Vol. 500: 121–137, 2014
doi: 10.3354/meps10663

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published March 17

Trophic structure of the abyssal benthic community in the Sea of Japan inferred from stable isotope and fatty acid analyses

Serguei I. Kiyashko[1,*], Vladimir I. Kharlamenko[1], Karen Sanamyan[2], Inna L. Alalykina[1,3], Laura Würzberg[4]

[1]A.V. Zhirmunsky Institute of Marine Biology, Far East Branch, Russian Academy of Sciences, Vladivostok 690059, Russia
[2]Kamchatka Branch of Pacific Institute of Geography, Far East Branch, Russian Academy of Sciences, Petropavlovsk-Kamchatsky 683000, Russia
[4]Far Eastern Federal University, School of Natural Sciences, Oktyabrskaya 29, Vladivostok 690091, Russia
[4]Biocenter Grindel and Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, Hamburg 20146, Germany

ABSTRACT: The abyss of the Sea of Japan represents an example of an isolated deep-sea environment that contains mostly endemic fauna and has a complicated Quaternary history. To determine the trophic structure and sources supporting this abyssal benthic community, the carbon and nitrogen stable isotope ratios and fatty acid (FA) compositions of key invertebrate species and sedimentary organic matter (SOM) were analysed. Samples were collected at a range of depths from 2481 to 3666 m in the deep-water basin of the Sea of Japan in August 2010. Species of the most abundant invertebrates—including polychaetes, sea anemones, peracarid crustaceans, bivalves and brittle stars—showed similar $\delta^{15}N$ values, corresponding to relatively high and similar trophic positions. Analysis of FA trophic markers showed that all of these equally ^{15}N-enriched omnivores, carnivores and scavenger species in the Sea of Japan abyssal environment fed mostly on sinking zooplankton animals. The resulting FA profiles of these species showed a high 18:1ω9/18:1ω7 ratio, and the 22:6ω3 and 20:5ω3 polyunsaturated FAs were the most abundant FAs. Only one macrobenthic species, the filter-feeding *Thyasira* (*Parathyasira*) sp., had low 22:6ω3 and 20:5ω3 FA proportions, but it exhibited significant levels of 18:2ω6 and 16:1ω10 FAs characteristic of the SOM of the deep waters of the Sea of Japan. These data reveal the dominant role of descending zooplankton as a food resource for mega- and macrobenthos in this marginal deep-water environment. Despite the proximity of the productive shelf area, which exports plant residues to the deep-water basin of the Sea of Japan, we found no isotopic or FA indications of feeding on allochtonous detritus of seagrasses or macroalgae among abyssal consumers. Our data did not support cannibalism as a feeding mode of the abundant abyssal carnivorous polychaetes, as had previously been suggested. Different key invertebrate species of the Sea of Japan abyssal food web occupied similar trophic positions and fed predominantly on descended zooplankton. We suggest that the simple structure of the Sea of Japan abyssal food web, lacking abundant deposit-feeder food chains, is the result of the young evolutionary age of this community rather than the low availability of bottom detritus or the specific structure of the pelagic community that provides abundant downward flow of zooplankton.

KEY WORDS: Abyssal zone · Sea of Japan · Benthic invertebrates · Feeding · Stable isotopes · Fatty acids

INTRODUCTION

Abyssal food webs, with the exception of areas of chemosynthesis, are rather uniform and characterised by the predominance of deposit feeders in the eutrophic regions of the global ocean floor (Sokolova 1972, 1997). Particulate organic carbon (POC) synthesised in the upper pelagic layers sinks mainly as seasonal pulses of diatoms and zooplankton faeces and is consumed by deep-sea detritivorous zooben-

*Corresponding author: sekiyash@mail.ru

thos and bacteria (Billett et al. 1983, Graf 1989, Witte et al. 2003, Mayor et al. 2012). However, regional changes in the pelagic food web can modify the composition and quantity of organic matter flowing from the pelagic zone to the bottom and affect the structure of the abyssal food web (Smith et al. 2008 and references therein). Comparative studies of particular abyssal food webs can reveal new features of biodiversity in the ocean.

The abyss of the Sea of Japan (SJ) represents an example of a very young isolated deep-sea community. The semi-closed marginal SJ, which has a greatest depth of approximately 3700 m, has its own deep waters formed by the sinking of cool surface water in severe winters and is separated from the north Pacific deep waters by the shallowness of the straits. The SJ deep waters are characterised by lower temperature (0.0 to 0.2°C), lower salinity (34.06 to 34.07‰) and an extremely high level of dissolved oxygen (>200 µmol kg^{-1}) (Zenkevich 1963, Gamo 2011) in comparison to the adjacent deep-water areas of the north Pacific (Watling et al. 2013). Another prominent feature of the SJ abyss is the specific character and very young age of its biota. It has been shown that the glacio-eustatic sea-level drop isolated the SJ from the Pacific Ocean during the last glacial maximum, resulting in water column stratification and anoxic conditions in the deep-water layer (Kido et al. 2007 and references therein). Consequently, the benthic communities that repopulated the SJ deep waters are likely to be younger than 17 kyr.

The species abundance of benthic fauna of the SJ decreases rapidly with increased water depth, and only some tens of invertebrate species have been recorded at depths >2000 m (Derjugin 1939, Zenkevich 1963). Few species contribute notably to the total biomass of the SJ abyssal benthos (Mokievskii 1954, Pasternak & Levenstein 1978), and most of them are apparently endemic. The abyssal species known to be in the adjacent north Pacific are absent in the SJ (Levenstein & Pasternak 1973). Despite low species abundance, the mean biomass of zoobenthos on the abyssal floor in the SJ is similar to or slightly higher than that in the abyssal area of the north-western Pacific (Pasternak & Levenstein 1978, Shuntov 2001). The polynoid polychaetes *Harmothoe* dominate in the SJ abyss, locally comprising up to 90% of the total benthos biomass and giving a carnivorous appearance to the whole abyssal community (Mokievskii 1954, Pasternak & Levenstein 1978). The food sources for these evidently carnivorous polychaetes remain unclear, given that the biomass of other small invertebrates in this benthic community is very low. Based on gut content analysis, even cannibalism was considered an important feeding mode for *Harmothoe derjugini,* which is endemic to the SJ abyss (Sokolova 1982). Recently, high abundance of small peracarid crustaceans in SJ deep waters was shown by a novel sampling approach (Brandt et al. 2013), and the isopod *Eurycope spinifrons* was recognised as the most important key species of the abyssal benthic community, presumably feeding on phytodetritus (Elsner et al. 2013).

Primary production in the SJ was evaluated as lower than that in other north Pacific seas (Shuntov 2001), and other organic matter flows were considered to support the SJ abyssal community in addition to the low POC fluxes to the seafloor. The deep-water pelagic communities of the SJ have a very low abundance of predatory zooplankton, bathypelagic fish and deep-water shrimp, which results in underconsumption of abundant interzonal zooplankton sinking to the bottom (Vinogradov 1973). It was supposed that the combination of cold water and the specific trophic structure of the bathypelagic communities in the SJ results in the large flow of interzonal zooplankton sinking to the abyssal floor, where it becomes the primary food for benthic animals (Vinogradov & Sazhin 1978). Horizontal flow of plant organic matter from the shelf has been hypothesized to be important for the abyssal benthos of the SJ (Mokievskii 1954, Elsner et al. 2013). Abundant seagrasses and macroalgae residues were obtained in many grab samples (Mokievskii 1954), and seagrass fragments were often recorded by underwater camera on the abyssal plain of the SJ (Brandt et al. 2013). The importance of enhanced flows of descending zooplankton or allochtonous plant residues for the development of the specific composition of abyssal benthos of the SJ has not yet been studied.

The study of abyssal species' diets is difficult, in part because some deep-water invertebrates are capable of surviving prolonged starvation, and may regurgitate ingested food upon lifting by trawl (Sokolova 1986). Alternative methods have been established to study trophic relationships in deep-sea ecosystems, such as the analysis of stable carbon and nitrogen isotopes or the fatty acid (FA) composition of consumers. The analysis of the natural ratios of stable carbon and nitrogen isotopes has been widely used for the study of trophic relationships in deep-sea ecosystems (Suchanek et al. 1985, Iken et al. 2001, Polunin et al. 2001, Blankenship & Levin 2007, Fanelli et al. 2009), providing time-

integrated averages of assimilated food items (e.g. Hobson & Welch 1992). However, analysis of the FA composition can significantly enhance the quality of deep-sea trophic studies because it captures more complex feeding interactions (Howell et al. 2003, Drazen et al. 2008a,b). Many potential food sources have specific FA compositions that can be used to trace their consumption by consumers. Therefore, FA analysis of consumers has been used extensively in the identification of trophic pathways in marine food webs (e.g. Dalsgaard et al. 2003, Kelly & Scheibling 2012).

The main goal of this study was to reveal the trophic structure in the abyssal food web of the SJ. To do this, we analysed stable carbon and nitrogen isotope ratios and FA compositions of the most abundant consumer species and probable food sources, and compared the obtained data with the assignment of species to functional groups based on the literature. We tested the following hypotheses: (1) the flow of descended interzonal zooplankton is a more important resource for the SJ abyssal benthos than POC flow, (2) allochtonous detritus of seagrasses and macroalgae could be a substantial subsidy for the SJ deep-water macro- and megabenthos, (3) different key species should use different organic matter sources and occupy different trophic positions and (4) cannibalism can be an important feeding strategy in allowing polynoid polychaetes to flourish in the SJ abyss.

MATERIALS AND METHODS

Study site and species sampling

Materials for this study were obtained in the northwestern part of the Japan Basin, the deepest and largest basin of the SJ. According to Derjugin (1939), the bottom of the SJ at depths >2000 m is an abyssal zone because of the uniformity of fauna, sediments and hydrological conditions. This point of view is supported by the existence of a clear boundary (benthic front) between deep water masses in the SJ at depths of 2000 to 2500 m, separating the extremely homogenous water mass below the boundary (the Bottom Water) from the deep water of the SJ (Gamo 2011). Given these peculiarities of the study area, we considered benthos collected in the SJ at depths >2000 m as a single abyssal community, even though the conventional upper limit of the abyssal zone is at a water depth of 3000 m (e.g. Smith et al. 2008). Sampling was performed in August 2010 during the joint Russian/German SoJaBio (Sea of Japan Biodiversity Studies) expedition onboard the RV 'Akademik M.A. Lavrentyev' (51st cruise) to the slope and deep-sea basin of the SJ. The stations for this expedition were located along 4 transects (see Malyutina & Brandt 2013). For this study, the most abundant macro- and megabenthic invertebrates were collected at all stations of these transects below a depth of 2000 m

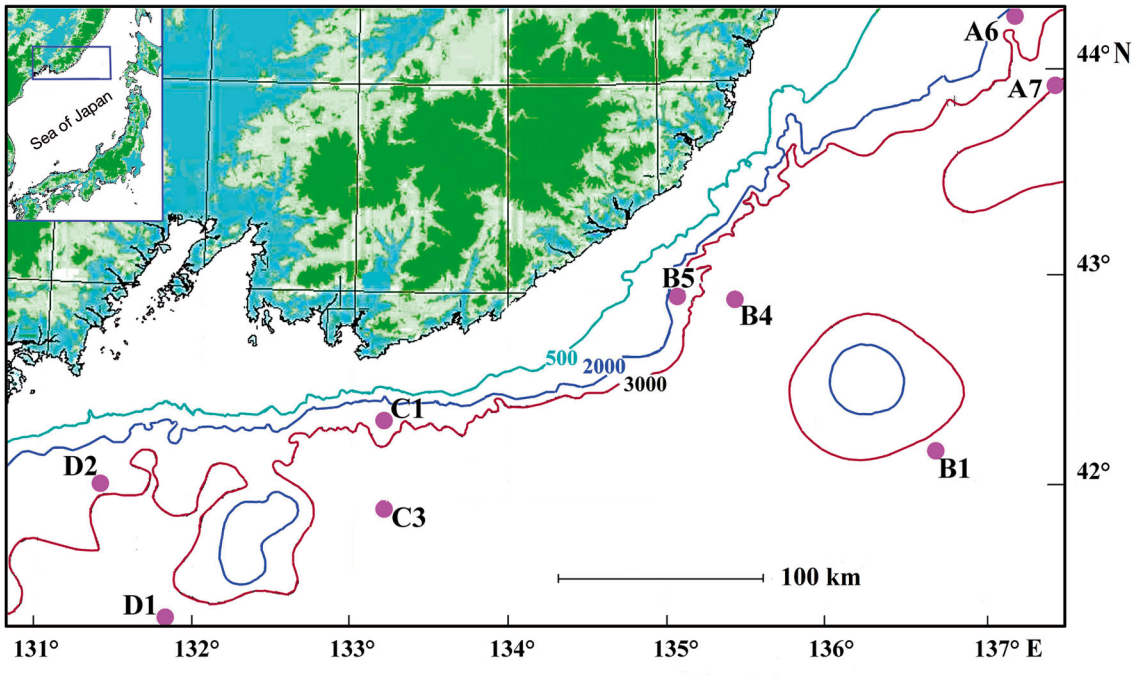

Fig. 1. SoJaBio study area in the Sea of Japan. Dots indicate sampling locations in abyssal zone

(Fig. 1) to obtain a sufficient amount of materials for stable isotope and FA analyses and to more completely represent the main species of the SJ abyssal community. A relatively high annual mean POC flux of 30.7 mg m^{-2} day^{-1} at a depth of 1 km was recorded in the deepest part of our study area (41.24° N, 132.35° E) (Otosaka et al. 2008). Nevertheless, we expected higher food availability for benthos sampled at the stations on the periphery of the Japan Basin floor in the vicinity of highly productive shelf waters (basin periphery stations: A6, B5, C1 and D2). During the sampling, seagrass residues were documented at the deepest stations (>3000 m) of all 4 transects by underwater cameras attached to an epibenthic sledge (Brandt et al. 2013), indicating the accumulation of plant debris in the deepest part of the Japan Basin (the deepest stations: A7, B1, B4, C3 and D1).

Animals were collected using an Agassiz trawl and epibenthic sledge (Malyutina & Brandt 2013). For analyses of sedimentary organic matter (SOM), 3 bottom-sediment cores were collected with a multiple corer at each sampling station, and the upper 3 cm layer was taken. Particulate organic matter (POM) was obtained by filtering approximately 300 cm^3 of the bottom water collected in the multiple corer over precombusted (at 450°C for 4 h) GF/F filters. These POM samples mainly contained resuspended matter from the flocculent layer of the bottom sediments rather than organic matter from the water column. For FA analysis of possible food sources, a composite sample of approximately 135 individual *Oolina lineata* foraminiferans was immediately separated manually under a dissecting microscope from the total meiobenthos obtained by the multiple corer at Stn B4 and processed in the same way as the invertebrate samples. The zooplankton sample including euphausiids *Thysanoessa* spp. was obtained by trawl in the northern part of the study area (44.5° N, 137.1° E) at a water depth of 1500 m. Animals were dissected on board after collection, and whole individuals or tissue subsamples were processed separately for isotope and FA analyses.

Stable isotope analysis

For the isotopic analysis, muscle tissues were sampled from molluscs and actinia, arm fragments were sampled from ophiuroids, and individuals without intestines were taken for crustaceans, polychaetes and ascidians. The individuals of all invertebrates species sampled on board were adults of the same size class. All samples were oven-dried at 60°C and stored in a desiccator. Dried samples were ground to a fine powder using an agate mortar and pestle, and 0.5 mg subsamples were packaged into tin caps. Because of the low lipid content of the majority of isotopic samples analysed, neither lipid extraction nor lipid correction was performed. An exception was made for amphipods because samples from these invertebrates contained some storage lipids (according to their high C/N ratio values) and subsamples of amphipods were re-analysed for $\delta^{13}C$ values after lipid removal by hexane (Logan & Lutcavage 2008). Subsamples of ophiuroids and crustaceans, which contained skeletal carbonate, and samples of SOM and POM were placed in silver cups, treated with 1 M HCl and re-analysed for carbon isotope compositions (Jaschinski et al. 2008).

For evaluation of probable ontogenetic variations in the nitrogen isotope composition of the polychaete *Harmothoe derjugini*, 20 individuals represented by different size classes were taken from a single sample obtained by epibenthic sledge at Stns A7–9 (water depth 3340 to 3347 m) (Alalykina 2013) and preserved on board in formalin because of logistical problems. According to a recent review of the literature and experimental data (Rennie et al. 2012 and references therein), preservation in formalin does not cause ecologically significant differences in $\delta^{15}N$ values among invertebrates samples of the same species. Because of fragmentation of some individuals during sampling, the width of the 10th segment without parapodia and setae was used to determine the size classes of polychaetes.

Isotopic analysis was performed at the Stable Isotope Laboratory (Far Eastern Geological Institute FEB RAS, Vladivostok) using a FlashEA 1112 elemental analyser coupled to a MAT 253 isotope mass spectrometer (ThermoQuest, Germany) by a ConFlo IV interface. Sample isotopic ratios were expressed in the conventional δ notation as parts per thousand (‰) according to the following equation:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample} - R_{standard})/ R_{standard}] \times 1000,$$

where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The δ values were expressed relative to the international reference standards of Pee Dee Belemnite for carbon, and atmospheric N_2 for nitrogen. The internal laboratory standard was measured after every sixth sample during analysis to control the data quality. Based on the SD of the replicates of the laboratory standard, the internal precision was ±0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$.

Fatty acid analysis

For FA analysis, samples were placed in vials containing a chloroform–methanol mixture immediately after collection and stored at −20°C. Lipids were extracted from all samples using the extraction method of Bligh & Dyer (1959). Fatty acid methyl esters (FAMEs) were prepared from the total lipids according to the generally accepted procedure of Carreau & Dubacq (1978) and purified with preparative thin layer chromatography in benzene. The 4,4-dimethyloxazoline derivatives of FAs were prepared according to Svetashev (2011). FAMEs were analysed on a Shimadzu GC 2010 chromatograph using a fused quartz capillary (30 m × 0.25 mm) column coated with SUPELCOWAX 10 (Supelco). FAs were identified based on the gas chromatography-mass spectrometry data from the FAMEs and from the 4,4-dimethyloxazoline derivatives of the FAs. Mass spectrometry was performed on a Shimadzu GCMS QP5050A spectrometer using MDN 5S columns (temperature gradient from 170° to 290°C at 2°C min^{-1}, and then held for 25 min). All spectra were obtained using the electron impact method at 70 eV.

Data analysis

Statistical analysis of the data was performed using Statistica v. 6.0 with one-way ANOVA and Tukey's test at a significance level of $p < 0.05$. Data were tested for normality and homogeneity of variance using the Shapiro-Wilks W and Levene's tests. FA profiles were compared between taxa using principal component analysis (PCA) with PRIMER v. 6 software. Only FAs that contributed >1.0% of the total FA in at least one sample were included in the statistical analysis. The values of FA contents were normalised before the PCA analysis for better visualisation of minor FAs as trophic markers; the mean was subtracted from values for each variable, and then the value was divided by the SD using the normalisation function in PRIMER v. 6.

The relative trophic position (TP) of the consumers (Table 1) was calculated using the following equation (Post 2002):

$$TP = \lambda + (\delta^{15}N_{consumer} - \delta^{15}N_{base})/\Delta\delta^{15}N,$$

where λ is the trophic position of the organism used to estimate $\delta^{15}N_{base}$, $\delta^{15}N_{consumer}$ is the $\delta^{15}N$ value of the species in question and $\Delta\delta^{15}N$ is the ^{15}N-enrichment factor per trophic level. We used a $\Delta\delta^{15}N$ value of 3.4‰ (Minagawa & Wada 1984, Post 2002). We chose the filter-feeding sponge Hexactinellida as the baseline species and assumed that it had a trophic position of 2 (Table 1).

RESULTS

Stable isotopes

We did not find significant differences in the $\delta^{13}C$ values of SOM sampled at different stations (1-way ANOVA, $F = 0.68$, $p = 0.42$). The $\delta^{15}N$ values of SOM were also similar among stations, except for significantly lower values at Stn B5 (ANOVA Tukey's HSD test, $p < 0.003$). The POM samples had lower $\delta^{13}C$ and $\delta^{15}N$ values than the SOM samples (Table 1). Deep-water zooplankton samples represented by *Thysanoessa* spp. had $\delta^{13}C$ and $\delta^{15}N$ values of −21.7 ± 0.4‰ and 8.9 ± 0.4‰, respectively.

A relatively narrow range of $\delta^{13}C$ values (ca. 3.5‰) was recorded for samples of benthic invertebrates. We found significant inter-specific differences in this narrow range of $\delta^{13}C$ values (Table 1) in which the actinia *Edwardsia sojabio* and the isopod *Eurycope spinifrons* were the most ^{13}C-depleted species, and the bivalves *Delectopecten vancouverensis* and *Thyasira* (*Parathyasira*) sp. were the most ^{13}C-enriched species. Generally, the invertebrate samples collected from the deepest stations had significantly lower $\delta^{13}C$ values than samples from the basin periphery stations (1-way ANOVA, $F = 28.21$, $p < 0.00001$). However, the samples from these 2 areas were composed mainly of different species. We found a considerable range of $\delta^{15}N$ values (approx. 8‰) for all samples of benthic invertebrates (Table 1). The following 6 species composed the main group in the middle of the $\delta^{15}N$ range: *D. vancouverensis*, *E. sojabio*, *E. spinifrons*, the amphipod *Anonyx derjugini* and the polychaetes *Harmothoe derjugini* and *Harmothoe impar impar* (Fig. 2). The mean $\delta^{15}N$ values for these species varied from 11.6 to 13.1‰ and were not significantly different (ANOVA Tukey's HSD test, $p > 0.08$).The lowest and highest $\delta^{15}N$ values were recorded for the unidentified glass sponge Hexactinellida (7.7‰) and the ascidia *Styela squamosa* (15.4‰). The bivalve mollusc *Thyasira* (*P.*) sp. had significantly lower $\delta^{15}N$ values than invertebrates from the main group. The mean $\delta^{15}N$ value of the brittle star *Ophiura leptoctenia* occupied an intermediate position between those of *Thyasira* (*P.*) sp. and the main group invertebrates. Samples of *Ophiura leptoctenia* found at 2 stations (A6 and D2) at similar water depths showed an

Table 1. $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SD) for benthic invertebrates, particulate organic matter (POM), and bottom sediments (SOM) from abyssal stations in the Sea of Japan. Species mean values (**bold**) marked with the same letters are not significantly different ($p > 0.05$, ANOVA Tukey's HSD test). TP: trophic position of consumers. Sampling gears—AGT: Agassiz trawl; EBS: epibenthic sledge; MUC: multiple corer

Group/source	Species	Station	Depth (m)	Gear	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	TP
Porifera	Hexactinellida	B5	2676	AGT	2	**-21.7^{bcde} ± 0.4**	**7.7 ± 0.3**	**2.0**
Cnidaria: Actinaria	*Edwardsia sojabio*	A6	2481	AGT	1	−22.9	12.4	3.4
		A7	3213	EBS	3	−23.6 ± 0.3	12.4 ± 0.4	3.4
		B4	3330	EBS	2	−23.6 ± 0.1	13.2 ± 0.1	3.6
		D2	2637	EBS	4	−22.9 ± 0.4	12.0 ± 0.6	3.3
						-23.2^{a} ± 0.4	**12.4^{bc} ± 0.6**	**3.4**
Mollusca: Bivalvia	*Delectopecten vancouverensis*	A6	2481	AGT	2	−20.5 ± 0.8	12.1 ± 0.5	3.3
		B5	2635	MUC	2	−20.3 ± 0.2	12.2 ± 0.1	3.3
		C1	2725	EBS	2	−19.9 ± 0.5	11.7 ± 0.1	3.2
		D2	2699	MUC	3	−20.4 ± 0.3	11.2 ± 0.4	3.0
						-20.3^{e} ± 0.4	**11.8^{c} ± 0.5**	**3.2**
	Thyasira (*Parathyasira*) sp.	B5	2635	MUC	6	−21.1 ± 0.2	9.4 ± 0.6	2.5
		C1	2787	AGT	3	−19.8 ± 0.1	11.1 ± 0.3	3.0
						-20.8^{e} ± 0.7	**9.9^{a} ± 1.0**	**2.7**
Crustacea: Amphipoda	*Anonyx derjugini*	A6	2481	AGT	4	−22.3 ± 0.6	13.0 ± 0.9	3.6
		D2	2637	EBS	3	−21.1 ± 0.2	13.1 ± 0.1	3.6
						-21.8^{bcd} ± 0.8	**13.1^{bc} ± 0.6**	**3.6**
Crustacea: Isopoda	*Eurycope spinifrons*	B4	3330	EBS	3	**-22.5^{ab} ± 0.5**	**11.6^{abc} ± 0.3**	**3.2**
Polychaeta	*Harmothoe impar impar*	A6	2481	EBS	1	−21.1	13.0	3.6
		B5	2676	AGT	6	−20.8 ± 0.7	13.2 ± 0.5	3.6
						-20.8^{de} ± 0.5	**13.1^{c} ± 0.6**	**3.6**
	Harmothoe derjugini	A7	3213	EBS	6	−21.5 ± 0.4	12.7 ± 0.3	3.5
		B1	3665	EBS	2	−22.8 ± 0.3	11.5 ± 0.1	3.1
		C3	3410	AGT	3	−21.7 ± 0.2	11.8 ± 0.9	3.2
		D1	3357	AGT	6	−22.1 ± 0.5	13.3 ± 0.4	3.6
						-21.9^{bc} ± 0.7	**12.6^{bc} ± 0.7**	**3.4**
Echinodermata: Ophiuroidea	*Ophiura leptoctenia*	A6	2481	AGT	3	−20.8 ± 0.1	13.0 ± 0.2	3.6
		D2	2637	EBS	2	−21.2 ± 0.1	9.1 ± 0.1	2.4
						-21.0^{cde} ± 0.2	**11.5^{ab} ± 2.1**	**3.1**
Ascidiacea	*Styela squamosa*	B5	2676	AGT	4	**-20.7^{de} ± 0.3**	**15.4 ± 0.6**	**4.3**
POM		B1	3666	MUC	1	−24.7	3.1	
		C3	3419	MUC	3	−24.4 ± 0.7	3.1 ± 2.2	
		D1	3358	MUC	1	−23.5	3.5	
						−24.3 ± 0.7	**3.2 ± 1.6**	
SOM		A6	2511	MUC	3	−22.5 ± 0.3	6.9 ± 0.1	
		A7	3344	MUC	3	−23.3 ± 0.6	7.4 ± 0.2	
		B1	3666	MUC	2	−23.2 ± 0.5	7.7 ± 0.1	
		B4	3333	MUC	3	−22.8 ± 0.4	7.3 ± 0.2	
		B5	2635	MUC	3	−23.2 ± 0.2	6.2 ± 0.2	
		C3	3421	MUC	3	−22.9 ± 0.6	7.2 ± 0.1	
		D1	3358	MUC	3	−22.8 ± 0.3	7.2 ± 0.2	
						−22.9 ± 0.4	**7.1 ± 0.5**	

extremely large $\delta^{15}N$ intra-specific difference of approximately 4‰ (Table 1). The intra-specific variations of $\delta^{15}N$ values of the other species studied were much lower and did not exceed a 1.8‰ difference between individuals collected at different stations.

We found no ontogenetic shift in the $\delta^{15}N$ values of the most abundant species in the SJ abyssal zone *Harmothoe derjugini*. No significant correlation of $\delta^{15}N$ signatures with an increase in body size (the width of body from 1.2 to 7.5 mm, n = 20) was observed ($R^2 = 0.06$, $p = 0.29$) for this species. Indeed, some large individuals were even depleted in ^{15}N compared to juveniles (see Fig. A1 in the Appendix).

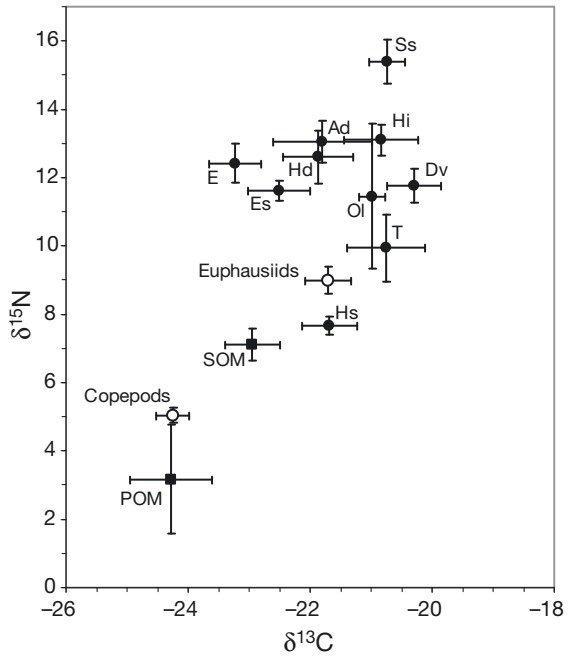

Fig. 2. $\delta^{13}C$ *versus* $\delta^{15}N$ biplot showing the stable isotope composition (mean ± SD) of benthic consumers, suspended particulate organic matter (POM), and sedimentary organic matter (SOM) collected in the abyssal zone (solid symbols) and mezooplankton (open symbols) in the Sea of Japan. Ad: *Anonyx derjugini*; Dv: *Delectopecten vancouverensis*; E: *Edwardsia sojabio*; Es: *Eurycope spinifrons*; Hd: *Harmothoe derjugini*; Hi: *Harmothoe impar impar*; Hs: Hexactinellid sponge; Ol: *Ophiura leptoctenia*; T: *Thyasira* (*Parathyasira*) sp.; Ss: *Styela squamosa*. Data on copepods (*Metridia pacifica*) from Park et al. (2011)

Fatty acid composition

The SOM and POM samples from all stations showed similar FA profiles (see Table A1). The main FA was 16:0, with average concentrations of 21.7% in SOM and 22.8% in POM. The second most prevalent FA was 18:1ω9, with average concentrations of 13.3% in SOM and 15.9% in POM. We found elevated average concentrations of 16:1ω10 (4.2% in SOM and 4.6% in POM), which exceeded the levels of 16:1ω7 in POM and some SOM samples. Polyunsaturated FAs (PUFA) were represented mainly by 18:2ω6, with average concentrations of 8.2% in SOM and 8.8% in POM. The concentrations of 20:5ω3 were, on average, 2.9% in SOM and 3.4% in POM. The concentrations of 20:4ω6 and 22:6ω3 were relatively low in all SOM and POM samples. Low proportions of odd and branched FAs were found in SOM and POM samples (generally <1% of total FAs). The levels of 18:1ω7 in SOM and POM were 3.8% and 2.3% on average, respectively.

In the lipids of the foraminifera *Oolina lineata*, the dominant FAs were 20:5ω3 (19.1%), 16:1ω7 (13.3%), 20:4ω6 (12.3%), 18:1ω9 (5.6%) and 16:4ω1 (5.6%).

We found no substantial differences in FA composition among samples of the same species of benthic invertebrates collected at different stations and pooled FA data from different sites (Table 2), with the exception of samples of the brittle star *Ophiura leptoctenia* from Stns A6 and D2, which showed large differences in the contents of all main FAs (ANOVA Tukey's HSD test, $p < 0.01$). The FA compositions of most invertebrate species were dominated by monounsaturated FAs (MUFAs), the content of which ranged from 31.2 to 53.5%. The levels of MUFAs were higher than the levels of PUFAs in 5 of the 9 species studied. In all species, 18:1ω9 was the major MUFA, with the exception of *O. leptoctenia,* for which 20:1ω13 was the major MUFA. High levels of 20:1 and 22:1 MUFAs were observed in *Delectopecten vancouverensis* and *Edwardsia sojabio*. The highest level of 18:1ω7 was found in lipids of *Eurycope spinifrons*, and the highest level of 16:1ω7 was found in *Anonyx derjugini* (Table 2). The total percentage of SFAs in the lipids of abyssal invertebrates ranged from 14.3 to 22.6%, with the highest values measured in *O. leptoctenia.* Among the saturated FAs (SFA), 16:0 was dominant in all invertebrates, and the content of 16:0 varied from 7.4% in *Styela squamosa* to 15.3% in *O. leptoctenia*. The proportion of other SFAs did not exceed 5% of the total FAs (Table 2). PUFA proportions ranged from 17.9% in *Thyasira* (*Parathyasira*) sp. to 40.1% in *O. leptoctenia.* In most species, the FA 20:5ω3 was the dominant PUFA, although 22:6ω3 was only the dominant PUFA in the polychaetes *Harmothoe derjugini* and *Harmothoe impar impar*. A high level of 22:5ω3 was observed in *E. sojabio*, and a high level of 24:6ω3 was detected in *O. leptoctenia* (Table 2).

Invertebrate species from the SJ abyssal zone were clearly separated by their FA compositions on the PCA plots (Fig. 3). The exceptions were 2 species of polychaetes, *Harmothoe derjugini* and *Harmothoe impar impar*, which showed a partly overlapping area on the PCA plot. The first 3 principal components together explained 58.4% of the total variance. The FAs that contributed most to the separation of species along PC1, which explains 23.2% of the total variance, were 22:1ω11, 20:1ω11, 22:2Δ7,15 and 20:2Δ5,13. The FAs that contributed most to the separation of species along PC2, which explains 19.0% of the total variance, were *anteiso*-17:0, 16:1ω5, 20:1ω9 and 20:5ω3. The FAs that contributed most to the separation of species along PC3, which explains

Table 2. Fatty acid composition (% of total fatty acids) of total lipids from benthic invertebrates (mean ± SD). Table contains only fatty acids with concentrations >1% in at least one sample. Prefixes '*i*' and '*a*': *iso* and *anteiso* methyl branching, respectively

Fatty acid	*Harmothoe derjugini* (n = 12)	*Harmothoe impar impar* (n = 5)	*Anonyx derjugini* (n = 7)	*Eurycope spinifrons* (n = 3)	*Edwardsia sojabio* (n = 6)	*Delectopecten vancouverensis* (n = 3)	*Thyasira* (*Parathyasira*) sp. (n = 5)	*Ophiura leptoctenia* Stn A6 (n = 3)	*Ophiura leptoctenia* Stn D2 (n = 3)	*Styela squamosa* (n = 5)
14:0	3.0 ± 0.6	2.9 ± 0.8	1.9 ± 0.7	2.1 ± 0.3	1.6 ± 0.6	3.6 ± 0.7	2.8 ± 0.3	5.1 ± 0.4	4.5 ± 0.4	1.9 ± 0.3
*ai*15:0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.1	0.2 ± 0.1	1.5 ± 0.5	0.4 ± 0.0	0.1 ± 0.0	0.3 ± 0.0
*i*16:0	0.1 ± 0.0	0.0	0.1 ± 0.0	0.2 ± 0.1	0.1 ± 0.1	0.3 ± 0.1	0.9 ± 0.2	0.2 ± 0.0	0.1 ± 0.0	0.5 ± 0.1
16:0	10.7 ± 0.9	11.1 ± 1.6	13.2 ± 1.6	10.4 ± 1.1	10.7 ± 2.2	11.8 ± 0.8	11.0 ± 3.1	7.5 ± 0.4	15.3 ± 1.8	7.4 ± 1.3
*ai*17:0	0.3 ± 0.1	0.1 ± 0.1	0.3 ± 0.1	0.6 ± 0.2	0.1 ± 0.1	0.6 ± 0.1	2.1 ± 1.2	0.2 ± 0.0	0.1 ± 0.0	0.5 ± 0.1
16:1ω5	0.4 ± 0.1	0.4 ± 0.1	0.1 ± 0.1	0.4 ± 0.1	0.2 ± 0.1	0.5 ± 0.1	5.0 ± 1.2	0.3 ± 0.0	0.2 ± 0.0	0.8 ± 0.2
16:1ω7	5.4 ± 1.5	4.8 ± 1.1	11.4 ± 2.5	10.4 ± 2.1	3.5 ± 1.3	6.7 ± 1.5	11.0 ± 1.8	3.7 ± 0.1	5.0 ± 0.3	7.2 ± 2.3
7Me16:1ω10	0.3 ± 0.0	0.2 ± 0.1	0.6 ± 0.2	0.7 ± 0.2	0.7 ± 0.2	0.5 ± 0.0	0.3 ± 0.3	0.6 ± 0.0	0.3 ± 0.0	1.3 ± 0.4
18:0	2.5 ± 0.4	2.1 ± 0.4	0.8 ± 0.2	1.8 ± 1.4	3.9 ± 0.4	2.9 ± 0.9	5.6 ± 1.7	4.4 ± 0.1	2.7 ± 0.5	3.7 ± 0.3
18:1ω11	2.5 ± 1.0	1.2 ± 0.9	0.0	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.1	0.0	1.5 ± 0.1	0.9 ± 0.0	0.5 ± 0.1
18:1ω9	6.8 ± 1.8	9.4 ± 2.7	27.4 ± 2.9	15.1 ± 0.9	9.4 ± 2.7	7.5 ± 1.5	11.1 ± 1.9	7.4 ± 0.9	14.1 ± 0.5	8.2 ± 2.7
18:1ω7	4.5 ± 0.3	6.1 ± 0.6	5.7 ± 0.7	7.2 ± 0.6	3.9 ± 0.8	4.1 ± 1.2	4.1 ± 0.3	4.5 ± 0.2	6.6 ± 0.2	4.0 ± 0.3
18:1ω5	0.9 ± 0.1	0.8 ± 0.3	0.8 ± 0.3	0.9 ± 0.0	1.1 ± 0.6	0.8 ± 0.1	1.2 ± 0.3	1.2 ± 0.1	0.4 ± 0.0	0.3 ± 0.1
18:2ω6	1.7 ± 0.3	2.3 ± 0.4	1.4 ± 0.3	1.8 ± 0.4	2.2 ± 0.9	1.6 ± 0.7	5.8 ± 1.6	1.5 ± 1.2	2.1 ± 1.2	1.9 ± 0.5
18:4ω3	0.6 ± 0.1	0.5 ± 0.3	0.7 ± 0.2	1.1 ± 0.1	0.2 ± 0.1	0.5 ± 0.1	0.7 ± 0.2	0.1 ± 0.0	0.1 ± 0.1	0.2 ± 0.1
20:1ω13	5.2 ± 0.9	5.0 ± 2.0	0.0	0.0	0.0	0.0	3.4 ± 0.6	8.5 ± 0.4	7.2 ± 1.6	0.0 ± 0.0
20:1ω11	0.0	0.0	2.4 ± 0.7	1.8 ± 0.6	5.0 ± 1.8	6.9 ± 0.6	0.0	0.0	0.0	2.7 ± 1.1
20:1ω9	1.8 ± 0.3	2.2 ± 0.9	2.4 ± 0.4	2.1 ± 0.8	2.9 ± 0.7	2.0 ± 0.4	1.1 ± 0.5	0.9 ± 0.2	2.2 ± 0.1	1.5 ± 0.4
20:1ω7	1.9 ± 0.6	1.4 ± 0.2	0.9 ± 0.4	0.5 ± 0.2	1.1 ± 0.2	2.1 ± 0.5	2.2 ± 0.2	0.6 ± 0.0	0.6 ± 0.1	1.1 ± 0.2
20:2Δ5,11	0.7 ± 0.3	1.0 ± 0.4	0.0	0.0	0.0	0.4 ± 0.0	0.5 ± 0.3	1.0 ± 0.0	1.1 ± 0.5	0.0
20:2Δ5,13	1.5 ± 0.5	1.8 ± 0.9	0.0	0.0	0.0	0.2 ± 0.0	0.5 ± 0.2	0.1 ± 0.0	0.2 ± 0.1	0.0
20:2ω6	0.9 ± 0.2	0.9 ± 0.1	0.4 ± 0.2	0.4 ± 0.3	0.6 ± 0.5	0.5 ± 0.0	0.7 ± 0.2	0.2 ± 0.0	0.1 ± 0.1	1.0 ± 0.9
20:4ω6	2.0 ± 0.3	1.2 ± 0.5	1.2 ± 0.4	2.3 ± 0.2	1.8 ± 0.4	1.9 ± 0.5	2.8 ± 0.7	1.6 ± 0.1	0.9 ± 0.1	7.0 ± 2.3
20:5ω3	15.4 ± 2.2	14.6 ± 3.0	10.6 ± 1.8	18.7 ± 3.3	18.7 ± 2.1	12.4 ± 0.3	4.8 ± 0.9	18.3 ± 0.1	14.8 ± 0.4	17.2 ± 3.8
22:1ω13	1.8 ± 0.6	1.2 ± 0.6	0.0	1.9 ± 0.8	0.0	0.0	1.0 ± 0.5	0.0	0.0	0.0
22:1ω11	0.0	0.0	1.3 ± 0.4	0.4 ± 0.2	5.3 ± 2.2	5.7 ± 0.7	0.0	2.3 ± 0.3	2.8 ± 0.4	4.7 ± 2.3
22:1ω9	0.4 ± 0.2	0.4 ± 0.4	0.6 ± 0.1	0.1 ± 0.1	2.2 ± 0.6	0.4 ± 0.4	0.2 ± 0.3	1.0 ± 0.1	2.1 ± 0.2	0.6 ± 0.1
22:2Δ7,13	1.0 ± 0.4	1.0 ± 0.3	0.0	0.0	0.0	0.3 ± 0.2	0.0	0.0	0.3 ± 0.1	0.0 ± 0.0
22:2Δ7,15	1.2 ± 0.2	1.9 ± 0.8	0.0	0.0	0.0	0.2 ± 0.3	0.2 ± 0.2	0.2 ± 0.0	0.0	0.0
22:5ω3	1.4 ± 0.3	0.9 ± 0.2	0.3 ± 0.0	0.6 ± 0.2	11.9 ± 4.0	1.5 ± 0.1	1.0 ± 0.2	0.1 ± 0.0	0.1 ± 0.0	1.2 ± 0.4
22:6ω3	15.9 ± 2.9	15.9 ± 3.3	7.2 ± 1.0	7.5 ± 2.5	2.0 ± 0.4	12.2 ± 0.9	2.2 ± 0.7	4.4 ± 0.4	1.9 ± 0.4	10.0 ± 2.0
24:6ω3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.7 ± 0.4	4.9 ± 0.7	0.0
Other fatty acids[a]	9.1	8.6	8.2	10.8	10.6	11.4	16.3	8.5	8.3	14.3

[a]Other fatty acids were 14:1ω7, *i*15:0, 15:0, 16:1ω10, 16:3ω4, 16:4ω1, *i*17:0, 17:0, 17:1ω8, *i*18:0, 18:3ω3, 19:0, 19:1ω8, 21:5ω3, 22:4ω6, 22:5ω6, 24:1ω9

16.2% of the total variance, were 16:1ω7, 18:1ω9, 18:0 and 24:6ω3 (Fig. 3).

DISCUSSION

Food sources for benthic invertebrates

Our mean estimates of isotopic compositions for abyssal SOM and POM collected with the multiple corer (Table 1) were similar to the $\delta^{13}C$ and $\delta^{15}N$ values of particles collected by sedimentary traps and the SOM in the Japan Basin reported previously (Nakanishi & Minagawa 2003). A comparison of SOM isotope data for the abyssal zone (Table 1) and the continental slope of the SJ (Kharlamenko et al. 2013; Table 1) showed no difference in $\delta^{13}C$ levels, and did not confirm the contribution of the ^{13}C-enriched organic matter of seagrasses (Kharlamenko et al. 2001) or macroalgae (France 1995) to the SOM at the deepest stations where seagrass debris was observed (Brandt et al. 2013).

The FA compositions of abyssal SOM samples (Table A1 in the Appendix) were similar to those of SOM samples from the continental slope of the SJ obtained during the SoJaBio expedition (Kharlamenko et al. 2013), indicating a similarity in sources of organic matter that contribute to the SJ abyssal and bathyal environments. Two characteristic features of all deep-water SOM samples from the SJ

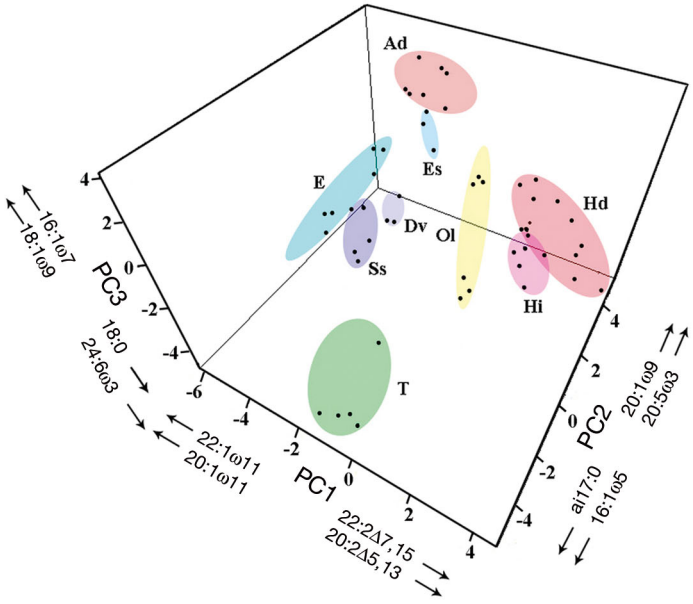

Fig. 3. Plot of the first 3 principal components derived from the fatty acid composition of individual specimens of invertebrates of the abyssal zone in the Sea of Japan. Arrows: fatty acids contributing most to the distribution of species along each component. Ad: *Anonyx derjugini*; Dv: *Delectopecten vancouverensis*; E: *Edwardsia sojabio*; Es: *Eurycope spinifrons*; Hd: *Harmothoe derjugini*; Hi: *Harmothoe impar impar*; Ol: *Ophiura leptoctenia*; T: *Thyasira* (*Parathyasira*) sp.; Ss: *Styela squamosa*

(high levels of 18:2ω6 and the presence of 16:1ω10) are not typical of deep-water marine sediments (Baird & White 1985, Baird et al. 1985). The FA 18:2ω6 has often been considered to be a marker of terrestrial organic matter in shallow-water marine SOM (Napolitano et al. 1997, Budge & Parrish 1998), although the sources of this FA in marine SOM can include fungi, macroalgae, protozoa, cyanobacteria (Findlay et al. 1990) and seagrasses (Khotimchenko 1993). Approximately 73% of the PUFAs preserved in the sediments in Trinity Bay, Newfoundland were shown to be composed of 18:2ω6 and 18:3ω3 in similar proportions. It was suggested that other PUFAs of marine origin, rather than these C_{18} PUFAs of terrestrial origin, were selectively consumed by zoobenthos (Budge & Parrish 1998). In the SOM and POM samples from the abyssal zone of the SJ, 18:2ω6 comprised 38-69% of the total PUFA content, whereas the levels of 18:3ω3 did not exceed 0.9% of the total FA content (Table A1). Terrestrial plant detritus, macroalgae and seagrasses have approximately equal 18:2ω6 and 18:3ω3 contents (Khotimchenko 1993, Budge & Parrish 1998, Khotimchenko 1998). Therefore, allochtonous detritus of seagrasses and macroalgae could not be a substantial contributor to the SOM of the SJ abyssal zone.

In deep-water SOM, the main C_{16} MUFA was usually 16:1ω7 (Baird & White 1985, Baird et al. 1985), and 16:1ω10 was rarely detected—and then as a minor component only (Baird & White 1985). As the main C_{16} MUFA, 16:1ω10 was found in the POM of several oceanic areas around Australia and in lipids derived from the cuticle and muscle of some crustaceans (Nichols et al. 1989), and also in the faecal pellets of copepods and euphausiids (Mayzaud et al. 2007). In some of our SOM samples and all of our POM samples, levels of 16:1ω10 were higher than those of 16:1ω7, indicating that zooplankton residues and faecal pellets are important sources for the SJ abyssal SOM.

The relatively high total PUFA content in our SOM samples was similar to that in SOM from the SJ continental slope (Kharlamenko et al. 2013) and other deep-water areas (Würzberg et al. 2011b). The contents of total organic carbon in the bottom sediments (0 to 1 cm layer) sampled in the Japan Basin and the continental slope of the SJ during the SoJaBio expedition varied from 0.90 to 2.54% (of dry matter) and showed no correlation with water depth (Trebukhova et al. 2013). Along with the high PUFA levels in SOM samples, these data suggested that the quantity and quality of SOM as a food source for benthic invertebrates were not generally depleted in the abyssal environment of Japan Basin compared to continental slope of the SJ and other deep-water eutrophic areas (Sokolova 1997).

The FA composition of *Oolina lineata* was characterised by elevated concentrations of 20:4ω6. Similar concentrations of this fatty acid were also found in other deep-sea benthic foraminifera (Suhr et al. 2003, Würzberg et al. 2011b). Given that consumers of the diatom-based epipelagic food web are usually depleted in 20:4ω6 (Dalsgaard et al. 2003), we used this FA as a marker for evaluation of benthic protists in the abyssal food web of the SJ.

The euphausiid *Thysanoessa* spp. and copepod *Metridia pacifica* were the most abundant interzonal mesozooplankton species entering the deep waters of the SJ (Vinogradov 1973, Vinogradov & Sazhin 1978). Data on the isotopic composition of the SJ zooplankton are extremely limited. The $\delta^{13}C$ and $\delta^{15}N$ values reported for *M. pacifica* from the sites (Park et al. 2011) corresponding to the southern part of our study area were lower than the values of the corresponding isotopic signatures of our euphausiid *Thysanoessa* spp. samples (Fig. 2). The large difference in $\delta^{15}N$ values (ca. 4‰) can be partly attributed

to the higher trophic status of omnivorous euphausiids compared to the primary consumer *M. pacifica* (Park et al. 2011). The differences in $\delta^{13}C$ values (approximately 2.5‰) of mesozooplankton species may indicate considerable spatial variations of isotopic values of the plankton food base in the study area, which corresponds to a known inshore–offshore isotopic trend (Miller et al. 2008).

Feeding mode of invertebrates

In our collection, specimens of the blind endemic polynoid polychaete *Harmothoe derjugini*, the most abundant species among the SJ deep-water macro- and megabenthos (Pasternak & Levenstein 1978), were found only at the deepest stations. Based on gut content analysis, *H. derjugini* has been classified as a carnivorous and even cannibalistic species, ingesting individuals of its own species in addition to slowly moving or immobile sunken planktonic amphipods (Sokolova 1982). Cannibalism presupposes that large individuals should occupy higher trophic positions and have significantly higher $\delta^{15}N$ values than small size classes of the same species (Hobson & Welch 1995). We found no significant trend in $\delta^{15}N$ values among different-sized individuals of *H. derjugini* collected at the same station, which suggested that both young and adult polychaetes shared the same diet and similar trophic status and did not support the notion that this species was primarily cannibalistic (Sokolova 1986). The FA profile of *H. derjugini* was similar to the profiles of deep-sea carnivorous polychaetes (Würzberg et al. 2011a) and was characterised by high 20:5ω3 and 22:6ω3 contents, indicating an epipelagic origin of the prey of this species (Dalsgaard et al. 2003). Relatively low C_{20} and C_{22} MUFA levels indicated that planktonic amphipods, which usually have a high abundance of 20:1ω9 and 22:1ω11 (Falk-Petersen et al. 1987), could not be an important source of food for the *H. derjugini* individuals that we collected. The FA 22:6ω3, which is one of the most important PUFAs in the higher trophic levels of pelagic food webs (Dalsgaard et al. 2003), was the main FA of *H. derjugini*, and its concentration was highest in this organism among all of the studied invertebrates (Table 2). Copepods were also noted as a possible food source for *H. derjugini* (Sokolova 1986). Notably, the consumption of copepods should be accompanied by an increase in the concentration of C_{22} and C_{20} MUFAs (Petursdottir et al. 2012), but this was not observed in the case of *H. derjugini*. One reason for this finding could be that the copepod *Metridia pacifica* dominated zooplankton in the SJ at depths >1000 m (Vinogradov & Sazhin 1978). This copepod species was characterised by low concentrations of C_{20} and C_{22} MUFAs and a high concentration of 22:6ω3 (El-Sabaawi et al. 2010). The high proportion of 22:6ω3 in the lipids of *H. derjugini* once again highlights that, in some cases, 22:6ω3 can serve as an indicator for a carnivorous diet of invertebrates (Kharlamenko et al. 1995).

Another abundant polychaete, identified as *Harmothoe impar impar* (a subspecies of eurybathic *H. impar* considered to be an active predator; Fauchald & Jumars 1979), was not found to co-occur with *Harmothoe derjugini* in our survey and was represented only by large adult individuals at the basin periphery stations. The compositions of FAs in our samples of *H. impar impar* were similar to those of *H. derjugini* (Table 2). Notable differences were only found in the proportion of some minor FAs, which did not exceed 2.5% of the total FA content. In the three-dimensional (3D) plot of the first 3 principal components derived from the FA composition of individual specimens of invertebrates in the SJ abyssal zone (Fig. 3), *H. impar impar* occupied the same area as *H. derjugini*, indicating a similar diet for these polychaetes. Similar high $\delta^{15}N$ values of both species (Fig. 2) confirmed the similarity in the trophic position of these polychaetes, which inhabit different depth ranges on the SJ abyssal floor. Notable ^{13}C-enrichment of *H. impar impar* from the basin periphery stations in comparison to *H. derjugini* from the deepest stations can be attributed to spatial ^{13}C-enrichment of mesozooplankton close to the mainland (Miller et al. 2008), which we believe are the main prey for both of these species, rather than to differences in diet.

The peracarid crustaceans *Anonyx derjugini* and *Eurycope spinifrons* were endemic to the abyssal zone of the SJ and constituted a separate group in Fig. 3. Lysianassid amphipods of the genus *Anonyx* were observed to feed on dead or weakened animals and showed typical adaptations necessary for scavenger feeding (Sainte-Marie 1984, Nygård et al. 2012). *A. derjugini* had high levels of 18:1ω9 and the highest 18:1ω9/18:1ω7 ratio among the studied invertebrates (Table 2). Large quantities of the FA 18:1ω9 can be synthesised by amphipods to overcome long periods of starvation, a common situation for scavengers (Nyssen et al. 2005). The 18:1ω9/18:1ω7 ratio was shown to reflect the peculiarities of this feeding behaviour and, to some degree, the trophic levels of the benthos, increasing from suspension feeders to predators and then to scavengers (Graeve et al.

1997). High $\delta^{15}N$ values of *A. derjugini* confirmed the high trophic position of this species, similar to that of the carnivorous polychaetes *Harmothoe derjugini* and *Harmothoe impar impar* (Fig. 2). On the 3D plot of the first 3 principal components derived from the FA compositions of individual specimens of invertebrates of the SJ (Fig. 3), *A. derjugini* was spatially distant from *H. derjugini* and *H. impar impar*, primarily because of its high concentration of 18:1ω9 and relatively low concentration of 22:6ω3. We propose that *A. derjugini* is a scavenger and feeds mostly on dead animals, in contrast to the *Harmothoe* species.

The endemic isopod *Eurycope spinifrons* was recently shown to be one of the most abundant species of abyssal invertebrates in the SJ (Brandt et al. 2013), and individuals of *E. spinifrons* at deeper stations grow larger because of reduced competition (Elsner et al. 2013). Isopods of the genus *Eurycope* were previously regarded as deposit-feeders, but because of the regular presence of the remains of animals in their guts, they have been referred to as carnivores (Sokolova 1986) or omnivores, given that they are capable of both deposit-feeding and predation (Sokolova 1997). Given that the guts of *E. spinifrons* individuals from the SJ contained mainly diatoms and some ciliates, flagellates and plant fibres, possibly from seagrasses, Elsner et al. (2013) suggested that this species mainly consumes phytodetritus. The FA profiles of *E. spinifrons* samples were similar to those of *Anonyx derjugini* (Fig. 3), indicating similarity in the food sources of these peracarid crustaceans. The mean $\delta^{15}N$ value of *E. spinifrons* was not significantly lower than that of the polychaetes *Harmothoe* and scavenger *A. derjugini* (Table 1). The 18:1ω9/18:1ω7 ratio of *E. spinifrons* confirmed the high trophic position of this isopod; this ratio was similar to those of the carnivores *Harmothoe* spp. but lower than that of *A. derjugini* (Table 2), as is typical for scavengers (Nyssen et al. 2005). Given that foraminifera could play an important role in the diet of some *Eurycope* species (Svavarsson et al. 1993), we compared the FA compositions of *E. spinifrons* with those of the foraminifera *Oolina lineata*, which was the most abundant species at the isopod collection site (Stn B4). Both species showed some similar features, including their high levels of 20:5ω3, C_{16} PUFAs and 16:1ω7, which are common indicators of consumers of diatom-based food webs (Kharlamenko et al. 2008). However, the concentration of 20:4ω6 in *E. spinifrons* was too low to determine whether this carnivorous species feeds upon foraminifera, because feeding on foraminifera may lead to higher concentrations of 20:4ω6 in the lipid compositions of isopods (Würzberg et al. 2011b). *E. spinifrons* showed no isotopic or FA signs of notable contribution of seagrasses or macroalgae detritus to its food sources. This species was among the most ^{13}C-depleted invertebrates in the SJ abyss (Fig. 2), whereas deep-water consumers that directly or indirectly derived a significant proportion of their nutrition from seagrasses detritus were shown to be highly ^{13}C-enriched (Suchanek et al. 1985).

The actinia *E. sojabio* appeared to be very common at abyssal depths in the SJ, dwelling in soft bottom sediments, and is not known in other regions (Sanamyan & Sanamyan 2013). Deep-sea anemones that inhabited soft bottom sediments were classified as carnivores that preyed upon slowly moving benthic isopods (Sokolova 1986). In terms of isotopic composition, *E. sojabio* is very similar to *Eurycope spinifrons*, the only isopod species recorded in the SJ abyss (Golovan et al. 2013), suggesting similar trophic positions and food sources for these 2 invertebrate species rather than a predator-prey relationship. The FA compositions of *E. sojabio* revealed high concentrations of the MUFAs C_{20} and C_{22}, which are characteristic of planktonic copepods and amphipods (Falk-Petersen et al. 1987). Moreover, *E. sojabio* showed the highest proportions of 20:5ω3 along with the lowest $\delta^{13}C$ values among the investigated the SJ abyssal invertebrates, suggesting that the most likely food for *E. sojabio* is planktonic crustaceans.

Pasternak & Levenstein (1978) identified the pectinid bivalve *Delectopecten vancouverensis* as an abundant species in the SJ abyssal zone. An interesting feature of the *D. vancouverensis* specimens collected in our survey was the attachment of many individuals of this species to the tubes of polychaetes a few inches above the soft bottom (Fig. 4). This position significantly narrowed the choice of potential food items. Most deep-sea pectinids are considered to be carnivores (Sokolova 1986) and have been shown to prey primarily upon benthic harpacticoid copepods (Hicks & Marshall 1985). The high $\delta^{15}N$ values and 18:1ω9/18:1ω7 ratio of *D. vancouverensis* from the SJ, which were similar to those of carnivorous polychaetes, confirmed the high trophic position of this bivalve mollusc. The FA profile of *D. vancouverensis* was similar to that of *Edwardsia sojabio* and characterised by high proportions of the MUFAs 20:1ω11 and 22:1ω11 in comparison to other studied species (Table 2). The presence of high concentrations of C_{20} and C_{22} MUFAs in the lipids of *D. vancouverensis* confirmed the important role of copepods as food for this carnivorous bivalve.

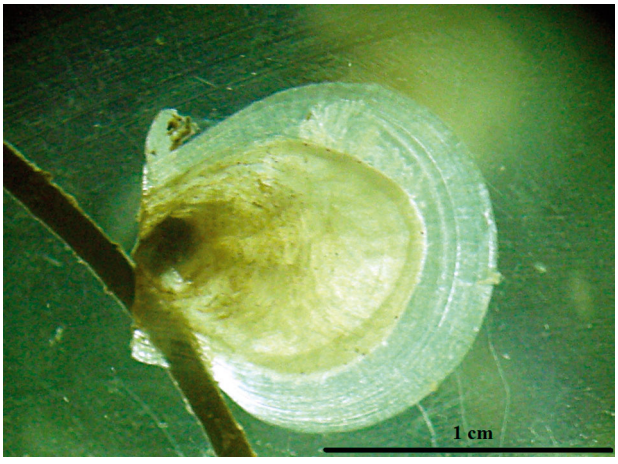

Fig. 4. Bivalve mollusc *Delectopecten vancouverensis* attached to the tube of a polychaete

All samples of the bivalve mollusc *Thyasira* (*Parathyasira.*) sp. were located away from the other species on the 3D plot of first 3 principal components (Fig. 3), indicating unusual food sources for this animal. Many thyasirid species may contain symbiotic bacteria in their gills (Southward 1986, Dufour 2005), and these chemoautotrophic symbionts may be the source of ^{13}C-depleted organic matter for their bivalve hosts (Dando & Southward 1986, Dando & Spiro 1993). Tissues of the symbiotrophic thyasirid showed lower δ^{13}C values than other sympatric bivalves (Dando & Spiro 1993). The FA composition of symbiont-containing thyasirids showed high proportions of 18:1ω7 and 20:1ω13 MUFAs and only low proportions of C_{20} and C_{22} PUFAs (Fullarton et al. 1995). Samples of *Thyasira* (*P.*) sp. from the abyssal zone of the SJ had δ^{13}C values similar to those of other bivalves from the continental slope of the SJ (Kharlamenko et al. 2013), and their FA compositions had low concentrations of 18:1ω7 and 20:1ω13 (Table 2) in contrast to known symbiotrophic thyasirids. It has been experimentally shown that the degree of thyasirid symbiotrophy strongly depends on the quantity of nutritive particles and concentration of reduced sulphur compounds in the local environment. With high concentrations of oxygen in the interstitial water and an abundance of organic matter, the δ^{13}C values of thyasirids did not differ from those of filter-feeders from the same community (Dufour & Felbeck 2006). The absence of reduced sulphur compounds in the SJ abyssal sediments or the absence of bacterial symbionts, as in other species of subgenus *Parathyasira* (Dufour 2005), may be the main reason for the lack of an isotopic and FA signature of symbiotrophy in our *Thyasira* (*P.*) sp. samples. However, this species drastically differed from other studied abyssal invertebrates by its low proportion of C_{20} and C_{22} PUFAs, its high levels of 18:2ω6 and the odd and branched bacterial FAs in its lipids. According to these FA characteristics, *Thyasira* (*P.*) sp. appeared to be the only species in the studied invertebrate community, relying mostly on SOM and bacteria associated with the sediment for food.

The stomach contents of *Ophiura leptoctenia* vary greatly depending on the location of the collection (Litvinova 1979). Thus, this brittle star may be a carnivore or deposit feeder, and the main food of *O. leptoctenia* was found to be euphausiids in most cases (Litvinova 1979). Our data confirmed the high degree of omnivory of *O. leptoctenia*, which used a carnivorous feeding mode together with detritophagy in the SJ abyssal zone. *O. leptoctenia* showed largest intraspecific difference in δ^{15}N values among samples collected at different sites. We considered this isotopic difference to mainly result from a shift in the trophic position of this omnivorous species rather than a consequence of spatial variations of the δ^{15}N of the food base, because other invertebrates collected at these stations had similar δ^{15}N values. The samples of *O. leptoctenia* characterised by high δ^{15}N values (Stn A6) had significantly higher concentrations of 22:6ω3 and 24:6ω3 (ANOVA Tukey's HSD test, $p < 0.001$) than individuals with low δ^{15}N values (Stn D2). The latter were characterised by a high 16:0 content and higher levels of MUFAs. On the 3D plot, they were located far from *Harmothoe derjugini* and other carnivores (Fig. 3).

The ascidia *Styela squamosa* was not abundant in the SJ abyssal zone and was collected at only one site (Stn B5) close to the continental slope. Because it had the highest δ^{15}N values recorded in this study, this species had the highest apparent trophic status among the studied invertebrates, but the reason for this ^{15}N-enrichment remains unknown. The main food source for the shallow-water filter-feeding *Styela* species is live microalgae (Jiang et al. 2008). The abyssal species *S. squamosa* lacked the opportunity to consume live microalgae, as confirmed by its high δ^{15}N values, it but could ingest suspended food particles of the same size class from the microbial food web. *S. squamosa* had a peculiar FA composition, i.e. high concentrations of both 20:4ω6 and 7Me16:1ω10 FAs. This last FA is considered to be typical for the microbial food web (Carballeira et al. 1996), and 20:4ω6 was abundant in the benthic protist *Oolina lineata* identified in our study. The combined FA and stable isotope results suggested that *S. squamosa* could be a 'top predator' of the relatively long microbial food web.

Trophic structure of abyssal community

We found no correlation between the $\delta^{15}N$ and $\delta^{13}C$ values measured in all invertebrate samples ($r = -0.02$, $N = 73$). In deep-sea communities, strong positive correlations between the $\delta^{15}N$ and $\delta^{13}C$ values of consumers point toward a single primary food source supporting the community (Polunin et al. 2001, Fanelli et al. 2011). The absence of such a correlation in the SJ community could reflect the heterogeneity of food sources entering this benthic food web. For example, the above-mentioned ^{13}C-enrichment of invertebrates collected at the basin periphery stations relative to those from the deepest stations may indicate the lateral transport of ^{13}C-enriched fresh organic matter from the shelf area. However, we did not observe corresponding ^{13}C enrichment for samples of the more refractory SOM from the abyssal plain (this study) in comparison to those from the continental slope (Kharlamenko et al. 2013).

Another reason for the absence of a correlation between $\delta^{15}N$ and $\delta^{13}C$ may be the minimal presence of macro- and megabenthic primary consumers among species abundant in the SJ abyssal zone. The simplicity of the food web structure in the SJ abyssal community recorded in the $\delta^{15}N$ versus $\delta^{13}C$ biplot (Fig. 2) suggests that the phytodetritus-based food chains are not well developed here. It appears that the core of this abyssal community consists of several invertebrate species of relatively high trophic status that consume only the most valuable part of possible food resources entering the deep-sea bottom from the pelagic environment (i.e. animal tissues).

Our analysis of the stable isotope and FA compositions of key invertebrate species corroborated the earlier assumptions that the abyssal zoobenthos of the SJ was mainly carnivorous (Pasternak & Levenstein 1978). The majority of the collected zoobenthic species showed high $\delta^{15}N$ values corresponding to trophic positions higher than the third trophic level. However, the $\delta^{15}N$ data alone may not be sufficiently robust to distinguish among the feeding guilds of deep-sea invertebrates (Gontikaki et al. 2011). Our data on FA trophic markers confirmed that all these equally ^{15}N-enriched omnivores, carnivores or scavenger species in the SJ abyssal environment fed mostly on sinking zooplankton animals and were loosely connected with food chains based on bottom detritus and SOM. The phenomenon of 'dead body rain' as the main food source for abyssal benthos is known in highly productive areas of the ocean, where large populations of commercially exploitable euphausiids have been found (Sokolova 1994, 1997). The absence of mesopelagic predators in the deep waters of the SJ was considered a cause of the predominance of carnivorous zoobenthos because of the abundance of zooplankton remains reaching the abyssal floor (Vinogradov 1973, Vinogradov & Sazhin 1978), and our data could corroborate this hypothesis. However, a relatively high downward flow of interzonal mesozooplankton could explain the abundance of carnivores among the SJ abyssal benthos but cannot be a cause of the scarcity of deposit-feeders in benthic communities.

The quantity and quality of SOM in the SJ abyssal zone did not sufficiently differ from that of adjacent areas sufficiently to prevent deposit-feeder distribution. However, only one consumer species, the filter-feeding *Thyasira* (*Parathyasira*) sp., was shown to be tightly associated with SOM as its food source in our study. Other macrobenthos, which can most likely be associated with SOM, were represented in the SJ abyss by several eurybathic and widespread polychaetes species (Alalykina 2013) and 2 species of small opportunistic tanaidacean crustaceans (Golovan et al. 2013), which were not included in our survey because of their low biomass. The meiofauna, another important trophic link connected with SOM, showed a density in SJ deep waters at least 10 times lower than what had been recorded for the adjacent Pacific Ocean, and polychaetes (most likely juveniles) were the most abundant meiobenthic group at all of the deepest stations of the SoJaBio expedition survey (Trebukhova et al. 2013).

This study of the trophic structure of the abyssal community of the SJ revealed the dominant role of descended zooplankton as a food resource for mega- and macrobenthos in this marginal deep-water environment. Despite the proximity of the productive shelf area, which provides plant residues to the deep-water basin of the SJ, we found no isotopic or FA indications of feeding on allochtonous detritus of seagrasses and macroalgae among abyssal consumers. Various key consumer species of the SJ abyssal food web occupied similar trophic positions and fed predominantly on descended zooplankton. Our data did not corroborate cannibalism as a feeding mode of the abundant abyssal carnivorous polychaetes as has been suggested.

We hypothesise that the specific food web structure of the SJ abyssal invertebrate community, which is characterised by the dominance of evidently endemic species that rely on 'the rain of corpses' and the absence of deposit feeders, is a result of the very short historical development of this isolated abyssal community following a deep-water anoxic event dur-

ing the Last Glacial Maximum. It is likely that we have only observed the initial step of the abyssal succession in which endemic carnivores have developed and exploited the most valuable food sources, but the trophic niches of deposit-feeders remain unoccupied.

Acknowledgements. We thank the officers and crew of the RV 'Akademik M. A. Lavrentyev' and all of the SoJaBio participants for their help and support. The foraminiferans analysed in this study were collected and identified by Franck Lejzerowicz, PhD student at the University of Geneva. The SoJaBio expedition was funded by a DFG grant to Angelika Brandt, University of Hamburg (Br 1121/37-1). This work was also supported by the Russian Foundation for Basic Research (Grant 11-04-01108-a), the Far Eastern Branch of the Russian Academy of Sciences (Grant 12-I-P4-02), and the Government of the Russian Federation (Grant 11.G34. 31.0010). We are grateful to the 3 anonymous reviewers for very insightful and thorough comments that greatly improved the initial version of this manuscript.

LITERATURE CITED

Alalykina I (2013) Preliminary data on the composition and distribution of polychaetes in the deep-water areas of the north-western part of the Sea of Japan. Deep-Sea Res II 86-87:164–171

Baird BH, White DC (1985) Biomass and community structure of the abyssal microbiota determined from the ester-linked phospholipids recovered from Venezuela Basin and Puerto Rico Trench sediment. Mar Geol 68:217–231

Baird BH, Nivens DE, Parker JH, White DC (1985) The biomass, community structure, and spatial distribution of the sedimentary microbiota from a high-energy area of the deep sea. Deep-Sea Res A 32:1089–1099

Billett DSM, Lampitt RS, Rice AL, Mantoura RFC (1983) Seasonal sedimentation of phytoplankton to the deep-sea benthos. Nature 302:520–522

Blankenship LE, Levin LA (2007) Extreme food webs: foraging strategies and diets of scavenging amphipods from the ocean's deepest 5 kilometers. Limnol Oceanogr 52: 1685–1697

Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. Can J Biochem Physiol 37: 911–917

Brandt A, Elsner N, Brenke N, Golovan O and others (2013) Epifauna of the Sea of Japan collected via a new epibenthic sledge equipped with camera and environmental sensor systems. Deep-Sea Res II 86-87:43–55

Budge SM, Parrish CC (1998) Lipid biogeochemistry of plankton, settling matter and sediments in Trinity Bay, Newfoundland. II. Fatty acids. Org Geochem 29: 1547–1559

Carballeira NM, Cruz C, Sostre A (1996) Identification of the novel 7-methyl-6-octadecenoic acid in *Holothuria mexicana*. J Nat Prod 59:1076–1078

Carreau JP, Dubacq JP (1978) Adaptation of macro-scale method to the micro-scale for fatty acid methyl transesterification of biological lipid extracts. J Chromatogr A 151:384–390

Dalsgaard J, St John M, Kattner G, Muller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46:225–340

Dando PR, Southward AJ (1986) Chemoautotrophy in bivalve molluscs of the genus *Thyasira*. J Mar Biol Assoc UK 66:915–929

Dando PR, Spiro B (1993) Varying nutritional dependence of the thyasirid bivalves *Thyasira sars*i and *T. equalis* on chemoautotrophic symbiotic bacteria, demonstrated by isotope ratios of tissue carbon and shell carbonate. Mar Ecol Prog Ser 92:151–158

Derjugin KM (1939) Zones and biocenoses of Peter the Great Bay (Sea of Japan). Volume in honor of scientific activity of N. M. Knipovich (1885–1939). Pishchepromizdat, Moscow, p 115–142

Drazen JC, Phleger CF, Guest MA, Nichols PD (2008a) Lipid, sterols and fatty acid composition of abyssal holothurians and ophiuroids from the North-East Pacific Ocean: food web implications. Comp Biochem Physiol B Biochem Mol Biol 151:79–87

Drazen JC, Phleger CF, Guest MA, Nichols PD (2008b) Lipid, sterols and fatty acids of abyssal polychaetes, crustaceans, and a cnidarian from the northeast Pacific Ocean: food web implications. Mar Ecol Prog Ser 372: 157–167

Dufour SC (2005) Gill anatomy and the evolution of symbiosis in the bivalve family Thyasiridae. Biol Bull 208: 200–212

Dufour SC, Felbeck H (2006) Symbiont abundance in thyasirids (Bivalvia) is related to particulate food and sulphide availability. Mar Ecol Prog Ser 320:185–194

El-Sabaawi RW, Sastri AR, Dower JF, Mazumder A (2010) Deciphering the seasonal cycle of copepod trophic dynamics in the Strait of Georgia, Canada, using stable isotopes and fatty acids. Estuar Coast 33:738–752

Elsner NO, Golovan OA, Malyutina MV, Brandt A (2013) Alone in the dark: distribution, population structure and reproductive mode of the dominant isopod *Eurycope spinifrons* Gurjanova, 1933 (Isopoda: Asellota: Munnopsidae) from bathyal and abyssal depths of the Sea of Japan. Deep-Sea Res II 86-87:103–110

Falk-Petersen S, Sargent JR, Tande KS (1987) Lipid composition of zooplankton in relation to the sub-arctic food web. Polar Biol 8:115–120

Fanelli E, Cartes JE, Rumolo P, Sprovieri M (2009) Food-web structure and trophodynamics of mesopelagic-suprabenthic bathyal macrofauna of the Algerian Basin based on stable isotopes of carbon and nitrogen. Deep-Sea Res I 56:1504–1520

Fanelli E, Papiol V, Cartes JE, Rumolo P, Brunet C, Sprovieri M (2011) Food web structure of the epibenthic and infaunal invertebrates on the Catalan slope (NW Mediterranean): Evidence from $\delta^{13}C$ and $\delta^{15}N$ analysis. Deep-Sea Res I 58:98–109

Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. Oceanogr Mar Biol Annu Rev 17:193–284

Findlay RH, Trexler MB, Guckert JB, White DC (1990) Laboratory study of disturbance in marine sediments—response of a microbial community. Mar Ecol Prog Ser 62:121–133

France RL (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Mar Ecol Prog Ser 124:307–312

Fullarton JG, Dando PR, Sargent JR, Southward AJ, Southward EC (1995) Fatty acids of hydrothermal vent *Ridgeia piscesae* and inshore bivalves containing symbiotic bac-

teria. J Mar Biol Assoc UK 75:455–468
Gamo T (2011) Dissolved oxygen in the bottom water of the Sea of Japan as a sensitive alarm for global climate change. Trends Analyt Chem 30:1308–1319
Golovan OA, Błażewicz-Paszkowycz M, Brandt A, Budnikova LL and others (2013) Diversity and distribution of peracarid crustaceans (Malacostraca) from the continental slope and the deep-sea basin of the Sea of Japan. Deep-Sea Res II 86-87:66–78
Gontikaki E, Mayor DJ, Narayanaswamy BE, Witte U (2011) Feeding strategies of deep-sea sub-Arctic macrofauna of the Faroe-Shetland Channel: combining natural stable isotopes and enrichment techniques. Deep-Sea Res I 58: 160–172
Graeve M, Kattner G, Piepenburg D (1997) Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? Polar Biol 18: 53–61
Graf G (1989) Benthic–pelagic coupling in a deep-sea benthic community. Nature 341:437–439
Hicks GRF, Marshall BA (1985) Sex selective predation of deep-sea meiobenthic copepods by pectinacean bivalves and its influence on copepod sex ratios. NZ J Mar Freshw Res 19:227–231
Hobson KA, Welch HE (1992) Determination of trophic relationships within a high arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar Ecol Prog Ser 84:9–18
Hobson KA, Welch HE (1995) Cannibalism and trophic structure in a high arctic lake—insights from stable isotope analysis. Can J Fish Aquat Sci 52:1195–1201
Howell KL, Pond DW, Billett DSM, Tyler PA (2003) Feeding ecology of deep-sea seastars (Echinodermata: Asteroidea): a fatty-acid biomarker approach. Mar Ecol Prog Ser 255:193–206
Iken K, Brey T, Wand U, Voigt J, Junghans P (2001) Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. Prog Oceanogr 50:383–405
Jaschinski S, Hansen T, Sommer U (2008) Effects of acidification in multiple stable isotope analyses. Limnol Oceanogr Methods 6:12–15
Jiang AL, Yu Z, Cai WG, Wang CH (2008) Feeding selectivity of the marine ascidian *Styela clava.* Aquacult Res 39:1190–1197
Kelly JR, Scheibling RE (2012) Fatty acids as dietary tracers in benthic food webs. Mar Ecol Prog Ser 446:1–22
Kharlamenko VI, Zhukova NV, Khotimchenko SV, Svetashev VI, Kamenev GM (1995) Fatty acids as markers of food sources in a shallow water hydrothermal ecosystem (Kraternaya Bight, Yankich Island, Kurile Islands). Mar Ecol Prog Ser 120:231–241
Kharlamenko VI, Kiyashko SI, Imbs AB, Vyshkvartzev DI (2001) Identification of food sources of invertebrates from the seagrass *Zostera marina* community using carbon and sulfur stable isotope ratio and fatty acid analyses. Mar Ecol Prog Ser 220:103–117
Kharlamenko VI, Kiyashko SI, Rodkina SA, Imbs AB (2008) Determination of food sources of marine invertebrates from a subtidal sand community using analyses of fatty acids and stable isotopes. Russ J Mar Biol 34:101–109
Kharlamenko VI, Brandt A, Kiyashko SI, Würzberg L (2013) Trophic relationship of benthic invertebrate fauna from the continental slope of the Sea of Japan. Deep-Sea Res II 86-87:34–42
Khotimchenko SV (1993) Fatty acids and polar lipids of seagrasses from the Sea of Japan. Phytochemistry 33: 369–372
Khotimchenko SV (1998) Fatty acids of brown algae from the Russian Far East. Phytochemistry 49:2363–2369
Kido Y, Minami I, Tada R, Fujine K, Irino T, Ikehara K, Chun JH (2007) Orbital-scale stratigraphy and high-resolution analysis of biogenic components and deep-water oxygenation conditions in the Japan Sea during the last 640 kyr. Palaeogeogr Palaeoclimatol Palaeoecol 247:32–49
Levenstein RY, Pasternak FA (1973) Studies of the bottom fauna in the sea of Japan on the 52nd cruise of the R/V 'Vityaz'. Oceanology (Mosc) 13:1098–1103
Litvinova NM (1979) On the feeding of brittle stars. Zool Zh 58:1501–1510
Logan JM, Lutcavage ME (2008) A comparison of carbon and nitrogen stable isotope ratios of fish tissues following lipid extractions with non-polar and traditional chloroform/methanol solvent systems. Rapid Commun Mass Spectrom 22:1081–1086
Malyutina MV, Brandt A (2013) Introduction to SoJaBio (Sea of Japan Biodiversity Studies). Deep-Sea Res II 86-87:1–9
Mayor DJ, Thornton B, Hay S, Zuur AF, Nicol GW, McWilliam JM, Witte UFM (2012) Resource quality affects carbon cycling in deep-sea sediments. ISME J 6: 1740–1748
Mayzaud P, Laureillard J, Merien D, Brinis A, Godard C, Razouls S, Labat JP (2007) Zooplankton nutrition, storage and fecal lipid composition in different water masses associated with the Agulhas and Subtropical Fronts. Mar Chem 107:202–213
Miller TW, Brodeur RD, Rau GH (2008) Carbon stable isotopes reveal relative contribution of shelf-slope production to the northern California Current pelagic community. Limnol Oceanogr 53:1493–1503
Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains—further evidence and the relation between $\delta^{15}N$ and animal age. Geochim Cosmochim Acta 48:1135–1140
Mokievskii OB (1954) Quantitative distribution of deep-sea bottom fauna of Japan Sea. Tr Inst Okeanol Akad Nauk SSSR 8:147–163
Nakanishi T, Minagawa M (2003) Stable carbon and nitrogen isotopic compositions of sinking particles in the northeast Japan Sea. Geochem J 37:261–275
Napolitano GE, Pollero RJ, Gayoso AM, MacDonald BA, Thompson RJ (1997) Fatty acids as trophic markers of phytoplankton blooms in the Bahia Blanca estuary (Buenos Aires, Argentina) and in Trinity Bay (Newfoundland, Canada). Biochem Syst Ecol 25:739–755
Nichols PD, Volkman JK, Everitt DA (1989) Occurrence of *cis*-6-hexadecenoic acid and other unusual monounsaturated fatty acids in the lipids of oceanic particulate matter. Oceanol Acta 12:393–403
Nygård H, Berge J, Soreide JE, Vihtakari M, Falk-Petersen S (2012) The amphipod scavenging guild in two Arctic fjords: seasonal variations, abundance and trophic interactions. Aquat Biol 14:247–264
Nyssen F, Brey T, Dauby P, Graeve M (2005) Trophic position of Antarctic amphipods—enhanced analysis by a 2-dimensional biomarker assay. Mar Ecol Prog Ser 300: 135–145
Otosaka S, Tanaka T, Togawa O, Amano H, Karasev EV, Minakawa M, Noriki S (2008) Deep sea circulation of particulate organic carbon in the Japan Sea. J Oceanogr 64:911–923

Park JI, Kang CK, Suh HL (2011) Ontogenetic diet shift in the euphausiid *Euphausia pacifica* quantified using stable isotope analysis. Mar Ecol Prog Ser 429:103–109

Pasternak FA, Levenstein RJ (1978) New data on the patterns of deep-sea bottom fauna distribution in the Sea of Japan. Oceanology (Mosc) 18:903–908

Petursdottir H, Falk-Petersen S, Gislason A (2012) Trophic interactions of meso- and macrozooplankton and fish in the Iceland Sea as evaluated by fatty acid and stable isotope analysis. ICES J Mar Sci 69:1277–1288

Polunin NVC, Morales-Nin B, Pawsey WE, Cartes JE, Pinnegar JK, Moranta J (2001) Feeding relationships in Mediterranean bathyal assemblages elucidated by stable nitrogen and carbon isotope data. Mar Ecol Prog Ser 220:13–23

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83: 703–718

Rennie MD, Ozersky T, Evans DO (2012) Effects of formalin preservation on invertebrate stable isotope values over decadal time scales. Can J Zool 90:1320–1327

Sainte-Marie B (1984) Morphological adaptations for carrion feeding in 4 species of littoral or circalittoral lysianassid amphipods. Can J Zool 62:1668–1674

Sanamyan N, Sanamyan K (2013) *Edwardsia sojabio* sp. n. (Cnidaria: Anthozoa: Actiniaria: Edwardsiidae), a new abyssal sea anemone from the Sea of Japan. Deep-Sea Res II 86-87:225–230

Shuntov VP (2001) Biology of far eastern seas of Russia. TINRO Centre, Vladivostok

Smith CR, De Leo FC, Bernardino AF, Sweetman AK, Arbizu PM (2008) Abyssal food limitation, ecosystem structure and climate change. Trends Ecol Evol 23:518–528

Sokolova MN (1972) Trophic structure of deep-sea macrobenthos. Mar Biol 16:1–12

Sokolova MN (1982) On the nutrition of the polychaete *Harmothoe derjugini* in the abyssal zone of the Sea of Japan. Tr Inst Okeanol Akad Nauk SSSR 117:76–80

Sokolova MN (1986) Feeding and trophic structure in the deep-sea macrobenthos. Nauka, Moscow

Sokolova MN (1994) Euphausiid 'dead body rain' as a source of food for abyssal benthos. Deep-Sea Res I 41: 741–746

Sokolova MN (1997) Trophic structure of abyssal macrobenthos. Adv Mar Biol 32:427–525

Southward EC (1986) Gill symbionts in thyasirids and other bivalve molluscs. J Mar Biol Assoc UK 66:889–914

Suchanek TH, Williams SL, Ogden JC, Hubbard DK, Gill IP (1985) Utilization of shallow-water seagrass detritus by Carribean deep-sea macrofauna: $\delta^{13}C$ evidence. Deep-Sea Res I 32:201–214

Suhr SB, Pond DW, Gooday AJ, Smith CR (2003) Selective feeding by benthic foraminifera on phytodetritus on the western Antarctic Peninsula shelf: evidence from fatty acid biomarker analysis. Mar Ecol Prog Ser 262:153–162

Svavarsson J, Gudmundsson G, Brattegard T (1993) Feeding by asellote isopods (Crustacea) on foraminifers (Protozoa) in the deep-sea. Deep-Sea Res I 40:1225–1239

Svetashev VI (2011) Mild method for preparation of 4,4-dimethyloxazoline derivatives of polyunsaturated fatty acids for GC-MS. Lipids 46:463–467

Trebukhova YuA, Miljutin DM, Pavlyuk ON, Mar'yash AA, Brenke N (2013) Changes in deep-sea metazoan meiobenthic communities and nematode assemblages along a depth gradient (North-western Sea of Japan, Pacific). Deep-Sea Res II 86-87:56–65

Vinogradov ME (1973) New data on the quantitative distribution of plankton in the deep layers of the Japan sea. Oceanology (Mosc) 13:1093–1097

Vinogradov ME, Sazhin AF (1978) Vertical distribution of the major zooplankton groups in the northern part of the Sea of Japan. Oceanology (Mosc) 28:312–319

Watling L, Guinotte J, Clark MR, Smith CR (2013) A proposed biogeography of the deep ocean floor. Prog Oceanogr 111:91–112

Witte U, Wenzhöfer F, Sommer S, Boetius A and others (2003) In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. Nature 424: 763–766

Würzberg L, Peters J, Schuller M, Brandt A (2011a) Diet insights of deep-sea polychaetes derived from fatty acid analyses. Deep-Sea Res II 58:153–162

Würzberg L, Peters J, Brandt A (2011b) Fatty acid patterns of Southern Ocean shelf and deep sea peracarid crustaceans and a possible food source, foraminiferans. Deep-Sea Res II 58:2027–2035

Zenkevich LA (1963) Biology of the seas of the USSR. George Allen and Unwin, London

Appendix. Additional data

Table A1. Fatty acid composition (mean ± SD) of sedimentary organic matter lipids (% of total fatty acids) sampled at various depths (m) in the abyssal zone of the Sea of Japan. Letter plus number IDs are station identifiers

Fatty acid	A6 2511 m (n = 3)	B5 2635 m (n = 2)	A7 3344 m (n = 3)	B1 3666 m (n = 2)	B4 3333 m (n = 3)	C3 3421 m (n = 4)	D1 3358 m (n = 3)
14:0	3.5 ± 0.1	4.9 ± 0.6	4.2 ± 0.7	6.4 ± 0.3	3.2 ± 1.4	3.9 ± 0.4	4.7 ± 0.4
14:1ω7	0.8 ± 0.1	0.6 ± 0.0	1.2 ± 0.3	0.8 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.7 ± 0.1
*ai*15:0	1.6 ± 0.3	1.8 ± 0.5	1.1 ± 0.2	1.5 ± 0.1	1.0 ± 0.3	1.2 ± 0.2	1.8 ± 0.3
15:0	2.2 ± 1.0	1.4 ± 0.0	2.1 ± 0.5	2.0 ± 0.2	1.4 ± 0.2	1.1 ± 0.1	1.3 ± 0.2
15:1ω7	0.6 ± 0.1	0.4 ± 0.0	0.7 ± 0.2	0.5 ± 0.0	0.4 ± 0.1	0.3 ± 0.0	0.4 ± 0.0
16:0	18.9 ± 0.7	23.2 ± 7.1	23.8 ± 1.0	30.0 ± 1.1	19.5 ± 2.1	18.8 ± 0.4	17.6 ± 3.8
16:1ω10	5.0 ± 0.4	3.8 ± 0.2	5.8 ± 1.2	3.9 ± 0.7	3.9 ± 1.1	3.1 ± 0.6	4.2 ± 0.2
16:1ω7	5.2 ± 1.5	7.1 ± 4.2	2.4 ± 0.5	3.0 ± 0.1	3.8 ± 1.0	7.3 ± 0.2	6.3 ± 0.2
16:1ω5	0.9 ± 0.3	1.7 ± 0.8	0.1 ± 0.0	0.6 ± 0.2	0.9 ± 0.5	1.1 ± 0.1	1.7 ± 0.2
*i*17:0	0.4 ± 0.1	0.6 ± 0.3	0.1 ± 0.1	0.3 ± 0.0	0.3 ± 0.0	0.6 ± 0.1	0.6 ± 0.2
*ai*17:0	0.4 ± 0.0	0.1 ± 0.2	0.3 ± 0.2	0.3 ± 0.1	0.5 ± 0.3	0.5 ± 0.0	0.3 ± 0.1
17:0	0.8 ± 0.1	0.9 ± 0.2	0.9 ± 0.2	0.9 ± 0.0	0.9 ± 0.3	0.5 ± 0.1	0.7 ± 0.1
17:1ω8	1.1 ± 0.1	0.9 ± 0.1	1.4 ± 0.1	0.9 ± 0.2	1.0 ± 0.3	0.6 ± 0.2	1.0 ± 0.2
18:0	5.9 ± 0.0	9.5 ± 6.0	8.3 ± 1.6	12.0 ± 0.5	7.0 ± 1.3	6.5 ± 0.6	5.7 ± 1.3
18:1ω9	13.6 ± 0.5	10.0 ± 1.4	17.0 ± 0.6	10.6 ± 2.4	14.8 ± 4.3	14.2 ± 1.6	12.6 ± 3.1
18:1ω7	3.8 ± 1.2	4.5 ± 2.0	1.5 ± 0.3	2.4 ± 0.1	3.2 ± 0.8	5.2 ± 1.1	5.9 ± 0.4
18:1ω5	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.0	0.3 ± 0.2	0.4 ± 0.3	0.2 ± 0.1	0.3 ± 0.2
*i*19:0	0.6 ± 0.1	0.5 ± 0.0	0.6 ± 0.1	0.2 ± 0.4	0.6 ± 0.2	0.6 ± 0.2	0.7 ± 0.0
18:2ω6	8.0 ± 0.6	4.8 ± 0.9	10.5 ± 1.6	6.0 ± 2.8	11.2 ± 4.4	11.0 ± 1.2	5.8 ± 1.8
19:1	0.2 ± 0.0	0.3 ± 0.0	0.3 ± 0.1	0.3 ± 0.0	0.4 ± 0.5	0.2 ± 0.1	0.1 ± 0.1
18:3ω3	0.9 ± 0.1	0.5 ± 0.1	0.6 ± 0.4	0.5 ± 0.3	0.8 ± 0.6	0.7 ± 0.3	0.5 ± 0.1
20:0	0.6 ± 0.0	0.9 ± 0.0	0.9 ± 0.1	1.2 ± 0.3	0.8 ± 0.3	0.7 ± 0.1	0.7 ± 0.1
20:1ω13	0.7 ± 0.1	0.4 ± 0.3	0.5 ± 0.3	0.5 ± 0.1	1.5 ± 2.1	0.3 ± 0.1	0.6 ± 0.3
20:2ω6	2.2 ± 0.9	1.5 ± 1.3	1.2 ± 0.4	0.9 ± 0.1	0.9 ± 0.4	0.4 ± 0.2	2.6 ± 1.4
20:4ω6	2.0 ± 0.5	1.4 ± 1.1	0.4 ± 0.3	0.3 ± 0.1	0.7 ± 0.4	1.7 ± 0.3	0.8 ± 0.2
20:5ω3	2.9 ± 0.5	2.7 ± 2.1	1.0 ± 0.6	0.9 ± 0.7	4.0 ± 4.3	5.9 ± 0.8	2.6 ± 1.9
22:1	0.8 ± 0.2	1.0 ± 0.0	0.8 ± 0.2	1.3 ± 0.3	1.1 ± 0.3	0.8 ± 0.2	0.9 ± 0.1
22:5ω3	1.1 ± 0.2	1.5 ± 0.1	1.2 ± 0.2	1.6 ± 0.2	1.3 ± 0.2	1.0 ± 0.2	1.4 ± 0.2
22:6ω3	0.9 ± 0.2	0.4 ± 0.4	0.3 ± 0.2	0.3 ± 0.2	0.7 ± 0.6	0.6 ± 0.1	0.9 ± 0.6
Others[a]	14.2	12.5	10.6	9.6	13.3	10.5	16.6

[a]Other fatty acids were 12:0, 7Me:16:1ω10, 16:2, 16:3ω4, 16:4ω1, 17:1, *i*18:0, 19:0, 19:1, *i*20:0, 23:0, 24:1ω9, 24:0, 25:0, 26:0

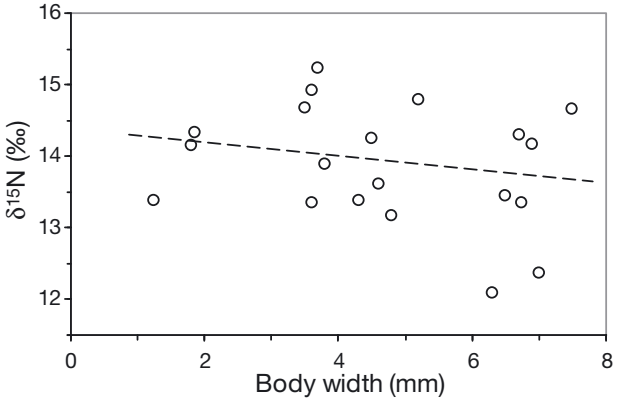

Fig. A1. *Harmothoe derjugini*. Stable nitrogen isotope ratios for individuals of various size. All individuals were taken from the only benthos sample obtained by epibenthic sledge at Stns A7–9 (water depth 3340 to 3347 m)

Editorial responsibility: Robert Stead, Puerto Montt, Chile

Submitted: April 24, 2013; Accepted: November 20, 2013
Proofs received from author(s): March 4, 2014