Assemblages of Harpacticoida (Crustacea: Copepoda) from the Ryukyu and Kuril Trenches, north-west Pacific Ocean

TOMO KITAHASHI[1], KIICHIRO KAWAMURA[2], GRITTA VEIT-KÖHLER[3], ROBERTO DANOVARO[4], JOHN TIETJEN[5], SHIGEAKI KOJIMA[1] AND MOTOHIRO SHIMANAGA[6]

[1]Atmosphere and Ocean Research Institute, the University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8564, Japan, [2]Fukada Geological Institute, 2-13-2 Honkomagome, Bunkyo, Tokyo 113-0021, Japan, [3]Senckenberg Research Institute, DZMB—German Centre for Marine Biodiversity Research, Südstrand 44, 26382 Wilhelmshaven, Germany, [4]Department of Life and Environmental Sciences, Polytechnic University of Marche, Via Brecce Bianche, 60131 Ancona, Italy, [5]Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th St New York, 10024, USA, [6]Aitsu Marine Station, Center for Marine Environment Studies, Kumamoto University, 6061 Aitsu, Matsushima, Kami-Amakusa, Kumamoto 861-6102, Japan

To examine the specific features of trench communities, spatial changes in the assemblages of harpacticoids were investigated at the family level around the Ryukyu Trench (the Ryukyu region) and Kuril Trench (the Kuril region). In the Ryukyu region, there were high average dissimilarities in the harpacticoid assemblages among the trench, trench slope and abyssal plain, indicating that the assemblage structures differ substantially between these topographic settings at the family level. Conversely, in the Kuril region, the average dissimilarities in harpacticoid assemblages between the trench and the trench slope and between the trench and the abyssal plain were lower than that between the slope and the abyssal plain. This result suggests that the hadal assemblage is a transition zone between the slope and the abyssal plain in this region. In addition, the analyses indicate that the composition of harpacticoid assemblages is influenced by the quantity of organic matter in the Ryukyu region, while sediment properties play a key role in the Kuril region. Comparisons of the assemblages between the two regions, however, revealed that the average dissimilarities between the trenches and between the abyssal plains were higher than that between the adjacent slopes. This result suggests that interchange among regions is difficult for deep-sea benthic animals, including harpacticoid copepods, likely due to the presence of physical barriers around trenches.

INTRODUCTION

Trenches present one of the last frontiers of deep-sea exploration (Rex & Etter, 2010). A trench is a narrow, elongated depression of the deep-sea floor associated with a subduction zone (Jackson, 1997). The world's trenches are distributed from boreal to subtropical regions, with a combined length of 40,000 km; therefore, information from trenches is necessary to fully understand marine biodiversity, spatial patterns of community structures, and the processes that regulate them.

Trenches are seafloor features that are isolated from each other (Angel, 1982), the upper boundary of which typically begins at a water depth of 6000 m. There is a paucity of information about meiofaunal abundances or compositions at higher taxonomic levels (e.g. George & Higgins, 1979; Tietjen *et al.*, 1989; Shirayama & Kojima, 1994; Richardson *et al.*, 1995; Danovaro *et al.*, 2002; Tselepides & Lampadariou, 2004; Itoh *et al.*, 2011). However, although meiofauna exceed megafauna and macrofauna in density

and biomass in the deep-sea (e.g. Rex *et al.*, 2006) and play an important role in the deep-sea ecosystem, there have been few previous studies of meiofaunal assemblages from trenches.

Todo *et al.* (2005) investigated the Challenger Deep and found that organic-walled foraminifera, which are rare in most deep-sea environments, dominated the assemblage of meiofaunal foraminifera. Low affinities between trench stations and adjacent slope stations have been reported for nematodes (Tietjen, 1989; Gambi *et al.*, 2003; Vanhove *et al.*, 2004). These studies, however, could not address whether trench communities are different from those in other environments, because they did not compare the trench stations with abyssal plain stations. Furthermore, a comparison between more than one trench regions has not been conducted to date.

Harpacticoids (Crustacea: Copepoda) are usually the second most abundant meiobenthic taxon in marine samples after nematodes (Giere, 2009). Jumars & Hessler (1976) reported that the diversity of harpacticoids in the Aleutian Trench was lower than that in the central North Pacific. However, the structure of assemblage was not mentioned.

The present study, in which the specific features of trench assemblages are examined, is the first step in investigating

Corresponding author:
T. Kitahashi
Email: tkitahashi-10a@nenv.k.u-tokyo.ac.jp

spatial changes in the assemblages of harpacticoids around trenches. We describe the harpacticoid assemblages at the family level in two trench regions around Japan: the Ryukyu Trench, which underlies an oligotrophic subtropical ocean, and the Kuril Trench, which is located below a highly productive boreal region (cf. Berger, 1989; NASA SeaWiFS Project: http://oceancolor.gsfc.nasa.gov/SeaWiFS/). In addition, we investigated the relationship between harpacticoid assemblages and environmental factors. Sajan *et al.* (2010) showed that the assemblage structure of nematodes at the family level had a similar pattern to that at the species level, and that analysis at the family level is sufficient to explain the depth gradient in the western Indian continental shelf. Although this consistency should not be assumed to exist in other regions (Narayanaswamy *et al.*, 2010), information at the family level is still useful for the analysis of assemblage structures. In the present study, we particularly focused on the following three questions associated with harpacticoid assemblages:

(1) Are trench assemblages different from those on the surrounding trench slope and abyssal plain? If the trench assemblage is different, the average dissimilarities between the adjacent slope and the trench and between the trench and the abyssal plain should be higher than that between the slope and the abyssal plain.
(2) Do the same factors influence the distribution pattern of the harpacticoid families in these two trench regions?
(3) Are the assemblages on the two different trenches isolated from each other? If trench assemblages are isolated from each other, the dissimilarity between trench stations should be much higher than that between the slopes and the abyssal plains.

MATERIALS AND METHODS

Sampling and sample processing

Meiofauna samples were collected from regions around the Kuril Trench (hereafter the Kuril region) and the Ryukyu Trench (hereafter the Ryukyu region) during two cruises of the research vessel 'Hakuho Maru', KH-01-2 in 2001 and KH-05-1 in 2005. We used a multiple corer (Barnett *et al.*, 1984), which can simultaneously collect up to eight sediment cores of 52.8 cm². Sampling stations were located along transects from the continental margins to the abyssal plains, traversing both trenches (Figure 1). We classified sampling stations into three topographic categories: trench (depth >6000 m); trench slope (adjacent slope landward from the trench); and abyssal plain (flat topography seaward from the trench). Sampling locations, depths and topographic categories of stations are listed in Table 1. One multiple corer deployment was conducted at each station, and three cores per deployment were used for meiofaunal analysis, because of limited ship time and demand for cores.

Shipboard, core samples were sliced horizontally into 0–1, 1–3 and 3–5 cm layers. The samples were fixed and preserved individually in 5% buffered seawater–formalin and stained with Rose Bengal (final concentration 0.05 g/l) within several hours. Only the 0–1 cm layer was analysed in the present study because most harpacticoids were distributed in this layer (Itoh *et al.*, 2011).
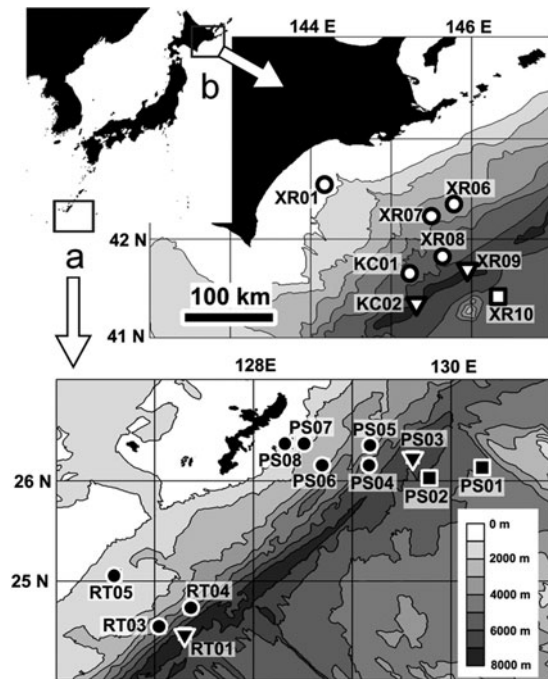

Fig. 1. Location of sampling stations (a) around the Ryukyu Trench (the Ryukyu region) and (b) around the Kuril Trench (the Kuril region), Japan. Solid and open points indicate the Ryukyu and Kuril region stations, respectively. Circles, triangles, and squares indicate trench slope, trench, and abyssal plain stations, respectively. Labels near to these symbols are the codes of the sampling stations listed in Table 1.

In the Ryukyu region, the entire sediment samples from each core were used for meiofaunal analysis. In the Kuril region, the sediment samples were quantitatively divided due to the high abundances of adult harpacticoids in this region (Table 2). First, a 9.0 cm² subcore was obtained for meiofaunal analysis. In Stations KC01, XR01, XR06, XR07, XR09 and XR10 (Figure 1), the harpacticoid abundances were low. Therefore, a quarter of the residual sediments around the subcores divided with a sediment divider were also used at these stations.

In the laboratory, samples were serially sieved onto 0.5, 0.25, 0.125 and 0.063 mm mesh nets. The retained harpacticoid specimens were transferred to flat-bottomed Petri dishes and examined to determine their developmental stages under a binocular stereoscopic microscope.

According to Huys *et al.* (1996), Boxshall & Halsey (2004) and Wells (2007), adult specimens were identified to the family level under a differential interference contrast microscope. Very few adult harpacticoids passed through the 0.063 mm mesh (0–6.3%), and damaged adults were omitted from the analysis due to identification problems. Harpacticoid density and family composition at each station were corrected with considering the differences in a fraction of the sediments and calculated based on the total number of adult harpacticoids from three cores.

Food supply (Soltwedel, 2000; Baguley *et al.*, 2006) and grain size (Montagna, 1982) have been suggested to affect the distribution patterns of meiofauna in the deep sea. Therefore, we examined chloroplastic pigment equivalents (CPE) as an indicator of the amount of organic matter supplied to the sea floor and the median diameter (MD) and sorting coefficient (SC) of sediments as parameters for grain

Table 1. Locations and topographic categories of the sampling stations.

Sampling station	Date	Latitude	Longitude	Depth (m)	Category
Ryukyu region					
PS01	20 May 2005	26°04.00′ N	130°20.00′ E	4910	Abyssal plain
PS02	21 May 2005	25°59.96′ N	129°50.02′ E	5710	Abyssal plain
PS03	22 May 2005	26°12.22′ N	129°39.38′ E	6340	Trench
PS04	23 May 2005	26°08.79′ N	129°06.62′ E	5330	Trench slope
PS05	23 May 2005	26°17.67′ N	129°06.86′ E	3850	Trench slope
PS06	23 May 2005	26°05.98′ N	128°42.98′ E	3030	Trench slope
PS07	24 May 2005	26°20.05′ N	128°30.02′ E	1960	Trench slope
PS08	24 May 2005	26°20.14′ N	128°21.48′ E	1290	Trench slope
RT01	16 May 2005	24°29.79′ N	127°20.88′ E	7150	Trench
RT03	17 May 2005	24°33.36′ N	127°02.93′ E	3830	Trench slope
RT04	18 May 2005	24°53.04′ N	127°25.05′ E	4240	Trench slope
RT05	10 May 2005	25°00.10′ N	126°42.11′ E	1890	Trench slope
Kuril region					
KC01	19 Sep 2001	41°43.66′ N	145°16.24′ E	5430	Trench slope
KC02	19 Sep 2001	41°20.98′ N	145°21.98′ E	7000	Trench
XR01	15 Sep 2001	42°34.05′ N	144°05.03′ E	560	Trench slope
XR06	16 Sep 2001	42°19.96′ N	145°48.03′ E	3320	Trench slope
XR07	17 Sep 2001	42°11.95′ N	145°31.08′ E	3730	Trench slope
XR08	20 Sep 2001	41°50.02′ N	145°37.88′ E	5730	Trench slope
XR09	20 Sep 2001	41°38.91′ N	145°58.59′ E	7090	Trench
XR10	22 Sep 2001	41°25.54′ N	146°23.45′ E	5570	Abyssal plain

size-distribution. The SC indicates the spread of the grain size, with small SC indicating 'well-sorted' homogeneous sediment (Giere, 2009). These data are summarized in Table 2. The CPE samples were treated in the laboratory according to the method of Greiser & Faubel (1988). The total amount of CPE in the top 0–1 cm layer of the sediment was measured for each core, and the mean value of three cores was regarded as the representative value for each station. MD and SC data were cited from Itoh *et al.* (2011). A small amount of sediment (<1 ml for the Kuril and Ryukyu samples) was taken from the top sediment layer of one core per station to determine the MD and SC. The sediments were dispersed into boiled water in a glass beaker and left for 24 hours. Trench sediments were further dispersed using an ultrasonic vibrator for 30–60 seconds immediately before measurement with a laser diffraction particle analyser (CIRAS Co. Ltd. 1064).

Statistical analyses

We used the following four multivariate analyses to decipher harpacticoid assemblages in the Ryukyu and Kuril regions: non-metric multi-dimensional scaling (nMDS), analysis of similarity (ANOSIM), similarity percentages (SIMPER) and BIO-ENV analyses. Prior to all analyses, abundance data

Table 2. Environmental variables, densities of adult harpacticoids, and the number of obtained specimens and families at each station. MD and SC values are cited from Itoh *et al.* (2011). CPE, chloroplastic pigment equivalents; MD, median diameter; SC, sorting coefficient of sediment grain size.

Sampling station	CPE (μg/cm²)	MD (μm)	SC	Density (ind./10 cm²)	Number of specimens	Number of families
Ryukyu region						
PS01	0.2	1.2	1.9	0.5	8	6
PS02	0.3	1.2	1.8	0.9	15	7
PS03	0.9	2.0	2.0	1.2	18	9
PS04	0.3	2.5	2.1	1.3	20	11
PS05	0.5	1.3	1.8	1.1	17	8
PS06	0.3	2.1	2.3	1.3	21	8
PS07	0.5	1.5	2.3	2.1	33	12
PS08	1.1	18.0	1.7	3.4	54	12
RT01	0.7	No datum	No datum	0.3	4	3
RT03	0.3	1.0	1.8	1.3	21	9
RT04	0.5	No datum	No datum	0.4	7	3
RT05	0.4	1.5	2.3	1.8	28	9
Kuril region						
KC01	7.6	8.0	2.0	10.7	31	7
KC02	6.8	3.8	2.1	16.4	34	6
XR01	17.2	No datum	No datum	10.5	63	10
XR06	5.3	12.0	2.0	4.0	20	7
XR07	7.3	10.0	1.9	8.3	43	10
XR08	9.3	7.7	2.0	21.6	40	12
XR09	22.4	5.4	2.1	5.4	32	7
XR10	3.8	5.7	2.3	4.1	20	10

were $\log_{10}(x + 1)$ transformed to reduce the contribution of abundant families and to focus on the whole assemblage pattern (Clarke & Warwick, 2001). In this study, the numbers of observed individuals varied from station to station (Table 2). Therefore, similarity or dissimilarity indices that were not influenced by different sample sizes were selected for the multivariate analyses. We adopted the Morisita–Horn dissimilarity index (Horn, 1966) because the use of this index has been recommended in such situations (Wolda, 1981). The nMDS is a method to visualize similarities in the assemblage structures across different stations. The nMDS attempts to plot the stations so that the rank order of distances between stations on the plot exactly agrees with the rank order of the matching dissimilarities (Clarke & Warwick, 2001). The ANOSIM is used to examine the statistical significance of differences in assemblage structures between different topographic categories within the same region or between different regions. First, the R statistic was computed based on the rank similarity matrix of the samples. Second, R was recalculated a large number of times under random permutations of the stations. Finally, the observed value of R was compared to its permutation distribution (Clarke & Warwick, 2001). The SIMPER analysis is used to determine the average of dissimilarities between different topographic categories and between different regions. In this analysis, dissimilarities were computed between every pair of stations in two different categories, and then their average was calculated (cf. Clarke & Warwick, 2001). When comparing the two different regions, we omitted Station XR01, which was the shallowest station in this study in order to compare the two regions based on the stations from the same depth-range. The BIO-ENV analysis is used to detect environmental factors that have the highest correlation with the changing pattern in an assemblage (Clarke & Warwick, 2001). This analysis can compare the rank dissimilarity matrices from biotic data against those from abiotic data (Clarke & Warwick, 2001). The Spearman coefficient (ρ_s) can evaluate the extent to which two matrices match (cf. Clarke & Warwick, 2001). The combination yielding the highest ρ_s was considered as the factor, or group of factors, that best explained the changing patterns in harpacticoid assemblages. The dissimilarity ranks are not mutually independent variables because they are based on a large number of strongly interdependent dissimilarity calculations. It is invalid, therefore, to statistically assess whether the obtained Spearman coefficient (ρ_s) is significant (cf. Clarke & Warwick, 2001). Therefore, we only evaluated the extent to which the two patterns match in the present study. For biotic data, the Morisita–Horn dissimilarity index was used, while for abiotic data, environmental variables were normalized, and the Euclidean distance was calculated in this analysis (cf. Clarke & Warwick, 2001). Environmental variables included water depth, CPE, MD and SC; stations for which MD and SC values were not obtained were excluded from this analysis. All multivariate analyses were performed with R (R Development Core Team, 2008), using the package *vegan* (Oksanen *et al.*, 2008).

Nematode data sets

To date, information about harpacticoid assemblages around trenches remains scarce. In contrast, the assemblage structures of nematodes around the Puerto Rico and Atacama Trenches have been reported by Tietjen (1989) and Gambi *et al.* (2003). Therefore, we compared the nematode family data from the Ryukyu and Kuril regions with the data from these existing studies. These data were treated using the same methods that were used for harpacticoid copepods and were analysed using the SIMPER analysis to obtain the average dissimilarity values between the trench and adjacent slope stations.

RESULTS

The density of adult harpacticoids, the number of specimens obtained and the number of observed families at each station are shown in Table 2. In total, 246 adult harpacticoids were identified in the Ryukyu region and 283 in the Kuril region (Table 3). Fourteen of twenty families were found in both regions, with four of the families that ranked in the top six abundant families being common between the two regions (Table 4). In the Ryukyu region, eighteen families were encountered, and Ectinosomatidae (15.8%), Pseudotachidiidae (15.1%), Zosimeidae (14.2%), Ameiridae (12.5%), Argestidae (12.1%) and Neobradyidae (9.3%) were dominant. In the Kuril region, sixteen families were encountered, and the most abundant families were Ectinosomatidae (23.9%), Ameiridae (17.3%), Pseudotachidiidae (14.3%), Idyanthidae (13.3%), Argestidae (9.8%) and Cletodidae (6.1%).

Comparison within the same regions

The observed families and their relative abundances in the topographic categories of each region are shown in Tables 5 and 6. Most of the families that appeared in one category were also found in other categories in both regions. The result of the nMDS based on the combined data from the Ryukyu and Kuril regions is shown in Figure 2. In the Ryukyu region, the stations in the same categories were not close to each other (Figure 2, solid plots), and no significant differences were detected among the different topographic categories (ANOSIM, $R = 0.17$, $P > 0.05$). In contrast, in the Kuril region, the stations in the same categories tended to be plotted near each other (Figure 2, open plots), with a significant difference being detected across the different topographic categories (ANOSIM, $R = 0.76$, $P < 0.01$).

SIMPER analyses showed that all dissimilarity values in harpacticoid assemblages across the different topographic categories were equally high (38.4–44.2%) in the Ryukyu region (Figure 3a). In contrast, in the Kuril region, the dissimilarity values between the trench slope and the trench (31.2%) and between the trench and the abyssal plain (28.3%) were lower than those between the slope and the abyssal plain (40.4%; Figure 3b). In contrast, for the nematode assemblages in the Puerto Rico and Atacama Trenches, the average dissimilarity values at the family level between the slope and trench stations were 28.2% and 25.4%, respectively.

According to the BIO-ENV analysis, the biotic and abiotic data in the Ryukyu region matched at the highest level ($\rho_s = -0.28$) when considering only the CPE. In contrast, the MD and SC showed the highest match against biotic data in the Kuril region ($\rho_s = 0.76$).

Table 3. The number of individuals of each family in the investigated sediments (see Materials and Methods) in the Ryukyu and Kuril regions.

Sampling station	Aegisthidae	Ameiridae	Ancorabolidae	Arenopontiidae	Argestidae	Canthocamptidae	Canuellidae	Cletodidae
Ryukyu region								
PS01	0	0	0	0	1	0	1	0
PS02	0	1	0	0	3	0	0	2
PS03	1	3	0	0	3	1	0	0
PS04	0	1	0	0	2	0	0	1
PS05	0	1	2	0	1	1	0	1
PS06	0	4	0	1	3	0	0	1
PS07	1	4	1	0	1	1	0	2
PS08	0	10	0	0	5	0	0	1
RT01	0	0	0	0	0	0	0	0
RT03	1	1	0	0	3	0	0	1
RT04	0	3	0	0	3	0	0	0
RT05	0	3	0	0	5	0	0	0
Kuril region								
KC01	0	5	0	0	0	0	0	0
KC02	0	16	0	0	7	0	0	0
XR01	0	2	1	0	1	1	0	3
XR06	0	1	0	0	0	0	0	0
XR07	0	2	0	0	3	1	0	1
XR08	0	4	1	0	7	1	0	5
XR09	0	2	0	0	4	0	0	4
XR10	1	7	0	0	2	1	0	2

Sampling station	Cletopsyllidae	Dactylopusiidae	Ectinosomatidae	Huntemaniidae	Idyanthidae	Leptastacidae	Miraciidae	Neobradyidae
Ryukyu region								
PS01	0	0	1	0	1	0	0	0
PS02	0	0	1	0	0	0	0	3
PS03	0	0	5	0	0	0	0	2
PS04	0	0	3	1	2	0	3	2
PS05	0	0	0	0	0	0	0	3
PS06	0	0	1	0	1	0	0	5
PS07	0	0	6	0	2	0	0	3
PS08	0	1	10	0	2	0	1	4
RT01	0	0	2	0	0	0	0	0
RT03	0	0	6	0	2	0	0	0
RT04	0	0	0	0	0	0	0	1
RT05	0	1	3	2	0	0	3	0
Kuril region								
KC01	0	0	11	0	4	1	0	2
KC02	0	0	2	0	6	0	0	1
XR01	0	0	25	0	2	0	10	0
XR06	0	0	8	1	2	0	3	0
XR07	0	0	12	0	3	0	7	1
XR08	1	0	9	0	5	0	1	0

Continued

Table 3. Continued

Sampling station	Aegisthidae	Ameiridae	Ancorabolidae	Arenopontiidae	Argestidae	Canthocamptidae	Canuellidae	Cletodidae
XR09	0	0	6	0	10	0	0	3
XR10	0	0	0	0	1	0	1	1

Sampling station	Normanellidae	Paramesochridae	Pseudotachidiidae	Zosimeidae	Total
Ryukyu region					
PS01	0	2	2	0	8
PS02	0	0	1	4	15
PS03	0	1	1	1	18
PS04	0	1	2	2	20
PS05	0	0	4	4	17
PS06	0	0	5	0	21
PS07	0	2	5	5	33
PS08	1	1	11	7	54
RT01	0	0	1	1	4
RT03	0	1	2	4	21
RT04	0	0	0	0	7
RT05	0	1	3	7	28
Kuril region					
KC01	0	0	7	1	31
KC02	0	0	2	0	34
XR01	0	0	14	4	63
XR06	0	0	3	2	20
XR07	0	0	9	4	43
XR08	0	1	4	1	40
XR09	0	0	3	0	32
XR10	0	1	3	0	20

Table 4. List of harpacticoid families collected in the Ryukyu and Kuril regions. Classification after Wells (2007).

Ryukyu region		Kuril region	
Family	**Relative abundance (%)**	**Family**	**Relative abundance (%)**
Ectinosomatidae	15.8	Ectinosomatidae	23.9
Pseudotachidiidae	15.1	Ameiridae	17.3
Zosimeidae	14.2	Pseudotachidiidae	14.3
Ameiridae	12.1	Idyantidae	13.3
Argestidae	12.3	Argestidae	9.8
Neobradyidae	9.3	Cletodidae	6.1
Idyanthidae	4.0	Miraciidae	5.4
Cletodidae	3.6	Zosimeidae	3.2
Paramesochridae	3.6	Neobradyidae	2.5
Miraciidae	2.8	Canthocamptidae	1.1
Aegisthidae	1.2	Cletopsyllidae	0.9
Ancorabolidae	1.2	Ancorabolidae	0.7
Canthocamptidae	1.2	Paramesochridae	0.7
Huntemaniidae	1.2	Leptastacidae	0.5
Dactylopusiidae	0.8	Aegisthidae	0.2
Arenopontiidae	0.4	Huntemaniidae	0.2
Canuellidae	0.4		
Normanellidae	0.4		

Comparison between the different regions

A tendency for separation between the two regions was observed, except for Station PS01 (Figure 2). However, no significant differences were noted between the two regions (ANOSIM, $R = 0.04$, $P > 0.05$) or across the topographic categories (ANOSIM, $R = 0.18$, $P > 0.05$). Assemblages were also compared between the same topographic categories in the two regions using SIMPER analysis (Figure 4). The average dissimilarity value between the Ryukyu and Kuril regions was 36.1%. Specifically, the average dissimilarity values between the different slopes, between the different trenches and between the different abyssal plains were 32.9%, 47.5% and 46.1%, respectively.

Global-scale comparison

To investigate spatial changes in assemblages at the family level on a global scale, we conducted a similarity analysis using the available data of harpacticoids from deep-sea sediments (water depth $>$1000 m) around the world and visualized the results using nMDS. Specifically, these data were obtained from the DEA site (south-east Pacific Ocean; Ahnert & Schriever, 2001), the Great Meteor Seamount (east Atlantic Ocean; George & Schminke, 2002), the Patagonian continental slope (Antarctic Ocean; George, 2005), the Angola Basin (South Atlantic Ocean; Rose et al., 2005), the Northern Gulf of Mexico deep-sea (Baguley et al., 2006) and the Porcupine Seabight (north-east Atlantic Ocean; Gheerardyn et al., 2010). In the present study, the data from the Ryukyu and Kuril regions were combined, and all the data were recalculated to provide the relative abundance; the Morisita–Horn index was used as a dissimilarity index. These studies used different systematic schemes; therefore family assignment was adjusted to that of Boxshall & Halsey (2004). The relative abundance of abundant families is shown in Table 7. Most of the abundant families were common among sites, despite differences in relative abundances. The result of the nMDS based on these data is shown in Figure 5. Similarity levels of $>$85% were observed between two stations in the Angola Basin (Rose et al., 2005) and among three regions in the Pacific Ocean, namely, the Ryukyu region, the Kuril region (this study) and the DEA site (Ahnert & Schriever, 2001). All sites clustered at a similarity level of 55%.

DISCUSSION

Harpacticoid assemblages in trenches: are trench assemblages different from those on the surrounding trench slope and abyssal plain?

Previous studies of meiofaunal assemblages, especially harpacticoids, from trenches remain limited. In the case of nematode

Table 5. List of harpacticoid families collected at each topographic category in the Ryukyu region. Classification after Wells (2007).

Trench slope		Trench		Abyssal plain	
Family	**Relative abundance (%)**	**Family**	**Relative abundance (%)**	**Family**	**Relative abundance (%)**
Pseudotachidiidae	15.9	Ectinosomatidae	34.3	Argestidae	17.4
Ectinosomatidae	14.4	Ameiridae	12.9	Zosimeidae	17.4
Zosimeidae	14.4	Argestidae	12.9	Neobradyidae	13.0
Ameiridae	13.4	Pseudotachidiidae	10.0	Pseudotachidiidae	13.0
Argestidae	11.4	Neobradyidae	8.6	Cletodidae	8.7
Neobradyidae	9.0	Zosimeidae	8.6	Ectinosomatidae	8.7
Idyanthidae	4.5	Aegisthidae	4.3	Paramesochridae	8.7
Miraciidae	3.5	Canthocamptidae	4.3	Ameiridae	4.4
Cletodidae	3.5	Paramesochridae	4.3	Canuellidae	4.4
Paramesochridae	3.0			Idyanthidae	4.4
Ancorabolidae	1.5				
Huntemaniidae	1.5				
Aegisthidae	1.0				
Canthocamptidae	1.0				
Dactylopusiidae	1.0				
Arenopontiidae	0.5				
Normanellidae	0.5				

Table 6. List of harpacticoid families collected at each topographic category in the Kuril region. Classification after Wells (2007).

Trench slope		Trench		Abyssal plain	
Family	**Relative abundance (%)**	**Family**	**Relative abundance (%)**	**Family**	**Relative abundance (%)**
Ectinosomatidae	31.3	Ameiridae	37.5	Ameiridae	34.7
Pseudotachidiidae	17.2	Idyanthidae	23.1	Argestidae	14.5
Idyanthidae	10.1	Argestidae	15.1	Cletodidae	14.5
Ameiridae	8.1	Ectinosomatidae	9.8	Pseudotachidiidae	12.1
Miraciidae	7.6	Pseudotachidiidae	7.5	Aegisthidae	4.0
Argestidae	7.4	Neobradyidae	4.0	Canthocamptidae	4.0
Cletodidae	6.6	Cletodidae	3.1	Idyanthidae	4.0
Zosimeidae	4.7			Miraciidae	4.0
Neobradyidae	1.7			Neobradyidae	4.0
Canthocamptidae	1.4			Paramesochridae	4.0
Cletopsyllidae	1.4				
Ancorabolidae	1.0				
Leptastacidae	0.7				
Paramesochridae	0.7				
Huntemaniidae	0.3				

assemblages, low percentages of similarity at the genus and species levels have been reported in comparative analyses of the trench and the adjacent slope stations in the Puerto Rico Trench (Tietjen, 1989), Atacama Trench (Gambi *et al.*, 2003) and South Sandwich Trench (Vanhove *et al.*, 2004).

In the present study, the average dissimilarity in harpacticoid assemblages at the family level between the trench stations and the slope stations was 40.6% in the Ryukyu region and 31.2% in the Kuril region (Figure 3). For nematodes, the average dissimilarity at the family level was 28.2% in the Puerto Rico Trench and 25.4% in the Atacama Trench. Although we should consider the difference in taxa, these data could suggest that there is much more divergence in the assemblages of the Ryukyu Trench and its slope than that reported for nematode assemblages in the Puerto Rico and Atacama Trenches. In contrast, the dissimilarity of harpacticoid assemblages in the Kuril Trench and its slope were comparable with that of the nematodes from the Puerto

Rico and Atacama Trenches. The abundant families in each topographic category, however, were quite similar in the Ryukyu and Kuril regions (Tables 5 & 6). Consequently, the differences in harpacticoid assemblages between these trenches and their adjacent slopes were primarily due to the relative abundances of families in the two regions. This finding is consistent with the results obtained from studying the nematode assemblage in the Puerto Rico Trench (Tietjen, 1989) but contrasts with the results obtained from the analysis of nematodes in the Atacama Trench, where a different composition of families was observed (Gambi *et al.*, 2003).

For a better understanding of the specific features of trench assemblages, comparisons were made not only with their adjacent slopes, but also with adjacent abyssal plains. This study presents the first systematic analysis of samples ranging from continental margins to abyssal plains, crossing trenches in two trench regions. In the Ryukyu region, the average dissimilarity values between the three topographic categories were all high (Figure 3A), suggesting that at the family level, the assemblage of the trench is equally different from that of the slope and abyssal plain. In contrast, in the Kuril region, the dissimilarity values between the slope and the trench and between the trench and the abyssal plain were lower than that between the slope and the abyssal plain (Figure 3B). This finding leads to the hypothesis that the hadal assemblage is a transition zone between the slope and the abyssal plain in this region. However, the differences in the relative abundances of families in the two habitats would affect the differences in harpacticoid assemblages between the trench and the abyssal plain for both regions, like between the trench and the trench slope. This corresponds with a previous study on large benthic fauna, which showed that hadal fauna are characterized by a relative abundance that is different to the neighboring abyssal zone (Wolff, 1970).

In the present study, we confirmed that differences in the harpacticoid assemblages among the trench slope, trench and abyssal plain were significant in the Kuril region but not the Ryukyu region. This led us to question why a significant difference arises in the assemblage structures between different topographic categories only in the Kuril region. One possible explanation is that the distances among
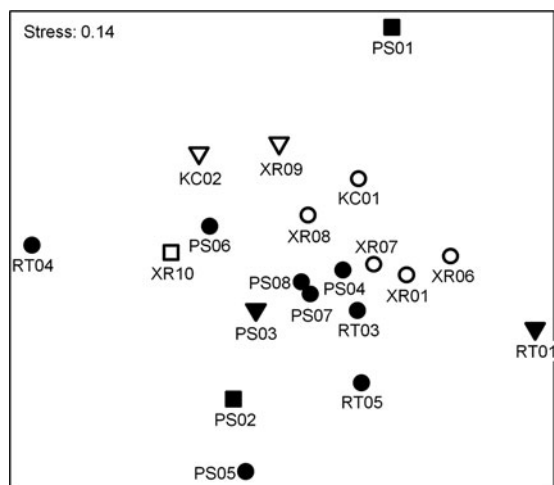

Fig. 2. The non-metric multidimensional scaling ordination based on combined data from the Ryukyu (solid plots) and Kuril regions (open plots). Circles, triangles, and squares indicate trench slope, trench, and abyssal plain stations, respectively. Labels near these symbols denote the code of the sampling stations (see Figure 1).

Table 7. Abundant families of harpacticoid copepods at deep-sea sites around the world. Classification after Boxshall & Halsey (2004).

Site	Code	Abundant families (relative abundance, %)	Citation
DEA site	DEA	Ameiridae (16.7), Ectinosomatidae (16.5), Argestidae (12.7), Tisbidae (11.2)	Ahnert & Schriever, 2001
Great Meteor Seamount	GMS	Miraciidae (26.1), Paramesochridae (21.0), Ectinosomatidae (16.3), Tisbidae (16.0)	George & Schminke, 2002
Patagonian continental slope	PSC	Ectinosomatidae (46.7), Ameiridae (24.2), Miraciidae (12.5)	George, 2005
Angola Basin M325	AB 325	Thalestridae (18.4), Tisbidae (15.4), Neobradyidae (14.1), Ectinosomatidae (12.7)	Rose et al., 2005
Angola Basin M346	AB 346	Argestidae (21.3), Thalestridae (20.1), Ameiridae (16.9), Ectinosomatidae (11.6)	Rose et al., 2005
Northern Gulf of Mexico	NGM	Tisbidae (33.0), Ectinosomatidae (13.3), Miraciidae (9.8), Ameiridae (8.2)	Baguley et al., 2006
Porcupine Seabight	PS	Ectinosomatidae (24.8), Ameiridae (21.1), Thalestridae (13.5), Argestidae (10.5)	Gheerardyn et al., 2010
Ryukyu region	Ryukyu	Tisbidae (18.2), Ectinosomatidae (15.8), Ameiridae (12.5), Argestidae (12.1)	This study
Kuril region	Kuril	Ectinosomatidae (24.0), Ameiridae (17.4), Tisbidae (16.5), Miraciidae (13.4)	This study

sampling stations influenced the results, but we cannot exclude that also the geological history of each trench may have affected the results.

Slight differences in assemblage structures are expected to occur when comparing different stations within the same topographic setting (Danovaro et al., 2009). In this study, stations of the same topography were located farther away from each other in the Ryukyu region than in the Kuril region (Figure 1). This may have resulted in the appearance of larger differences in assemblage structures between stations of the same topography in the Ryukyu region, thus masking differences between topographies. In contrast, the significant difference recorded in the Kuril region may have appeared as a result of stations with the same topography being located closer to each other (Figure 1), leading to smaller differences between stations of the same topographic settings. Alternatively, according to Hall (2002), the Kuril Trench is older than the Ryukyu Trench. Thus, considerable differences in the harpacticoid assemblages may have developed in each topographic setting around the Kuril region over a longer period, whereas no significant differences may exist around the Ryukyu region due to its shorter geological history.

Environmental factors that influence harpacticoid assemblages: do the same factors influence the distribution pattern of the harpacticoid families in the two trench regions?

The sorting coefficient (SC) has been suggested to influence the distribution of macrofaunal diversity (Etter & Grassle, 1992). For harpacticoids, several environmental factors have been suggested to influence them. Baguley et al. (2006) suggested that POM flux is strongly related to harpacticoid diversity in the deep-sea sediments of the Gulf of Mexico. Montagna (1982) found that four species of Cerviniidae appeared at different depths and attributed this phenomenon to species adaptations to the different sedimentary environments. Shimanaga et al. (2008) reported that bathymetric changes in the composition of Cerviniidae species are regulated by certain factors associated with water depth.

The BIO-ENV analysis showed that the distribution pattern of harpacticoid families in the Ryukyu region was most correlated with CPE concentrations ($\rho_s = -0.28$), suggesting that the amount of organic matter supplied to the sea floor may influence the harpacticoids in this region. In contrast, the MD and SC were most closely associated with the distribution pattern of harpacticoid families in the Kuril region ($\rho_s = 0.76$), suggesting that sediment properties influence harpacticoid assemblages in this region.

Harpacticoid assemblages in the Ryukyu and Kuril regions appeared to be affected by different environmental factors. This observation led us to question why different factors affect harpacticoid assemblages in the Ryukyu and Kuril regions. One possible explanation is the differences in the supply of organic matter. In the Ryukyu region, organic fluxes were much lower than in the Kuril region (Itoh et al., 2011). Consequently, competition for food in the Ryukyu region should be more severe, with food availability possibly influencing the harpacticoid assemblages. In the Kuril region, competition for food may be less severe, allowing
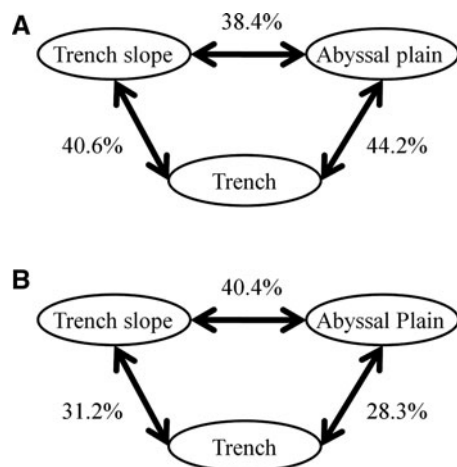

Fig. 3. Average dissimilarities between the trench slope, trench, and abyssal plain stations in (A) the Ryukyu region and (B) Kuril region.

other factors to affect the harpacticoid assemblage. Another possible explanation is associated with the topographical features of the Kuril region. The Kushiro Submarine Canyon, which is one of the largest submarine canyons around the Japanese islands (Ogawa *et al.*, 1993), is located near the sampling stations in this region. As a result, frequent turbidities disturb the sea floor (Noda *et al.*, 2008), and these factors may influence harpacticoid assemblages in this region.

It is possible that the method of determining MD and SC values affected our analysis. The sediment samples obtained from the trenches were treated using an ultrasonic vibrator. This treatment may disintegrate larger particles, such as faecal pellets in the sediment, possibly influencing the results.

Independence of trench assemblages: are the assemblages on the two different trenches isolated from each other?

Trenches are spatially isolated environments that are separated by shallower areas (Jamieson *et al.*, 2009) and are therefore expected to contain distinct assemblages. When the same topographies were compared between the Kuril and Ryukyu regions, the average dissimilarities between the trenches and between the abyssal plains were higher than that between the trench slopes (Figure 4). This finding indicates that between these two regions, the habitats in the trenches and the abyssal plains are more isolated from each other than those in the trench slopes. This observation is contrary to the findings of Gheerardyn & Veit-Köhler (2009) and Menzel *et al.* (2011), which show that the distribution-ranges of benthic harpacticoid species can span thousands of kilometres and cross abyssal plains, ridge structures and complete oceans. Our results may be different because of the Izu-Ogasawara arc and trench, which are located between the two regions, and may prevent the expansion of harpacticoid distribution ranges. Interchange among regions may be difficult for deep-sea benthic animals, including harpacticoid copepods, likely due to the presence of physical barriers around trenches. Therefore, more detailed studies on the depth range of species are required to determine factors that may limit their dispersal.

Distribution of harpacticoid families around the world

Dominant families of harpacticoids do not drastically differ on a global scale (Table 7). In addition, two stations in the Angola
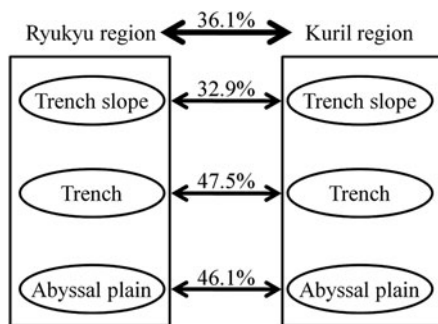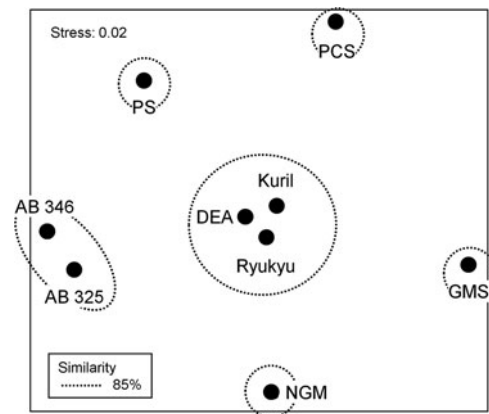

Fig. 5. The non-metric multidimensional scaling ordination based on data of the present study and data from previous studies. Existing studies comprise the DEA site, south-east Pacific Ocean (Ahnert & Schriever, 2001); Great Meteor Seamount (GMS), east Atlantic Ocean (George & Schminke, 2002); Patagonian continental slope (PCS), Southern Ocean (George, 2005), Angola Basin (Angola M325 (AB 325) and M346 (AB 346)), South Atlantic Ocean (Rose *et al.*, 2005); Northern Gulf of Mexico deep sea (NGM; Baguley *et al.*, 2006); and Porcupine Seabight (PS), north-east Atlantic Ocean (Gheerardyn *et al.*, 2010). Contour lines indicate 85% similarity.

Basin and three regions in the Pacific Ocean (the Ryukyu region, the Kuril region and the DEA site) formed clusters with 85% similarity (Figure 5). This finding suggests that harpacticoid assemblages in nearby regions are similar with respect to the relative abundance of families.

In the present study, we analysed the harpacticoid assemblages at the family level. However, it should be noted that further studies at the genus or species level are needed. Analysis at the genus or species level may reveal more detailed patterns of the harpacticoid assemblages than those shown in this study and may provide further information on trench assemblages. Unfortunately, species-level analyses present a major challenge as more than 95% of deep-sea harpacticoid specimens are new to science (cf. Seifried, 2004). In addition, identifications based on morphological characteristics should be performed with caution. For example, molecular studies on shallow-water harpacticoids have revealed that presumably cosmopolitan harpacticoid species are actually 'species complexes' (i.e. composed of several sibling species: Schizas *et al.*, 1999; Rocha-Olivares *et al.*, 2001). Therefore, molecular analyses of deep-sea harpacticoids are required in association with the classical taxonomic approach to provide a clear picture of the deep-sea biodiversity patterns.

Fig. 4. Average dissimilarities between the Ryukyu and Kuril regions.

Research Center, Japan Hydrographic Association and data from Basic Maps of Sea (Continental Shelf) No. 6311 and No. 6315 (published by Japan Coast Guard).

REFERENCES

Ahnert A. and Schriever G. (2001) Response of abyssal Copepoda Harpacticoida (Crustacea) and other meiobenthos to an artificial disturbance and its bearing on future mining for polymetallic nodules. *Deep-Sea Research II* 48, 3779–3794.

Angel M.V. (1982) Ocean trench conservation. *Environmentalist* 2, 1–17.

Barnett P.R.O., Watson J. and Connelly D. (1984) A multiple corer for taking virtually undisturbed samples from shelf, bathyal and abyssal sediments. *Oceanologica Acta* 7, 399–408.

Baguley J.G., Montagna P.A., Lee W., Hyde L.J. and Rowe G. (2006) Spatial and bathymetric trends in Harpacticoida (Copepoda) community structure in the northern Gulf of Mexico deep-sea. *Journal of Experimental Marine Biology and Ecology* 330, 327–341.

Berger W.H. (1989) Global maps of ocean productivity. In Berger W.H., Smetacek V.S. and Wefer G. (eds) *Productivity of the ocean: present and past*. Chichester: John Wiley & Sons, pp. 429–455.

Boxshall G.A. and Halsey S.H. (2004) *An introduction to copepod diversity*. London: The Ray Society.

Clarke K.R. and Warwick R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation*. 2nd edition. Plymouth, UK: Plymouth Marine Laboratory.

Danovaro R., Bianchelli S., Gambi C., Mea M. and Zeppilli D. (2009) α-, β-, γ-, δ- and ε-diversity of deep-sea nematodes in canyons and open slopes of north-east Atlantic and Mediterranean margins. *Marine Ecology Progress Series* 396, 197–209.

Danovaro R., Gambi C. and Della Croce N. (2002) Meiofauna hotspot in the Atacama Trench, eastern South Pacific Ocean. *Deep-Sea Research I* 49, 843–857.

Etter R.J. and Grassle J.F. (1992) Patterns of species diversity in the deep sea as a function of sediment particle size diversity. *Nature* 360, 576–578.

Gambi C., Vanreusel A. and Danovaro R. (2003) Biodiversity of nematode assemblages from deep-sea sediments of the Atacama Slope and Trench (South Pacific Ocean). *Deep-Sea Research I* 50, 103–117.

George K.H. (2005) Sublittoral and bathyal Harpacticoida (Crustacea: Copepoda) of the Magellan region. Composition, distribution and species diversity of selected major taxa. *Scientia Marina* 69, 147–159.

George K.H. and Schminke H.K. (2002) Harpacticoida (Crustacea, Copepoda) of the Great Meteor Seamount, with first conclusions as to the origin of the plateau fauna. *Marine Biology* 144, 887–895.

George R.Y. and Higgins R.P. (1979) Eutrophic hadal benthic community in the Puerto Rico Trench. *Ambio Special Report* 6, 51–58.

Gheerardyn H. and Veit-Köhler G. (2009) Diversity and large-scale biogeography of Paramesochridae (Copepoda, Harpacticoida) in South Atlantic Abyssal Plains and the deep Southern Ocean. *Deep-Sea Research I* 56, 1804–1815.

Gheerardyn H., De Troch M., Vincx M. and Vanreusel A. (2010) Diversity and community structure of harpacticoid copepods associated with cold-water coral substrates in the Porcupine Seabight (North-East Atlantic). *Helgoland Marine Research* 64, 53–62.

Giere O. (2009) *Meiobenthology*. 2nd edition. Berlin: Springer.

Greiser N. and Faubel A. (1988) Biotic factors. In Higgins R.P. and Thiel H. (eds) *Introduction to the study of meiofauna*. Washington, DC: Smithsonian Institution Press, pp. 79–114.

Hall R. (2002) Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences* 20, 353–431.

Horn H.S. (1966) Measurement of 'overlap' in comparative ecological studies. *American Naturalist* 100, 419–424.

Huys R., Gee J.M., Moore C.G. and Hamond R. (1996) *Marine and brackish water harpacticoid copepods, Part 1*. Shrewsbury, UK: Field Studies Council.

Itoh M., Kawamura K., Kitahashi T., Kojima S., Katagiri H. and Shimanaga M. (2011) Bathymetric patterns of meiofaunal abundance and biomass associated with the Kuril and Ryukyu trenches, western North Pacific Ocean. *Deep-Sea Research I* 58, 86–97.

Jackson J.A. (1997) *Glossary of geology*. 4th edition. Alexandria, VA: American Geological Institute.

Jamieson A.J., Fujii T., Mayor D.J., Solan M. and Priede I.G. (2009) Hadal trenches: the ecology of the deepest places on Earth. *Trends in Ecology and Evolution* 25, 190–197.

Jumars P.A. and Hessler R.R. (1976) Hadal community structure: implications from the Aleutian Trench. [Reprint from] *Journal of Marine Research* 34, 547–560.

Menzel L., George K.H. and Martínez Arbizu P. (2011) Submarine ridges do not prevent large-scale dispersal of abyssal fauna: a case study of *Mesocletodes* (Crustacea, Copepoda, Harpacticoida). *Deep-Sea Research I* 58, 839–869.

Montagna P. (1982) Morphological adaptation in the deep-sea benthic harpacticoid copepod family Cerviniidae. *Crustaceana* 42, 37–47.

Narayanaswamy B.E., Bett B.J. and Hughes D.J. (2010) Deep-water macrofaunal diversity in the Faroe–Shetland region (NE Atlantic): a margin subject to an unusual thermal regime. *Marine Ecology* 31, 237–246.

Noda A., TuZino T., Furukawa R., Joshima M. and Uchida J. (2008) Physiographical and sedimentological characteristics of submarine canyons developed upon an active forearc slope: the Kushiro Submarine Canyon, northern Japan. *Geological Society of America Bulletin* 120, 750–767.

Ogawa Y., Kobayashi K., Tamaki K., Thu M.K. and Hanamura Y. (1993) Topography of the western part of the Kuril Trench off Hokkaido based on the Sea Beam map and 3.5 kHz profiles. In Kobayashi K. (ed.) *Preliminary Report of the Hakuho Maru Cruise KH 92-3. Ocean Research Institute*. Tokyo: University of Tokyo, pp. 10–25.

Oksanen J., Kindt R., Legendre P., O'Hara B., Simpson G.L., Solymos P., Stevens M.H.H. and Wagner H. (2008) *vegan: Community Ecology Package*. (available: http://cran.r-project.org/ and http://vegan.r-forge.r-project.org/).

R Development Core Team (2008) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. (available: http://www.R-project.org).

Rex M.A. and Etter R.J. (2010) *Deep-sea biodiversity: pattern and scale*. 1st edition. Cambridge, MA: Harvard University Press.

Rex M.A., Etter R.J., Morris J.S., Crouse J., McClain C.R., Johnson N.A., Stuart C.T., Deming J.W., Thies R. and Avery R. (2006) Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Marine Ecology Progress Series* 317, 1–8.

Richardson M.D., Briggs K.B., Bowles F.A. and Tietjen J.H. (1995) A depauperate benthic assemblage from the nutrient-poor sediments of the Puerto Rico Trench. *Deep-Sea Research I* 42, 351–364.

Rocha-Olivares A., Fleeger J.W. and Foltz D.W. (2001) Decoupling of molecular and morphological evolution in deep lineages of a

meiobenthic harpacticoid copepod. *Molecular Biology and Evolution* 18, 1088–1102.

Rose A., Seifried S., Willen E., George K.H., Veit-Köhler G., Bröhldick K., Drewes J., Moura G., Martínez Arbizu P. and Schminke H.K. (2005) A method for comparing within-core alpha diversity values from repeated multicorer samplings, shown for abyssal Harpacticoida (Crustacea: Copepoda) from the Angola Basin. *Organisms Diversity and Evolution* 5, 3–17.

Sajan S., Joydas T.V. and Damodaran R. (2010) Depth-related patterns of meiofauna on the Indian continental shelf are conserved at reduced taxonomic resolution. *Hydrobiologia* 652, 39–47.

Schizas N.V., Street G.T., Coull B.C., Chandler G.T. and Quattro J.M. (1999) Molecular population structure of the marine benthic copepod *Microarthridion littorale* along the south-eastern and Gulf coasts of the USA. *Marine Biology* 135, 399–405.

Seifried S. (2004) The importance of a phylogenetic system for the study of deep-sea harpacticoid diversity. *Zoological Studies* 43, 435–445.

Shimanaga M., Nomaki H. and Iijima K. (2008) Spatial changes in the distributions of deep-sea 'Cerviniidae' (Harpacticoida, Copepoda) and their associations with environmental factors in the bathyal zone around Sagami Bay, Japan. *Marine Biology* 153, 493–506.

Shirayama Y. and Kojima S. (1994) Abundance of deep-sea meiobenthos off Sanriku, north-eastern Japan. *Journal of Oceanography* 50, 109–117.

Soltwedel T. (2000) Metazoan meiobenthos along continental margins: a review. *Progress in Oceanography* 46, 59–84.

Tietjen J.H. (1989) Ecology of deep-sea nematodes from the Puerto Rico Trench area and Hatteras Plain. *Deep-Sea Research* 36, 1579–1594.

Tietjen J.H., Deming J.W., Rowe G.T., Macko S. and Wilke R.J. (1989) Meiobenthos of the Haatras Abyssal Plain and Puerto Rico Trench: abundance, biomass and associations with bacteria and particulate fluxes. *Deep-Sea Research I* 36, 1567–1577.

Todo Y., Kitazato H., Hashimoto J. and Gooday A.J. (2005) Simple foraminifera flourish at the ocean's deepest point. *Science* 307, 689.

Tselepides A. and Lampadariou N. (2004) Deep-sea meiofaunal community structure in the eastern Mediterranean: are trenches benthic hotspots? *Deep-Sea Research I* 51, 833–847.

Vanhove S., Vermeeren H. and Vanreusel A. (2004) Meiofauna towards the South Sandwich Trench (750–6300 m), focus on nematodes. *Deep-Sea Research II* 51, 1665–1687.

Wells J.B.J. (2007) *An annotated checklist and keys to the species of Copepoda Harpacticoida (Crustacea)*. Aukland, New Zealand: Magnolia Press.

Wolda H. (1981) Similarity indices, sample size and diversity. *Oecologia* 50, 296–302.

and

Wolff T. (1970) The concept of the hadal or ultra-abyssal fauna. *Deep-Sea Research* 17, 983–1003.

Correspondence should be addressed to:
T. Kitahashi
Atmosphere and Ocean Research Institute, the University of Tokyo
5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8564, Japan
email: tkitahashi-10a@nenv.k.u-tokyo.ac.jp