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Population structure of the hadal amphipod *Bathycallisoma (Scopelocheirus) schellenbergi* (Birstein and Vinogradov, 1958) in the Kermadec Trench and New Hebrides Trench, SW Pacific

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Highlights:

- The hadal amphipod, *Bathycallisoma schellenbergi*, was sampled across its full depth range within two hadal trenches.
- Their minimum depth range was 1000 m shallower in the shallower trench (New Hebrides).
- Their maximum abundance occurred 1000 m deeper in the deeper trench (Kermadec).
- Relative trends in population structure were the same in both trenches but occurred over different depths.
- The lower depth limit for juveniles was the same in both trenches.
- Trench morphology and ecological interactions influence population structure rather than hydrostatic pressure alone.

Abstract

Deep sea animals inhabiting the hadal zone (>6,000 m deep) are frequently reported to occupy large bathymetric ranges, but details of intra-specific population structure and the underlying drivers remain poorly understood. Here we describe the population structure of the dominant SW Pacific

hadal amphipod, *Bathycallisoma schellenbergi*, across its bathymetric range in the Kermadec (10,047 m) and New Hebrides (7156 m) trenches and explore the factors likely responsible for the observed patterns. These two trenches are relatively close geographically but underlie different water masses and are topographically isolated by the Kermadec fore-arc. The minimum depth of *B. schellenbergi* was ~1000 m shallower in the New Hebrides Trench than in the Kermadec Trench although similar patterns of ontogenetic stratification were present; juveniles were restricted to depths <~7000 m, larger adults were deeper toward the trench axes, regardless of absolute depth. We suggest that the increased juvenile presence around the abyssal-hadal transition zone is driven by reduced competition and a relaxation of pressure effects on metabolism. Evidence is also presented for morphological heterogeneity indicating geographic isolation between the two trenches. Interestingly, the absence of another major scavenging amphipod, *Hirondellea dubia*, at mid-trench depths corresponded to maximum densities of *B. schellenbergi*, a trend that was reversed towards the trench axes regardless of actual depth. This suggests that the population structure and amphipod assemblages are more affected by how trench topography influences the distribution of food and potential ecological interactions, rather than simply by the effects of hydrostatic pressure.

Introduction

The last decade had seen a renaissance in scientific endeavour at hadal depths (6000 - 11,000 m, Jamieson, 2015). The technical challenges of undertaking biological research of such an extreme environment has favoured the use of baited cameras and traps (Blankenship et al., 2006; Fujii et al., 2013, 2010, Jamieson et al., 2009ab, 2011ab), which in turn focuses effort on the bait-attending communities. These communities are dominated by snailfish, scavenging amphipods and predatory decapods in the upper trench depths (6000 – 8000 m) (Jamieson et al., 2009ab), whereas the deeper depths are dominated almost exclusively by scavenging amphipods. Amphipods, predominantly of the superfamily Lysianassoidea, play a key role in the hadal food web as prey to the larger organisms in the upper depths (Jamieson et al., 2009a, 2009b; Linley et al., 2016a) and through overwhelming dominance of the scavenging fauna at greater depths (Blankenship et al., 2006; Hessler et al., 1978).

Amphipods are ideal taxon in which to study population structure at hadal depths as they are readily sampled in adequate numbers to permit meaningful study. Furthermore, the recent increases in sampling effort at hadal depths over extensive bathymetric ranges and across multiple trenches is permitting inferences to be made on community and population structure at both intra- and inter-trench levels for the first time (Fujii et al., 2013; Lacey et al., 2016). As such, hadal amphipods have

60 been the subject of numerous and diverse studies in recent years (Blankenship et al., 2006;
61 Blankenship and Levin, 2007; Jamieson et al., 2011a; Kobayashi et al., 2012; Eustace et al., 2013,
62 2016; Ritchie et al., 2015, 2016; Lacey et al., 2016).

63 Hadal trenches do not form part of the continental shelf-slope-rise to abyssal plain continuum, but
64 rather are deep and geographically sporadic clusters of disjunct and isolated environments. Indeed
65 despite comprising only 0.24% of the world's ocean area, the hadal zone represents 45% of the
66 oceans' depth range (Jamieson, 2015). Hadal amphipods, particularly of the superfamily
67 Lysianassoidea, have been widely reported from bathyal, abyssal and hadal depths but are often
68 unique to a single trench, or adjoining trenches, and therefore exhibit a high level of trench
69 endemism at species level (Belyaev, 1989). Amphipod communities have been found to be divided
70 by a distinct 'ecotone' beyond the abyssal-hadal transition zone, and are not simply extensions of
71 shallower bathyal and abyssal communities (Fujii et al., 2013; Jamieson et al., 2011a; Lacey et al.,
72 2016).

73 Bathymetric trends in diversity and abundance of deep sea amphipods appear broadly consistent
74 between trenches studied to date; namely a decrease in diversity and increase in abundance with
75 depth (Blankenship et al., 2006, Jamieson et al., 2009a, Fujii et al., 2013). The physiological effects of
76 hydrostatic pressure are believed to play a key role in the structuring of species' bathymetric ranges
77 (Pradillon and Gaill, 2007). However, the community composition and bathymetric ranges of species
78 have been found to differ between trenches, potentially due to a combination of trench topography
79 and the supply and distribution of nutrients from overlying waters, rather than high hydrostatic
80 pressure alone (Fujii et al., 2013; Lacey et al., 2016). The vertical population structure of species
81 inhabiting multiple trenches would therefore be expected to differ in each trench.

82 With increasing sampling effort at abyssal and hadal depths, many abyssal species are being found
83 to have cosmopolitan distributions. However, *Bathycallisoma* (syn. *Scopelocheirus*) *schellenbergi*
84 (Birstein and Vinogradov, 1958) has arguably the widest known geographic distribution of any
85 amphipod found in the trenches (Lacey et al., 2013). *Hirondellea dubia* (Hirondelleidae, Dahl 1959),
86 another endemic hadal species, appears to be restricted to the trenches of the southwest Pacific;
87 the Kermadec, Tonga and New Hebrides trenches (Blankenship et al., 2006; Dahl, 1959). Whereas *H.*
88 *gigas* (Birstein and Vinogradov, 1955) has been recorded in all northwest Pacific trenches studied to
89 date (France, 1993), three further species of *Hirondellea* have been identified from the Peru-Chile
90 Trench in the southeast Pacific (Kilgallen, 2014). Species of the genera *Eurythenes*, *Paralicella* and
91 *Abyssorchomene* are often found in the upper hadal depths of some trenches as a result of as yet

unresolved extensions from their otherwise cosmopolitan abyssal distributions (Fujii et al., 2013; Lacey et al., 2016).

The vertical population structure of hadal amphipod species remains largely unknown. Most studies to date have either been based on collections from a single depth (Hessler et al., 1978; Perrone et al., 2002; Thurston et al., 2002) or are concerned with community composition and bathymetric trends in diversity (Blankenship et al., 2006; Fujii et al., 2013; Jamieson et al., 2011a, 2010). The exceptions are the reports of bathymetric ontogenetic stratification of *Hirondellea dubia* and *B. schellenbergi* from the Tonga Trench (Blankenship et al. 2006), *H. gigas* from the Izu-Bonin Trench (Eustace et al., 2013) and morphotypes of *Eurythenes gryllus sensu lato* from the Peru-Chile Trench (Eustace et al., 2016). In these studies juveniles were found to dominate the population at the shallower ends of the species' bathymetric range, with larger brooding females at the deeper end of their range.

This study examined the population structure of *B. schellenbergi* over its entire bathymetric range in two contrasting trenches in the southwest Pacific, the Kermadec Trench (10,047 m) and the New Hebrides Trench (7156 m), and examines the drivers of the observed trends. Comparison between these two trenches allows us explore how population structure is affected by depth (hydrostatic pressure) and trench morphology. We examine two contrasting hypotheses: (H1) the vertical population structure of *B. schellenbergi* is the same in both trenches but truncated at the lower end of their range in the shallower, New Hebrides Trench (depth-driven) or, alternatively, (H2) any trends in population structure found in the Kermadec Trench are compressed within the smaller vertical range available in the New Hebrides Trench (topography-driven).

Materials and Methods

Study sites

The Kermadec Trench lies ~120 km off the coast of North Island, New Zealand, in the southwest Pacific Ocean and runs parallel to the Kermadec Ridge (Fig. 1.). The Kermadec Trench is the fifth deepest trench in the world, reaching 10,047 m depth (Angel 1982), and is approximately 1500 km long and 60 km wide. The trench has the characteristic V-shaped cross section topography, formed by tectonic subduction of the downriding Pacific Plate under the Australian Plate.

The New Hebrides Trench is ~1000 km north east of the Kermadec Trench and is entirely partitioned from the Kermadec Trench by the Kermadec fore-arc and South Fiji Basin at bathyal and abyssal

depths respectively. It is a subduction trench wherein the Australian Plate subducts north-eastward beneath the overriding Vanuatu archipelago. The trench runs for ~ 2000 km with a maximum depth of 7156 m.

The Kermadec Trench and New Hebrides Trench underlie close, but different, biogeochemical provinces (South Pacific Subtropical Gyre or SPSG and the Western Pacific Archipelagic Deep Basins or ARCH respectively), which have similar surface primary production rates of 87 and 100 g C m⁻² y⁻¹ respectively at provincial level (Longhurst et al., 1995) and a mean POC flux to the seafloor of 1.64 ± 0.45 and 0.86 ± 0.75 g C m⁻² y⁻¹ ± S.D. respectively at individual trench level (Jamieson 2015). The bathyal depths of the South Fiji Basin may act as a barrier to connectivity between the hadal populations of the two trenches. The SFB was sampled in order to assess whether *B. schellenbergi* inhabit these depths outside the trench environment.

Figure 1. Map showing the SW Pacific study area. Empty circles are stations absent of *B. schellenbergi*, filled circles are stations where *B. schellenbergi* were present. NHT = New Hebrides Trench, KT = Kermadec Trench, SFB = South Fiji Basin. The dashed line represents the Kermadec Fore-arc.

137 Sample collection

138 Out of the 31 stations sampled, *B. schellenbergi* were retrieved from seven stations within the
 139 Kermadec Trench from 6097 m to 8487 m and from four stations within the New Hebrides Trench
 140 between 5600 and 6948 m depth (Table 1).

141 **Table 1.** Details of the deployments within the Kermadec Trench (KT), New Hebrides Trench (NHT) and South
 142 Fiji Basin (SFB). Gear indicates if the funnel traps were attached to the LATIS, FT: Fish Trap, HL: Hadal Lander or
 143 OBS: Obulus. Bottom time is in decimal hours. Total number denotes the number of *B. schellenbergi*
 144 individuals identified in each subsample, parentheses denote the percentage in each subsample.

Area	Depth (m)	Station	Date	Gear	Latitude	Longitude	Bottom time (hours)	Total number (percentage of subsample) for <i>B. schellenbergi</i>
KT	1490	KAH1301/19	28.01.13	LATIS	39°00.19'S	178°34.50'E	07.2	0
KT	2197	KAH1301/04	21.01.13	FT	33°59.52'S	179°53.44'W	10.7	0
KT	3268	KAH1301/07	22.01.13	FT	33°59.99'S	179°20.35'W	13.0	0
KT	4193	KAH1301/10	23.01.13	FT	34°00.00'S	179°01.32'W	12.5	0
KT	5242	KAH1301/13	24.01.13	FT	34°00.01'S	178°41.07'W	12.1	0
KT	6097	KAH1202/04	19.02.12	LATIS	32° 40.76'S	176°45.95'W	12.0	1 (0.6)
KT	6709	KAH1202/09	22.02.12	LATIS	32° 22.70'S	177°05.62'W	11.2	145 (52.9)
KT	6968	KAH1109/07	28.11.11	OBS	32° 37.77'S	177°14.63'W	11.5	58 (49.2)
KT	7000	KAH1109/03	28.11.11	LATIS	32° 33.42'S	177°14.59'W	12.7	123 (84.8)
KT	7291	KAH1109/13	01.12.11	LATIS	32° 35.22'S	177°17.73'W	08.4	237 (98.1)
KT	7884	KAH1109/09	29.11.11	LATIS	32° 36.98'S	177°21.49'W	09.0	141 (67.4)
KT	8487	KAH1202/06	20.02.12	LATIS	32° 39.92'S	177°27.93'W	12.1	5 (3.9)
KT	9053	KAH1202/08	21.02.13	LATIS	31°58.71'S	177°23.31'W	10.5	0
KT	9908	KAH1109/12	30.11.11	LATIS	32°01.594'S	177°22.26'W	14.4	0
NHT	2000	KAH1310/31	23.11.13	FT	21°16.58'S	168°12.53'E	15.2	0
NHT	2500	KAH1310/37	26.11.13	FT	21°13.15'S	168°40.04'E	15.0	0
NHT	3374	KAH1310/24	20.11.13	HL	21°07.68'S	168°11.07'E	12.5	0
NHT	3400	KAH1310/23	20.11.13	FT	21° 06.80'S	168° 09.87'E	17.1	0
NHT	4700	KAH1310/29	22.11.13	FT	20° 56.08'S	168° 28.60'E	15.5	0
NHT	4835	KAH1310/28	22.11.13	AL	20° 57.00'S	168° 29.41'E	14.0	0
NHT	5180	KAH1310/16	17.11.13	FT	20° 54.72'S	168° 32.25'E	14.3	0
NHT	5300	KAH1310/26	21.11.13	FT	20° 49.99'S	168° 31.52'E	18.0	0
NHT	5600	KAH1310/34	25.11.13	FT	20° 45.52'S	168° 29.15'E	15.5	14 (7.6)
NHT	6000	KAH1310/33	24.11.13	FT	20° 47.67'S	168° 32.77'E	14.2	238 (86.5)
NHT	6228	KAH1310/20	19.11.13	HL-C	20° 49.31'S	168° 34.99'E	12.1	198 (90.9)
NHT	6948	KAH1310/27	21.11.13	HL-C	20° 38.91'S	168° 36.83'E	17.5	137 (28.6)
SFB	4100	KAH1310/03	09.11.13	LATIS	25° 08.56'S	171° 04.16'E	12.6	0
SFB	4100	KAH1310/04	09.11.13	FT	25° 08.62'S	171° 05.78'E	08.2	0
SFB	4100	KAH1310/07	10.11.13	LATIS	24°58.24''S	171° 03.42'E	14.3	0
SFB	4100	KAH1310/08	10.11.13	FT	24° 58.32'S	171° 04.94'E	13.0	0
SFB	4100	KAH1310/39	29.11.13	FT	27° 44.84'S	174° 14.97'E	15.0	0

145

Samples used in this study were taken using small baited funnel traps and cages of varying size mounted upon a series of deep-sea lander vehicles; LATIS, the Fish Trap, OBULUS and Hadal-Lander (Jamieson 2015). Regardless of delivery vehicle, the traps were small baited invertebrate funnel traps of 12 cm diameter x 30 cm long, baited with ~100g of mackerel (*Trachurus* sp.). Each vehicle was equipped with a temperature and pressure sensor (SBE-39; SeaBird Electronics, USA) which recorded at 30 second intervals throughout each deployment.

Sample processing

Amphipod specimens were preserved in 99 % ethanol within 1 hour of recovery. On return to the laboratory samples were transferred to 70 % ethanol for species identification and counting. At depths where catch numbers exceeded 300 individuals, a subset of ~200 amphipods was attained using a Folsom Plankton Splitter. The catches from the New Hebrides Trench were identified in their entirety. Individuals were identified to species level where possible following Barnard and Karaman (1991) with updates and some changes to family level, sub-family level or informal groupings after Lowry and Stoddart (1990, 1994, 1995, 2010, 2011), Stoddart and Lowry (2004), Lowry and De Broyer (2008) and Horton and Thurston (2013). Identification was undertaken using a Wild Heerbrugg Wild M8 dissection microscope. The *B. schellenbergi* components of the samples were used for the analysis in this study. Determination of sex was based on the presence of penile papillae in males and oostegites in females. Specimens lacking both papillae and oostegites were assumed to be juvenile. Damaged individuals for which sex could not be confidently determined were classed as “unknown” and excluded from sex-ratio analyses.

Total length was measured dorsally from the tip of the rostrum to the anterior end of the telson in undamaged, straight posture individuals using digital callipers. Many individuals were damaged or preserved in postures that rendered accurate total body length measurement impossible. The coxa 4 (C4) diagonal length was used as a proxy for total body length (Blankenship et al., 2006; Duffy et al., 2013). C4 measurements were taken using digital callipers under a stereomicroscope. These data were correlated to the total body length of undamaged individuals. Total body length for all remaining individuals was estimated using the C4 measurement as a proxy.

Statistical analyses

All statistical analyses were conducted in R v.3.1.3 (R Core Team, 2015). The efficacy of C4 length as a proxy for total length was assessed using linear regression ($\alpha = 0.05$). To test whether the populations displayed the same relationship between C4 and total length, a general linear model

(GLM) was used to test for homogeneity of regression slopes using an interaction between slope and trench ($\alpha = 0.05$).

To identify significant bathymetric changes in the size structure of the populations, C4 length frequency histograms were compared across depths using the non-parametric Kolmogorov-Smirnov (KS) test ($\alpha = 0.01$) following Blankenship et al. (2006). The increased acceptance threshold was proposed by Blankenship et al. (2006) to prevent erroneous rejection of the null hypothesis resulting from the sensitivity of the KS test to errors in the extreme tails that may arise from bias during subsampling.

The C4 length frequencies of females, juveniles and males were not normally distributed (KS, $p < 0.05$). As the assumptions for parametric tests were not met, the effect of sex on C4 length was examined using the non-parametric Kruskal-Wallis (KW) test ($\alpha = 0.05$). When a significant difference was detected, pairwise comparisons were conducted. The Mann-Whitney non-parametric test was conducted to test for significant differences in length between the two trenches ($\alpha = 0.05$). To determine if there was male or female bias (deviation from 1:1) in the sex ratios a one tailed binomial test was applied ($\alpha = 0.05$). Differences in calculated length (mm) were tested using Mann-Whitney due to non-normal distributions ($\alpha = 0.05$).

Results

In the New Hebrides Trench *B. schellenbergi* were recovered from all stations between 5600 m and 6948 m depth, the deepest station sampled (total range = 1348 m), and in the Kermadec Trench they were recovered from all stations between 6097 m and 8487 m depth (total range = 2390 m; Fig. 2). A total of 587 and 710 individual *B. schellenbergi* were sampled from the New Hebrides Trench and Kermadec Trench respectively. No individuals were caught shallower in either trench, and were not found deeper than 8487 m in the Kermadec Trench. No *B. schellenbergi* were found at the four stations across the adjoining South Fiji Basin (~ 4100m). A total of 587 and 651 individuals were measured and sexed in the New Hebrides and Kermadec trenches respectively. In both trenches, males, females and juveniles were present but no ovigerous females were identified.

B. schellenbergi was one of 21 species identified in the Kermadec Trench and one of 19 species identified from the New Hebrides Trench catches (see Lacey et al., 2016). The lowest catch proportion of *B. schellenbergi* in the New Hebrides Trench was at 5600 m (8 %), yet at the following two depths, 6000 and 6228 m, they comprised 87 % and 91 % of the catch respectively (238 and 198 individuals). The proportion decreased at the maximum sample depth (6948 m) to 29 % of the total

catch (137 individuals; Table 1). The highest proportions in the Kermadec Trench were between 7000 m and 7884 m, 67 and 98 % of the catch (123 to 147 individuals). The lowest proportions were from the stations at the extremes of its observed range; 0.06 % at 6097 m and < 4 % at 8487 m (1 and 5 individuals).

Figure 2. A. Total number of individual *B. schellenbergi* recovered at each sampling depth in the New Hebrides Trench (dark grey dots) and Kermadec Trench (light grey dots).

Body size

In the New Hebrides Trench there was a strong positive correlation between total body length and coxa 4 (C4) length (Fig. 3; $n = 404$, $R^2 = 0.96$) permitting the use of C4 measurements as a proxy for total body length using the equation $L = 8.511 \times C4 + 3.3291$, where L is the estimated total body length and $C4$ is the diagonal measure of C4. Likewise, in the Kermadec Trench there was also a strong positive correlation between total body length and C4 length ($n = 59$, $R^2 = 0.90$), therefore, $L = 6.036 \times C4 + 4.393$. The morphometric relationship between C4 and total length (mm) was significantly different between the populations of the two trenches (GLM: $df = 1$, $F = 105.15$, $p < 0.001$) (Fig. 3).

Figure 3. Linear correlation between total body length and coxa 4 length of A) *Bathycallisoma schellenbergi* from the New Hebrides Trench: $n = 404$, $R^2 = 0.96$, $y = -0.2699 + 0.1128x$ and the Kermadec Trench: $n = 59$, $R^2 = 0.90$, $y = -0.1702 + 0.1483x$. Circles: Kermadec Trench, triangles: New Hebrides Trench. 95% confidence intervals represented by grey shading, Kermadec Trench 95% CI was too small for visualisation.

The New Hebrides Trench females ranged in total length from 20.8 to 45.6 mm ($32.6 \text{ mm} \pm 6.2 \text{ S.D.}$), males ranged in total body length from 19.1 to 37.4 mm ($28.5 \text{ mm} \pm 4.2 \text{ S.D.}$) and juveniles ranged in total length from 5.3 to 21.78 mm ($16.5 \text{ mm} \pm 4.0 \text{ S.D.}$). Sex could not be determined for two individuals (12.9 and 31.8 mm). The Kermadec Trench females ranged in total length from 17.2 to 47.4 mm ($33.6 \text{ mm} \pm 5.88 \text{ S.D.}$), males ranged from 12.24 to 40.50 mm ($27.73 \text{ mm} \pm 4.17 \text{ S.D.}$) and juveniles from 4.2 to 2.2 mm ($16.65 \text{ mm} \pm 4.47 \text{ S.D.}$). Sex could not be determined for 11 individuals ranging from 12.24 to 31.56 mm ($19.73 \text{ mm} \pm 6.76 \text{ S.D.}$).

C4 length was significantly different between sexes in both the New Hebrides Trench (KW: $\chi^2 = 362.8$, $p < 0.001$) and Kermadec Trench (KW: $\chi^2 = 369.6$, $p < 0.001$) (Fig. 4A). Pairwise tests revealed that females were significantly bigger than both males and juveniles and juveniles were significantly smaller than both males and females ($p < 0.001$) (Table 2). The mean total length of *B. schellenbergi* did not differ between the two populations ($p > 0.05$) (Fig. 4B).

Figure 4. Box plots showing the distribution of data of A) Coxa 4 length (mm) of *Bathycallisoma schellenbergi* by sex (denoted by line type) from the Kermadec Trench (KT) and New Hebrides Trench (NHT) and B) Total length (mm) of *B. schellenbergi*, including estimated total length from coxa 4 length, of all individuals by trench. For diagram explanation see Supplementary Figure 1.

Table 2. Pairwise Kruskal Wallis tests comparing the coxa 4 lengths of males, females and juveniles of *Bathycallisoma schellenbergi* within the New Hebrides Trench (NHT) and Kermadec Trench (KT).

Trench	Sex	Female		Male	
		χ^2	p	χ^2	p
NHT:	Male	10.007	<0.001		
	Juvenile	26.823	<0.001	18.215	<0.001
KT:	Male	11.579	<0.001		
	Juvenile	26.691	<0.001	12.169	<0.001

Sex ratios

Within the New Hebrides Trench the sex ratio of the overall catch was ~1:1 (male:female), with males and females comprising 37 and 39 % of the catch respectively and juveniles comprising 25 %. Sex could not be determined for 13 individuals. Juveniles dominated at 5600 m (92 %, n = 13) and comprised smaller proportions at greater depths; 19 % at 6000 m, 41 % at 6228 m and 3 % at 6948 m. Male:female ratios were male biased at 6000 m (48 % *B. schellenbergi* catch) and 6228 m (35 %) and female biased at 6948 m (65 %) (Table 3, Fig. 5A).

Within the Kermadec Trench females were the most abundant, comprising 58 % of the total *B. schellenbergi* catch. Juveniles comprised 21 % and males 19 % of the total catch. Sex could not be

determined for 11 individuals. Juveniles dominated at 6709 m only and were present in low proportions (<10 %) at the remaining depths. The male:female ratio was 1:1 at 6709 m but showed a female bias between 7000 – 7884 m (70 – 76 % of total catch) (Fig. 5B). Only five individuals were recovered at 8487 m with an male:female ratio of 1:1.5 (Table 3). It must be noted however that the sex ratios reported for both species do not include ovigerous females due to presumed baited trap avoidance. Therefore the true female proportion is likely to be under-reported.

The deepest catch in the New Hebrides trench yielded the largest average individual size (33 mm length). The average sizes at 6628 m and 6000 m were 24 and 27 mm respectively. Only 13 individuals at 5600 m were available for measurement, 12 of which were < 20 mm total length and a single individual ~32 mm estimated total length (Fig. 6). Pairwise tests revealed significant differences in the size frequency distributions between all stations (Fig. 6, Table 4, KS: $p < 0.001$). The smaller average size at 6228 m is likely due to the larger proportion of males than females at this depth.

Pairwise tests for the Kermadec Trench population revealed significant differences in the size frequency distributions between 6709 m and all other depths (Fig. 6, Table 4, KS: $p < 0.001$). The animals recovered from 6709 m were markedly smaller than those of the deeper traps. There was no significant difference between the size-frequency distributions at 7000 m and 7884 m (Mean C4 = 4.64 and 4.69 mm respectively). The presence of animals with C4 lengths between 1.49 and 2.75 mm resulted in the significant difference with both the 7000 m and 7884 m samples.

Figure 5. Relative proportions of females (black), males (dark grey) and juveniles (pale grey) of *Bathycallisoma schellenbergi* by depth in A) the New Hebrides Trench and B) the Kermadec Trench. Ratios are presented in Table 5.

Table 3. Total counts of females, males and juveniles for all samples of *Bathycallisoma schellenbergi* and results of a one-tailed binomial test to determine significant bias. Data for Kermadec Trench stations 6968 and 7000 m were pooled.

Trench	Depth (m)	Totals			Male: Female ratio	Mature: Juvenile ratio
		Female	Male	Juvenile		
NHT	5600	1	0	13	0 ^{ns}	0.08**
	6000	78	115	45	1.47**	4.29***
	6228	47	69	82	1.47*	1.41*
	6948	89	44	4	0.49***	33.25***
KT	6709	18	15	112	0.83 ^{ns}	0.29***
	7000	85	38	0	0.45***	0***
	7291	181	39	17	0.22***	12.94**
	7884	107	33	1	0.31***	140**
	8487	3	2	0	0.67 ^{ns}	0 ^{ns}

*p < 0.05; **p < 0.01; ***p < 0.001; ns: non-significant.

Table 4. Significance values resulting from pairwise Kolmogorov Smirnov tests comparing size-frequency distributions of *Bathycallisoma schellenbergi* within the New Hebrides Trench and Kermadec Trench.

New Hebrides Trench				Kermadec Trench			
Depth (m)	6000 m	6228 m	6948 m	Depth (m)	7000 m	7291 m	7884 m
5600	<0.001	<0.001	<0.001	6709	<0.001	<0.001	<0.001
6000		<0.001	<0.001	7000		<0.001	0.215
6228			<0.001	7291			<0.01

Figure 6. Length frequency distributions of *Bathycallisoma schellenbergi* by depth from the New Hebrides Trench and Kermadec Trench. The Kermadec Trench stations 6097 m (n = 1) and 8487 m (n = 5) were excluded due to low numbers. Data for Kermadec Trench stations 6968 and 7000 m were pooled.

Discussion

Geographic and bathymetric distribution

All marine organisms have upper and lower bathymetric limits (Tyler and Young, 1998) and hydrostatic pressure is the single largest environmental gradient (MacDonald 1997). The physiological effects of hydrostatic pressure are varied (DeLong and Yayanos, 1985; Gross and Jaenicke, 1994; Pradillon and Gaill, 2007; Thatje et al., 2010). As such, hydrostatic pressure is frequently suggested as a dominant physical force preventing vertical range expansion (Belyaev, 1989; Carney, 2005). *B. schellenbergi* inhabits a wide bathymetric range, spanning nearly 3000 m,

and so must have a range of physiological adaptations to counteract the perturbing effects of high pressure and low temperature (Somero, 1992).

In the Kermadec Trench, the entire depth range of *B. schellenbergi* appears to have been successfully sampled. Low numbers of individuals were captured at ~6000 and ~8500 m with no individuals found shallower or deeper respectively. Likewise in the New Hebrides Trench, the low numbers found at 5600 m (with none found shallower or indeed across the South Fiji Basin) and consistently high numbers down to the (relatively shallow) the maximum sampled depth (only 208 m shallower than the maximum trench depth) of the New Hebrides Trench, also suggest that the entire depth range was captured. In both trenches *B. schellenbergi* reached maximum catch densities in the upper trench depths; 6000 m in the New Hebrides Trench and 7000 m in the Kermadec, a difference of 1000 m. These data, combined with other studies (Blankenship et al. 2006) show that *B. schellenbergi* dominates the catch assemblages at ~ 6500 to 7500 m in the Kermadec and Tonga Trenches (maximum depth 10,017 and 10,800 m respectively). At depths >8500 m another major scavenging amphipod, *Hirondellia dubia*, dominates the assemblage (Lacey et al., 2016) and *B. schellenbergi* were not observed > 9000 m depth. A similar pattern is observed in the shallower New Hebrides Trench (maximum depth ~7000 m) whereby *B. schellenbergi* dominated the catches recovered between ~ 6000 and 6200 m and *H. dubia* dominated at the deepest sites. This pattern is conserved over the two trenches in terms of 'shallow', mid-trench' and 'deep-trench' but the actual depth (or hydrostatic pressure) differs. If hydrostatic pressure was the sole driver of the population structure, then the trend in the New Hebrides trench would mirror that of the Kermadec but then truncate at 7500 m. This was not the case, leading us to reject our depth-driven hypothesis (H1). Instead it appears the structure of the population is scaled to the topography of the trench (H2), with the same pattern occurring at shallower depths in shallower trenches. Were it not for one individual at 6097 m, the minimum depths would be 1000 m shallower in the New Hebrides Trench. Likewise, the depth of maximum abundance is 1000 m deeper in the Kermadec Trench.

It is unlikely that strict upper and lower pressure tolerances within the hadal zone are driving this zonation, as highlighted in this study. However, physiologically mediated interactions may be a factor. Within the Kermadec Trench *B. schellenbergi* reached maximum catch densities toward the centre of their observed bathymetric range. Contrary to the findings of Blankenship *et al.*, (2006), *H. dubia* were nearly absent from catches towards the centre of their observed bathymetric range, with numerous juveniles in the shallower regions and abundant adults at the deeper extent of its range (Lacey et al., 2016). This could be indicative of a physiological advantage for *B. schellenbergi* under

shallower conditions, allowing competitive exclusion of *H. dubia*. This hypothesis is further supported by the similar pattern within the New Hebrides Trench in which *B. schellenbergi* dominates at ~ 6000 m depth, and the proportion of *H. dubia* increased at the maximum depth (Fig. 7).

Figure 7. The relative catch proportions of *Bathycallisoma schellenbergi* (closed circles) and *Hirondellea dubia* (open triangles) from the New Hebrides, Kermadec and Tonga Trenches. Dashed lines denote maximum trench depth. The Tonga Trench data is adapted from Blankenship et al., (2006), *H. dubia* data from New Hebrides and Kermadec trenches from Lacey et al., (2016).

Morphological variation

The significant difference in the slope of the relationship between C4 and body length between the two populations of *B. schellenbergi* may be the result of genetic drift in the absence of gene flow between trenches, as shown in *H. gigas* by France (1993). The Kermadec fore-arc, and the South Fiji Basin (~4000 m depth) would form a physical barrier to dispersal for hadal species between the two trenches and indeed no *B. schellenbergi* were recovered from the South Fiji Basin. A lower limit to the physiological tolerance of hydrostatic pressure, preventing *B. schellenbergi* from inhabiting the

abyssal depths of the South Fiji Basin (~4000 m) would prevent connectivity between the trenches and may explain such a divergence.

The geological record across the Southwest Pacific convergence zones may offer further insight into the morphological divergence of these two populations. According to plate tectonic modelling software (GPlates Geological Information Model, v 1.5.0, underpinned by Seton et al. 2012), up to 20 million years ago (Ma) the Kermadec-Tonga and New Hebrides trenches were part of a continuous convergence zone running north east from New Zealand's current position. At approximately 14 Ma a distinct bending of the convergence zone occurred at what is now the position of the Island of Fiji, where-in a westerly migration of the convergence zone is seen to occur, in what later becomes the New Hebrides Trench. The formation of the New Hebrides Trench, with morphology similar to that of present day, occurs between 11 and 5 Ma. Although these models are somewhat crude, the timescales are considerably less than the best estimates of the invasion of the deep sea by the Amphipoda. Corrigan et al. (2013) estimated that colonisation of the deep sea by the Amphipoda occurred around the Cretaceous-Paleogene boundary (66 Ma), with some lineages dating to the Eocene-Oligocene transition (33.9 Ma), both of which considerably predate the splitting of the convergence zone. It is therefore feasible that common ancestral populations were indeed isolated from one another during the division of the Kermadec-Tonga-New Hebrides convergence zone. This isolation may account for the observed difference between the present-day populations.

Deep water masses pose an alternative hypothesis here as they are often proposed as a driver of zonation albeit not fully understood (Carney, 2005). However, a faunal divide in this region (at the Tasman Front that marks the path of the East Australian Current) has been detected in other taxa (Clark et al., 2003; O'Hara et al., 2011; Zintzen et al., 2011). Differences in productivity, standing crop and phytoplankton size distribution either side of the front results in the Kermadec side experiencing greater nitrogen flux over the thermocline, and is therefore exploited by phytoplankton (Ellwood et al., 2013). Increased phytoplankton growth depletes nutrients, increases phytoplankton standing stock, and increases larger zooplankton size classes (Baird et al., 2008; Ellwood et al., 2013) which ultimately may alter the food supply reaching the trenches either side of the Tasman Front. This however, may be more likely to alter the species' size and reproductive strategies rather than morphology, which again is perhaps better explained by physical isolation. The body sizes of *B. schellenbergi* in this study were not significantly different between the two trenches, suggesting no nutritional advantage in the less oligotrophic Kermadec Trench.

Influence of trench topography

The steep slopes of hadal trenches are understood to generate a gravity driven down-slope transport of sediment, resulting in an accumulation of organic material at the trench axis (Danovaro et al., 2003; Ichino et al., 2015). This accumulation of food along the trench axis, the “trench resource accumulation depth” (TRAD, Jamieson et al., 2010), should result in nutrient impoverished upper trench slopes, creating a different quality habitat to the sediment rich trench axis (Jamieson 2015). It may be then that *B. schellenbergi* is better suited to the upper trench slopes whereas *H. dubia* dominates in the sediment rich TRAD, explaining the conserved bathymetric patterns presented here.

Deep sea lysianassoid amphipods are commonly considered to be generalist scavengers with high trophic plasticity; thought to be advantageous in such a nutrient poor environment, in which any food resource must be utilised effectively (Blankenship and Levin, 2007). Conversely specialisation in the nutrient poor trenches may help limit competitive interactions. The presence of Hironnellidae along the trench axes in all hadal trenches studied to date suggests a TRAD specialisation. Likewise the cosmopolitan distribution of *B. schellenbergi* in the upper trench slopes indicates an optimal niche habitat, regardless of depth. This theory is further supported by the apparent niche overlap of *B. schellenbergi* and another lysianassoid, *Eurythenes gryllus*, both of which are understood to have similar feeding ecologies (Blankenship and Levin, 2007; Ingram and Hessler, 1983). *E. gryllus* is typically found at abyssal depths, however in the Peru Chile Trench, from which *B. schellenbergi* is absent, *E. gryllus* is present in high numbers, and penetrates 2000 m deeper than their typical depth range elsewhere (Thurston et al., 2002; Eustace et al., 2016). Fujii et al. (2013) postulate that competitive exclusion may prevent cohabitation in the upper trenches. This is supported by the similarly large body size of these two species in comparison to the majority of other hadal species of amphipods. We suggest that these large benthopelagic species inhabit the larger but nutrient impoverished upper trenches whereas *Hirondellea* species are specialised to the deeper, relatively enriched, trench axes regardless of trench depth.

Figure 10A shows that in other known populations of *B. schellenbergi*, the depth range spans close to the maximum depth of mid-depth trenches, e.g. the Puerto Rico and South Orkney trenches (8526 and 6820 m; Lacey et al., 2013 and Vinogradov and Vinogradov, 1993 respectively) and is absent from the bottom few thousand metres of the deeper trenches (e.g. Kermadec and Tonga trenches; Blankenship et al., 2006). A caveat to interpreting the results of this study and in comparison with the studies listed above is the lack of replicates at each station inherent in the limitations imposed

on deep sea sampling. Moreover, the possibility of a chrono-biological effect to hadal species distributions cannot be discounted without seasonal comparisons.

It also interesting to note that typical trench topography is such that the inhabitable area decreases exponentially with depth, similar to an inverted mountain (Fig. 10B). Whereas *B. schellenbergi* inhabits depths of the Kermadec Trench of ~6500 to ~8500 m, accounting for ~85% of the trench area, *H. dubia* dominates at depths >8500 m, representing <20% of the trench. Increasing numbers of *H. dubia* with depth have been previously reported (Blankenship et al., 2006; Lacey et al., 2016). It could therefore be postulated that one species occupies a greater area with lower concentration of available food and slightly relaxed hydrostatic pressure, and the other inhabits high pressure environments in higher densities, with greater feeding opportunities but suited to survival in a far smaller space. It is also worth noting that at depths <8500 m there are a range of larger predators known to prey upon amphipods (Jamieson et al. 2009ab; 2011ab; Linley et al., 2016a, b) whereas areas >8500 m there are, to date, no known predators, adding another element to the contrasting habitat preference of the two species.

Figure 10. (A) Black bars represent known depth ranges of *B. schellenbergi* against maximum trench depths (grey square) in the (i) South Orkney Trench (Vinogradov and Vinogradov, 1993), (ii) New Hebrides Trench (this study), (iii) the Kermadec Trench (this study and Blankenship et al., 2006), (iv) the Tonga Trench (Blankenship et al., 2006) and (v) The Puerto-Rico Trench (Schellenberg, 1955, Lacey et al., 2013). (B) Black bars

demonstrate exponential decrease in area with depth within the Kermadec Trench, in 500m depth bins. Grey circles give the cumulative percentage of area with increasing depth. Data modified from Jamieson (2015).

Ontogenetic stratification

Ontogenetic stratification was evident in *B. schellenbergi* in both trenches with juveniles dominating the shallowest depths, agreeing well with the population structure observed for the Tonga Trench (Blankenship et al., 2006). However, while juveniles were largely absent from deeper catches in the Kermadec Trench, in the New Hebrides Trench they accounted for ~20 % and ~40 % of the catches at 6000 and 6228 m respectively. This difference may be attributed to the topography of the trenches and relative depths of the populations. The maximum depth of the Kermadec Trench population is ~1000 m deeper than the New Hebrides Trench population (6948 m) which appeared to be constrained by the maximum depth of the trench. The virtual absence of juveniles >7000 m in the Kermadec Trench is reflected in the similarly adult dominated catch at 6948 m in the New Hebrides Trench.

We suggest that the bathymetric distribution of juveniles does not relate to the distribution of food because the characteristic V-shape of trenches causing a topographic funnelling of organic matter downslope towards the trench axis (Glud et al., 2013; Ichino et al., 2015). Rather, their distribution likely has a physiological and ecological basis. For example, it has been postulated that juveniles inhabit shallower depths to relieve pressure-induced metabolic limitations (Somero and Siebenaller, 1979), allowing them to ingest and assimilate food more rapidly (Blankenship et al., 2006; Eustace et al., 2013). Indeed juveniles became absent at ~ 7000 m in both trenches, regardless of minimum range and trench depths. The increased amount of available space at shallower depths may also offer reduced rates of intra- and interspecific competition for resources. Abundance of scavengers at baited traps increases with depth within the hadal zone, representing a greater density of individuals towards the trench axis and greater competition for resources. We therefore suggest that the ontogenetic stratification observed in *B. schellenbergi* is due to both physiological constraints related to pressure and an ecological strategy to reduce competition for food.

How juveniles are transported to shallow depths remains unresolved. It is widely considered unlikely that the juveniles themselves undergo a vertical migration and more likely that females release their brood at shallower depths (Eustace et al., 2013). No ovigerous females, i.e. individuals with a full marsupium, were caught in the baited traps, in accordance with other studies of deep-sea Lysianassidae (Perrone et al. 2002; Blankenship et al., 2006; Eustace et al. 2013; Kraft et al., 2013),

therefore the true female proportion is likely to be under-reported. It has been suggested that feeding cessation is employed by near-mature females (Bregazzi, 1972) and during incubation to prevent expulsion of the brood (Christiansen et al., 1990; Johnson et al., 2001). Direct observation of shallow water ovigerous Lysianassoid females actively avoiding feeding events also suggests a predator/cannibalism avoidance strategy (Bregazzi, 1972) as ovigerous females can be more susceptible to predation (Lewis and Loch-Mally, 2010). Until ecological sampling at hadal depths can be achieved without the current reliance on baited traps, the ovigerous female proportion of the population cannot be determined. As this study did not assess reproductive structures we cannot make any further inferences into potential reproductive mechanisms behind the observed stratification.

There was some evidence that males dominate the sex ratio at shallower depths and are replaced by females with increasing depth. In the NHT males dominated between 6000 and 6228 m, switching to a female bias at the deepest NHT depth (6948 m). The deeper KT depths were also dominated by females. This may suggest a bathymetric trend in population structure in which males dominate at shallower depths, switching to a female bias at ~7000 m, a pattern truncated by the topography of each trench. The sex ratios here differ to those reported by Blankenship et al. 2006, which did not significantly deviate from a 1:1 ratio at four depths between 6834 m and 8237 m in the Kermadec Trench in October 2001. This suggests that the pattern observed here may not be maintained through time. Further sampling across seasons and within other trenches with differing topographies is required to understand the prevalence of the observed population structures.

Other considerations

B. schellenbergi has an exceptionally widespread geographic distribution, between often extremely isolated hadal trenches in the North and South Atlantic (Lacey et al., 2013; Schellenberg, 1955; Vinogradov and Vinogradov, 1993), Indian Ocean (Birstein and Vinogradov, 1964) and North and South West Pacific (Birstein and Vinogradov, 1958, 1970; Blankenship et al., 2006; Dahl, 1959; Jamieson et al., 2009a; Nagata, 1963). Furthermore, it is apparently absent from the Peru-Chile Trench in the Southeast Pacific (Fujii et al., 2013). *B. schellenbergi* has also been recently reclassified from *Scopelocheirus schellenbergi* (Barnard, 1964; Dahl, 1979) based on morphological analysis (Kilgallen and Lowry, 2015). However, a recent study by Ritchie et al. (2015) using genetic data from multiple trenches, suggests that the Scopelocheiridae do not form a monophyletic group with the Lysianassoidea superfamily, ubiquitous at hadal depths. Moreover, samples that were identified under the synonyms *Bathycallisoma*- and *Scopelocheirus schellenbergi* were not genetically resolved.

This species offers an interesting subject for future study due to its biogeographical distribution including extremely disparate populations, large bathymetric range, apparent significance in hadal scavenging communities and the evolutionary distance from the other species with which it cohabits. Assessment of hadal populations of *B. schellenbergi* using molecular methods may challenge the assumption that *B. schellenbergi* is a true cosmopolitan species, instead comprising multiple cryptic species, as has been found for bathyal and abyssal species (France., 1994; France and Kocher, 1996; Havermans et al., 2013).

Conclusions

The hadal amphipod *B. schellenbergi* was sampled across its full depth range within the Kermadec and New Hebrides Trenches. Their minimum depth and depth of maximum abundance were 1000 m deeper in the Kermadec Trench, likely reflecting its greater maximum depth. The relative trends in vertical population structure were conserved in both trenches regardless of depth, with the exception that juveniles were consistently found at a maximum depth of ≤ 7000 m in both trenches. Evidence of morphological heterogeneity in the two populations is likely driven by geographical isolation and physical partitioning by the Kermadec fore-arc and South Fiji Basin, rather than water mass boundary effects. We conclude that the vertical distribution of *B. schellenbergi* reflects a variety of interacting ecological and physiological factors that vary with trench morphology, rather than the influence of hydrostatic pressure alone.

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730 **Supplementary material**

Supplementary Figure 1. An example box plot displaying an example distribution of data based on the minimum, first quartile, median, third quartile, maximum and outlying values.