

Spatial and temporal heterogeneity in the distribution of an Antarctic amphipod and relationship with the sediment

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ABSTRACT: The nearshore Antarctic environment is subject to increasing anthropogenic impact, yet the ecological processes influencing some of its most dominant species remain poorly understood. We examined patterns of the distribution and abundance of the Antarctic amphipod *Orchomenella franklini* in relation to the local environment. Samples of benthic sediment were collected in East Antarctica across several spatial and temporal scales and were analysed for the abundance of *O. franklini* and various sediment properties. *O. franklini* was found to reach extremely high densities ($>41\,000\text{ m}^{-2}$), yet abundance was strongly heterogeneous on all spatial scales tested. Temporal variation in abundance was also significant and was location-specific, potentially reflecting fluctuations in food supply and variable conditions resulting from ice disturbance. Principal component analysis and generalised additive modelling revealed evidence of a relationship between the distribution of *O. franklini* and the sediment, which was consistent with its deposit-feeding trophic niche. Generally, the abundance of *O. franklini* increased with decreasing sediment grain size and increasing trace element concentration. Abundance also peaked at high (though not maximum) total organic carbon content. This is one of the first empirical demonstrations of a correlation between discrete physical sediment traits and the abundance of an infaunal benthic species in the Antarctic, with evidence consolidated from 2 geographic regions. The influence of local conditions on the abundance of *O. franklini* provides insight on the heterogeneity of Antarctic benthic ecosystems.

KEY WORDS: Benthic sediment · Peracarid crustacean · Population density · Metals · Grain size · Anthropogenic impact · Environmental change

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INTRODUCTION

Predicting the potential response of nearshore marine ecosystems to environmental change requires a thorough understanding of the ecological processes structuring populations (Harley et al. 2006). This is crucial for the Antarctic benthic fauna, which are considered particularly vulnerable to change because of their limited potential for migration and characteristic traits including delayed maturity, slow growth and tolerance of only a narrow range of physical conditions (Peck et al. 2004, Peck 2005). Despite

its isolation, the Antarctic nearshore environment is subject to increasing anthropogenic impact including localised pollution and broader climate change (see Clarke & Harris 2003, Aronson et al. 2011). While there has been extensive research on patterns of Antarctic benthic community composition (e.g. Dayton et al. 1974, Stark 2000, Thatje et al. 2005, Barnes & Conlan 2007, Gutt 2007), there are very few ecological studies on individual species distributions and their relationship with the physical environment (Gutt 2007). Improved knowledge of the population ecology of benthic species is urgently required to

provide a baseline for the mandatory monitoring of anthropogenic impacts in Antarctica (Anisimov et al. 2007, Hughes 2010).

Existing autecological studies of Antarctic benthic species are largely restricted in temporal and/or spatial coverage because of the logistical difficulties of sampling such an extreme environment (Arntz et al. 1992, Griffiths 2010). Additionally, there has been a historic emphasis on the relatively stable sea temperatures and circumpolar currents of the Antarctic coastline as drivers of a uniform suite of fauna (e.g. Hedgpeth 1970, White 1984, Gutt 2000). Thus, there has been limited exploration of the effect of natural spatial environmental heterogeneity (other than ice disturbance; Gutt 2001, Gerdes et al. 2003, Teixidó et al. 2007, Smale et al. 2008) on benthic population ecology (Gutt 2007). Similarly, knowledge of the temporal processes structuring the Antarctic benthos is largely focused on the predictable, seasonal cycles that characterise polar environments (e.g. sunlight/sea ice/phytoplankton; Tucker 1988, Arntz et al. 1992, Obermüller et al. 2010). Very little is known about stochastic, inter-annual fluctuations in abundance and distribution. However, recent studies are beginning to demonstrate that inter-annual variability in the environment may have an important influence on local population structure (e.g. Chiantore et al. 2002, Thrush & Cummings 2011, Dayton et al. 2013).

Particular uncertainty surrounds the relationship between sediment attributes and benthic species distributions in Antarctica. One theory is that Antarctic benthic invertebrates are largely opportunistic in substrate choice, given that similar assemblages can be associated with markedly different substrates (Gutt 2007). Yet isolated studies suggest that Antarctic benthic macrofauna may indeed be affected by broad sediment type (Barry et al. 2003), total organic carbon (TOC) (Lenihan et al. 2003) and metal contamination of sediments (Lenihan et al. 2003, Stark et al. 2003b). These studies explored patterns at community levels; however, there is very little empirical research on the relationships of individual Antarctic benthic species to sediment properties. Improving our understanding of these relationships is important, given that marine sediments are being altered by ongoing localised pollution (e.g. hydrocarbon and heavy metal contamination) in the Antarctic (Aronson et al. 2011). Inshore soft sediments are also likely to be affected on a broader scale by climate change. Mechanisms include expanding anoxic zones because of decreasing oxygen content (Anisimov et al. 2007, Brierley & Kingsford 2009) and increased tur-

bulence because of more regular storm activity and reductions in sea ice (e.g. Stammerjohn et al. 2008).

Amphipod crustaceans are a particularly appropriate group with which to explore ecological patterns in the Antarctic benthos, as they are highly abundant and widespread, and most species are endemic to the region (Jażdżewski et al. 1991, Brandt 1999, De Broyer et al. 2003). Amphipods are considered suitable indicators for environmental monitoring (e.g. Thomas 1993, Duquesne et al. 2000, Bach et al. 2010), and understanding their ecology can provide a context against which the significance of impacts can be interpreted. The amphipod *Orchomenella franklini* (Walker, 1903) is believed to be one of the most abundant infaunal members of the nearshore Antarctic (Tucker & Burton 1988, Stark 2000, Knox 2007), and it is ubiquitous around the Antarctic coast (Lowry & Bullock 1976, De Broyer et al. 2007). It is representative of many Antarctic benthic infaunal species, with brooding reproduction synchronised to the summer phytoplankton bloom and a relatively long lifespan (Baird & Stark 2013). While *O. franklini* is known to have a patchy distribution (Stark 2000), one study found it to be unaffected by substrate type (Tucker 1988). Yet its trophic position as a deposit-feeder (Gillies et al. 2013) suggests a potential relationship with the sediment (as well as hydrodynamic processes such as wave action, upwelling and stratification). We used *O. franklini* to study (1) the degree of spatial and temporal variability in Antarctic nearshore populations over multiple scales and (2) the potential influence of sediment properties on Antarctic nearshore populations.

MATERIALS AND METHODS

Sampling

Samples of *Orchomenella franklini* were collected from 2 regions adjacent to the research stations Casey (66° S, 110° E) and Davis (68° S, 78° E) in East Antarctica (Fig. 1). The nearshore marine environment of Casey has experienced a range of human impacts, including heavy metal contamination from an abandoned waste site and secondary treated sewage exposure, providing varied sediment conditions (for more detail, see Stark et al. 2003a). Marine sediments at Davis also vary in their proximity to a simple macerated sewage outfall, and while most sampled areas represented semi-protected conditions (similar to Casey), there exists a gradient of exposure to swell which increases from north to

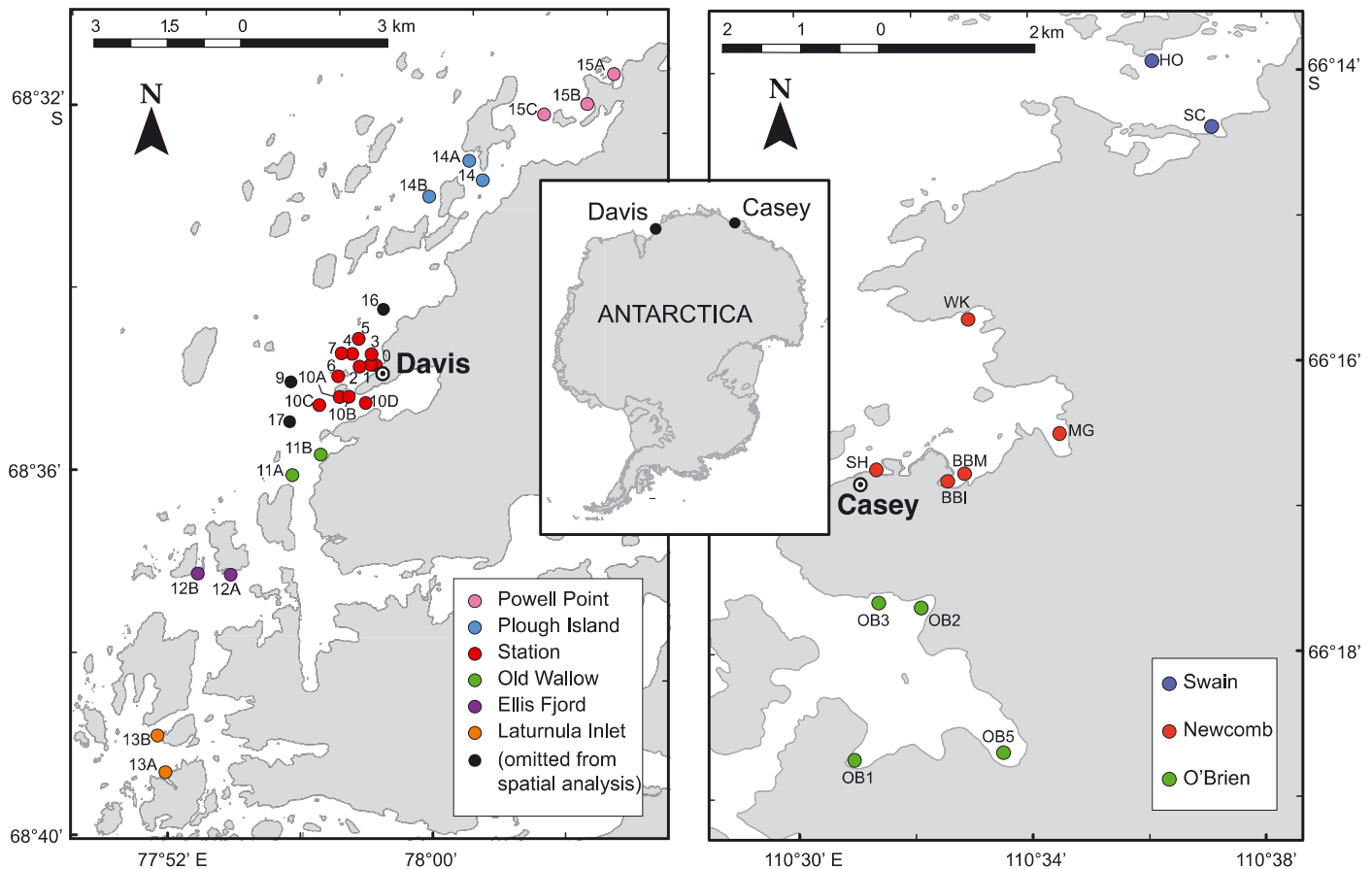


Fig. 1. *Orchomenella franklini*. Sample collection stations at Casey and Davis, with inset showing the positions of Casey and Davis on the Antarctic coast. All locations are coloured by the broad area in which they were placed to analyse spatial patterns of abundance. BBI: Brown Bay Inner, BBM: Brown Bay Middle, HO: Honkala, MG: McGrady Cove, OB1: O'Brien Bay 1, OB2: O'Brien Bay 2, OB3: O'Brien Bay 3, OB5: O'Brien Bay 5, SC: Stevenson Cove, SH: Shannon Bay, WK: Wilkes

south (for more detail, see Stark et al. 2011). To assess spatial variability in abundance of *O. franklini* over several scales, a hierarchical nested sampling design was used within both the Casey and Davis regions. To ensure that samples were quantitatively comparable, SCUBA divers used plastic cores of uniform size and shape (10 cm in diameter \times 10 cm deep) to sample the benthic sediment (all cores were taken at ≤ 23 m depth). Four replicate faunal cores were taken within a plot (covering < 10 m² area), and at least 2 plots (spaced between 10 and 100 m apart) were sampled within a location. Locations themselves were between 100 and 2500 m apart. For the purposes of this study, locations were grouped into areas > 2 km apart and broadly represent bays or inlets separated by terrestrial features (Fig. 1, Table 1). Only locations that fitted this hierarchical classification were used to test for spatial variability; however, at Davis, 3 additional locations were sampled to provide extra data for sediment modelling (see Table 1).

At Casey, cores were also taken during several years from 1997 to 2006 (see Table 1) to test for temporal variability.

To explore relationships between the environment and the distribution of *Orchomenella franklini*, cores were also taken to analyse sediment properties. Sediment cores (5 cm in diameter \times 10 cm deep) were sampled by divers with the same spatial design as cores used for abundance estimates, with 2 cores taken per plot (but only for a subset of the sampling years at Casey; see Table 1). All equipment associated with the sampling and processing of sediment cores was washed prior to use in 10% nitric acid.

Abundance of *Orchomenella franklini*

Faunal cores were sieved on a 1 mm mesh and sorted under a dissecting microscope to remove and count *Orchomenella franklini*. While a sieve mesh

Table 1. *Orchomenella franklini*. Core samples from Casey and Davis, detailing the geographic area and location (see Fig. 1), number of plots and date sampled. Four replicate cores were sampled within each plot for abundance data. Plots shown in **bold** had a subset of cores sieved on both a 1 and 0.5 mm mesh (all others were sieved to 1 mm only). Plots from which 2 extra cores were taken for sediment data are indicated (Y)

Davis				Casey			
Area	Location	No. of plots (date sampled)	Sediment data	Area	Location	No. of plots (date sampled)	Sediment data
Station	0	2 (Mar 2010)	Y	Newcomb	Brown Bay Inner	4 (Oct 1997)	
	1	2 (Feb 2010)	Y			4 (Jan 2003)	
	2	2 (Feb 2010)	Y			4 (Nov 2005)	
	3	2 (Feb 2010)	Y			4 (Nov 2006)	Y
	4	2 (Feb 2010)	Y			4 (Oct 1997)	
	5	2 (Feb 2010)	Y			4 (Dec 1997)	
	6	2 (Mar 2010)	Y			6 (Dec 1998)	
	7	2 (Mar 2010)	Y			4 (Jan 2003)	
	10A	2 (Feb 2010)	Y			4 (Jan 2004)	
	10B	2 (Mar 2010)	Y			4 (Dec 2005)	Y
	10C	2 (Mar 2010)	Y			4 (Nov 2006)	Y
	10D	2 (Mar 2010)	Y			4 (Jan 2003)	
	Old Wallow	11A	2 (Feb 2010)			Y	Shannon Bay
11B		2 (Feb 2010)	Y	4 (Jan 2003)			
Ellis Fjord	12A	2 (Feb 2010)	Y	Wilkes	4 (Nov 2006)	Y	
	12B	2 (Feb 2010)	Y		4 (Dec 1997)		
Laternula Inlet	13A	2 (Feb 2010)	Y		4 (Jan 1999)		
	13B	2 (Feb 2010)	Y		4 (Jan 2003)		
Plough Island	14	2 (Feb 2010)	Y		4 (Jan 2004)		
	14A	2 (Feb 2010)	Y		4 (Dec 2005)	Y	
	14B	2 (Feb 2010)	Y	O'Brien	O'Brien Bay 1	4 (Nov 1997)	
						4 (Jan 2003)	
Powell Point	15A	2 (Mar 2010)	Y		O'Brien Bay 2	4 (Dec 2005)	Y
	15B	2 (Mar 2010)	Y			4 (Nov 1997)	
	15C	2 (Mar 2010)	Y			4 (Nov 1998)	
(Data for sediment models only)	9	2 (Mar 2010)	Y		O'Brien Bay 3	4 (Jan 2003)	Y
	16	2 (Feb 2010)	Y			4 (Nov 2006)	
	17	2 (Mar 2010)	Y			4 (Nov 1997)	
				Swain	Honkala	4 (Feb 2003)	
						O'Brien Bay 5	4 (Dec 2005)
					Stevenson Cove	4 (Dec 2006)	Y
						4 (Dec 2006)	Y

size of 0.5 mm is required to retain all specimens of *O. franklini*, efficiency can be maximised by estimating relative abundance from a 1 mm mesh (see Thompson et al. 2003). To validate this, 132 cores from a range of locations were sieved at both mesh sizes (see Table 1), and the correlation between 1 mm-derived abundance estimates and total (i.e. 0.5 mm-derived) abundance was tested using linear regression performed in R software, version 2.12.2 (R Core Development Team 2011). Estimates of abundance derived from a 1 mm mesh size were strongly correlated with total abundance ($R^2 = 0.96$, $p < 0.001$); thus, we regarded our use of 1 mm fractions valid to explore relative patterns in abundance.

Sediment properties

Sediment cores were analysed for grain sizes, TOC and trace elements including heavy metals (a full list of measured parameters is provided in Table S1 in the Supplement, available at www.int-res.com/articles/suppl/m502p169_supp.pdf). For grain size estimation, the outer 5 mm edge of the core was removed to eliminate edge bias and coring effects, and the remainder was weighed and dried in an oven at 45°C. The dry sample was reweighed and sieved through a 2 mm mesh. The <2 mm fraction and the >2 mm fraction were then weighed separately, and a sub-sample of the <2 mm fraction was taken for grain

size analysis using a Mastersizer 2000 particle size analyser at Macquarie University. TOC analysis was carried out on a homogenised wet sub-sample of sediment weighed into a pre-combusted crucible and dried at 105°C. The dried sample was reweighed and placed in a muffle furnace for 4 h at 550°C, and total carbon was calculated as loss of mass on ignition. Analysis of bioavailable metals and trace elements was carried out on <2 mm fractions, as this provides a more realistic estimate of metals in the sediment than <63 µm fractions (a common alternative) or whole sediment (Loring 1991, Scouller et al. 2006). A weak acid extraction was performed on a sub-sample of homogenised wet sediment, mixed with 30 ml of 1 M HCl in a polypropylene centrifuge tube and tumbled for 4 h. The mixture was then centrifuged for 15 min at 12 000 rpm, and the supernatant was filtered through a 0.45 µm membrane cartridge filter. Filtered supernatant was analysed by inductively coupled plasma mass spectrometry at Central Science Laboratories, University of Tasmania.

Statistical analyses

To test for spatial and temporal variation in the abundance of *Orchomenella franklini*, we used permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001, McArdle & Anderson 2001), a permutation-based equivalent to ANOVA, which is suitable for unbalanced datasets and departures from assumptions of normality. This was performed with the PERMANOVA+ package for PRIMER 6 software (Anderson et al. 2008). For all analyses, a $\log(x+1)$ transformation was applied to abundance data to address heterogeneity of variance. PERMANOVA analyses used a Euclidean distance similarity matrix, and significance was assessed with 10 000 data permutations. If analyses yielded negative variance components, these were set to zero, the respective factor was removed from the analysis and estimates were recalculated, as recommended by (Fletcher & Underwood 2002). Variance components were converted to percentage total variance to compare the relative magnitude of variation at each spatial/temporal scale (Graham & Edwards 2001).

To test for variation at each spatial scale, we used a 3-factor nested design with Area, Location nested within Area and Plot nested within Location (all factors were considered random, see Underwood 1997). Tests were restricted to locations that had been sampled within a single 30 d period to remove any confounding effect of sampling year or month (*Or-*

chomenella franklini has a synchronised annual brood release, implying a concentrated recruitment of juveniles over the austral summer months; Baird & Stark 2013). This resulted in 1 test for spatial variation at Davis (where all locations were sampled between February 12 and March 12, 2010) and 3 tests at Casey (8 locations sampled between January 8 and February 8, 2003; 6 locations sampled between November 18 and December 16, 2005; and 6 locations sampled between November 8 and December 7, 2006). We tested for inter-annual variation in abundance using a 2-factor PERMANOVA with Year and with Plot nested within Year. To isolate the effect of Year from any confounding spatial and monthly effects, inter-annual comparisons were restricted to data from the same location and sampling month. This resulted in 5 tests for temporal variation, all from locations at Casey.

We tested for spatial variability in the sediments from Casey and Davis using analysis of similarities (ANOSIM), performed with PRIMER 6 software. All sediment variables were standardised, and a Euclidean distance matrix was generated. ANOSIM analyses were performed for Casey and Davis separately, with Location and Area as factors. To explore the distribution of *Orchomenella franklini* in relation to the local environment, we examined relationships between individual sediment parameters and abundance data. Principal component analysis (PCA) was used to simplify the representation of sediment variability, as it is suitable for multivariate analysis of environmental data (Clarke & Warwick 2001) and can account for co-correlation of variables. PCA was done for all standardised sediment properties observed within each plot (i.e. averaged over 2 replicate sediment cores), from which patterns of sediment variation could be interpreted by PCA loadings on the first 2 principal component axes. Ordinated points in the PCA of sediment properties were then scaled to represent the mean abundance of *O. franklini* in that particular plot (i.e. averaged over 4 replicate faunal cores) so that patterns of abundance could be qualitatively related to sediment variation. Furthermore, generalised additive modelling (GAM) was used to model *O. franklini* abundance as a function of the first 2 principal components, which was overlaid as contours on PCA plots. While a Poisson distribution is the standard model used for count data, the abundance of *O. franklini* was extremely over-dispersed. Therefore, it was more appropriate to homogenise variance with a square-root transformation and fit a normal distribution. All PCAs were carried out in R, and GAM was performed using the mgcv package for R (Wood 2006).

RESULTS

Spatial and temporal patterns of abundance

Orchomenella franklini reaches astounding abundances in the shallow Antarctic benthos. The highest mean abundance of *O. franklini* within a plot was from Brown Bay Middle at Casey (BBM in Fig. 1) in December 2005, with an average of 329 (± 51 SE) ind. core⁻¹. Extrapolating from the surface area sampled by a core, this gives a maximum density of 41 889 (± 6494 SE) ind. m⁻² of benthic sediment.

The abundance of *Orchomenella franklini* was heterogeneous, with significant variation revealed at all spatial scales examined, for all sampling periods tested. PERMANOVA revealed significant differences in abundance among plots at both Casey and Davis, indicating patchiness on scales as fine as 10 to 100 m (Table 2, Figs. 2 & 3). Variation in abundance was also significant among locations within both of the regions (Table 2, Figs. 2 & 3). However, the majority of variance in abundance at Casey was attributed to areas (63 to 72%; Table 2, Fig. 2), whereas areas at Davis did not differ significantly from each other. Rather, the majority of variation in abundance at Davis was attributed to location (82%; Table 2, Fig. 3).

The abundance of *Orchomenella franklini* at Casey also appears to fluctuate significantly over time. Differences in abundance among years were observed for 2 of the 3 locations tested, with sampling year explaining between 66 and 75% of the variance in abundance at these locations (Table 3, Fig. 4). However, the nature of these inter-annual fluctuations was clearly location-specific. For example, from the years 1997 to 2006, there appears to be an increase in abundance at O'Brien Bay 2 yet a decrease in abundance at Wilkes (Fig. 4).

Relationship between sediment properties and distribution

Sediment traits differed significantly among locations at both Casey and Davis (ANOSIM global test statistic: $R > 0.6$, $p < 0.001$ for both regions). However, only at Casey were sediments found to vary significantly among areas (Casey: $R = 0.21$, $p = 0.004$; Davis: $R =$

0.14, $p = 0.06$), mirroring the result for spatial analysis of abundance. There were also differences in the range of some sediment parameters at Casey and Davis. Casey showed higher variability in trace metal concentrations (Fig. 5a), whereas Davis was characterised by wider variability in grain size (Fig. 5b).

For all Casey and Davis data combined, the first 2 principal components of a PCA ordination of all sediment parameters explained 60% of observed environmental variation. Using these 2 principal components as a surrogate for sediment variation, a GAM analysis explained 43% of variation in the abundance of *Orchomenella franklini*. This model predicted an increase in abundance with decreasing grain size, although optimum abundance occurred before grain size reached minimum values (Fig. 6a). Abundance was also predicted to increase with increasing TOC, with a peak in abundance occurring at moderately high values, before TOC reached its maximum (Fig. 6b). Higher abundances were also predicted in sediments with trace metal concentrations towards the upper limit of their ranges, in particular Cu, Fe, Pb (Fig. 6c), Mg, Sb, Sn and Zn.

To determine if the observed relationship between sediment parameters and abundance was equally evident within both study regions, PCAs were also

Table 2. *Orchomenella franklini*. Results of the 3-factor nested permutational multivariate analysis of variance for spatial variation in abundance. Tests were restricted to data from the same 30 d sampling period

Factor	df	MS	F	p	% total variance component
Casey (Jan–Feb 2003)					
Area	1	232.22	9.35	0.021	62.59
Location (Area)	6	24.72	16.51	<0.001	26.39
Plot (Location(Area))	24	1.50	4.79	<0.001	5.38
Residual	95	0.31			5.64
Casey (Nov–Dec 2005)					
Area	1	124.20	9.93	0.032	69.79
Location (Area)	4	12.51	13.65	<0.001	19.31
Plot (Location(Area))	18	0.92	3.63	<0.001	4.42
Residual	69	0.25			6.48
Casey (Nov–Dec 2006)					
Area	2	37.84	9.21	0.049	72.15
Location (Area)	3	4.15	9.68	<0.001	14.13
Plot (Location(Area))	17	0.43	2.34	0.009	3.55
Residual	65	0.19			10.17
Davis (Feb–Mar 2010)					
Area	5	6.13	0.32	0.911	0
Location (Area)	18	19.31	20.91	<0.001	81.57
Plot (Location(Area))	24	0.92	3.16	<0.001	6.62
Residual	138	0.29			11.80

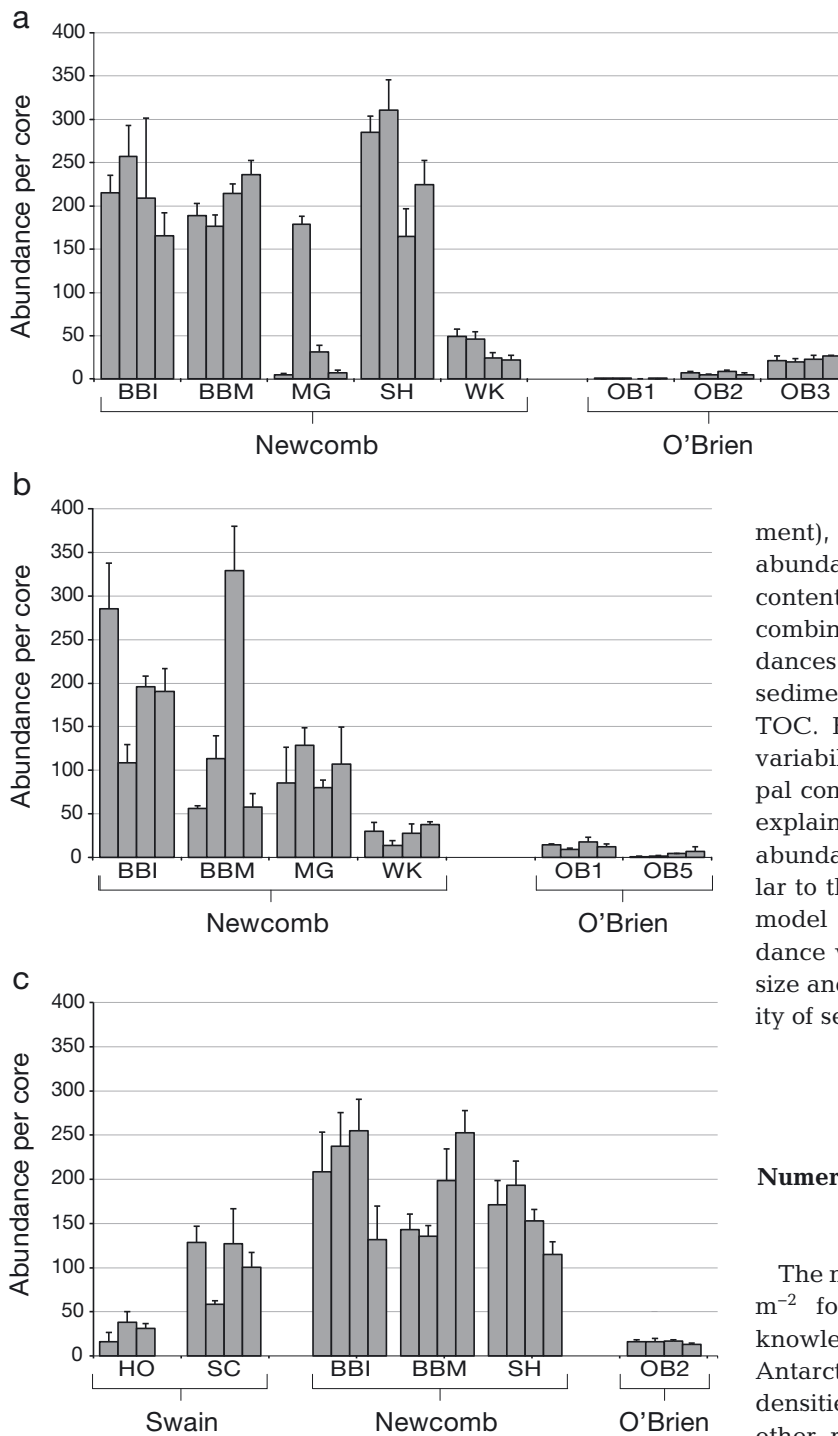


Fig. 2. *Orchomenella franklini*. Mean abundance \pm SE ($n = 4$) at each of 4 plots within locations at Casey, sampled during (a) January to February 2003, (b) November to December 2005 and (c) November to December 2006. Locations are subdivided into areas, as indicated by square brackets labelled on the x-axis. BBI: Brown Bay Inner, BBM: Brown Bay Middle, HO: Honkala, MG: McGrady Cove, OB1: O'Brien Bay 1, OB2: O'Brien Bay 2, OB3: O'Brien Bay 3, OB5: O'Brien Bay 5, SC: Stevenson Cove, SH: Shannon Bay, WK: Wilkes

generated for Casey and Davis data independently. For Casey, the first 2 components of a PCA of sediment variables explained 58% of the total variation, and the resultant GAM using the first 2 principal components explained 43% of the variation in abundance of *Orchomenella franklini*. This model predicted higher abundance in sediments with higher metal bioavailability, supporting similar predictions generated from the combined dataset. The strongest drivers of this pattern at Casey were the heavy metals Cu, Fe, Pb (Fig. S1 in the Supplement), Sn and Zn. Relationships between abundance and sediment grain size and TOC content were not as evident for Casey as in the combined model. However, the lowest abundances of *O. franklini* were still predicted in sediments with highest grain size and lowest TOC. For Davis, 67% of the total sediment variability was explained by the first 2 principal components, and the corresponding GAM explained 49% of the variation in *O. franklini* abundance (Fig. S2 in the Supplement). Similar to the model based on combined data, the model for Davis predicted increasing abundance with increasing TOC, decreasing grain size and increasing trace element bioavailability of sediments.

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DISCUSSION

Numerical dominance, spatial patchiness and temporal heterogeneity

The maximum density estimate of 41 861 ind. m^{-2} for *Orchomenella franklini* is, to our knowledge, the highest yet recorded for any Antarctic macrobenthic species. Maximum densities of soft-substrate benthic fauna from other regions of Antarctica have been estimated at 17 000 ind. m^{-2} for all species combined (Jażdżewski et al. 1991). Clearly, this confirms previous postulations that *O. franklini* is one of the most dominant members of the shallow benthos at Casey and Davis (e.g. Tucker & Burton 1988, Stark 2000). However, the distribution of *O. franklini* is remarkably heterogeneous. Significant variability in abun-

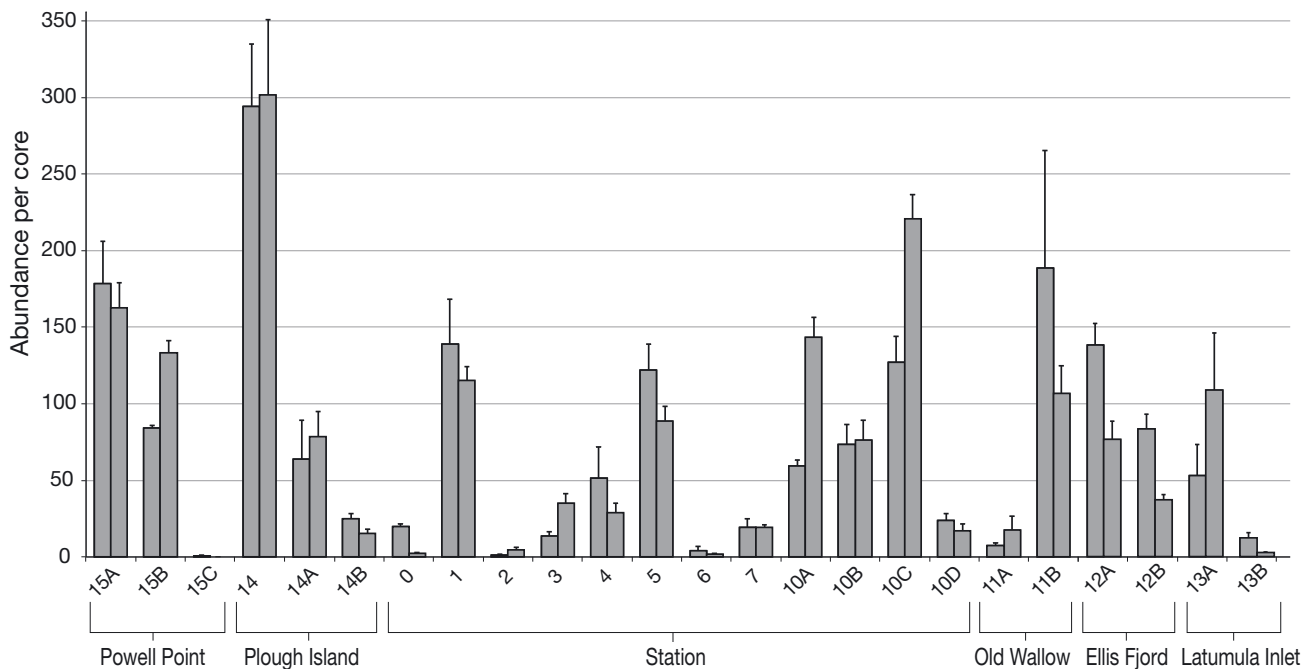


Fig. 3. *Orchomenella franklini*. Mean abundance (\pm SE) at each of 2 plots within locations at Davis (all sampled between February 12 and March 12, 2010). Locations are subdivided into areas, as indicated by square brackets labelled on the x-axis.

Table 3. *Orchomenella franklini*. Results of the 2-factor permutational multivariate analysis of variance for inter-annual variation in abundance at Casey. Note that only the results for the effect of Year are shown; variation because of Plot was statistically significant in all comparisons made. Significant values ($p < 0.05$) in **bold**

Location	Month	Years compared	p-value from ANOVA	% total variance explained by year
Brown Bay Middle	December	1997, 1998, 2005	0.25	10
Brown Bay Middle	January	2003, 2004	0.14	27
O'Brien Bay 2	November	1997, 1998, 2006	<0.01	66
Wilkes	December	1997, 2005	<0.05	64
Wilkes	January	1999, 2003, 2004	<0.001	75

dance was observed over spatial scales as small as 10 to 100 m (i.e. among plots) at both Casey and Davis. The majority of variation in abundance occurred on the largest spatial scale at Casey (i.e. among areas) yet on the intermediate scale at Davis (i.e. among locations); areas at Davis were not significantly different, largely because of extreme variation between locations within areas. This may indicate that areas at Casey are characterised broadly by different sediment attributes, while areas at Davis have more heterogeneous sediments, as supported by the ANOSIM results. However, it is acknowledged that more locations were sampled within areas at Davis compared to Casey, increasing the chance that local variability

would obscure any discrete differences among areas. Additionally, locations sampled at Davis were occasionally associated with more exposed coastline than at Casey. Nonetheless, it is interesting to note that populations of *O. franklini* from Davis have been found to harbour higher genetic diversity than those from Casey, which may also indicate greater environmental complexity at Davis (Baird et al. 2012).

Inter-annual fluctuations in the abundance of *Orchomenella franklini* were also demonstrated and appeared to be location-specific, although comparisons were limited. Localised temporal differences in abundance could potentially reflect fluctuations in food supply because of inter-annual sea ice variability. *O. franklini* is a deposit-feeder dependent on benthic and pelagic carbon supply to the sediment, derived from phytoplankton, macroalgae, benthic diatoms and sea ice algae (Gillies et al. 2012, 2013). The breakout of sea ice increases light levels in coastal ecosystems, stimulating primary production of phytoplankton, macroalgae and benthic diatoms, thus increasing food availability on local scales (e.g. Dayton et al. 1986,

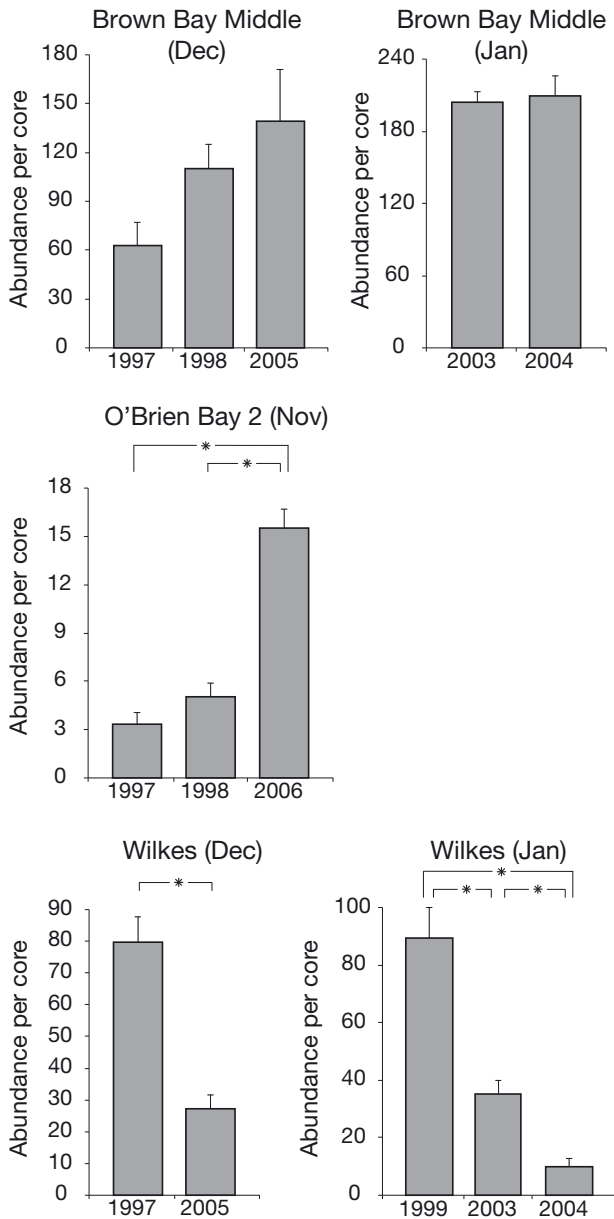


Fig. 4. *Orchomenella franklini*. Mean abundance (+SE) in cores (minimum $n = 16$) sampled in the same month across different years at Casey locations. Note that years are not continuous along the x-axis; only years with data are shown. Asterisks indicate significant differences ($p < 0.05$) between years (as determined by post hoc pairwise comparisons)

Clark et al. 2013). Sea ice and corresponding phytoplankton fluctuations have been directly linked to inter-annual variation in the abundance of several benthic invertebrates in the Ross Sea (Thrush & Cummings 2011). Similarly, food supply has been linked to population fluctuations in benthic amphipods from the northern high latitudes (Lehtonen & Andersin 1998). Another explanation could be

localised ice disturbance (e.g. ice scour, anchor ice), which is temporally sporadic and has a marked effect on the macrobenthos of many nearshore regions in Antarctica (e.g. Gutt 2001, Gerdes et al. 2003, Thrush et al. 2006, Smale et al. 2008). Most likely, the observed temporal fluctuations reflect a combination of these environmental factors.

Distribution in relation to sediment features

The distribution of *Orchomenella franklini* appeared to be related to the grain size, TOC and trace element concentration of sediments. Their relative influence must be interpreted with caution, as these variables are known to be correlated, with smaller grain sizes generally having higher TOC and trace element bioavailability (Goldberg et al. 1975, Horowitz 1985). For the model that combined all data, there was an increase in abundance with decreasing grain size, with a peak in abundance at moderately small grain sizes (approximately 85 to 200 μm) rather than absolute minimum values. Abundance also increased with TOC content, with highest abundances observed at moderately high (approximately 10.5 to 12% of sediment mass) rather than maximum values of TOC; this pattern was also supported by the individual models for Casey and Davis. Although we cannot determine the relative influence of TOC and grain size in driving this pattern, given their correlative nature, both relationships are consistent with the deposit-feeding lifestyle of *O. franklini*. Deposit-feeders directly ingest sediment particles to derive their food and are therefore predicted to favour smaller particle sizes and sediments richer in organic carbon (Whitlatch 1981). Amphipods in particular have been shown to prefer smaller grain sizes even when compared to other deposit-feeders (Fenchel et al. 1975, Taghon 1982). Fine grain sizes and high TOC content are also often associated with sulphide-rich, hypoxic sediments (Hyland et al. 2005), which *O. franklini* appears to be able to tolerate to a certain degree. Deposit-feeding amphipods from northern latitudes have been shown to tolerate hypoxic and sulphide-rich sediments by creating microhabitats where sulphide is rapidly oxidised through burrowing activity (Modig & Ólafsson 2001). The lowered abundance of *O. franklini* in sediments with the finest grain sizes and highest TOC content is likely to reflect avoidance of the most hypoxic, or even anoxic, sediments. Patches of anoxic sediment have previously been observed in the nearshore environment of Casey (Stark et al. 2003b, Pow-

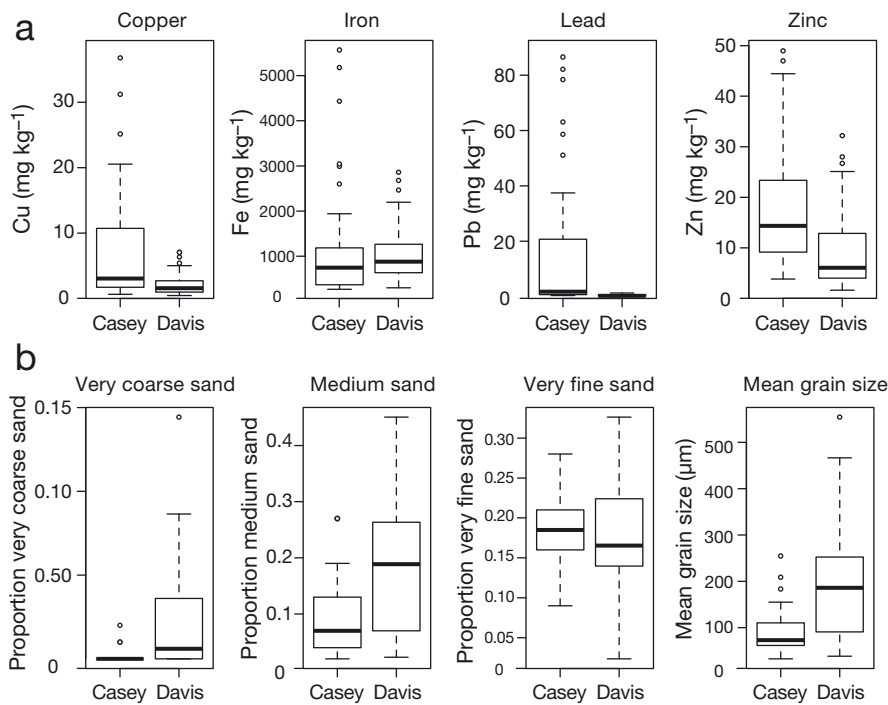


Fig. 5. Properties of benthic sediments sampled in East Antarctica. (a) Boxplots of copper, iron, lead and zinc concentrations in Casey and Davis sediments, showing the wider range of values measured at Casey; (b) boxplots of grain size for Casey and Davis sediments, showing the wider variability in grain sizes at Davis. Boxes encompass 50% of data, or the interquartile range (IQR), for a given variable, with a bold line representing the median. Dashed lines extend to maximum and minimum values, unless they exceed $1.5 \times$ IQR beyond the limits of the box, in which case they are shown as circles

ell et al. 2012) and are known to be detrimental to benthic species worldwide (Diaz & Rosenberg 1995), including *O. franklini* (Powell et al. 2012).

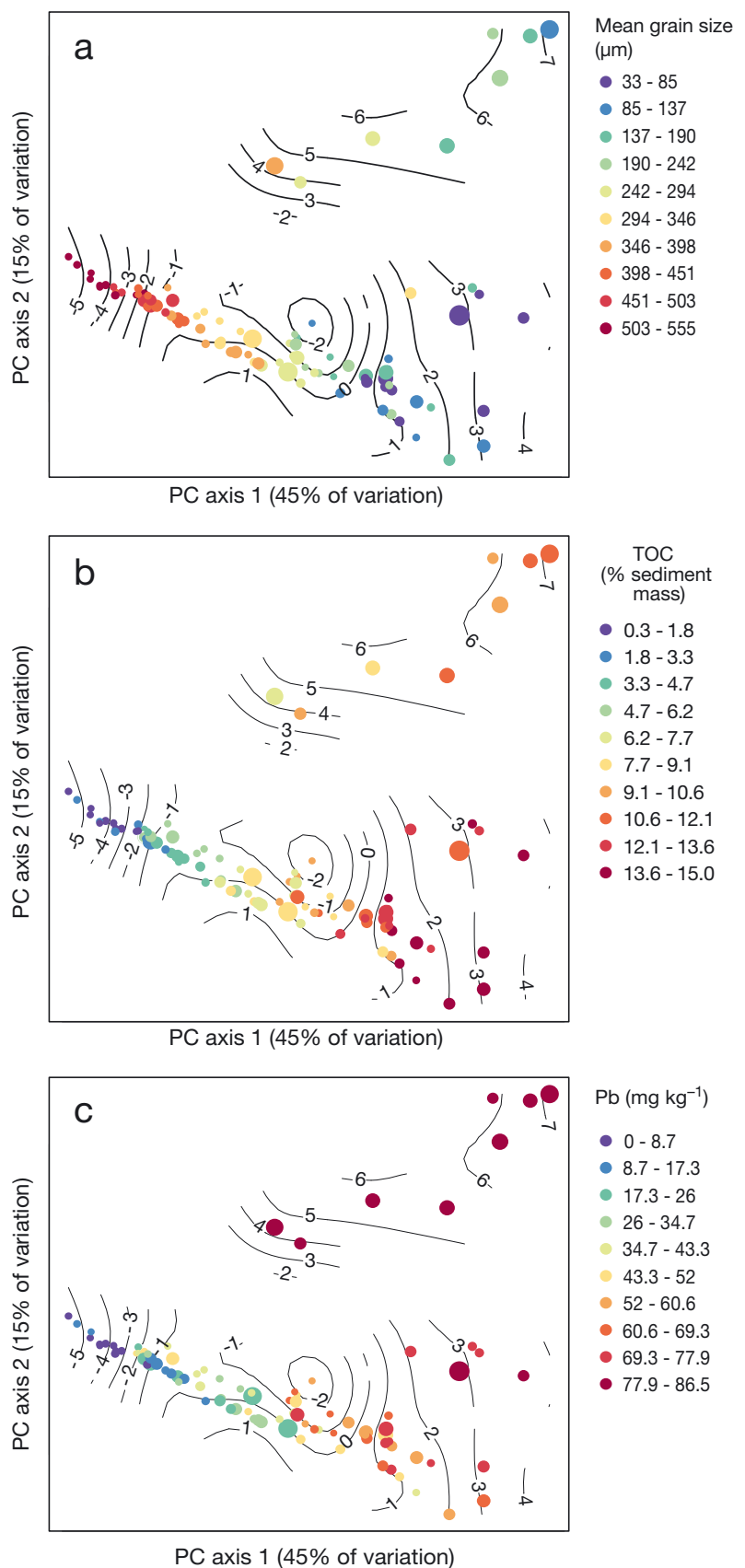
For both Casey and Davis, as well as for the combined dataset, a higher abundance of *Orchomenella franklini* was consistently predicted for sediments with higher trace element concentrations in particular metals. At Davis, however, the range of metal concentrations was just a fraction of that at Casey; therefore, this pattern likely reflects the correlation between finer-grained sediments and higher trace element bioavailability rather than indicating an affinity for high metal concentrations per se. At Casey, however, where grain sizes were much less variable and a clear relationship between abundance and grain size was lacking, the relationship observed for several trace metals may indicate a genuine influence of metal bioavailability on distribution. It is possible that at Casey (where most metals reached higher concentrations and showed stronger relationships to abundance than at Davis), *O. franklini* has a competitive advantage in sediments with higher heavy metal bioavailability. A study involving field manipulation of sediments at Casey also showed little effect of elevated metal concentrations on benthic fauna, attributed largely to the abundant presence of gammarid amphipods including *O. franklini* (Stark et al. 2003c). Many crustaceans including amphipods have the ability to regulate uptake and excretion of bioavailable trace metals in sediments (Rainbow

1997, Nassiri et al. 2000). Potentially, this enables *O. franklini* to thrive in the more contaminated sediments at Casey, where species unable to regulate internal levels of metals might be excluded. The burrowing of benthic amphipods can also contribute to bioturbation and associated redistribution of metals (Nedwell & Walker 1995, Modig & Ólafsson 2001, Marsden & Rainbow 2004), potentially making them more available to other infauna, thus reducing intraspecific competition. Recently, genetic evidence of selection pressures acting differentially on Davis and Casey populations of *O. franklini* have also been reported (Baird et al. 2012). Localised adaptation to specific regions within the Antarctic benthos has only recently begun to be explored, as the stability of the environment has long fostered the view of a relatively homogenous fauna (Hedgpeth 1970, Dell 1972, Arnaud 1977, White 1984). Observations for *O. franklini* suggest that local adaptation should be considered a potentially important force structuring populations, particularly in light of the continuing localised pollution of Antarctic marine habitats (Lenihan et al. 1990) which is likely to increase environmental disparity between areas.

Models based on the first 2 principal components from PCA analysis of sediment parameters only explained up to half of the variance in *Orchomenella franklini* abundance; thus, many additional factors are likely contributing to the observed distribution. Depth, largely through its influence on other vari-

ables, has a strong effect on the abundance of many Antarctic invertebrates (e.g. Gambi et al. 1994, Barry et al. 2003, Barnes & Conlan 2007); however, its effect on *O. franklini* cannot be determined from this study, as depth differed by less than 10 m for >80% of samples. Other potential factors include the extent of sea ice cover (and therefore sunlight exposure), hydrodynamics of the water column such as turbidity and current speeds, concentration of phytoplankton and cryopelagic organisms resulting in patchy food distribution, ice disturbance (see Gutt 2000, Barnes & Conlan 2007) and the density of other species that may have an effect via competition or predation. Nonetheless, the discovery of discernible patterns in abundance with respect to sediment characteristics has important implications for our understanding of the Antarctic benthos. While the effects of ice disturbance to benthic community composition and distribution have been thoroughly demonstrated (e.g. Barnes 1999, Gutt 2001, Gerdes et al. 2003, Brown et al. 2004), the present study indicates that sediment properties may also be important factors contributing to the biological heterogeneity of the Antarctic benthos. However, these relationships are likely to be highly complex, with deposit-feeder distributions generally influenced by dynamic sedimentary and hydrodynamic processes along with microbial and meiofaunal communities (Snelgrove & Butman 1994). The

Fig. 6. Principal components analysis ordination of sediment parameters for Casey and Davis data combined. The first 2 principal components account for 60% of environmental variation. Points are scaled by mean abundance of *Orchomenella franklini*, and contours represent predictions of relative abundance based on generalised additive modelling (GAM) of square-root-transformed abundance data. GAM explains 43% of the variance in abundance. Points are coloured by (a) mean grain size, (b) total organic carbon (TOC) content and (c) lead concentration (all parameters increase from cool to warm colours). Maximum abundance values are predicted for sediments with (a) moderately low mean grain size, (b) moderately high TOC and (c) concentrations of lead in the upper ranges for the region (correlated with several other metals and TOC; see text). PC: principal component



near-bed flow regime may be very influential in determining sediment conditions (Snelgrove & Butman 1994) and thus animal distributions. Investigations of hydrodynamic conditions would further aid our understanding of biological heterogeneity.

Implications and further research

To date, autecological studies of Antarctic benthic invertebrates are limited in spatial and/or temporal scope. Consequently, population dynamics and ecological processes are largely generalised from discrete observations, providing very limited baselines for monitoring human impacts (Lenihan 1992, Stark et al. 2003a). Benthic amphipods are often proposed as candidates for monitoring Antarctic nearshore ecosystems (e.g. Duquesne et al. 2000), given their trophic importance (Nedwell & Walker 1995, Dauby et al. 2003) and widespread high abundances (Jażdżewski et al. 1991, De Broyer et al. 2003). Our results indicate that even the most ubiquitous Antarctic benthic amphipods may exhibit marked spatial and temporal patchiness over several scales. This heterogeneity must be considered in the design of future studies aimed at monitoring benthic invertebrate communities. *Orchomenella franklini* may be considered an opportunistic species, given its association with high sediment organic matter (and corresponding sediment hypoxia) and moderate levels of metal contamination. Large increases in abundance may be a particularly effective indicator of human impacts such as increased sediment organic content from sewage outfalls, metal contamination or increased sedimentation resulting from land-based physical disturbance.

Until recently, there has also been extremely limited empirical evidence of relationships between specific sediment attributes and Antarctic benthic species distributions (Gutt 2000, 2007). Observations for *Orchomenella franklini* provide evidence of a relationship between sediment parameters and benthic species distribution in East Antarctica. It is highly probable that faunal distribution is driven by a combination of sediment conditions and hydrodynamics and near-bed flow, as has been proposed for other regions (Snelgrove & Butman 1994). The influence of sediments may be more important to deposit-feeders generally, because of their substantial reliance on the sediment for survival. Many Antarctic benthic fauna, however, are capable of switching their trophic mode or have a wide trophic niche (Gillies et al. 2013), suggesting that the simple

dichotomy between suspension and deposit-feeding communities (Gutt 2007) may not be valid, as has been suggested by Snelgrove & Butman (1994) and Pearson (2001). Future research in this field should also consider that distributional relationships with the local environment may differ between regions of the Antarctic dependent on the range of conditions present (Griffiths 2010), particularly the level of anthropogenic contamination.

On a local scale, future disturbance of the Antarctic nearshore environment through human presence (e.g. increased number of stations and shipping) is likely to increase sediment hypoxia (e.g. through sewage-derived eutrophication) and contribute ongoing metal pollution (Anisimov et al. 2007). On a broader scale, increased storm activity because of future climate change is predicted to affect the turbidity of oceanic waters and alter hydrodynamic conditions (Harley et al. 2006, Australian Government 2009), which may alter sediment nutrients and grain sizes. These predicted changes in sediment properties are likely to alter the abundance and distribution of *Orchomenella franklini*. Given the numerical dominance of this species, its importance as a prey item (La Mesa et al. 2007) and its likely role in bioturbation (Nedwell & Walker 1995), any changes in its abundance are likely to have a wider effect on the Antarctic nearshore benthic ecosystem.

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