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Deep-sea amphipod community structure across abyssal to hadal depths in the Peru-Chile and Kermadec trenches

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ABSTRACT: Deep-sea necrophagous amphipods were sampled from 5 stations across the abyssal and hadal zones (4602 to 8074 m depth) of the Peru-Chile Trench (SE Pacific Ocean) and combined with comparative data taken from 7 stations at corresponding depths (4329 to 7966 m) in the Kermadec Trench (SW Pacific Ocean) to investigate the diversity and structure of the amphipod communities in the South Pacific Ocean. Four distinctive community groups were identified and their relationships with environmental factors were examined using a total of 6 variables (latitude, longitude, hydrostatic pressure, primary productivity, temperature, sediment characteristics), of which pressure (i.e. depth) and longitudinal (i.e. geographic isolation or dispersal distance) gradients best explained the observed variation in the amphipod assemblage structure. The composition of the abyssal community was dominated by cosmopolitan species belonging to the genera *Paralicella*, *Abyssorchomene* and *Eurythenes*. The 2 most dissimilar groups corresponded to the sites at deeper, hadal depths in both trenches: the hadal Kermadec sites (6890 to 7966 m), dominated by *Hirondellea dubia*, and the hadal Peru-Chile sites (7050 to 8074 m), characterised by the presence of *E. gryllus* and 3 undescribed *Hirondellea* species. The number of amphipod species decreased significantly with increasing depth across all the sampling stations, but the decreasing trend diverged markedly between the 2 hadal trench communities, possibly due to the stark contrast in overlying surface productivity between the 2 regions. Thus the environmental forcing exerted by the pressure and longitudinal gradients on the scavenging amphipod community structure is likely to be further influenced by the surface production and associated flux of food material to the trenches.

KEY WORDS: Amphipoda · Hadal zone · Community structure · Peru-Chile Trench · Kermadec Trench · Pacific Ocean

INTRODUCTION

Scavenging amphipods are an abundant and ubiquitous component of the deep-sea benthic community and are thought to play an important role in the interception, consumption and subsequent dispersal of surface-derived organic matter (e.g. Thurston 1979, Smith & Baldwin 1984, Blankenship et al. 2006). The success of the scavenging lysianassoid amphipods in the deep sea may be attributed to both trophic plasticity (Blankenship & Levin 2007) and their ability to cope with extreme hydrostatic pressure and low temperatures (e.g. MacDonald 1978, Yayanos 1981). These abilities are likely to be responsible for their success on abyssal plains (e.g. Smith & Baldwin 1984) and in the hadal zone (e.g.

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Hessler et al. 1978, Blankenship et al. 2006), where habitats are characterised by low food supply, high pressure and low temperatures (e.g. Jamieson et al. 2010).

Scavenging amphipods can be readily recovered in large numbers using simple baited traps and have therefore been the subject of diverse and detailed studies: e.g. population biology (e.g. Perrone et al. 2002), population genetics (e.g. France & Kocher 1996), dietary composition (e.g. Blankenship & Levin 2007) and physiological adaptation (e.g. Tamburri & Barry 1999). With few exceptions, the majority of studies on deep-sea amphipods originate from bathyal (1000 to 3000 m) or abyssal (3000 to 6000 m) depths. The last decade, however, has seen an increase in sampling effort at hadal depths (>6000 m), and results have demonstrated the overwhelming dominance of amphipods within the scavenging community, particularly at depths below 8000 m in trench environments (Blankenship et al. 2006, Jamieson et al. 2009a, 2011).

The HADEEP project is a collaborative programme initiated in 2006 in order to undertake direct studies on the distribution and behaviour of the deep-living benthic scavenging fauna of the abyssal to hadal boundary. As part of the programme, both baited landers and traps (Jamieson et al. 2009b,c) have been deployed across bathymetric gradients in several of the trenches of the Pacific Rim in order to categorise the bait-attending hadal community, including the Amphipoda (e.g. Jamieson et al. 2009a, 2011, 2012). One such sampling campaign was carried out on the RV 'Sonne' cruise SO209 in 2010 to investigate the scavenging communities of the Peru-Chile Trench in the southeast Pacific.

Most biological sampling campaigns around the Peru-Chile Trench have concentrated on benthic sampling at depths <4000 m (usually <2000 m; e.g. Gallardo et al. 1995) or biological processes within the oxygen minimum zone (e.g. Levin et al. 2002) or at cold seep sites (e.g. Quiroga & Sellanes 2009). There are, however, a few reports from depths >6000 m. For example, Hessler et al. (1978), in a review of baited camera studies in the Philippine Trench, reported on a series of deployments in the Peru-Chile Trench during the Scripps Institution of Oceanography 'Southtow' expedition in 1972. Images from bathyal to abyssal depths (2103 to 4609 m) showed mostly amphipods as well as 3 fish species, natant decapods and the occasional octopod or ophiuroid. In contrast, hadal site images (6767 to 7196 m) contained almost exclusively amphipods. In 1997, an array of 6 baited traps was deployed at 7800 m in the Atacama sector of the Peru-Chile Trench and recovered a total of 942 amphipod samples. These comprised mainly *Eurythenes gryllus* (Fig. 1a) and an undescribed species of *Hirondellea* (Perrone et al. 2002, Thurston et al. 2002). These 2 studies offered the first detailed account of the amphipod assemblage of this trench, but all samples were taken from only one depth.

The present study expands on that of Thurston et al. (2002) and Perrone et al. (2002) by examining the amphipod community structure from 5 depths across the abyssal-hadal transition zone to the deepest point of the Peru-Chile Trench in the southeast Pacific Ocean. Data on amphipod assemblages were previously ob-

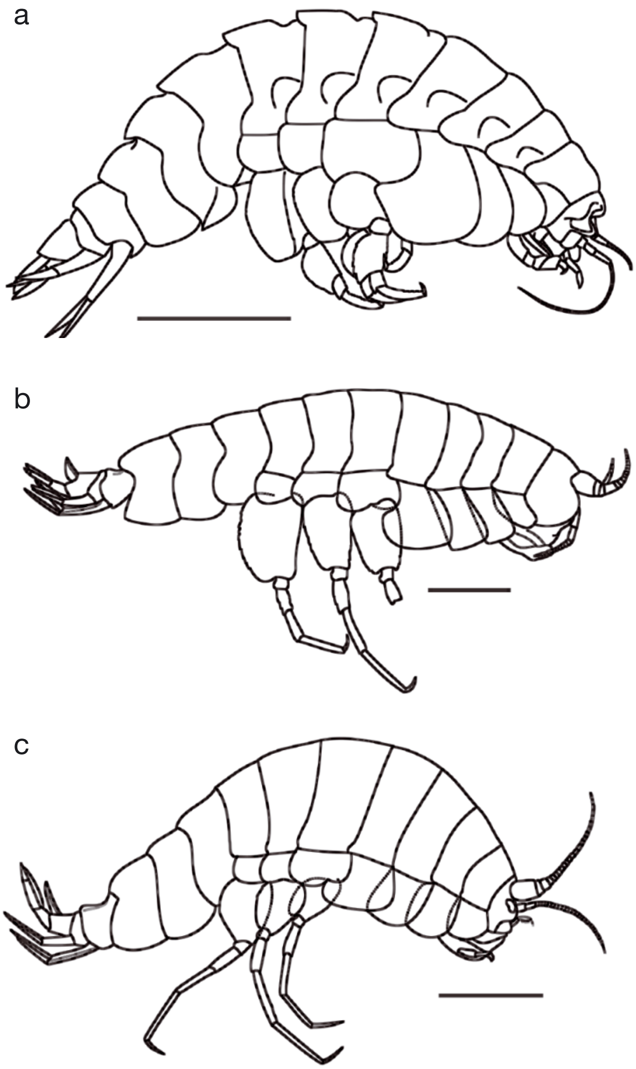

Fig. 1. (a) *Eurythenes gryllus* (Lichtenstein in Mandt, 1822) (Eurytheneidae); scale bar = 20.0 mm. (b) *Hirondellea dubia* Dahl, 1959 (Hirondelleidae); scale bar = 2.0 mm. (c) *Paralicella tenuipes* Chevreux, 1908 (Alicellidae); scale bar = 2.0 mm

tained from corresponding depths in the Kermadec Trench in the southwest Pacific Ocean (Jamieson et al. 2011). These 2 data sets are combined here in order to identify the relationship between environmental factors and variation in community structure from abyssal to hadal depths. The aim of this study is to examine the general hypothesis that amphipod community structures at abyssal depths are characterised by cosmopolitan species whereas community structures at hadal depths differ among individual trenches as a result of geographic isolation and variation in local environmental characteristics.

MATERIALS AND METHODS

Study sites

The Peru-Chile Trench runs southward from off the coast of Ecuador to central Chile (6° S, 82° W to 39° S, 75° W) and is the deepest environment in the southeast Pacific Ocean (Fig. 2). The trench is approximately 5900 km long and 64 km wide and covers an area of approximately 590 000 km^2. Topographically, it is a classic trench with V-shape cross section. It is formed by tectonic subduction; the eastern edge of the Nazca Plate subducts under the South American Plate. The trench is intercepted by the Nazca Ridge. To the north of the ridge, at a point often referred to as the Milne-Edwards Deep, it reaches a maximum depth of ~6500 m. In the southern sector, referred to as the Atacama Trench, it culminates in 2 deep areas, the Bartholomew Deep (7154 m) and the Richards Deep (8065 m). Given that this study includes data from both north and south of the Nazca Ridge, the study area is referred to as the Peru-Chile Trench.

The comparative data, derived from Jamieson et al. (2011), is from a series of samples taken in the Kermadec Trench off the coast of New Zealand, southwest Pacific Ocean (Fig. 2). The Kermadec Trench is located approximately 10 000 km west of the Peru-Chile Trench at slightly lower latitudes between 26 and 36°S, reaching a maximum depth of 10 047 m. The seafloor between the 2 trenches is mostly at abyssal depths (4000 to 5000 m) with the exception of the shallower East Pacific Rise which runs approximately north to south at 110°W.

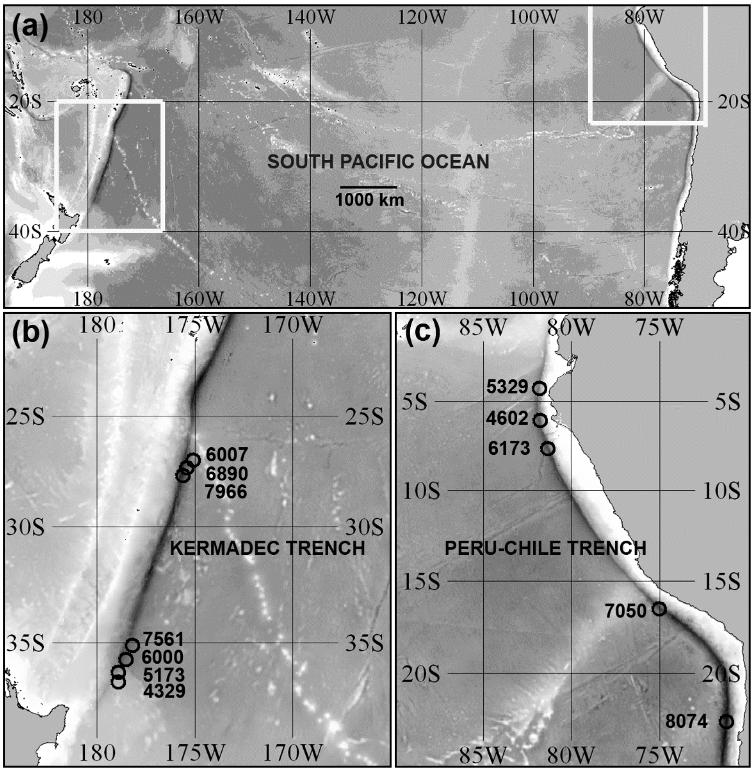

Fig. 2. Study areas for sampling of deep-sea amphipod assemblages: locations of (a) the Peru-Chile and Kermadec trenches in the South Pacific Ocean, and deployment stations, with depths (m), in (b) the Kermadec Trench and (c) the Peru-Chile Trench

Sampling equipment

The study was undertaken using a free-fall baited camera lander (Hadal-Lander B; Jamieson et al. 2009b,c, 2011). Multiple-baited invertebrate funnel traps were coupled to the lander system. Each trap was 30 cm long by 12 cm in diameter with a funnel opening of 2.5 cm in diameter. Each trap was baited with approximately 200 g of locally sourced tuna (*Thunnus* sp.). A trap was coupled to the base of each of the 3 lander footpads at 0 metres above bottom (mab). Individual traps were also coupled to the lander at 1 and 2 mab. Further traps were attached to the buoyancy modules on the mooring line at 20, 30, 40, 50, 60 and 90 mab. In September 2010, the Hadal-Lander B was deployed 5 times at the depths of 4602, 5329 and 6173 m in the northern 'Milne-Edwards' sector and at 7050 and 8074 m in the southern 'Atacama' sector of the Peru-Chile Trench (Fig. 2c). The 8074 m deployment was located in the Richards Deep. The lander was left on the seafloor for a nominal 24 h period (range 11 to 23 h; see Table 1). Samples from 7 deployments in the Kermadec Trench were available, ranging in depth from 4329 to 7966 m (Fig 2b; see Table 2).

Environmental variables

The lander was equipped with a CTD sensor (SBE 19plus V2, SeaBird Electronics) recording salinity, temperature (°C) and pressure (dbar) at 10 s intervals. Pressure was converted to seawater depth following Saunders (1981). Estimates of mean annual primary production rates (mg C m^{-2} d^{-1}) were obtained from the Vertically Generalized Production Model of Behrenfeld & Falkowski (1997) based on MODIS satellite ocean colour data from between mid-2002 and the end of 2011 (www.science.oregonstate.edu/ocean.productivity/). The values for sampling stations were extracted using cells nearest to the station positions in the Peru-Chile and Kermadec trenches at a resolution of 0.083 degrees (nominally 9 km). 'Sediment softness' was assessed visually by reference to the vertical position of the camera's scale bar which also acted to secure the bait. This bar, 1 cm in diameter, was positioned to lie directly on the sediment-water interface assuming no sinking occurs. Sediment softness was recorded as: (1) no sinking; (2) bar and bait in contact with sediment surface; (3) bar and bait partially buried; (4) bar and bait completely sunk in sediment.

Sample treatment and identification

The invertebrate samples from the traps were preserved in 99% ethanol within 1 h of recovery and returned to the laboratory for sorting, species identification and counting. For subsequent analyses, samples taken from the pelagic traps and the bottom traps at each sampling station were pooled together because the pelagic components did not retrieve any significant amphipod catches. The traps at 50 and 60 mab caught nothing at all stations. *Eurythenes gryllus* (Fig. 1a) was the only species to enter the pelagic traps, albeit in low numbers; 1 and 2 individuals at 20 and 90 mab respectively (4602 m), 2 individuals in each of the 40 and 90 mab traps at 5329 m, a single individual at 30 mab at 6173 m and 11 individuals at 7050 m.

Data analysis

Multivariate community analysis was conducted using PRIMER v6 (Clarke & Warwick 2001) in order to identify structure and trends in the amphipod data from the Peru-Chile and Kermadec trenches. Amphipod trap counts were first divided by the duration of deployment (h) to standardise and fourth-root transformed to down-weight the influence of highly abundant species. Cluster analysis (group-average linkage) was performed on a resemblance matrix (Bray-Curtis similarity index) of the transformed abundance data. A similarity profile (SIMPROF) permutation test (significance level $p < 0.05$) was used to identify statistically significant patterns of multivariate structure in the grouping of samples, i.e. to identify 'communities' (Clarke et al. 2008). Trap deployment time can be regarded as a measure of sampling effort, and varied from 9.5 to 47 h among the sites studied. In order to avoid any possible effect of sample-size bias as a result of these differences in deployment time, a RELATE test was conducted to assess the correlation between the amphipod multivariate structure and the trap-time before using further test routines in the multivariate statistical package PRIMER v6 (Clarke & Warwick 2001). A non-metric multidimensional scaling (nMDS) was then conducted to illustrate the degree of similarity across the sampling locations on a 2-D ordination plane based on Bray-Curtis similarity measure. SIMPER (similarity percentage) analysis was also performed in order to identify those species most responsible for the differences between the community groups as well as the similarity within the groups identified by the cluster analysis.

A total of 6 environmental variables, latitude, longitude, hydrostatic pressure, primary productivity (natural-log transformed), bottom temperature and sediment softness, were selected and normalised to generate a resemblance matrix (Euclidean distance) for conducting BIO-ENV stepwise (BEST) analysis and principal component analysis (PCA). The environmental variables considered are all potential drivers of benthic community composition and distribution: latitude and longitude describe the relative geographic position of the sampling sites, and thus the relative isolation and dispersal distance from one site to another; pressure is an important factor controlling the distribution of organisms in the deep sea (e.g. Carney 2005); surface water primary productivity is a useful proxy for the amount of food supplied to seafloor animals (e.g. Stockton & DeLaca 1982), including scavenging animals such as amphipods that feed upon the carcasses of relatively large organisms that derive their nutritional requirements from productivity in surface waters; temperature influences the physiology of organisms to the extent that it exerts control over the occurrence of particular species (e.g. Danovaro et al. 2004); sediment softness was used to provide an indication of substratum conditions at the sampling stations, in particular the organic matter content of the seafloor sediment, which is broadly reflected by the fine particle content of the substratum (e.g. Danovaro et al. 2003) and generally equates to the 'softness' of the sediment; salinity was not included in the analyses as there was little variation in the observed values across sampling stations where the measurement was made. The BEST procedure was used to examine rank correlations between the multivariate patterns of amphipod assemblage and identify the subsets of environmental variables that best explained the overall pattern. PCA was used to identify those environmental variables that correlate with the multivariate pattern of the amphipod assemblage, as well as to reveal which environmental variables explain particular aspects of the observed structure.

To further explore the relationship between amphipod communities and environmental factors, a simple linear regression analysis was performed to identify the possible role of depth in explaining the observed variation in amphipod species richness across sampling sites and cluster groups. Individual-based rarefaction curves (Gotelli & Colwell 2001) were produced to estimate the total number of amphipod species for each cluster group, in order to assess the adequacy of sampling for characterising the amphipod community in this study. These analyses were performed using 'Vegan' package (Oksanen et al. 2013) in R v.2.13.1 (R Development Core Team 2011).

RESULTS

Environmental conditions

There was a systematic difference in bottom temperature between the 2 trenches (Tables 1 & 2). In the Peru-Chile Trench, the temperature ranged from 1.80°C at the shallowest site (4602 m) to 2.25°C at

Table 1. All data from the deployment of 'Hadal-Lander B' (free-fall baited camera lander) at 5 stations in the Peru-Chile Trench (see 'Materials and methods' for explanation of the method used to estimate primary productivity; sediment softness was recorded on a scale from 1 [hardest] to 4 [softest]), number of amphipods recovered (by species and station) and number of species recovered at each station

	Depth (m)				
	4602	5329	6173	7050	8074
Station	SO209/11	SO209/03	SO209/19	SO209/35	SO209/48
Date (dd.mm.yy)	03.09.10	01.09.10	05.09.10	10.09.10	13.09.10
Latitude	06° 12.42′ S	04° 27.02′ S	07° 48.04′ S	17° 25.47′ S	23° 22.47′ S
Longitude	81°40.13′ W	81° 54.72′ W	81° 17.01′ W	73° 37.01′ W	71° 19.97′ W
Bottom time (hh:mm)	20:26	11:09	18:40	22:51	20:25
Pressure (dbar)	4685.9	5426.4	6299.0	7208.5	8278.9
Temperature (°C)	1.8	1.87	1.98	2.07	2.25
Salinity	34.69	34.69	34.69	34.69	34.69
Primary productivity (mg C m^{-2} d^{-1})	2065.2	2144.5	1463.7	859.4	873.3
Sediment softness	3	3	2	4	2
Amphipod species					
Abyssorchomene chevreuxi	313	24	44	–	–
A. distinctus	34	1	–	–	–
Eurythenes gryllus	254	21	32	261	54
Paralicella caperesca	72	174	43		–
P. tenuipes	–	5	7	14	–
Tectovalopsis sp.	1	–	–	–	–
Valettietta sp.	11	–	–	–	–
Princaxelia sp.	–	3	–	–	–
Hirondellea sp. 1	–	–	4	–	–
Hirondellea sp. 2	–	–	2	15	104
Hirondellea sp. 3	–	–	–	33	–
Tryphosella sp.	–	–	–	1	–
aff. *Tryphosella* sp.	–	–	–	–	9
Total no. of ind.	**685**	**228**	**132**	**324**	**167**
No. of species	6	6	6	5	3

Table 2. As in Table 1, except for the deployment of 'Hadal-Lander' at 7 stations in the Kermadec Trench. Data derived from Jamieson et al. (2011)

	Depth (m)						
	4329	5173	6000	6007	6890	7561	7966
Station	KAH0910/08	KAH0910/02	KAH0910/06	KT1a	KT2a	KAH0910/07	KT3a
Date (dd.mm.yy)	09.11.09	05.11.09	07.11.09	07.07.07	08.07.07	08.11.09	10.07.07
Latitude	36° 45.31′ S	36°31.02′ S	36°10.07′ S	26°43.94′ S	26°48.73′ S	35°45.10′ S	26°54.96′ S
Longitude	179°11.52′ W	179°12.03′ W	179°00.27′ W	175°11.33′ W	175°18.10′ W	178°52.55′ W	175°30.73′ W
Bottom time (hh:mm)	12:10	09:30	12:41	17:28	12:16	13:33	46:57
Pressure (dbar)	4405.6	5275.5	6130.7	6133.0	7049.2	7754.4	8170.3
Temperature (°C)	1.06	1.09	1.17	1.16	1.31	1.4	1.46
Salinity	34.70	34.69	34.69	–	–	34.69	–
Primary productivity ($mg\ C\ m^{-2}\ d^{-1}$)	554.4	552	531.6	261.5	261.8	518.9	265.2
Sediment softness	1	2	1	2	2	1	1
Amphipod species							
Paralicella tenuipes	1	18	–	–	–	–	–
Paralicella caperesca	12	620	5	78	–	–	–
Cyclocaris tahitensis		–	–	2	–	–	–
Eurythenes gryllus	3	7	1	2	–	–	–
Rhachotropis sp.	–	4	–	–	–	–	–
Hirondellea dubia	–	–	2	2	127	279	361
Paracallisoma sp.	1	1	–	–	–	–	–
Scopelocheirus schellenbergi	–	–	–	1	10	–	–
Abyssorchomene chevreuxi	–	13	–	–	–	–	–
Abyssorchomene distinctus	2	1	–	–	–	–	–
Abyssorchomene musculosus	3	1	–	–	–	–	–
Orchomenella gerulicorbis	–	37	14	1471	–	1	–
Tryphosella sp.	–	–	–	1	–	–	–
Valettietta anacantha	–	–	–	20	–	–	–
Total no. of ind.	**22**	**702**	**22**	**1577**	**137**	**280**	**361**
No. of species	6	9	4	8	2	2	1

the deepest site (8074 m), whereas the Kermadec Trench showed a temperature range from 1.06°C (4329 m) to 1.46°C (7966 m). Although adiabatic heating (Jamieson et al. 2010) was assumed to be responsible for these similar increases in bottom temperature with increasing depth, the Peru-Chile trench was approximately 0.75°C warmer than the Kermadec Trench at corresponding depths. Salinity in both trenches was essentially constant at 34.69 at all the sampling stations where the measurement was made (Tables 1 & 2). The long-term averages of surface primary production rates at over the Peru-Chile Trench were markedly higher (859.4 to 2144.5 $mg\ C\ m^{-2}\ d^{-1}$) than those over the Kermadec Trench (261.5 to 554.4 $mg\ C\ m^{-2}\ d^{-1}$) (Tables 1 & 2). Sediment softness was generally higher at stations in the Peru-Chile Trench than in the Kermadec Trench (Tables 1 & 2).

Amphipoda

The baited traps collected a total of 1536 amphipods in the Peru-Chile Trench (Table 1). A total of 13 species of amphipod were identified, comprising 3 from the family Alicellidae (23%), 3 Hirondelleidae (23%), 2 Uristidae (15%), 2 Lysianassidae (15%, one putative) and 1 species each of Eurytheneidae, Valettiopsidae and Pardaliscidae (8% each) (Table 1). The most numerically dominant species was *Eurythenes gryllus* (Lichtenstein, 1822) (Eurytheneidae) (Fig. 1a), which was found at all depths and comprised more than twice the total number of individuals of other species. Other abundant species included *Paralicella caperesca* (Shulenberger & Barnard, 1976) (Alicellidae) and *Abyssorchomene chevreuxi* (Stebbing 1906) (Uristidae), both mostly confined to abyssal stations (4602 to 6173 m). At hadal depths (6173 to 8074 m), the most dominant species other than *E. gryllus* were of the Hirondelleidae family. Three undescribed species were determined, *Hirondellea* sp. 1, 2 and 3; of these *Hirondellea* sp. 2 was dominant, particularly at deeper sites (Table 1). The data from the Kermadec Trench are shown in Table 2 and a detailed account of the sampling campaigns can be found in Jamieson et al. (2011).

Amphipod community structure

Cluster analysis and SIMPROF test revealed 4 distinctive amphipod assemblage groups, or communities (Fig. 3a). Although the trap deployment time varied substantially, ranging from 9 to 47 h (Tables 1 & 2), the RELATE test did not suggest that the main analysis was confounded by sample size effect ($\rho = 0.21$, $p > 0.05$). The nMDS plot illustrated the clear separation of these amphipod community groups (Fig. 3b). The most dissimilar groups corresponded to the sites at hadal depths: the deepest 3 Kermadec sites (Group 1: 6890, 7561 and 7966 m) and the 2 deepest Peru-Chile sites (Group 4: 7050 and 8074 m) (Fig. 3). Other groups comprised 2 stations from the Kermadec Trench at the boundary of the hadal zone (Group 2: 6000 and 6007 m), and a mixture of 3 stations from Peru-Chile Trench and 2 stations from Kermadec Trench (Group 3). These 5 stations in Group 3 corresponded to abyssal depths: 4602, 5329 and 6173 m (Peru-Chile sites) and 4329 and 5173 m (Kermadec sites).

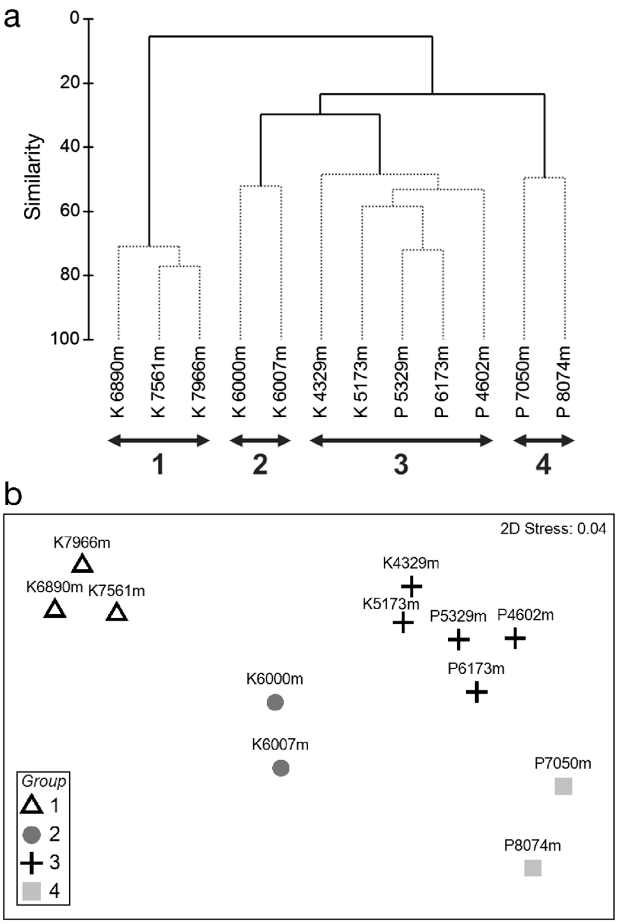

Fig. 3. Multivariate analysis of amphipod assemblage composition in deep-sea trenches. (a) Dendrogram based on fourth-root transformation, Bray-Curtis similarity and group-average clustering. Four main groups of sites (black branches) were identified based on the similarity profile (SIMPROF) permutation test ($p < 0.05$). (b) Non-metric multidimensional scaling (nMDS) ordination, based on fourth-root transformation and Bray-Curtis similarity. Sites identified by P: Peru-Chile Trench; K: Kermadec Trench; and sampling depth

The amphipod species and their percentage contributions which accounted for most of the similarity (> 90 %) within cluster groups based on the SIMPER analysis are shown in Table 3. Groups 2, 3 and 4 showed an average similarity of around 50 %, whereas Group 1 had a higher average similarity level of 73.1 % (Table 3). *Hirondellea dubia* (Fig. 1b) was the sole species responsible for the similarity within Group 1 (Kermadec hadal sites), whereas *Eurythenes gryllus* and *Hirondellea* sp. 2 were the 2 species which contributed most, and almost equally to the average similarity within Group 4 (Peru-Chile hadal sites) (Table 3). The number of species responsible for the average similarities within the groups generally increased from deeper hadal to shallower abyssal groups, and *H. dubia*, *Paralicella caperesca* and *E. gryllus* made multiple contributions to average faunal similarities across groups, namely between Groups 1–2, 2–3 and 3–4 (Table 3).

The average dissimilarity level between Groups 1 and 4 was the highest (100.0 %), followed by 99.5 % between Groups 1 and 3 (Table 3). Average abundances of *Hirondellea dubia* were higher in Group 1 and those of *Eurythenes gryllus* were higher in Group 3 and 4; however, the occurrence of *Paralicella caperesca* in Group 3 contributed to the majority of the dissimilarity in both cases. The third highest average dissimilarity (86.4 %) was between Groups 2 and 4, and the occurrence of *Orchomenella gerulicorbis*, *Hirondellea* sp. 2 and *P. caperesca* contributed the majority of the dissimilarity observed. Groups 2 and 3 showed the least average dissimilarity of 70.1 %, with majority of dissimilarity accounted for by the almost exclusive occurrence of *O. gerulicorbis* in Group 2, the total absence of both *Abyssorchomene chevreuxi* and *P. tenuipes* (Fig. 1c) in Group 2, and variation in the abundance of *P. caperesca* across the 2 groups.

Table 3. Results of SIMPER analysis of amphipod community structure in the Peru-Chile and Kermadec trenches, showing (dis)similarities within and between the 4 cluster groups identified (see Fig. 3a), and percentage contributions of amphipod species which accounted for most (>90 %) of those values

	Group 1	**Group 2**	**Group 3**	**Group 4**
Group 1	(Similarity = 73.1 %) Species % *Hirondellea dubia* 100	(Dissimilarity = 76.4 %) Species % *Orchomenella gerulicorbis* 28.4 *Hirondellea dubia* 23.0 *Paralicella caperesca* 18.8 *Eurythenes gryllus* 10.2 *Scopelocheirus schellenbergi* 6.6 *Valettietta* sp. 6.4	(Dissimilarity = 99.5 %) Species % *Hirondellea dubia* 21.5 *Paralicella caperesca* 18.2 *Eurythenes gryllus* 13.1 *Abyssorchomene chevreuxi* 11.6 *Paralicella tenuipes* 7.5 *Abyssorchomene distinctus* 6.5 *Orchomenella gerulicorbis* 3.7 *Scopelocheirus schellenbergi* 3.5 *Abyssorchomene musculosus* 3.1 *Paracallisoma* sp. 2.6	(Dissimilarity = 100.0 %) Species % *Hirondellea dubia* 28.1 *Eurythenes gryllus* 23.1 *Hirondellea* sp. 2 18.7 *Hirondellea* sp. 3 7.3 *aff. Tryphosella* 6.9 *Paralicella tenuipes* 5.9 *Scopelocheirus schellenbergi* 4.5
Group 2		(Similarity = 52.2 %) Species % *Orchomenella gerulicorbis* 35.0 *Paralicella caperesca* 27.1 *Hirondellea dubia* 19.9 *Eurythenes gryllus* 18.1	(Dissimilarity = 70.1 %) Species % *Orchomenella gerulicorbis* 20.6 *Abyssorchomene chevreuxi* 12.8 *Paralicella caperesca* 8.4 *Paralicella tenuipes* 8.0 *Hirondellea dubia* 7.6 *Eurythenes gryllus* 7.3 *Abyssorchomene distinctus* 7.0 *Valettietta* sp. 5.0 *Abyssorchomene musculosus* 3.3 *Cyclocaris tahitensis* 2.8 *Paracallisoma* sp. 2.8 *Tryphosella* sp. 2.4 *Scopelocheirus schellenbergi* 2.4	(Dissimilarity = 86.4 %) Species % *Orchomenella gerulicorbis* 22.1 *Hirondellea* sp. 2 15.4 *Paralicella caperesca* 13.0 *Eurythenes gryllus* 12.3 *Hirondellea dubia* 7.7 *Hirondellea* sp. 3 6.3 *aff. Tryphosella* 5.6 *Paralicella tenuipes* 5.1 *Valettietta* sp. 4.8
Group 3			(Similarity = 54.3 %) Species % *Paralicella caperesca* 33.9 *Eurythenes gryllus* 25.1 *Abyssorchomene chevreuxi* 17.5 *Paralicella tenuipes* 11.4 *Abyssorchomene distinctus* 9.2	(Dissimilarity = 72.5 %) Species % *Paralicella caperesca* 20.4 *Hirondellea* sp. 2 14.1 *Abyssorchomene chevreuxi* 13.2 *Abyssorchomene distinctus* 7.2 *Eurythenes gryllus* 6.7 *Hirondellea* sp. 3 6.5 *Paralicella tenuipes* 6.4 *aff. Tryphosella* 5.6 *Abyssorchomene musculosus* 3.4 *Paracallisoma* sp. 2.9 *Orchomenella gerulicorbis* 2.7 *Tryphosella* sp. 2.7
Group 4				(Similarity = 49.6 %) Species % *Eurythenes gryllus* 58.6 *Hirondellea* sp. 2 41.4

Environmental drivers

BEST analysis revealed that the 4 best subsets of environmental variables, which generated the highest rank correlation with the amphipod multivariate data, were combinations of pressure, longitude, sediment softness and primary productivity (Table 4). The combination of pressure and longitude produced the highest correlation ($\rho = 0.64$, $p < 0.001$). While pressure and longitude appeared in every combination of the 4 best subsets selected in the procedure, neither latitude nor temperature were selected in a single combination (Table 4).

The PCA of environmental variables showed the influence of those associated with geographical and depth dimensions along the first 2 PC axes, which explained 88% of the total variance (Fig. 4). PC Axis 1 was influenced by longitude, latitude, productivity and sediment softness, variables potentially associated with geographical isolation (physical distance between stations along longitudinal or latitudinal gradients) and regional differences in environmental characteristics between the trenches. PC Axis 2 was dominated by pressure alone, reflecting the environmental forcing associated with the depth gradient. Temperature contributed to some degree to distinguishing between both the geographical and depth-related grouping of stations (Fig. 4).

The number of amphipod species decreased significantly with increasing depth across all the sampling stations ($n = 12$, $R^2 = 0.55$, $F = 12.47$, $p < 0.01$) (Fig. 5a). However, in relation to community groups, this declining trend in species richness diverged with increasing depth (Fig. 5a). Overall examinations of individual-based rarefaction curves by cluster groups (Fig. 5b) also suggested that estimated number of species in Group 4 (Peru-Chile hadal sites) was consistently higher than that in Group 1 (Kermadec hadal sites) and demonstrated that sampling was adequate to characterise the amphipod community structure in this study.

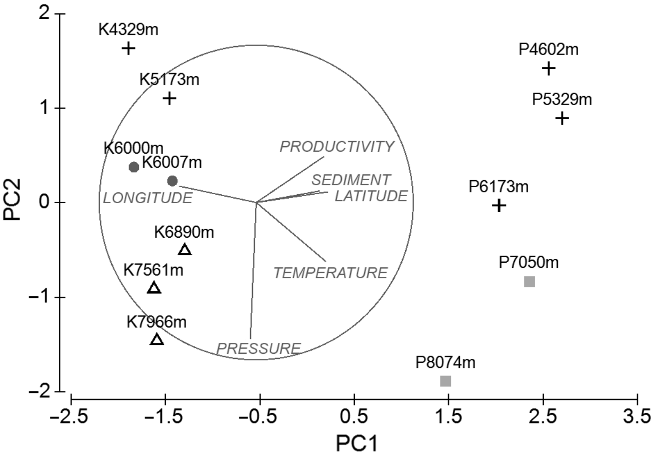

Fig. 4. Principal component analysis (PCA) of the influence of 6 environmental variables on amphipod community structure in deep-sea trenches. Sites identified by P: Peru-Chile Trench; K: Kermadec Trench; and sampling depth. Symbols represent the groups of sites identified by cluster analysis (see Fig. 3)

Table 4. Results of BIO-ENV stepwise (BEST) analysis of potential drivers of deep-sea amphipod community structure in the Peru-Chile and Kermadec trenches, showing the 4 subsets of combinations of 6 environmental variables that generated the highest Spearman's rank correlations (ρ) with the community structure, and results for the individual variables (in parentheses). PRE: hydrostatic pressure; LON: longitude; SED: sediment softness; PRO: surface primary productivity; TEM: bottom temperature; LAT: latitude

Variables	Correlation (ρ)	p-value
PRE, LON	0.64	< 0.001
PRE, SED, LON	0.55	< 0.001
PRE, LON, PRO	0.55	< 0.01
PRE, SED, LON, PRO	0.54	< 0.01
(PRE)	0.41	< 0.01
(TEM)	0.36	< 0.05
(LON)	0.36	< 0.05
(PRO)	0.34	< 0.05
(LAT)	0.12	ns
(SED)	0.12	ns

DISCUSSION

The scavenging amphipod community composition of the Peru-Chile Trench was similar to that found in the Kermadec Trench as well as other deep-sea environments, where the abyssal zones are dominated by cosmopolitan deep-sea species of the genera *Paralicella, Abyssorchomene* and *Eurythenes* (Shulenberger & Hessler 1974, Dahl 1979, Thurston 1990). The shift from these abyssal genera to the hadal genus *Hirondellea* is also typical of trench environments (Hessler et al. 1978, Blankenship et al. 2006, Jamieson et al. 2011). However, while the Kermadec Trench fauna was dominated by *Hirondellea dubia* at deeper hadal depths, *E. gryllus* remained an important species, coexisting with the 3 undescribed species of *Hirondellea*, at hadal depths in the Peru-Chile Trench.

The amphipod assemblages of the Kermadec and Peru-Chile Trenches appeared to be influenced by a

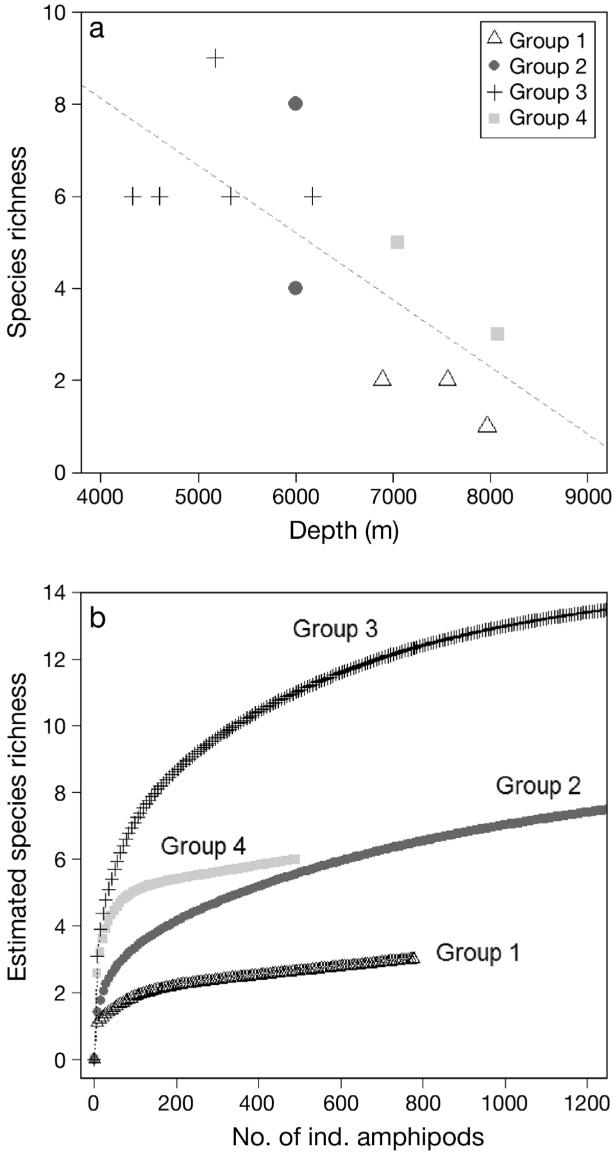

Fig. 5. (a) Relationship between the amphipod species richness and depth, showing the line (dashed) fitted by linear regression analysis ($y = -0.00146x + 13.987$, n = 12, $R^2 = 0.55$, $F = 12.47$, $p < 0.01$). Symbols represent the groups of sites identified by cluster analysis (Fig. 3). (b) Rarefaction curves for the 4 cluster groups showing the estimated number of amphipod species per number of individuals sampled

combination of both hydrostatic pressure and longitudinal gradients. Pressure appeared to be the most important environmental factor shaping the structure of the amphipod assemblage, with clear separation of abyssal and hadal communities along the vertical depth (pressure) gradient. The abyssal amphipod community (Group 3) had a relatively high degree of similarity irrespective of trench location, suggesting a high degree of connectivity across the vast stretches of the abyssal plain between the 2 trenches. There appear very few physical impediments to dispersal between the 2 regions at these depths, with abyssal areas being almost contiguous along the longitudinal gradient between the edges of the Peru-Chile and Kermadec trenches. In the deeper hadal zone, however, there was no similarity between the communities from each trench (Group 1 and 4), suggesting that at these depths the trench fauna are either physically isolated and/or the environmental conditions experienced by each trench are sufficiently differentiated to account for the faunal differences. The Peru-Chile and Kermadec Trenches are approximately 10 000 km apart and this geographical isolation, together with the vertical barrier imposed by the hydrostatic pressure, may be responsible for the total dissimilarity in community structure observed between the 2 trenches at hadal depths. The combined vertical and horizontal isolation could result in allopatric speciation (e.g. France & Kocher 1996). Support for this contention is provided in this study by the different species of *Hirondellea* found in each trench. Other trench studies have shown that, for example, *Hirondellea gigas* is the single dominant amphipod species at hadal depths in northwest Pacific trenches (Kurile-Kamchatka, Japan, Izu-Bonin, Mariana, Yap, Palau and Philippine trenches; Kamenskaya 1981, France 1993), whereas *H. dubia* is dominant in southwest Pacific trenches (Kermadec and Tonga trenches; Blankenship et al. 2006). In the only amphipod study at hadal depths in the Peru-Chile trench prior to this study (Perrone et al. 2002), only 1 undescribed *Hirondellea* species was documented, collected from 7800 m.

The presence of the *Eurythenes gryllus* at hadal depths in the Peru-Chile Trench was noted in contrast to its absence at such depths in the Kermadec Trench. *E. gryllus* is one of the most bathymetrically and geographically widespread marine species. It is found throughout all oceans (Barnard 1961, Thurston 1990) and appears to have the widest bathymetric range (>7500 m) of any amphipod, from 550 m (Weddell Sea; De Broyer et al. 2007) to 8074 m (this study. However, it is thought to be a cold-water stenotherm species, inhabiting shallower depths at the poles but restricted to deeper, colder waters at low latitudes (Thurston et al. 2002). Data from this study and other literature demonstrates that *E. gryllus* is capable of surviving hydrostatic pressures to 8074 m at lower latitudes in the Peru-Chile Trench where temperatures are warmer (up to 2.25°C), yet does not penetrate far beyond 6000 m at higher latitudes in the Kermadec Trench (deepest record = 6007 m; Jamieson et al. 2011) or in the neighbouring Tonga Trench (deepest record = 6252 m; Blankenship et al. 2006) where temperatures are colder. This somewhat contradicts the expected distribution of *E. gryllus* based purely on the cold-water stenotherm hypothesis. The incursion of Antarctic water in the form of the Lower Circumpolar Deep Water mass (LCDW) into the Kermadec Trench makes it one of the coldest trenches, with bottom temperatures of 1.2 to 1.8°C (Belyaev 1989). The apparent absence of this species from the deepest parts of the Kermadec and Tonga trenches suggests that temperature may not be the only environmental driver responsible for both bathymetric and geographic distribution of *E. gryllus*.

With respect to the feeding behaviour of deep-sea scavenging amphipods, both *Eurythenes gryllus* and *Scopelocheirus schellenbergi* belong to a 'benthopelagic guild' (Ingram & Hessler 1983, Blankenship & Levin 2007), members of which specialise in foraging for large carrion items from above the sea floor near the top of the Eckman layer. In contrast, members of a 'demersal guild', which include *Hirondellea* spp. and *Paralicella* spp., remain closely associated with seafloor and tend to be more facultative in their scavenging behaviour. In the Kermadec and Tonga trenches, the lower depth range of *E. gryllus* corresponds with the upper depth limit of *S. schellenbergi*. The apparent absence of *Scopelocheirus* spp. or other members of benthopelagic guild from the Peru-Chile Trench may have therefore allowed *Eurythenes gryllus* to extend its vertical range to fill this niche in this environment. This, however, is only a postulation and Sainte-Marie (1992) emphasises that the concept of benthopelagic and demersal guilds needs to be critically evaluated.

Primary productivity of the surface waters above the trenches, or rather the amount of potential food for scavenging organisms derived from this productivity, was implicated by our analysis as an important driver of amphipod community composition. The Peru-Chile Trench is situated within the CHIL biogeographic province (Longhurst et al. 1995) and lies below the Humboldt Current and the Peruvian upwelling system, which makes this trench system one of the most productive areas of the world (up to 19.9 g C m^{-2} d^{-1}; Daneri et al. 2000). Analysis of organic content of the sediment has suggested that the Peru-Chile Trench is an example of a eutrophic hadal environment, which has resulted from organic enrichment by topographic accumulation of organic matter transported down-slope (Danovaro et al. 2003). This contention is supported by this study as the degree of sediment softness was found to be generally higher in the Peru-Chile Trench than in Kermadec Trench. In contrast, the Kermadec region is relatively oligotrophic with a mean annual primary production rate of 87 g C m^{-2} y^{-1} compared to 269 g C m^{-2} y^{-1} in the Peru-Chile region (Longhurst et al. 1995), suggesting that food availability in the Kermadec region is considerably lower than that in the Peru-Chile region. The bathymetric and biogeographic distribution of *Eurythenes gryllus*, and thus the difference in the hadal communities between the 2 trench systems, might be driven not only by temperature and/or physical isolation but also by food availability, illustrating the potential roles that various environmental conditions could interplay in structuring benthic communities across the deepest parts of the multiple hadal trench ecosystems (Jamieson et al. 2010).

The distinct amphipod assemblage identified at the shallowest extent of the hadal zone in the Kermadec Trench (~6000 m; Group 2) was not mirrored by a community at a similar depth in the Peru-Chile Trench (i.e. the assemblage found at 6173 m, grouped with the abyssal community of Group 3). The reason for this contrast may be related to the position of the sampling stations relative to the morphology of the 2 trenches. Jamieson et al. (2011) proposed that the precise location of the ecotone between abyssal and hadal communities could be influenced by abrupt changes in topography as the abyssal plains drop away into the trench. In the Kermadec Trench, the stations at 6000 and 6007 m (Group 2) were both situated on a relatively shallow sloping seafloor in close proximity to a marked slope change at ~6400 m (Jamieson et al. 2011); whereas in the Peru-Chile trench, there was no such topographical demarcation observed, at least between the locations of the 3 stations at 4602, 5329 and 6173 m that were grouped into the same abyssal community (Group 3). An alternative explanation for the grouping of the amphipod assemblage at the 6173 m with the abyssal sites is that all these stations were located in the northern Milne-Edwards sector of the trench, whereas the hadal stations were located in the southern Atacama Trench sector. However, our analysis showed that latitudinal gradient did not significantly influence the structure of the deep-sea amphipod assemblage, suggesting that the north–south alignment of the trench axes observed in both trenches could act as dispersal corridor and thereby facilitate similarity among the fauna along a latitudinal gradient. In this study, both 'longitude' and 'latitude' were used as a measure of geographic distance between sites, which gives an indication of relative isolation of one site from another (potential dispersal distance) along respective directions. Our results thus indicate that for those organisms inhabiting across abyssal-hadal zones, migrating in a west–east (longitudinal) direction may be totally different from travelling in a north–south (latitudinal) direction at the ocean-basin scale, due partially to: the presence of relatively few physical impediments but relatively long physical distance across the vast abyssal plains in a longitudinal direction; the prevailing direction of the deep-water currents; and the orientation of trench axes (often aligned in a north–south direction, particularly in the southern hemisphere).

The number of amphipod species caught by the traps decreased significantly with increasing depth across all the sampling stations. Comparisons of rarefaction curves also showed that at hadal depths, the expected number of species was consistently higher for the community in the Peru-Chile trench (Group 4) than for the community in the Kermadec trench (Group 1). This pattern may be attributable to either a greater quantity of food or a greater variety of resource types reaching the seafloor of the Peru-Chile trench, which would potentially permit resource partitioning by enhanced numbers of species, thus minimising the risk of exclusion resulting from inter-specific competition (Levin et al. 2001). In the case of oligotrophic Tonga and Kermadec trenches, evidence from stable isotope analysis of 3 amphipod species (*Hirondellea dubia*, *Scopelocheirus schellenbergi* and *Uristes* sp.) coexisting at shallower hadal depths, indicated a form of character displacement (e.g. diet partitioning) that is likely to be driven by interspecific competition (Blankenship & Levin 2007). However, *H. dubia* becomes a single species dominating at deeper depths of the Tonga and Kermadec trenches (Blankenship & Levin 2007, this study), and the isotopic signatures of *H. dubia* in the deepest Tonga Trench pointed to a detrital-based food chain, suggesting that such trophic shifts together with a marked reduction in species richness may well be dictated by the extreme food limitation or the unavailability of desired resource types (e.g. carrion) at these depths in the oligotrophic trenches (Blankenship & Levin 2007). In addition, the Peru-Chile Trench is situated very close to the South American land mass over its entire length while the Kermadec Trench only connects to the relatively small North Island of New Zealand at its most southern point. These geographical settings combined with the contrast in surface productivity (Longhurst et al. 1995, Daneri et al. 2000, this study) suggest that the quantity of organic matter of both terrestrial and marine origin is substantially higher in the Peru-Chile Trench than in the Kermadec trench and is likely an important driver of the observed differences in community structure between the 2 hadal communities.

Overall, the analysis presented in this study suggests that hydrostatic pressure (depth), longitudinal gradient and possible influence of food supply are likely to drive the amphipod community structures observed in the 2 trenches, as also reported from shallower abyssal environments (Levin et al. 2001, Wei et al. 2010). Our results, however, were based on a modest dataset obtained from only 2 trench environments in the South Pacific Ocean, and it was therefore not possible to determine the extent to which each of the key environmental factors was responsible for the particular patterns observed. Constraints in sample sizes and limitation in geographical coverage are inherent in trench investigations, making it difficult to explicitly identify possible environmental drivers and their relative importance for community structure. Further sampling using sediment corers or tethered sediments traps at hadal depths in these trenches has yet to be undertaken, which could provide quantitative analysis to identify the relative importance of food supply and examine the possibility of resource partitioning. The systematic 3-D mapping of resource distribution in the hadal trenches will also be paramount in disentangling the effects of environmental factors such as food supply, temperature, deep-water currents, substratum type and topography in driving the ecology of deep-sea hadal trench communities.

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