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Influence of the Leeuwin Current on the epipelagic euphausiid assemblages of the south-east Indian Ocean

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Abstract

The Leeuwin Current is an anomalous eastern boundary current which transports warm, low salinity water poleward off Western Australia. This study investigated epi-pelagic euphausiids in the Leeuwin Current system from 22°S - 34°S focusing on the latitudinal gradient in species richness and whether variability in euphausiid assemblages was associated with an increase in seawater density across latitude. Twenty-eight species of euphausiids (including five new records) were identified from the study area. Species richness remained relatively constant across latitude as the distribution of seven tropical species, including the dominant *Pseudeuphausia latifrons*, extended south of 30°S. Euphausiid assemblages from the northern shelf stations were distinct from the oceanic, shelf break and southern shelf assemblages which, though clustering together, showed evidence of latitudinal shifts and day/night influence, particularly at oceanic stations. Distance-based linear models confirmed that, of the environmental variables examined, mean seawater density was the only significant explanatory variable accounting for 32%, 27% and 71% of the variation for shelf, shelf break and night oceanic assemblages, respectively. This study provides the first account of the diversity, distribution and abundance of euphausiids along the entire western seaboard of Australia and enhances understanding of the influence of the Leeuwin Current on holoplanktonic biota.

KEY WORDS: Oceanography, boundary current, Euphausiacea, water mass, krill

Introduction

Euphausiids are holoplanktonic, vertically migrating crustaceans and the distributions of the 86 species known from the world's oceans are relatively well documented (Brinton et al., 2000). They generally have affinities with tropical, subtropical, temperate or polar marine environments, although some are cosmopolitan in their distribution. Euphausiids follow the same global trend as many other marine biota, with the number of species decreasing with increasing latitude (Letessier et al., 2009; Tittensor et al., 2010; Letessier et al., 2011). However, their distribution patterns are known to be influenced by ocean currents (Mauchline & Fisher, 1969; Pillar et al., 1989; Barange & Pillar, 1992) and, in particular, western boundary currents can disrupt the latitudinal gradient in species richness by transporting waters with tropical characteristics and complement of plankton towards temperate environments (Wang & Chen, 1963; Griffiths, 1979; Gibbons et al., 1995). In the south-east Indian Ocean, the Leeuwin Current (LC), an anomalous, poleward flowing eastern boundary current, occurs off Western Australia. This current enables tropical corals, fishes and other taxa to exist as far south as the Houtman Abrolhos Islands (29°S) and Rottnest Island (32°S) (Maxwell & Cresswell, 1981; Wilson & Allen, 1987; Hutchins & Pearce, 1994; Fox & Beckley, 2005) but its influence has not been investigated with respect to the distribution of epi-pelagic euphausiids.

The LC comprises warm, low salinity, Tropical Surface Water (TSW) sourced from the Indo-Australian basin, with inputs from the Indonesian Throughflow, the South Java Current, the South Equatorial Current and the Eastern Gyral Current (Meyers et al., 1995; Feng & Wijffels, 2002; Domingues et al., 2007). As the LC flows poleward along the shelf break, cooler, more saline Sub Tropical Surface Water (STSW) is entrained into the current and, together with evaporative cooling, results in longshore temperature and salinity gradients from north to south along the Western Australian coast (Woo et al., 2006; Weller et al., 2011). The strength of the LC is intensified during the austral autumn/winter months, when maximum poleward geostrophic transport can reach 5 Sv (Feng et al., 2003), and the current, after passing Cape Leeuwin (34°S), extends eastward across the Great Australian Bight towards Tasmania (Cresswell & Golding, 1980; Ridgway & Condie, 2004).

Studies on the euphausiids within the LC are few, particularly for a region that supports southern blue fin tuna, migratory baleen whale populations and globally important colonies of seabirds, all of which are known consumers of euphausiids (Surman & Wooler, 2003; Rennie et al., 2009; Itoh et al., 2011). Four euphausiid species, namely, *Pseudeuphausia latifrons* (Sars, 1883), *Euphausia hemigibba* Hansen, 1910, *Euphausia recurva* Hansen, 1905 and *Thysanopoda tricuspidata* Milne-Edwards, 1837, have been previously reported from the LC (Wilson et al., 2003; Rennie et al., 2009), and 22 species were identified within a mesoscale eddy of the LC located between 31°S - 34°S and 112°E - 115°E (Sutton et al., 2015). Eleven species have been recorded in the headwaters of the LC between 20°S - 26°S, 105°E - 118°E (Taniguchi, 1974) and, in oceanic waters west of the LC, 31 euphausiid species were reported to occur along the 110°E meridian between 9°S - 32°S during the 1962 - 1965 International Indian Ocean Expedition (McWilliam, 1977).

The primary aim of this study was to examine the diversity, distribution and abundance of epipelagic euphausiids off the western seaboard of the Australian continent (22°S - 34°S) and relate these to prevailing oceanographic conditions. As the study area is dominated by the LC, the specific research questions were: a) does species richness of epi-pelagic euphausiids decline with increasing latitude and b) are epi-pelagic euphausiid assemblages off Western Australia structured by the change in seawater density across latitude?

Methods

Study area

A multi-disciplinary survey of the LC system between 22°S - 34°S and 111°E - 115°E was conducted during the late austral autumn from 16 May - 5 June 2007 aboard the R.V. *Southern Surveyor* (voyage SS04/07). Thirteen cross-shelf transects were sampled at each degree of latitude off the coast of Western Australia, encompassing shelf (~ 50 m depth), shelf break (~ 200 m) and oceanic (1000 - 2000 m) stations (Fig. 1). The concurrent studies of physical oceanography (Weller et al., 2011), nutrients (Thompson et al., 2011), primary production (Lourey et al., 2012), larval fishes (Holliday et al., 2012) and chaetognaths (Buchanan & Beckley 2016) identified physical and biological structuring in a system with dynamic longshore and cross-shelf transport.

Oceanographic and biological sampling

Abiotic and biotic properties of the water column at each station were sampled using a Seabird SBE 911 instrument (CTD) mounted in a 24 Niskin bottle rosette. The CTD was equipped with a dual temperature and conductivity sensor, an oxygen sensor and a Chelsea TGI fluorometer. Chlorophyll *a* was determined from water samples collected at the surface, 10, 25, 50, 75 and 100 m depths, and at the chlorophyll *a* maximum when present (Lourey et al., 2012). Temperature and salinity were used to calculate a mean seawater density for each station (0 – 150 m depth), expressed at sigma-t (σ_t).

After oceanographic measurements were taken, irrespective of whether it was day or night, zooplankton samples were collected using a bongo net (355 µm and 100 µm meshes, net diameters of 0.5 m). Two replicate oblique tows from a maximum depth of 150 m (or shallower on the shelf) to the surface were conducted at each station. The bongo net was towed at a speed of 2 knots for approximately 15 minutes. To determine the volume of water sampled, General Oceanics flowmeters were mounted in the mouth of both nets and were connected to an electronic interface in order to monitor the tow profile and volume of seawater sampled. Zooplankton samples were preserved in 5% buffered formaldehyde in seawater and the 355 µm mesh samples were used for identification and quantification of euphausiids. As the plankton samples were required to be intact for other projects, estimates of mesozooplankton abundance were made by pouring the zooplankton sample through a 1 mm sieve and measuring the settled volume of the < 1 mm zooplankton in a graduated cylinder after a 24 h period (Gibbons, 1999; Suthers & Rissik, 2009); settled volumes were expressed in mL m^{-3}.

Euphausiid identification

Immature and mature euphausiids were counted using a dissecting microscope and identified using relevant literature (Baker et al., 1990, Brinton et al., 2000). Zooplankton was subsampled with a Folsom splitter and a minimum of 200 euphausiids (100 immature and 100 mature specimens of all species combined) were counted from the sub-samples before estimates were made of the total concentration (Gibbons, 1999). Concentrations of euphausiids were expressed as the average number of individuals per 1000 m^{-3} ± standard error. Damaged or indistinguishable immature and mature specimens were grouped as unidentified. Euphausiid species were classified as tropical, subtropical or temperate based upon geographical distributions given by Brinton et al. (2000).

Statistical analyses

As euphausiids undergo pronounced diel vertical migration, stations were classified *a priori* as day or night. Univariate analyses were performed on total euphausiid concentrations using the non-parametric Kruskal-Wallis test for independent samples (IBM SPSS Statistics 21), to assess if total concentrations differed across day and night and across isobath (shelf, shelf break and oceanic).

For multivariate analyses of euphausiid assemblages, the PRIMER v6 PERMANOVA+ software package was used (Anderson et al., 2008; Clarke & Gorley, 2015). A fourth root transformation was applied to euphausiid concentrations to reduce the relative importance of abundant species, and a Bray-Curtis resemblance matrix was constructed. Non-metric multidimensional scaling ordination was used to assess the spatial relationships among assemblages, and one-way analysis of similarity (ANOSIM) was used to test for differences in assemblages across day and night for each isobath (Clark & Warwick, 2001).

To determine which abiotic and biotic properties of the water column structured euphausiid assemblages, mean seawater density (0 - 150 m), mean dissolved oxygen (0 -150 m), surface chlorophyll *a*, depth integrated chlorophyll *a* (0 - 100 m) and mesozooplankton settled volume (0 - 150 m), were correlated with euphausiid assemblages using distance-based linear models (DISTLM) (Anderson, 2001). These models were constructed using the step-wise selection procedure with the adjusted R^2 as the selection criterion, and were used to determine the subset of environmental variables that best correlated with euphausiid assemblages. Square root transformations were applied to the environmental data, and the data were normalised and constructed into a resemblance matrix based on Euclidean distance. Draftsman plots revealed if co-correlation existed between environmental variables ($r^2 > 0.7$), which resulted in the removal of mean dissolved oxygen due to its positive correlation with mean seawater density.

Results

The oceanographic environment

The LC was the dominant feature in the south-eastern Indian Ocean during May - June 2007 and was most evident along the shelf break where it transported warm waters southwards from 22°S to 34°S (Fig. 1). At shelf and shelf break stations the water column was generally well-mixed, but for oceanic stations as far north as 25°S, the water column was more stratified with shallower mixed layers (Fig. 2). For all stations, a gradual shift from a TSW signature (> 22°C, < 35.5 psu, 22.9 - 24.6 σ_t) to a STSW signature (< 22°C, > 35.7 psu, 24.8 - 26.2 σ_t) was evident (Fig. 2; Fig. 3). In the top 150 m of the water column (matching the extent of epi-pelagic zooplankton sampling), a decrease in mean temperature corresponded to an increase in mean salinity and mean dissolved oxygen and overall, an increase in mean seawater density occurred with an increase in latitude (Fig. 3).

In general, surface chlorophyll *a* and depth-integrated chlorophyll *a* increased from north to south (Fig. 4a & b). Mesozooplankton settled volume decreased from 2.31 ml m^{-3} at 22°S to 0.40 ml m^{-3} at 34°S for shelf stations, but showed no obvious patterns for shelf break and oceanic stations (Fig. 4c).

Euphausiid diversity, abundance and distribution

A total of 28 euphausiid species was identified from the LC study area (Fig. 5a) and overall, there was no evidence of a decline in species richness with increasing latitude ($r^2 = 0.0005$) (Fig. 5b). Five of these species were new records for the south east Indian Ocean, namely, *Euphausia fallax* Hansen, 1916, *Nyctiphanes australis* Sars, 1883, *Stylocheiron indicum* Silas & Mathew, 1967, *Stylocheiron insulare* Hansen, 1910, and *Stylocheiron robustum* Brinton, 1962 (Fig. 5a). Of the nine tropical species identified across the study area (*Euphausia diomedeae* Ortmann, 1894, *Euphausia fallax* Hansen, 1916, *Euphausia sanzoi* Torelli, 1934, *P. latifrons*, *S. indicum, S. insulare*, *Stylocheiron microphthalma* Hansen, 1910, *Thysanopoda astylata* Brinton, 1975 and *T. tricuspidata*), all except *S. indicum* and *T. tricuspidata* were recorded south of 30°S (Fig. 5). The number of species recorded was higher for oceanic (26 in total) and shelf break (22 in total) stations than shelf stations (14 in total) (Fig. 6a). The occurrence of some species was also affected by whether the samples were collected during the day or night; only 17 species were collected from day stations whereas all 28 species were recorded at night stations.

The highest total euphausiid concentrations were recorded at shelf stations at 22°S and 27°S, reaching 50,858 inds·1000 m^{-3} and 16,649 inds·1000 m^{-3}, respectively (Fig. 6b); these samples were mainly comprised of juvenile *P. latifrons*. Generally, though, total concentrations at all other stations ranged between 130 - 4191 inds·1000 m^{-3}, and decreased from north to south. More specimens were caught during the night (1671 ± 251 inds·1000 m^{-3}) than during the day (820 ± 169 inds·1000 m^{-3}) ($p = 0.010$, $n = 39$, Kruskal-Wallis), and there were no significant differences in total concentration across isobath ($p = 0.676$, $n = 39$, Kruskal-Wallis).

Pseudeuphausia latifrons, *E. recurva* and *Stylocheiron carinatum* Sars, 1883 were the most common and abundant species throughout the study area and together, they accounted for over 75% of euphausiids. *Pseudeuphausia latifrons*, a tropical neritic species, was identified from every station sampled in the study area and concentrations decreased from north to south (Fig. 7a). The subtropical/temperate oceanic species, *E. recurva*, was mostly identified from stations in the southern part of the study area (29°S - 34°S), but with some occurrences between 25°S - 27°S (Fig. 7b); concentrations increased towards the south. *Stylocheiron carinatum* is typically cosmopolitan and it was collected at most stations throughout the study area with similar concentrations across latitude (Fig. 7c).

Euphausiid assemblages and environmental correlations

A nMDS ordination of euphausiid assemblages showed that shelf stations, particularly those from the north of the study area, were largely distinct from shelf break and oceanic stations which were clustered together (Fig. 8a). Whether stations were sampled during the day or night (Fig. 8b) was not significant for shelf assemblages (ANOSIM $R = 0.074$, $P = 0.219$, $n = 13$) or shelf break assemblages ($R = 0.212$, $P = 0.061$, $n = 13$) but was significant for oceanic assemblages ($R = 0.915$, $P = 0.006$, $n = 13$).

In the distance-based linear model for shelf assemblages, all four environmental variables together explained 48% of the total variation (Table 1). Mean seawater density was, however, the only significant explanatory variable accounting for 32% ($P = 0.002$). For the fitted model, the distance-based redundancy bi-plot showed axes 1 and 2 to explain 69% and 24% of the variation, respectively (Fig. 9a). The change in euphausiid assemblages from 22°S - 34°S corresponded with increasing seawater density.

For euphausiid assemblages along the shelf break, all four environmental variables together explained 61% of the total variation (Table 1). Mean seawater density was again the only significant variable accounting for 27% ($P = 0.001$). For the fitted model, axes 1 and 2 explained 53% and 26% of the variation, respectively (Fig. 9b). Similarly, the change in euphausiid assemblages across latitude corresponded with increasing seawater density.

The significant day/night effect on oceanic euphausiid assemblages was taken into account for the distance-based linear model. For assemblages sampled during the day, although the four environmental variables explained 86% of the variation, none of the variables was significant (Table 1). For assemblages sampled at night, the four environmental variables explained 77% of the variation (Table 1). Mean seawater density was the only significant explanatory variable explaining 51% of the variation (P = 0.004). For the fitted model, axes 1 and 2 explained 68% and 20% of the variation in night assemblages, respectively (Fig. 9c).

Discussion

This study ascertained that, over the 22° - 34°S study area off Western Australia, the total number of species of epi-pelagic euphausiids did not decline with increasing latitude but remained relatively stable confirming that the anomalous LC disrupts the expected latitudinal gradient in euphausiid species richness. However, the mix and concentrations of species contributing to euphausiid assemblages at shelf, shelf break and oceanic stations over the study area did vary, and assemblages were shown to be significantly structured by seawater density, which increased across latitude.

Twenty eight euphausiid species were identified from the LC study area and comprised nine tropical, 15 tropical/subtropical, three subtropical/temperate and one temperate species (Brinton et al., 2000). This mix of euphausiid species in the LC study area could be explained by entrainment of species from source waters or surrounding water masses. For example, tropical Indo-Australian endemics such as *S. insulare*, *E. fallax* and *E. sanzoi* could have been funnelled into the LC via the catchment waters of the Indonesian Throughflow. *Stylocheiron robustum*, which has a distribution across the central Indian Ocean basin (Brinton et al., 2000), was recorded at oceanic stations 25°S and 34°S, and is probably indicative of eastward flows into the LC (Domingues et al., 2007; Menezes et al., 2014). The subtropical/temperate species, *E. recurva*, *Euphausia similis* Sars, 1883, *N. australis*, and *Thysanoessa gregaria* Sars, 1883 (Brinton et al., 2000), were all present in the south where the influence of STSW created a cooler, more saline environment (Domingues et al., 2007; Woo & Pattiaratchi, 2008).

The occurrence of the tropical species, *E. diomedeae*, *E. sanzoi*, *E. fallax S. insulare*, *S. microphthalma*, *T. astylata* and, particularly, *P. latifrons*, at southern latitudes confirms the influence of the southward flowing LC on the distribution of holoplanktonic biota. Such poleward dispersal of tropical euphausiid species is not unusual in western boundary currents. For example, *E. diomedeae* and *P. latifrons* have been recorded to be transported northwards in the western Pacific by the Kuroshio Current (Wang & Chen, 1963, Brinton et al., 2000) and the southward dispersal of *P. latifrons* is known for both the Agulhas and East Australian Currents (Griffiths 1979; Gibbons et al. 1995).

In the northern hemisphere, *Nyctiphanes simplex* Hansen, 1911 has been used as a biological tracer to determine the direction of transport of warm water off Oregon during an El Niño event (Keister et al., 2005). It is proposed here that *P. latifrons*, a typically tropical and neritic species (Brinton et al., 2000), could be similarly used as a tracer of longshore and cross-shelf transport of LC waters. Not only was *P. latifrons* found at every degree of latitude in the survey area but also at every station in shelf break and oceanic waters, which for a coastal species, could be achieved by cross-shelf transport via meanders and eddies (Holliday et al., 2011; Holliday et al., 2012; Paterson et al., 2013).

Numerically, three species, *P. latifrons*, *E. recurva* and *S. carinatum* were dominant and constituted 75% of all euphausiids sampled in the LC study area. It appears to be a common finding that euphausiid assemblages are numerically dominated by only a few euphausiid species, with the remaining species found in relatively low abundances. Off Baja California, *Nyctiphanes simplex* dominates assemblages (Gomez-Gutierrez et al., 1995), *Euphausia lucens* Hansen, 1905, *Euphausia hanseni* Zimmer, 1915 and *Nyctiphanes capensis* Hansen, 1911 dominate in the Benguela Current (Pillar et al., 1992), *Euphausia mucronata* Sars, 1883 dominates in the Humboldt Current system (Antezana, 2010) and *Euphausia pacifica* Hansen, 1911 is very abundant in the Oyashio and Kuroshio Currents (Taki, 1998; Taki, 2008).

Examination of the relationships between euphausiid assemblages across the study area indicated that those at northern shelf stations were distinct from the oceanic, shelf break and southern shelf assemblages. Within these nMDS groupings there was evidence of a latitudinal shift from 22° - 34°S. However, for oceanic assemblages sampled during the day, this pattern was disrupted, presumably due to the diel vertical migration of many euphausiid species over the deeper water column (Mauchline & Fisher, 1969). Assemblages sampled at the oceanic stations during the day had fewer species and lower concentrations and thus did not cluster with oceanic stations sampled at night. Depth-stratified sampling during both day and night would be required to confirm the effects of diel vertical migration on assemblages. Further, euphausiids are also known to exhibit net avoidance particularly during the day (Brinton, 1967; Wiebe et al., 1982), so use of bongo nets in this study might have influenced capture rates.

Euphausiids are well-known to be linked with the physical properties of water masses (Brinton, 1975; Dadon & Boltovsky, 1982; Gibbons et al., 1995; Tarling et al., 1995). Seawater density is indicative of water mass and, in the LC study area, both TSW (22.9 - 24.6 σ_t) and STSW (24.8 - 26.2 σ_t) were the dominant water masses. Distance-based linear models confirmed that mean seawater density was the only significant explanatory variable accounting for 32%, 27% and 71% of the variation for shelf, shelf break and night oceanic assemblages, respectively. Lower density waters, i.e. TSW, had higher total concentrations of euphausiids, particularly of tropical species, such as *P. latifrons,* whereas higher density waters, i.e. STSW, had lower overall concentrations, but greater concentrations of subtropical and temperate species, such as *E. recurva*. Likewise, in the California Current, changes in the euphausiid assemblages and dominant species were, in part, attributed to the mixing of species from the different water masses in the region (Youngbluth, 1976).

Besides the physical properties of the water column, other factors, particularly food availability, are known to affect euphausiids (Youngbluth, 1975, Hu, 1978, Gibbons, 1993, Taki, 2008). As they feed on a range of phytoplankton and zooplankton species (Mauchline & Fisher, 1969), chlorophyll *a* and mesozooplankton settled volume were included as environmental variables in the distance-based linear modelling in this study. Although increases in surface and depth integrated chlorophyll *a*, and a decrease in mesozooplankton settled volume from north to south explained some of the variation in euphausiid assemblages, these were not found to be significant variables in the model.

Although euphausiid diversity, distribution and abundance are relatively well known across the oceans (e.g. Brinton, 2000; Letessier et al., 2009; Letessier et al., 2011), until this study, the influence of the unusual LC on euphausiids in the south-east Indian Ocean was unknown. The presence of the poleward flowing LC results in a disruption of the typical latitudinal gradient in species richness by dispersing tropical species beyond their normal distribution limits to mix with subtropical and temperate species off Western Australia. The oceanographic property of mean seawater density was established to be the best explanatory variable in structuring epi-pelagic euphausiid assemblages and emphasizes the influence of boundary currents on holoplanktonic biota.

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Table 1 The percentage of the variance in euphausiid assemblages explained by each environmental explanatory variable included in the distance-based linear models for shelf, shelf break and oceanic stations. Due to the significant influence of day and night on oceanic assemblages, models were performed separately. Environmental variables explaining a significant percentage of variation are denoted by an asterisk

Fig. 1 a) Sea surface temperature for the 5 June 2007, showing the warm, southward flowing Leeuwin Current (LC), Tropical Surface Water (TSW) and cooler Sub Tropical Surface Water (STSW) in the south-east Indian Ocean (adapted from Weller et al., 2011). b) Zooplankton sampling locations at shelf, shelf break and oceanic stations. The 200 m isobath is indicated by the dashed line

Fig. 2 Temperature and salinity profiles (0 - 150 m) of shelf, shelf break and oceanic water columns at 22°S, 29°S and 34°S in the south-east Indian Ocean. Solid line indicates temperature (°C) and dashed line indicates salinity (psu)

Fig. 3 (a) Temperature and salinity profile of the water column, to 2000 m depth, across the Leeuwin Current study area in the south-east Indian Ocean. Box indicates 0 - 150 m of the water column which is expanded to show the correlations between b) mean temperature and mean salinity c) mean temperature and mean dissolved oxygen and d) latitude and mean seawater density for shelf, shelf break and oceanic environments.

Fig. 4 a) Surface chlorophyll *a* concentration, b) depth integrated chlorophyll *a* (0 - 150m) and c) mesozooplankton settled volume for shelf, shelf break and oceanic stations across the Leeuwin Current study area in the south-east Indian Ocean. Grey and black circles distinguish stations sampled during the day and night, respectively

Fig. 5 a) The euphausiid species and their respective latitudinal ranges (°S) recorded across the Leeuwin Current survey area in the south-east Indian Ocean in 2007. Previously known distribution ranges are given based on Brinton et al. (2000) and are indicated by * tropical, $^{\#}$ tropical/subtropical, ^ subtropical/temperate and $^{+}$ temperate. Species of a genus that could not be distinguished are indicated as sp. and spp. refers to more than one species of the same genus that could not be distinguished. b) The total number of euphausiid species identified at each latitude between 22°S - 34°S. Only euphausiids that were identified to species level were included.

Fig. 6 a) The number of euphausiid species identified and b) total euphausiid concentrations for all the shelf, shelf break and oceanic stations over the Leeuwin Current study area in the south-east Indian Ocean. Grey and black circles indicate stations sampled during the day and night, respectively

Fig. 7 Concentrations (1000·m^{-3}) of the three dominant euphausiid species at shelf, shelf break and oceanic stations in the Leeuwin Current study area in the south-east Indian Ocean, a) *Pseudeuphausia latifrons*, b) *Euphausia recurva* and c) *Stylocheiron carinatum*. Scales are the same for all three species and grey and black circles indicate stations sampled during the day and night, respectively

Fig. 8 nMDS ordinations showing similarities in euphausiid assemblages in the south-east Indian Ocean, defined by latitude and a) isobath (shelf, shelf break, oceanic), b) day and night

Fig. 9 Distance-based redundancy bi-plots for a) shelf, b) shelf break and c) oceanic night euphausiid assemblages, showing the influence of environmental variables