripedia	*Verum striolatum*	PS68/276-1	1500	M	SF	2	−21.45	0.13	11.3	0.1
Cirripedia	*Verum striolatum*	PS68/272-2	1900	M	SF	1	−22.18		10	
Mysida	*Boreomysis* sp.	PS68/247-1	3100	Abdomen of 1	HBPF	1	−0.58		14.2	
Amphipoda	Corophiidae	PS68/276-1	1500	1 whole ind.	n.d.	1	−21.18		9.15	
Amphipoda	*Eurythenes gryllus*	PS68/278-1	2400	Gutted telson of 1	P/S	8	−22.08	0.12	14.8	0.6
Amphipoda	*Eurythenes gryllus*	PS68/247-1	3100	Gutted telson of 1	P/S	3	−22.76	0.37	12.8	0.4
Amphipoda	*Eurythenes gryllus*	PS68/270-1	3600	Gutted telson of 1	P/S	4	−21.65	0.33	12.7	0.7
Amphipoda	*Halirages quadridentatus*	Victor-255	5400	Gutted telson of 1	P/S	6	−21.31	0.15	10	0.2
Amphipoda	*Haploops* sp.	PS68/272-2	1900	1 whole ind.	SF	6	−22.14	0.14	8.7	1
Amphipoda	*Leptamphopus* sp.	Victor-256	2400	3 whole ind.	DF	2	−0.99	0.15	7.63	0.5
Amphipoda	*Liljeborgia fissicornis*	PS68/276-1	1500	1 whole ind.	P/S	1	−19.75		10.9	
Amphipoda	Lysianassidae cf. *tryphosa*	Victor-255	5400	3 whole ind.	P/S	3	−23.36	0.18	14.2	0.2
Amphipoda	*Amphipoda* sp. 1	PS68/272-2	1900	1 whole ind.	n.d.	2	−21.89	0.95	8.41	0.9
Amphipoda	*Amphipoda* sp. 2	PS68/276-1	1500	4 whole ind.	n.d.	1	−21.54		6.08	
Amphipoda	Amphipoda sp. 3	PS68/272-2	1900	1 whole ind.	n.d.	1	−21.11		7.64	
Amphipoda	*Unciola* sp.	PS68/276-1	1500	2 whole ind.	DF	2	−21.14	0.06	5.63	0.7
Cumacea	*Diastylis* spp.	PS68/276-1	1500	1 whole ind.	DF	3	−21.59	0.16	5.4	0.3
Isopoda	*Caecognathia stygia*	PS68/276-1	1500	3 whole ind.	DF	1	−21.94		9.72	

Table 2 (*continued*)

Taxonomic group	Taxon	Station No.	Depth (m)	Sampling	Feeding type	*n*	δ^{13}C (‰)	SEM	δ^{15}N (‰)	SEM
Isopoda	*Caecognathia stygia*	PS68/272-2	1900	1 whole ind.	DF	2	−22.08	0.04	10.4	0.5
Isopoda	*Mesidothea megalura*	PS68/276-1	1500	Abdomen of 1	P/S	3	−0.19	0.03	10.7	0.2
Isopoda	*Mesidothea megalura*	PS68/272-2	1900	Abdomen of 1	P/S	8	−0.07	0.28	10.1	0.4
Isopoda	*Mesidothea megalura*	PS66/118-1	2400	Abdomen	P/S	8	−19.59	0.35	11.3	0.5
Isopoda	*Mesidothea megalura*	PS68/247-1	3100	Abdomen of 1	P/S	1	−19.58		10.5	
Decapoda	*Bythocaris* spp.	PS66/103-1	1300	Gutted abdomen of 1	P/S	5	−18.26	0.08	15.2	0.2
Decapoda	*Bythocaris* spp.	PS68/272-2	1900	Gutted abdomen of 1	P/S	6	−19.62	0.17	13	0.2
Decapoda	*Bythocaris* spp.	PS66/118-1	2400	Gutted abdomen of 1	P/S	5	−19.41	0.24	13.2	0.2
Decapoda	*Bythocaris* spp.	PS68/260-1	3600	Gutted abdomen of 1	P/S	6	−19.7	0.19	13.8	0.1
Decapoda	*Bythocaris* spp.	PS68/256-1	3900	Gutted abdomen of 1	P/S	3	−0.49	0.07	13.8	0.1
Echinodermata										
Crinoidea	*Bathycrinus* cf. *carpenteri*	PS68/272-2	1900	3 pooled	SF	3	−23.12	0.22	8.28	0.9
Crinoidea	*Bathycrinus* cf. *carpenteri*	PS66/118-1	2400	5 pooled	SF	5	−22.17	0.25	10.4	0.7
Crinoidea	*Bathycrinus* cf. *carpenteri*	PS68/247-1	3100	5 pooled	SF	1	−22.84		11	
Asteroidea	*Bathybiaster vexillifer*	PS66/103-1	1300	Arm of 1	P/S	5	−17.1	0.2	15.8	0.1
Asteroidea	*Bathybiaster vexillifer*	PS68/276-1	1500	2 arms of 1	P/S	8	−17.08	0.18	16.8	0.3
Asteroidea	*Bathybiaster vexillifer*	PS68/272-2	1900	Arm of 1	P/S	2	−17.05	0.62	17	0.4
Asteroidea	*Hymenaster pellucidus*	PS68/276-1	1500	3 arms of 1	P/S	3	−19.49	0.24	13.1	0.7
Asteroidea	*Hymenaster pellucidus*	PS68/272-2	1900	Arm of 1	P/S	3	−19.89	0.11	11.9	0.7
Asteroidea	*Hymenaster pellucidus*	PS66/118-1	2400	1 arm	P/S	1	−19.54		24.6	
Asteroidea	*Poraniomorpha tumida*	PS68/247-1	3100	Arm of 1	P/S	4	−17.27	0.7	21.3	0.4
Ophiuroidea	*Ophiocten* cf. *gracilis*	PS66/103-1	1300	15 arms of various ind.	DF	5	−0.14	0.35	12.6	0.3
Ophiuroidea	*Ophiocten* cf. *gracilis*	PS68/276-1	1500	5 arms	DF	6	−0.49	0.12	11	0.6
Holothuroidea	*Kolga hyalina*	PS68/247-1	3100	Body wall of 1	DF	3	−0.26	0.24	8.87	0.3
Holothuroidea	*Elpidia heckeri*	Victor-255	5400	Body wall of 1	DF	2	−22.24	0.91	5.98	0.9
Chordata										
Ascidiacea	Ascidiacea	PS68/276-1	1500	1 whole ind.	SF	1	−18.93		13.1	
Rajiformes	*Amblyraja hyperborea*	PS66/103-1	1300	m	P/S	1	−0.36		12.4	
Teleostei	*Gaidropsarus argentatus*	PS66/103-1	1300	m	P/S	1	−19.97		13	
Teleostei	*Lycodes frigidus*	PS68/272-2	1900	m	P/S	6	−19.3	0.12	13.6	0.1
Teleostei	*Lycodes frigidus*	Victor-256	2400	m	P/S	23	−0.66	0.2	12.4	0.2
Teleostei	*Lycodes frigidus*	PS68/247-2	3100	m	P/S	3	−19.34	0.29	14.1	0.2
Teleostei	*Lycodes frigidus*	PS68/260-1	3600	m	P/S	1	−19.83		14.6	
Teleostei	*Lycodes squamiventer*	PS66/103-1	1300	m	P/S	12	−18.59	0.06	13.9	0.1
Teleostei	*Lycodes squamiventer*	PS68/276-1	1500	m	P/S	5	−18.74	0.23	13.3	0.3
Teleostei	*Lycodonus flagellicauda*	PS68/276-1	1500	m	P/S	2	−19.92	0.14	13	0.6
Teleostei	Paralepididae	PS68/272-2	1900	m	Decomposing	1	−22.39		10.8	
Cetacea	Whale bone	Victor-255	5400	Section	Decomposed	6	−16.18	0.17	10.2	0.1

Food sources	POM (surface)	PS68/245-1	10	Filtrate	1	n.a.	6.03	
	POM (surface)	PS68/245-1	20	Filtrate	1	n.a.	4.66	
	POM (surface)	PS68/245-1	30	Filtrate	1	n.a.	5.1	
	POM (surface)	PS68/245-1	50	Filtrate	1	n.a.	4.55	
	POM (bottom)	PS66/134-1	2400	Filtrate	13	n.a.	4.43	0.2
	POM (bottom)	PS64/399-1	2200	Filtrate	19	n.a.	4.43	0.3
	Sediment	PS70/191-2	1292	Chamber	3	n.a.	5.28	
	Sediment	PS70/163-1	1304	Multiple corer	3	n.a.	5.69	0.28
	Sediment	PS70/159-1	1565	Multiple corer	3	n.a.	5.52	0.04
	Sediment	PS70/174-1	2354	Multiple corer	1	n.a.	5.86	
	Sediment	PS70/206-1	2400	Chamber	3	n.a.	5.26	0.13
	Sediment	PS70/169-1	2414	BWS	3	n.a.	5.43	0.02
	Sediment	PS70/175-1	2477	Multiple corer	1	n.a.	5.89	
	Sediment	PS70/200-1	2644	Multiple corer	3	n.a.	5.58	0.04
	Sediment	PS70/183-1	2990	Multiple corer	3	n.a.	5.21	0.05
	Sediment	PS70/184-1	3593	Multiple corer	3	n.a.	4.85	0.03
	Sediment	PS70/211-1	4065	Multiple corer	3	n.a.	4.77	0.07
	Sediment	PS70/212-1	5140	Multiple corer	3	n.a.	4.22	0.07
	Sediment	PS70/219-1	5586	Chamber	3	n.a.	5.41	0.04

Abbreviations: (SEM) standard error of the mean, (P/S) Predator/scavenger, (SF) suspension feeder, (DF) deposit feeder, (HBPF) hyperbenthic particle feeder, (n.d.) not defined, (n.a.) not available, (M) muscle tissue, (POM) particulate organic matter, (ind.) individual, (BWS) bottom water sampler.

Overall, the stable nitrogen and carbon content of 73 taxa, was analysed (430 samples in total, including POM and sediment samples). Based on information from the literature and advice from specialists, organisms were assigned to one of the following functional groups: predator/scavenger, suspension feeder, deposit feeder. If the taxonomic resolution was too low, or if no trophic information was available, the organisms were excluded from this analysis.

We tested for significant differences in the δ^{15}N signatures of different functional groups, phyla and organisms collected from different depths using analysis of variance (ANOVA) and Tukey's pairwise comparisons. We applied linear regression analysis to test if the δ^{15}N signatures of organisms varied as a function of depth. For all statistical analyses we used the MINITAB 14© package.

3. Results

3.1. General food web structure

The δ^{15}N values of POM from the euphotic zone were higher (mean $\delta^{15}\text{N} = 5.4 \pm 0.5$‰ SEM) than those recorded at 800 m depth (4.6 ± 0.3‰) and at the sea floor (4.4 ± 0.2‰). The δ^{15}N ratios of POM collected by sediment traps deployed at 800 m and above the sea bed were similar (ANOVA: $F_{(2,49)} = 0.16$, $p = 0.85$). The δ^{15}N values of sediments were slightly higher than most POM samples (Table 2). We used the mean δ^{15}N values of POM collected by bottom sediment traps as a baseline as we consider this a key source of food for benthic organisms.

There was a considerable range of δ^{15}N values in the food web sampled (Table 2): it ranged from 3.0‰ for Foraminifera to 21.4‰ for starfish (*Poraniomorpha tumida*). If we use the mean $\text{POM}_{\text{bottom}}$ value of 4.4‰ as a baseline and assume a progressive δ^{15}N enrichment of 3.8‰ per trophic step, the HAUSGARTEN food web encompassed five trophic levels (Fig. 2).

While the majority of deposit feeders (15 taxa) occupied the first and second trophic level (10.2 ± 0.3‰), most suspension feeders (25 taxa) fed at the second and third (11.2 ± 0.2‰) and most predators/scavengers (19 taxa) occupied the third trophic level (13.2 ± 0.2‰) (Fig. 2). There were significant differences in the δ^{15}N signatures between each of these groups (ANOVA, $F_{(2,358)} = 43.74$, $p < 0.001$).

Predators/scavengers had the highest range of δ^{15}N values (13.5‰) followed by suspension (11.4‰) and deposit (10.1‰) feeders.

All organisms except for Foraminifera were enriched in δ^{15}N relative to POM (Table 2). *Poraniomorpha tumida* was the only species to occupy the fifth trophic level with the highest mean δ^{15}N recorded (21.4 ± 0.4‰) followed by the anthozoan *Bathyphellia margaritacea* and the starfish *Bathybiaster vexillifer* (Table 2). The majority of organisms occupied the second and third trophic levels (Fig. 2). Cumaceans (*Diastylis* spp.), amphipods and hydrozoans had the lowest mean δ^{15}N (first trophic level). Molluscs occupied exclusively the second, and fish and rays occupied the third trophic level.

Table 2 shows that there was great variability in taxon/species isotopic enrichment: the range of δ^{15}N values exceeded two trophic levels in nemerteans and the sponge *Caulophacus arcticus* and one level in *Eurythenes gryllus*, *Haploops* sp., *Mesidothea megalura*, *Amphianthus* spp., *Colossendeis proboscidea*, *Gersemia rubiformis*, *Mohnia* spp., *Esperiopsis* sp., *Thenea abyssorum*, *Radiella sol*, *Tentorium semisuberites*, *Bathycrinus* cf. *carpenteri*, *Hamingia arctica*, *Bathyarca frielei*, *Katadesmia kolthoffi*, *Ophiocten* cf. *gracilis* and *Kolga hyalina*.

3.2. Bathymetric patterns

Regression analysis revealed that the δ^{15}N signatures of bottom sediments decreased with increasing water depth (Fig. 3). By contrast, the δ^{15}N signatures of all organisms taken together were not affected by depth (Fig. 4a). However, analyses of different feeding types indicate that the δ^{15}N signatures of suspension feeders increased with increasing depth (Fig. 4c). Increasing numbers of carnivorous sponges have been discovered recently, some of which are closely related to those sampled here. If sponges were excluded, however, the increase of δ^{15}N of suspension feeders with depth was even more pronounced ($\delta^{15}\text{N}_{\text{SF}} = 6.95 + 0.00147$ depth, $n = 81$, $r^2 = 0.38$, $p < 0.0001$). The δ^{15}N of sponges alone was not affected by depth ($\delta^{15}\text{N}_{\text{sponges}} = 11.87 - 0.00021$ depth, $n = 43$, $r^2 = 0.005$, $p < 0.0001$). By contrast, the δ^{15}N signatures of deposit feeders decreased as a function of depth (Fig. 4d). In turn, there was no significant relationship between depth and the δ^{15}N of predators/scavengers (Fig. 4d). The low r^2-values indicate a poor regression fit.

The δ^{15}N values of most species/taxa tested were not affected by depth. However, the δ^{15}N of *B. margaritacea* and *B. vexillifer* increased significantly with increasing depth, whereas they showed a significant decrease with increasing depth in *E. gryllus* (Fig. 5a, c, and i).

4. Discussion

Naturally occurring stable nitrogen isotopes have been used widely as tracers in marine food webs as they produce estimates of trophic position that simultaneously capture trophic interactions of the reticulate pathways of communities (Hobson and Wassenaar, 1999). The popularity of the approach to assessing individual species' ecology is due to the fact that conventional tools for dietary analyses are rather limited. While it cannot provide the taxonomic detail of stomach contents analysis and direct observation, it is less time-consuming, gives information on long-term feeding habits and organisms that macerate their prey beyond recognition (Sherwood and Rose, 2005). Although recent years have seen a considerable research effort in food web ecology using this method, few studies have considered depth-related changes in food webs. Our results indicate that most functional groups are affected by depth in a different way.

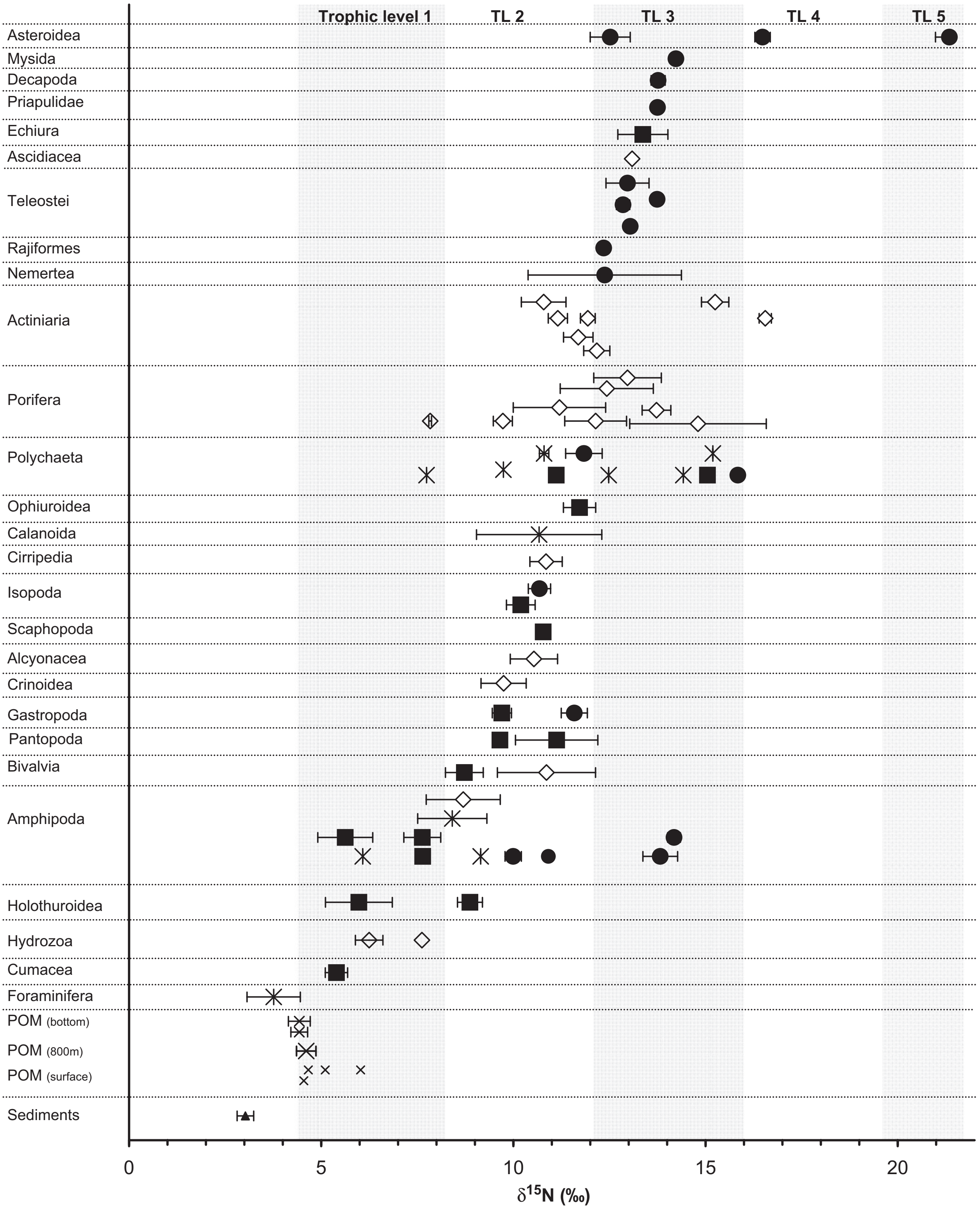

Fig. 2. Distribution of mean δ^{15}N signatures of sediments, POM and organisms from HAUSGARTEN by taxonomic groups. Trophic levels are indicated by grey shading in 3.8‰ enrichment steps using bottom POM (2462 and 2393 m) as a baseline. Bars indicate standard error. Symbols denote feeding types: (Ӿ) not defined, (●) predator/scavenger, (◇) suspension feeder and (■) deposit feeder.

4.1. *Characterisation of the food web*

4.1.1. *General food web structure*

It is likely that the benthic fauna at HAUSGARTEN utilises two to four different pathways of food: fresh surface-derived POM, (reworked) refractory bottom sediments and particles that trickle down-slope. Furthermore, large quantities of ice algae, particulate lithogenic and organic matter are trapped during freezing of the sea-ice in shallow waters, transported with the ice and released during melting processes (Nürnberg et al., 1994). It could therefore be argued that a multiple-source food web model (Søreide et al., 2006) should be used to distinguish between the qualitatively different inputs. However, in contrast to the input of sympagic (ice-related) systems, the δ^{15}N signatures of sediments were only slightly higher than those of POM. Therefore, it would be difficult to distinguish between different sources.

Aquatic food webs rarely encompass more than four to five trophic steps (Hall and Raffaelli, 1993). The food web sampled at HAUSGARTEN covered five trophic levels. While Polunin et al. (2001) reported a food chain of four trophic steps from the bathyal Mediterranean, Iken et al. (2001) found only three trophic levels at the Porcupine Abyssal Plain. Arctic food webs encompassed four trophic levels in the Canadian Arctic Basin (Iken et al., 2005), 4.7 in the Barents Sea (Tamelander et al., 2006) and five trophic levels in a Northeast Water Polynya (Hobson et al., 1995) and Lancaster Sound (Hobson and Welch, 1992). Spanning five trophic levels, the HAUSGARTEN food web clearly represents one of the longest food-chains, a situation that appears to be quite common in Arctic and deep-sea environments. Long food chain length indicates that nutrients are often recycled because of food limitation. Ecosystem size is a crucial determinant of food-chain length in aquatic systems although it is not yet clear which aspects of ecosystem size are most important (Post, 2002a). In larger ecosystems, such as those found in the deep sea (Danovaro et al., 2008), food chains might become more diverse, allowing greater dietary specialisation that could result in an increase in their lengths.

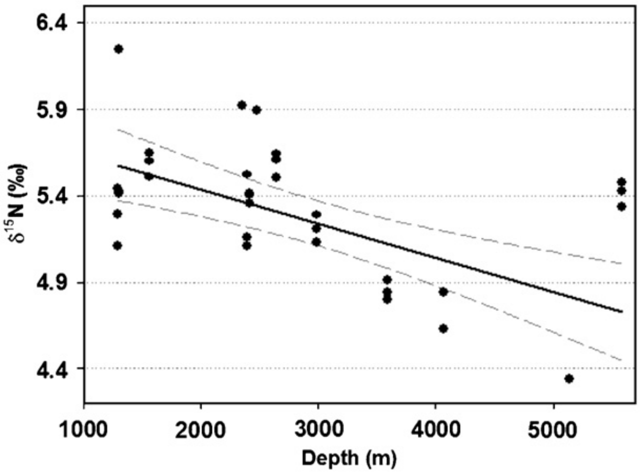

Fig. 3. Relationship between δ^{15}N signatures of sediment samples and water depth ($\delta^{15}N_{SED} = 5.833–0.000198$ depth, $n = 35$, $r^2 = 0.35$, $p < 0.001$). Dashed lines represent 95% confidence intervals.

It should be noted, however, that our five trophic level estimate has to be treated with care, as it is based on the use of bottom POM as a reference. Rather than using sediments as a baseline, which would constitute chiefly a baseline of deposit feeders, we decided to use bottom POM collected by sediment traps for three reasons: (1) The sediment trap fitted to the benthic lander was suspended only 1–2 m above the seafloor. Therefore, it can be assumed to capture particles of various pathways (sedimenting labile POM, re-suspended refractory bottom

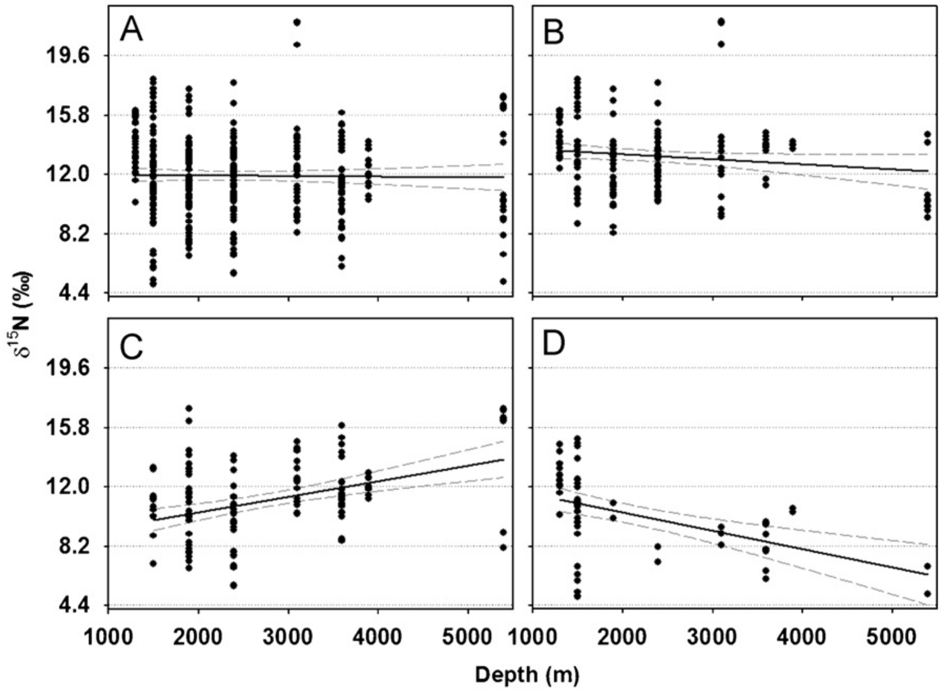

Fig. 4. Relationship between δ^{15}N signatures and water depth for (A) all organisms sampled ($\delta^{15}N_{all} = 12–0.000039$ depth, $n = 380$, $r^2 > 0.001$, $p = 0.77$), (B) predators/scavengers ($\delta^{15}N_{P/S} = 13.89–0.00032$ depth, $n = 176$, $r^2 = 0.019$, $p = 0.071$), (C) suspension feeders ($\delta^{15}N_{SF} = 8.386+0.00099$ depth, $n = 123$, $r^2 = 0.15$, $p < 0.001$) and (D) deposit feeders ($\delta^{15}N_{DF} = 12.64–0.00117$ depth, $n = 59$, $r^2 = 0.229$, $p < 0.001$). Dashed lines represent 95% confidence intervals.

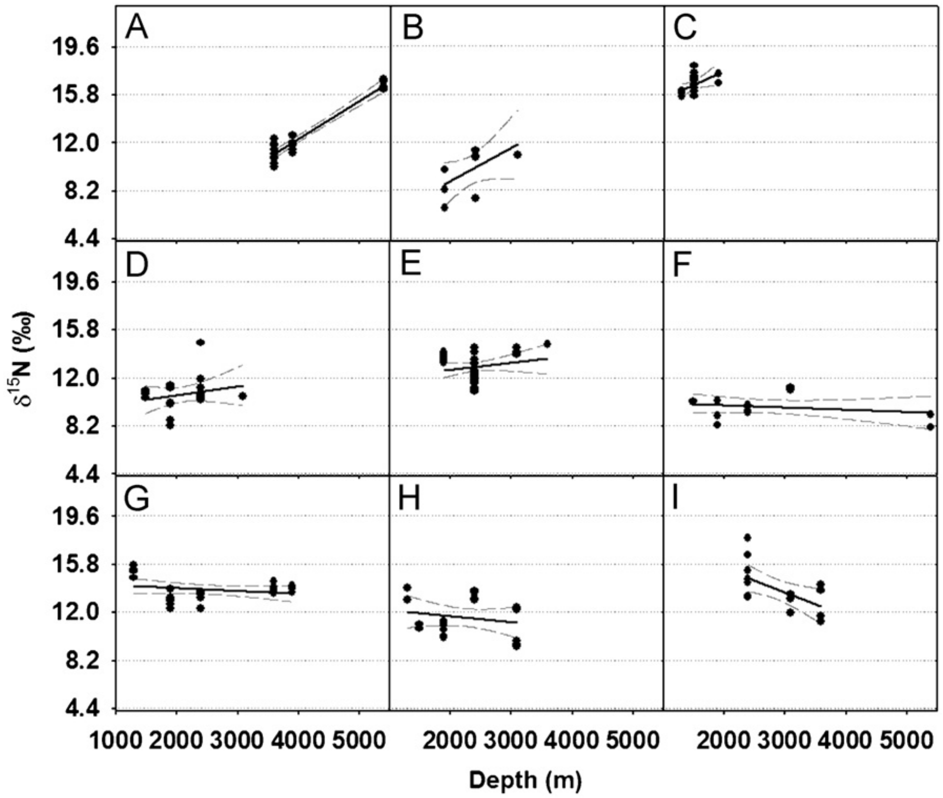

Fig. 5. Relationship between δ^{15}N signatures and water depth for (A) *Bathyphellia margaritacea* ($\delta^{15}N = 0.25+0.0030$ depth, $r^2 = 0.94$, $p<0.001$), (B) *Bathycrinus* cf. *carpenteri* ($\delta^{15}N = 3.67+0.00263$, $r^2 = 0.33$, $p = 0.11$), (C) *Bathybiaster vexillifer* ($\delta^{15}N = 13.28+0.00216$, $r^2 = 0.29$, $p = 0.039$), (D) *Mesidothea megalura* ($\delta^{15}N = 9.17+0.00072$, $r^2 = 0.05$, $p = 0.34$), (E) *Lycodes frigidus* ($\delta^{15}N = 11.59+0.00052$, $r^2 = 0.04$, $p = 0.28$), (F) *Cladorhiza gelida* ($\delta^{15}N = 10.23-0.00018$, $r^2 = 0.05$, $p = 0.41$), (G) *Bythocaris* spp. ($\delta^{15}N = 14.35-0.00023$ depth, $r^2 = 0.06$, $p = 0.24$), (H) *Mohnia mohni* and *Tacita danielsseni* ($\delta^{15}N = 12.63-0.00047$ depth, $r^2 = 0.04$, $p = 0.42$), and (I) *Eurythenes gryllus* ($\delta^{15}N = 19.15-0.00186$ depth, $r^2 = 0.33$, $p = 0.025$). Dashed lines represent 95% confidence intervals.

sediments, particles from the nepheloid layer), which are used by a broader range of benthic biota. (2) The bottom POM value is more robust as it represents the mean δ^{15}N signature over a year. (3) It enabled a comparison with data from other studies in the Arctic, which use POM as a baseline (Hobson and Welch, 1992; Hobson et al., 1995; Iken et al., 2005; Søreide et al., 2006; Tamelander et al., 2006).

4.1.2. Functional groups

While we tried to assign the organisms to feeding groups as accurately as possible, it should be noted that 100% dependable autecological information is lacking for many deep-sea species. Furthermore, some species can switch between different feeding modes so as to capitalise on the most abundant source of food (e.g. Lopez and Levinton, 1987). Therefore, our results have to be treated with caution.

The majority of taxa sampled at HAUSGARTEN were suspension feeders, followed by predators/scavengers and deposit feeders. This may result from the use of an Agassiz trawl as the main sampling gear.

While it is not surprising that predators/scavengers had the highest δ^{15}N signatures at HAUSGARTEN it is puzzling that suspension feeders had higher δ^{15}N signatures than deposit feeders assuming that deposit feeders utilise organic matter that has been more often reworked (Lopez and Levinton, 1987) and is therefore enriched in δ^{15}N. Furthermore, suspension feeders may also feed on re-suspended matter (Iken et al., 2001) meaning that they utilise the same food repository as deposit feeders. However, several authors reported higher δ^{15}N values in tissues of suspension compared with deposit feeders (e.g. Iken et al., 2001; Lovvorn et al., 2005; Mintenbeck et al., 2007). Some of the taxa classified as suspension feeders may be micro- or macrophagous, e.g. sponges (Vacelet and Boury-Esnault, 1995) and anthozoans. Indeed, when these groups were omitted there were no significant differences between deposit and suspension feeders but the number tested also decreased from 124 to 36 individuals. Still, the vacuolated ectoderm of the anthozoan *Bathyphellia margaritacea* contained foreign particles, which indicates a true suspension-feeding mode (Riemann-Zürneck, 1997).

Predators/scavengers had the highest spread of δ^{15}N values, which encompassed 3.5 trophic levels. This is hardly surprising as the group included both scavengers and predators. It shows that they had a broad trophic niche width (Bearhop et al., 2004), possibly due to opportunistic dietary habits (Sweeting et al., 2005), which may indicate food limitation. More surprisingly, the δ^{15}N values of suspension feeders spanned three trophic levels. For comparison, in the German Bight, their range of δ^{15}N was only 1.5‰ (Dannheim, 2007). The broad range in δ^{15}N could be caused by size-selective feeding habits facilitated by the different feeding apparatus of different taxa. In addition, food limitation and temporary starvation may have contributed to the broad range observed as it can lead to an enrichment of δ^{15}N in animal tissues (Hobson et al., 1993; Frazer et al., 1997; Adams and Sterner, 2000; Kurle and Worthy, 2002; Olive et al., 2003; Cherel et al., 2005; Gaye-Siessegger et al., 2007). Nutritional stress may cause an increase of catabolic muscle protein breakdown. As the lighter nitrogen isotope is no longer replaced by dietary protein, the remaining tissues are enriched in the heavier isotope (increased fractionation).

The spread of deposit feeders over two trophic levels could be explained by different feeding strategies. While those feeding at a lower trophic level may select freshly deposited (isotopically lighter) surficial material, those occupying a higher level may feed less selectively on (sub-surface) material that has been repeatedly reworked and is therefore enriched in δ^{15}N (Iken et al., 2005). To avoid errors from misclassification, we did not distinguish between surface and sub-surface deposit feeders in our study.

4.1.3. *Species/taxon level*

The trophic positions revealed by our analyses did not always match our preconceptions. For example, the starfish *Poraniomorpha tumida* had the highest δ^{15}N signature recorded at HAUSGARTEN. The same was reported for a shallower food web in the Barents Sea (Tamelander et al., 2006), although at HAUSGARTEN the δ^{15}N of *P. tumida* was one trophic level higher. No information was found on the feeding behaviour, but the high δ^{15}N signatures strongly suggest a scavenging feeding mode. Similarly, Iken et al. (2001) reported highest δ^{15}N values for a starfish and a polychaete rather than for the known predatory/scavenging species of fish or amphipods of the Porcupine Abyssal Plain. The authors concluded that the latter were decoupled from the POM-based food web and fed on less frequently recycled abysso-pelagic prey and large food falls. Although food falls may occasionally subsidise fish populations, we found primarily small benthic invertebrates in fish stomachs from HAUSGARTEN (Bergmann, unpublished). Furthermore, the trophic level of fish was approximately one level higher than that of their identified prey. Therefore, the trophic level of *P. tumida* was probably higher because they fed at a higher trophic level than fish.

The enrichment between certain primary consumers and their food source (e.g. cumaceans, amphipods, sea pens) was much lower than the assumed fractionation of 3.8‰ per trophic step. Congeneric cumaceans from the deep Arctic Canada Basin had also unexpectedly low δ^{15}N values, and Iken et al. (2005) suggested that they capitalise on very fresh and thus isotopically light phytodetritus. Post (2002b) stated that 3.4‰ is a valid estimate of trophic fractionation only when averaged over multiple trophic pathways and that any single trophic transfer is likely to range between 2‰ and 5‰ (Adams and Sterner, 2000). This may explain the low enrichment of some consumers relative to their food source.

4.2. *Bathymetric patterns in food supplies*

Only some 1–10% of the POM produced at the surface sinks to the sea floor (De La Rocha and Passow, 2007; Klages et al., 2003), and the amount of POM that reaches the seafloor decreases with increasing depth (Suess, 1980; Peinert et al., 2001) with the sharpest decrease in the twilight zone (Buesseler et al., 2007). Organisms from the deep Arctic seafloor are therefore subject to increasing food limitation. At HAUSGARTEN, the annual input of refractory particulate organic carbon and nitrogen beyond 300 m varies from 1.6 to 2.5 and 0.2 to 0.3 g m^{-2}, respectively (Bauerfeind et al., in revision), and food availability decreases as a function of depth (Soltwedel et al., 2005). Fig. 3 suggests that the quality of food supplies is also affected by depth. According to the ‘temperature-substrate limitation hypothesis’ (Mincks et al., 2005) the decrease in POM reaching the bottom, as well as decreasing temperatures along the HAUSGARTEN depth transect (Bauerfeind, unpublished data), may lead to decreasing microbially mediated mineralisation rates. Indeed, bacterial viability decreased as a function of depth at HAUSGARTEN (Quéric et al., 2004). The decreased turnover may have led in turn to the decreased δ^{15}N of sediments with depth. Ultimately, it is microbial breakdown that renders organic matter in sediments available to benthic biota (Lovvorn et al., 2005). Therefore, we consider depth as an indicator of food availability and suspect that the benthic assemblages and food webs present at different depths have been shaped by decreasing food supplies.

Mintenbeck et al. (2007) hypothesised that the δ^{15}N signatures of POM increase with increasing depth because of biodegradation in the water column of the Weddell Sea. However, the mean δ^{15}N values of POM samples from bottom and mid-water sediment traps recorded in our study were similar, which is corroborated by measurements from other years and HAUSGARTEN stations nearby (Bauerfeind, unpublished data). Similarly, Holmes et al. (1999) found that the δ^{15}N signatures of POM remain fairly constant below the euphotic zone. Accordingly, it could be argued that the δ^{15}N values of all organisms taken together were not affected by depth.

4.3. *Bathymetric patterns in functional groups*

Intriguingly, the δ^{15}N signatures of suspension feeders increased as a function of depth as also reported for the Weddell Sea (Mintenbeck et al., 2007). The comparison of bathymetric patterns in different functional groups in this study has to be treated with some caution as the species composition varied. However, a few species occurred at three or more depths allowing a direct comparison. As with all suspension feeders, the δ^{15}N signatures of *B. margaritacea* and the crinoid *B.* cf. *carpenteri* increased with increasing depth; the range of this increase exceeded one trophic level. This could have several explanations. (1) The HAUSGARTEN stations are positioned along the continental slope. Therefore, it is possible that benthic organisms also utilise particles that are transported down-slope or re-suspended sediments that may carry different δ^{15}N signatures compared with less degraded surface-POM. It could be hypothesised that the relative importance of such particles increases with depth since the quantity of surface POM decreases as a function of depth (Suess, 1980). Unfortunately, we were unable to sample the bottom POM at all of the HAUSGARTEN stations to verify this. (2) The bottom fauna may be increasingly exposed to food limitation and starvation. The increase in δ^{15}N with depth might thus reflect increasing nutritional stress due to lowered particle availability. However, the fact that suspension feeder densities at HAUSGARTEN increase as a function of depth (Jaeckisch, 2004) supports the first explanation.

The δ^{15}N of sponges were unexpectedly high for a group classified as suspension feeders. However, over recent years more and more sponges have been classified as carnivorous (Vacelet and Boury-Esnault, 1995; Vacelet, 2006; Ereskovsky and Willenz, 2007). Some of these (e.g. *Cladorhiza, Esperiopsis*) are closely related to those sampled in this study. Alternatively, high δ^{15}N values of sponges could be due to symbiotic bacteria (Iken et al., 2001). The mesohyl of *Tentorium semisuberites* from HAUSGARTEN harbours Archaea indicating "microbial farming" (Pape et al., 2006). Both carnivory and symbiotic bacteria may therefore explain the unexpectedly high δ^{15}N signatures recorded. Similar to those of predators/scavengers, the δ^{15}N signatures of all sponges or of *Cladorhiza gelida* alone were not affected by depth. Macrophagy may be a more effective feeding strategy than microphagous suspension-feeding in food-limited deep-sea environments (Vacelet and Boury-Esnault, 1995) such as HAUSGARTEN.

Strikingly, the δ^{15}N signatures of deposit feeders followed the opposite trend: the δ^{15}N values decreased with increasing water depth. This is consistent with a reduction in bacterial viability and abundance of sediment-inhabiting bacteria with increasing water depth recorded at HAUSGARTEN (Quéric et al., 2004). As mentioned above, decreasing concentrations of organic matter and temperatures – as found along the HAUSGARTEN transect – may lead to decreased microbially mediated mineralisation rates (Mincks et al 2005). Organic matter in sediments is indigestible by macrofauna and becomes available to deposit feeders only through microbial breakdown (Lovvorn et al., 2005). Under oxic conditions, microbial degradation of organic matter leads to an enrichment of δ^{15}N in sediments (Macko and Estep, 1984; Holmes et al., 1999; Freudenthal et al., 2001). A decrease in bacterial abundance and viability with depth therefore also explains the recorded decrease in δ^{15}N of sediments with growing depth. The lower δ^{15}N signature of their food source is reflected, in turn, in the tissues of deposit feeders. Furthermore, as food supplies decrease with increasing depth, deposit feeders may rely increasingly on smaller particles, which have larger surface to volume ratios compared to larger particles. This may maximise food uptake (Lopez and Levinton, 1987). Small particles are characterised by lower δ^{15}N signatures (Rau et al., 1990). Their preferential ingestion may therefore also contribute to the decreasing δ^{15}N signatures recorded.

Since none of the deposit-feeding species was sampled at more than two depth strata we were unable to corroborate the depth-related patterns at the species level. Our findings concur with photographic evidence from HAUSGARTEN indicating decreasing surface deposit feeder densities as a function of depth (Jaeckisch, 2004).

The δ^{15}N values of predators/scavengers and of most individual predatory/scavenging taxa were not affected by depth. Likewise, Polunin et al. (2001) detected depth-related differences only in two out of 20 species of predators/scavengers from the deep Mediterranean. Predators/scavengers may have to adopt a degree of omnivory to be able to make ends meet in environments as food-limited as the deep sea. Indeed, stomach content analysis of the same individual fish used for stable isotope analyses revealed that they fed on a mixture of benthic invertebrates (Bergmann, unpublished data: amphipods, cumaceans, copepods, isopods, tanaids, polychaetes) with different feeding modes. The opposite depth patterns in the δ^{15}N of suspension and deposit feeders may thus have been evened out in the tissues of their consumers.

By contrast, the δ^{15}N signatures of the amphipod *Eurythenes gryllus* decreased with depth. While this species has been reported from various baited trap and food fall experiments around the globe (e.g. Hessler et al., 1978; Premke et al., 2003) it may switch to different food sources, e.g. bottom POM, during periods of carrion scarcity (Charmasson, 1998). When removing the hindgut whilst sampling tissue from the abdomen, we also found sediments. If carrion becomes scarcer with depth *E. gryllus* may increasingly adopt a diet including particles or deposit-feeding prey. As argued above, these sources are increasingly depleted in δ^{15}N, which may have caused the depth-related δ^{15}N depletion observed.

Surprisingly, the δ^{15}N signatures of the starfish *B. vexillifer* increased with increasing water depth. The dominant prey of conspecifics from the Rockall Trough included irregular echinoids, gastropods and bivalves (Tyler et al., 1993). As macrofaunal abundance and biomass decreases with increasing water depth in the HAUSGARTEN area (Włodarska-Kowalczuk et al., 2004), starfish may increasingly suffer starvation or feed on food falls reflected in growing δ^{15}N values.

5. Conclusions

The bathymetric patterns in δ^{15}N were different in all feeding groups. While the δ^{15}N signatures of predators/scavengers were not affected by depth, those of suspension feeders increased with depth, and the reverse was found for deposit feeders. Suspension feeders feed on POM, which decreases in availability with increasing depth. As a result, suspension feeders may rely increasingly on particles that trickle down the HAUSGARTEN slope and carry higher δ^{15}N values. The fact that suspension feeder densities increase with depth (Jaeckisch, 2004) indicates the importance of this food source at HAUSGARTEN. Deposit feeders feed on material recycled by sediment-inhabiting bacteria, which may be less and less reworked as their biomass decreases with depth (Quéric et al., 2004). The decreasing food availability may lead to the decreasing surface deposit feeder densities observed as a function of depth (Jaeckisch, 2004). Our results highlight the need for a depth-stratified approach to analyses of deep-sea food webs.

A more comprehensive sampling approach including samples from ice cores would allow us to determine the importance of sympagic input to deep benthic communities below the marginal ice zone. Extraction of lipids prior to stable isotope analyses, or the use of fatty acid trophic biomarkers, would enable us to infer the sources of carbon used by benthic organisms and increase the dietary resolution.

Our results cast new light on a food web located in an area that may already be affected by climate change or soon become so. Changes in food-web relationships could markedly alter benthic community and trophic structure, thereby influencing food availability up to apex consumers. Time-series measurements of the isotopic signature of longer-lived key benthic species may allow us to infer trophic changes in response to climate change.

Acknowledgements

We thank the officers and crews of RVs *Polarstern* and *L'Atalante* and the ROV team of "*Victor 6000*" for their support. S. Bury, A. Pappert and M. Volkenandt assisted with the preparation of samples. U. Struck undertook the isotope-ratio mass spectrometry analysis and K. Beyer gave practical instructions on the methodology. R. Bramber, A. Brandt, S. Gromisz, J. Guerrero, D. Jones, M. Kędra, P.R. Møller, U. Mühlenhardt-Siegel, D. Piepenburg, M. Ramos, A.V. Rogacheva, O.S. Tendal, M. Türkay, K. von Juterzenka, A. Warén and J.M Węsławski kindly identified fauna from reference samples and provided information on feeding habits. The suggestions of three anonymous referees improved an earlier version of the manuscript. This is publication awi-n17402 of the Alfred Wegener Institute for Polar and Marine Research.

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