Euphausiid assemblages in and around a developing anticyclonic Leeuwin Current eddy in the south-east Indian Ocean

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The composition, distribution and abundance of euphausiids in and around an anticyclonic eddy of the Leeuwin Current were investigated in the south-east Indian Ocean off Western Australia (31°–34°S). In total, 22 euphausiid species were identified, two of which, *Euphausia sanzoi* and *Thysanopoda astylata*, are new records for the south-east Indian Ocean. In addition, five species represent new records for Australian EEZ waters and seven are new records for the latitude of the eddy field. *Euphausia recurva* and *Stylocheiron carinatum* were the most abundant species in the Leeuwin Current and eddy perimeter, reaching mean abundances of 135.5 ± 22.3 m^{-2} and 70.5 ± 12.2 m^{-2}, respectively. *Pseudeuphausia latifrons* was the most abundant species over the shelf (52.1 ± 14.0 m^{-2}). Species richness was greater in the eddy and surrounding oceanic waters (18–20 species) than on the adjacent shelf (11 species). Of the water column properties included in a multivariate multiple regression analysis, only depth made a significant contribution to explaining the variation in euphausiid assemblages, probably due to mixing of water masses in the developing eddy. This study has revealed the influence of mixing processes associated with a Leeuwin Current eddy on holoplanktonic euphausiids in the south-east Indian Ocean.

KEYWORDS: Euphausiacea, warm core eddy, boundary current, entrainment, new records

INTRODUCTION

Despite the importance of euphausiids (krill) in marine food webs, there have been no studies dedicated to describing the distribution and abundance of euphausiid species within the Leeuwin Current system of the south-east Indian Ocean. During earlier plankton investigations further offshore of the Leeuwin Current system during the International Indian Ocean Expedition, 32 euphausiid species were recorded in oceanic waters along the 110°E meridian (9°–32°S) (McWilliam 1977). To the north of Western Australia, 12 euphausiid species, including *Euphausia recurva* Hansen 1905 and *Pseudeuphausia latifrons* (Sars 1883), have been recorded in the head waters of the Leeuwin Current (Taniguchi 1974; Wilson *et al.* 2003). Within the Australian Exclusive Economic Zone, eight euphausiid species are expected to occur off south-western Australia between 31° and 34°S (Davie 2002).

The Leeuwin Current is an anomalous, poleward flowing, eastern boundary current off the coast of Western Australia (Cresswell & Golding 1980; Ridgway & Condie 2004; Waite *et al.* 2007a). Like other boundary currents, it has an important influence upon longshore and cross-shelf variability and transport of planktonic biota and is responsible for southward (temperate) range extensions of tropical species (Maxwell & Cresswell 1981; Hutchins and Pearce 1994; Fox & Beckley 2005; Pearce *et al.* 2011). The Leeuwin Current is increasingly energetic and variable along its southwards trajectory and the formation of meso-scale perturbations such as meanders and anticyclonic eddies enhance shelf-ocean exchange (Weller *et al.* 2011; Holliday *et al.* 2012). Such meso-scale features are more frequent during the austral autumn and winter months when the Leeuwin Current is strongest and opposing southerly winds are weak (Feng *et al.* 2003). These features drive the cross-shelf variability of planktonic biota and there are important latitudinal differences in the dispersal or retention of shelf waters that correspond with regions of recurrent meso-scale instability (Feng *et al.* 2010; Holliday *et al.* 2012).

Detailed *in situ* investigations of a developing anticyclonic eddy of the Leeuwin Current and surrounding waters (Paterson *et al.* 2008; Holliday *et al.* 2011) provided the context to examine the euphausiid assemblages off south-western Australia in the late austral autumn. This particular eddy was defined as a mix of Leeuwin Current, oceanic, and shelf waters and its constituent ichthyoplankton assemblage reflected the different source waters (Paterson *et al.* 2008; Holliday *et al.* 2011). The aim of this study was to document the euphausiid assemblage within an eddy of the Leeuwin Current system in the south-eastern Indian Ocean.

METHODS

Sampling

This study is based upon intensive oceanographic (Paterson *et al.* 2008) and biological (Holliday *et al.* 2011) sampling of a developing anticyclonic eddy and surrounding waters off the coast of south-western Australia (31°–34°S; up to 200 nm offshore) over the period 2–28 May 2006. The developing eddy was identified through sequential satellite observations of sea surface temperature and sea surface height anomaly (Fig. 1). A meander was initially formed which developed into the anticyclonic eddy, continuing to circulate after the 26 day sampling period during May 2006. The eddy then broke away and, by mid-August, had drifted further westward. Altimetry and satellite images of sea-surface temperature were sourced from the Integrated Marine Observing System (IMOS) website (www.oceancurrent.imos.org.au).

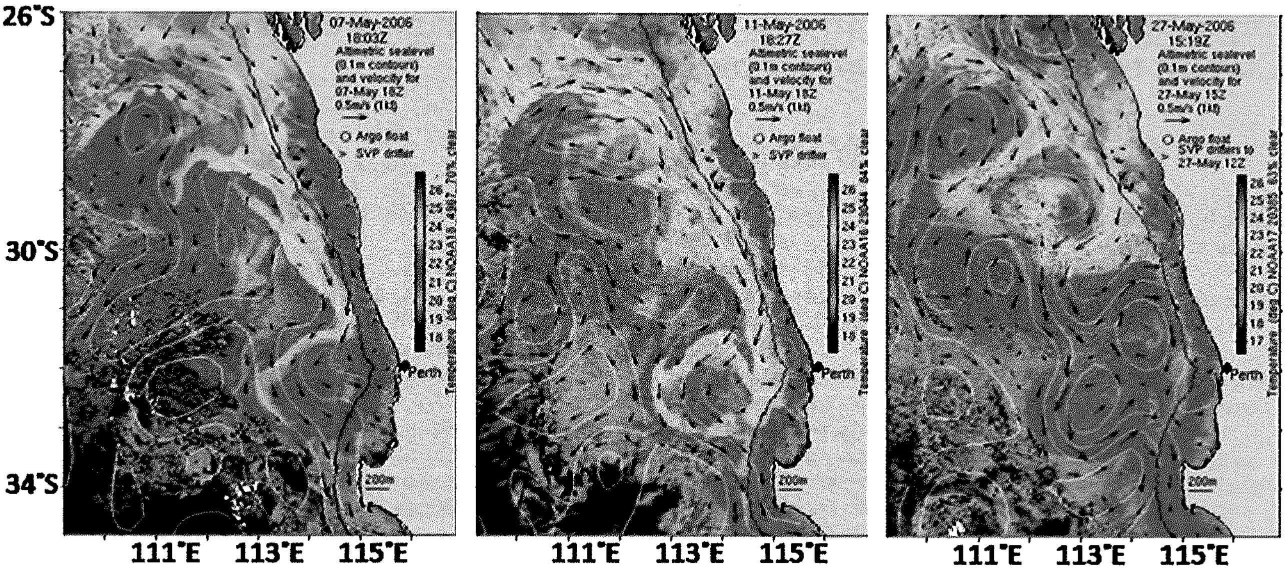

Figure 1. Satellite sea surface temperature images showing the development of an anticyclonic eddy at 32°S from 7–27 May 2006 within the south-east Indian Ocean (Source: www.oceancurrent.imos.org.au/).

Zooplankton samples were taken at 18 stations within the Leeuwin Current, the meander/ developing eddy, adjacent shelf and surrounding oceanic waters (Fig. 2). The locations of sampling stations were primarily determined by the trajectories of Iridium satellite-tracked drifting buoys (Fastwave Communications Pty Ltd), which were deployed during the voyage, as well as the use of near real time satellite imagery (sea surface temperature and surface chlorophyll *a*). The imagery aided in the distinction of eddy (centre and perimeter), adjacent continental shelf, Leeuwin Current and surrounding oceanic waters (Paterson *et al.* 2008; Holliday *et al.* 2011).

A conductivity-temperature-depth-oxygen (CTD-O2) instrument was used to measure vertical profiles of the water column immediately prior to zooplankton sampling. The Seabird SBE 19+ CTD-O2 was also equipped with a Chelsea TGI fluorometer to measure fluorescence, a proxy for chlorophyll *a*, and was cast from the surface to 500 m depth, or to ~ 10 m above the sea bottom for shelf stations. The mixed layer depth was determined when a change in potential density of 0.125kg m^{-3} from that at 10 m depth occurred (Levitus 1982; Feng *et al.* 2007)

Zooplankton samples were collected at night using a 1 m^2, multiple opening and closing EZ net equipped with a General Oceanics flowmeter (10 nets, mesh size of 335 μm); this technique has been successfully used for collecting depth-stratified samples of fish larvae in this region (Muhling & Beckley 2007; Muhling *et al.* 2007). Two replicate tows were conducted to 200 m depth or to ~10 m above the seafloor on the shelf for all stations except P1, LC2, P5 and O13. Samples were preserved in a 5% buffered formalin seawater solution. For the purposes of this paper in documenting the euphausiid assemblages of the region, abundances of euphausiids at each station were derived by integrating the concentrations from each depth stratum, and were expressed as the number under 1 m^2.

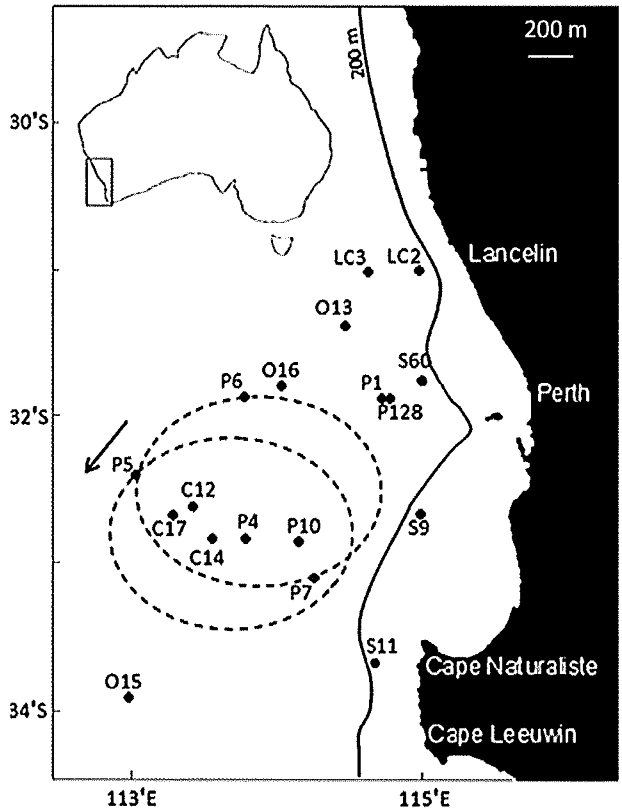

Figure 2. Location of stations within and around the Leeuwin Current anticyclonic eddy (dashed lines) where euphausiid samples were collected (adapted from Holliday *et al.*, 2011). Arrow indicates the propagation direction of the eddy. Letters correspond to station groupings for statistical purposes: LC = Leeuwin Current; P = eddy perimeter; C = eddy centre; S = shelf, O = oceanic.

With the aid of a Folsom plankton splitter to sub sample (Gibbons 1999) and relevant taxonomic keys (Baker *et al.* 1990; Gibbons 1999), adult and juvenile euphausiids were counted and identified to species level. A minimum of 100 specimens were identified from the sub samples before an estimate of the whole sample was made. Damaged or indistinguishable juvenile specimens were grouped as unidentified. The difficult "*Euphausia gibba* species complex" comprises *Euphausia gibba* Sars 1883, *Euphausia paragibba* Hansen 1910, *Euphausia pseudogibba* Ortmann 1893, and *Euphausia hemigibba* Hansen 1910, and distinguishing between species is only based on minute morphological features (Baker *et al.* 1990) that could not be definitively recognised in all specimens. As *E. hemigibba* occurs throughout the south-east Indian Ocean (Brinton *et al.* 2000) and along the 110°E meridian (McWilliam 1977), specimens from this group were ascribed to this species in this study. The species pair *Thysanopoda astylata* and *Thysanopoda aequalis* is also difficult to distinguish and, in this study, thickness of the frontal plate was used, in addition to the defining feature of a flagellum-like spine on the third thoracic leg in adult males of *T. aequalis* (Baker *et al.* 1990).

Statistical analyses

For statistical analyses, stations were grouped *a priori* depending on their location within the eddy field, and were classified as Leeuwin Current meander/ eddy perimeter, eddy centre, oceanic, or shelf as per Holliday *et al.* (2011). As the study was of a Lagrangian design, it is recognised that the *a priori* locations were not represented by an equal number of stations, which could present a bias towards the observed species richness of Leeuwin Current meander/ eddy perimeter stations. Euphausiid assemblage structure (excluding unidentified and damaged specimens) across the eddy field was examined using the Primer-6 software package (Clarke & Gorley 2006) and, prior to analysis, data were fourth root transformed and a Bray-Curtis resemblance matrix was constructed. Non-metric multidimensional scaling ordination plots (nMDS) were used to assess the spatial relationships among euphausiid assemblages within, and among, sampling locations. A one-way analysis of similarity (ANOSIM) was then applied to determine significant spatial differences between euphausiid assemblages in relation to location, and a one-way similarity percentage routine (SIMPER) was used to show the dissimilarities of the assemblages between each of the locations.

A multivariate multiple regression analysis, using the distance-based linear modelling technique (DistLM) (Anderson 2001) was used to evaluate the relationship between water column properties (predictors) and euphausiid assemblages (response matrix). Mean values for the mixed layer of temperature, salinity, fluorescence, dissolved oxygen, surface chlorophyll *a* and depth were used by the model to determine how much variation in euphausiid assemblages was explained by the variation in water column properties. Prior to the analysis, data for the water column properties were examined using a draftsman scatter plot to determine appropriate data transformations according to the skewness and curvilinearity of the data (Clarke & Ainsworth 1993). Temperature was subjected to a log (x+1) transformation, all variables were normalised and a resemblance matrix was constructed using Euclidean distance. Subsequently, salinity was removed from the analysis because of its strong negative correlation with temperature. Results were represented in a two-dimensional distance-based redundancy (dbRDA) biplot, in which the water column properties identified in the DistLM were used to constrain the ordination of euphausiid assemblages.

RESULTS

The studied anticyclonic eddy was formed from a meander of the Leeuwin Current during April 2006 and was sampled during its developing phase from 2–28 May (Paterson *et al.* 2008; Holliday *et al.* 2011) (Fig. 1). Most of the Leeuwin Current's volume was deflected offshore to circulate around the eddy perimeter and feed into the eddy. The eddy's connection with Leeuwin Current and shelf waters, as it developed from the meander, was evident from the strong cross shelf exchange observed in synoptic sea surface temperature and chlorophyll *a* data. Mixing between the eddy and surrounding water masses was responsible for the modification of the physio-chemical and biological signature of the eddy (Paterson *et al.* 2008).

Holliday *et al.* (2011) identified three distinct water masses within the eddy field based on temperature and salinity properties, Leeuwin Current (> 23.0°C, < 35.4 psu), modified Leeuwin Current (21.5–22.5°C, 34.4–35.7 psu), and Sub-Tropical Surface Water (18–20.5°C, 35.8–35.9 psu) (Table 1). Leeuwin Current water was identified upstream of the eddy (LC2 & LC3), whilst the eddy centre and Leeuwin Current meander/ eddy perimeter stations were characterised by modified Leeuwin Current water, indicative of the mixing and water exchange with surrounding source waters. Oceanic stations (O13, O15 & O16) were characterised by Sub-Tropical Surface Water. Mixed layer depths varied across the eddy field, with shelf and eddy stations having a more homogenous water column structure. Eddy centre stations had deeper mixed layers, deepening with development from 70 m at E12 (16-May) to 119 m at E17 (22-May). Relatively high nutrient and chlorophyll *a* concentrations were also identified within the eddy (Paterson *et al.* 2008).

Twenty two euphausiid species from seven genera were identified from the 18 stations that were sampled within the eddy field (Table 1). Assemblages were dominated by *E. recurva*, *Stylocheiron carinatum* Sars 1883 and *P. latifrons*. *Euphausia sanzoi* Torelli 1934 and *T. astylata* Brinton 1975 have not previously been recorded for the south-east Indian Ocean, and are new records for the region. Furthermore, *Nematobrachion flexipes* (Ortmann 1893), *Stylocheiron microphthalma* Hansen 1910, *Stylocheiron suhmi* Sars 1883, *T. aequalis* Hansen 1905 and *Nematoscelis microps* Sars 1883 have been reported for the south-east Indian Ocean, but are new records for Australian Exclusive Economic Zone. Within Australian waters, *P. latifrons*, *Nematoscelis atlantica* Hansen 1910, *Stylocheiron abbreviatum* Sars 1883, *Stylocheiron affine* Hansen 1910, *S. carinatum*, *Thysanopoda monacantha* Ortmann 1893 and *Thysanopoda tricuspidata* Milne-Edwards 1837 represent new distribution records for the southerly latitudes encompassed by the eddy (31–34°S). Previously, their distributions were regarded as restricted to lower latitudes (Davies 2002).

Table 1. Euphausiid species and mean abundance (number under 1 $m^2 \pm$ SE down to 200 m, or 80 m for shelf stations S9 and S11) within the Leeuwin Current eddy field, and their documented geographic distributions as per Brinton et al. (2000). Total number of each species examined per replicate per location are also given (#). [1] indicates a new record for the south-east Indian Ocean, [2] indicates a new record for the Australian Exclusive Economic Zone, and [3] indicates new distribution records within the 31–34°S range of the Leeuwin Current eddy (Davie, 2002).

	LC/eddy perimeter			Eddy centre			Oceanic			Shelf			Geographic distribution
# of zooplankton samples	18			6			6			6			
Species	Mean (m^{-2})	S.E.	#	Mean (m^{-2})	S.E.	#	Mean (m^{-2})	S.E.	#	Mean (m^{-2})	S.E.	#	
Euphausia hemigibba	12.2	3.5	494	10.9	3.1	181	7.7	0.6	165	0	–	0	Tropical/subtropical
Euphausia mutica	6.9	1.5	136	7.0	1.6	73	0.7	0.4	15	0.1	0.06	3	Tropical/subtropical
Euphausia recurva	135.5	22.3	5097	89.3	22.1	1322	31.4	8.8	670	1.2	0.7	28	Subtropical
Euphausia sanzoi [1]	0.1	0.1	10	0.3	0.1	8	0.2	0.1	5	7.2	6.1	107	Tropical/subtropical
Euphausia similis	6.1	2.2	145	1.0	0.3	12	2.6	1.0	72	0.2	0.2	6	Cosmopolitan
Euphausia spinifera	0.04	0.04	1	0	–	0	0.2	0.1	7	0	–	0	Subtropical
Nematobrachion flexipes [2]	0.5	0.3	12	0	–	0	0.2	0.1	6	0	–	0	Tropical/subtropical
Nematoscelis atlantica [3]	3.1	0.9	122	0.8	0.4	14	3.8	1.3	113	0	–	0	Subtropical
Nematoscelis microps [2]	0.3	0.3	14	0	–	0	0.04	0.04	1	0	–	0	Tropical/subtropical
Nematoscelis spp.	6.9	1.5	298	3.0	0.9	61	5.8	1.6	176	0.3	0.3	3	Tropical/subtropical
Pseudeuphausia latifrons [3]	30.8	10.3	457	52.8	40.6	235	4.5	2.7	52	52.1	14.0	655	Tropical/subtropical
Stylocheiron abbreviatum [3]	8.8	1.5	398	7.1	2.9	130	5.0	0.7	139	0.9	0.6	15	Tropical/subtropical
Stylocheiron affine [3]	6.4	1.3	168	6.5	1.1	123	3.2	0.8	89	2.0	1.3	42	Tropical/subtropical
Stylocheiron carinatum [3]	70.5	12.2	2195	63.7	11.8	924	15.8	3.5	289	25.3	10.1	403	Tropical/subtropical
Stylocheiron microphthalma [2]	0.1	0.1	30	0.4	0.3	3	0	–	0	0.1	0.1	3	Tropical
Stylocheiron suhmi [2]	20.4	2.5	774	23.5	4.3	375	5.0	0.4	99	10.1	4.4	136	Tropical/subtropical
Stylocheiron spp.	41.4	13.3	1294	17.7	6.4	254	5.9	1.9	119	7.7	2.8	142	Tropical/subtropical
Thysanoessa gregaria	1.0	0.5	178	0.4	0.2	7	2.7	1.2	91	0	–	0	Subtropical/temperate
Thysanopoda aequalis [2]	0.3	0.2	17	0.4	0.2	21	0.3	0.1	8	0	–	0	Tropical/subtropical
Thysanopoda astylata [1]	0.6	0.2	38	1.3	0.4	69	0.4	0.2	62	0	–	0	Tropical
Thysanopoda monacantha [3]	0.3	0.1	5	0	–	0	0.04	0.04	1	0	–	0	Tropical/subtropical
Thysanopoda pectinata	0	–	0	0.1	0.1	1	0	–	0	0	–	0	Tropical/subtropical
Thysanopoda obtusifrons	0.3	0.2	17	0.1	0.1	2	0.1	0.04	3	0	–	0	Tropical/subtropical
Thysanopoda tricuspidata [3]	0	–	1	0.1	0.1	1	0.04	0.04	1	0.02	0.02	1	Tropical/subtropical
Thysanopoda spp.	4.1	0.9	155	0.8	0.2	13	0.5	0.3	9	0.1	0.04	2	Tropical/subtropical
Unidentified specimens	71.9	11.2		81.6	14.5		40.0	10.2		62.4	19.3		
Total abundance	428.9			368.8			136.3			169.8			

Euphausiid species richness was similar at oceanic (20 species), Leeuwin Current meander /eddy perimeter (20 species) and eddy centre (18 species) locations, but only 11 species were identified in shelf waters (Table 1). Ten species were shared across the four locations. Some species, namely *N. flexipes, N. microps, S. microphthalma* and most of the *Thysanopoda* spp., were considered rare based on their low abundances and presence at only a few stations throughout the eddy field (Table 1).

Euphausia recurva was most abundant at Leeuwin Current meander/ eddy perimeter stations with a mean of 135.5 (s.e. ± 22.3) individuals under 1 m^2 down to 200 m (Table 1). Mean abundances were considerably lower for the shelf stations (1.2 ± 0.7 m^{-2}). *Stylocheiron carinatum* showed a similar trend of highest mean abundance at Leeuwin Current meander/ eddy perimeter stations (70.5 ± 12.2 m^{-2}), which was greater than at both shelf and oceanic stations. The shelf and eddy centre contained the highest mean abundances of *P. latifrons*, at 52.1 ± 14 m^{-2} and 52.8 ± 40.6 m^{-2}, respectively; abundance of this species was considerably lower for oceanic stations at 4.5 ± 2.7 individuals under 1 m^2 down to 200 m depth. Considering abundance by water mass, modified Leeuwin Current water had the highest total mean abundance of euphausiids under 1 m^2 (380.3 ± 43.8 m^{-2}), followed by Leeuwin Current water (276.9 ± 72.0 m^{-2}) and sub-tropical surface water (138.6 ± 22.9 m^{-2}) (Fig. 3).

Ordination showed a clear spatial separation of the euphausiid assemblage of shelf stations from the all other stations (Fig. 4). High within-group variability of the shelf assemblage is demonstrated by the considerable spatial separation between each of the shelf samples. The close grouping of Leeuwin Current meander /eddy perimeter, eddy centre and oceanic stations is indicative of their similar euphausiid assemblages. Overall, there was a significant difference between euphausiid assemblages (ANOSIM: *R statistic* = 0.425; p = 0.008) that was driven by strong separation of the shelf assemblage from all other locations within the eddy field. The shelf was significantly different from Leeuwin Current meander/eddy perimeter stations (*R statistic* = 0.93; p = 0.005), but there were no significant differences between any other pairwise tests of assemblages from the four location groups (Table 2).

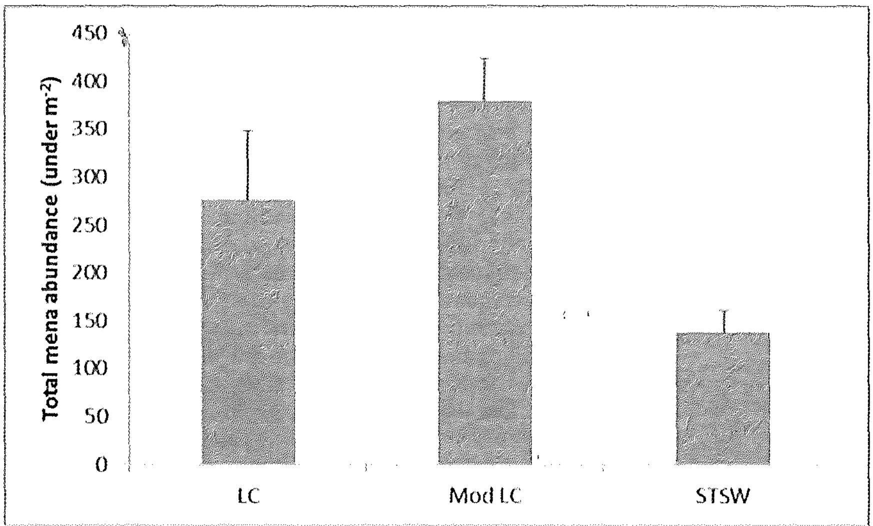

Figure 3. Total mean abundance of juvenile and adult euphausiids, under 1 m^2, for Leeuwin Current water (LC), modified Leeuwin Current water (Mod LC) and Sub-Tropical Surface Water (STSW). Standard error bars are included.

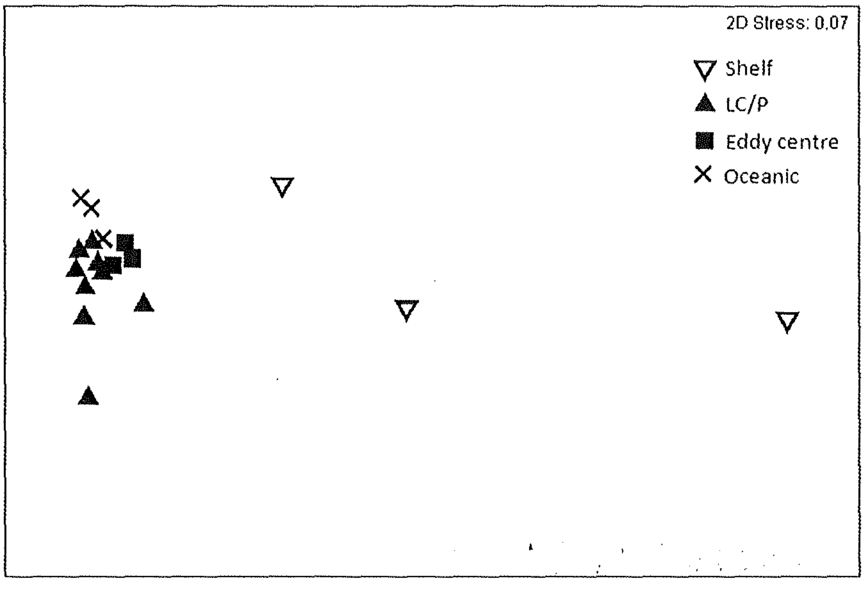

Figure 4. A two-dimensional nMDS ordination of euphausiid assemblages classified according to location in the Leeuwin Current eddy field, south-east Indian Ocean.

Table 2. One-way ANOSIM and SIMPER of euphausiid assemblages, according to *a priori* location groupings. Shading indicates the assemblage typical for each location; un-shaded are comparisons between locations, with significant differences marked with an asterisk. The four species contributing the highest abundances are listed for the location comparisons and superscript denotes the location in which each species was most common and abundant. Ave. Diss. = average dissimilarity, C = eddy centre, LC/P = Leeuwin Current meander/ eddy perimeter, O = oceanic, S = shelf.

	LC/ eddy perimeter	Eddy centre	Oceanic	Shelf
LC/eddy perimeter	Ave. Diss. = 21.9% *E. recurva* *Stylocheiron* spp. *S. carinatum* *S. suhmi*			
Eddy Centre	R= –0.06, p= 0.5 Ave. Diss. = 20.6%	Ave. Diss. = 14.4 % *E. recurva* *S. carinatum* *S. suhmi* *Stylocheiron* spp.		
Oceanic	R= 0.27, p= 0.12 Ave. Diss.= 24.1%	R= 0.93, p=0.10 Ave. Diss.= 20.4%	Ave. Diss. = 14.9% *E. recurva* *S. carinatum* *E. hemigibba* *S. suhmi*	
Shelf	*R= 0.93, p= 0.005 Ave. Diss.= 50.6% *E. recurva* (LC/P) *E. hemigibba* (LC/P) *Stylocheiron* spp.(LC/P) *Thysanopoda* spp.(LC/P)	R= 0.48, p= 0.10 Ave. Diss.= 47.4%	R= 0.59, p=0.10 Ave. Diss. = 51.3%	Ave. Diss. = 43.9% *P. latifrons* *S. carinatum* *S. suhmi*

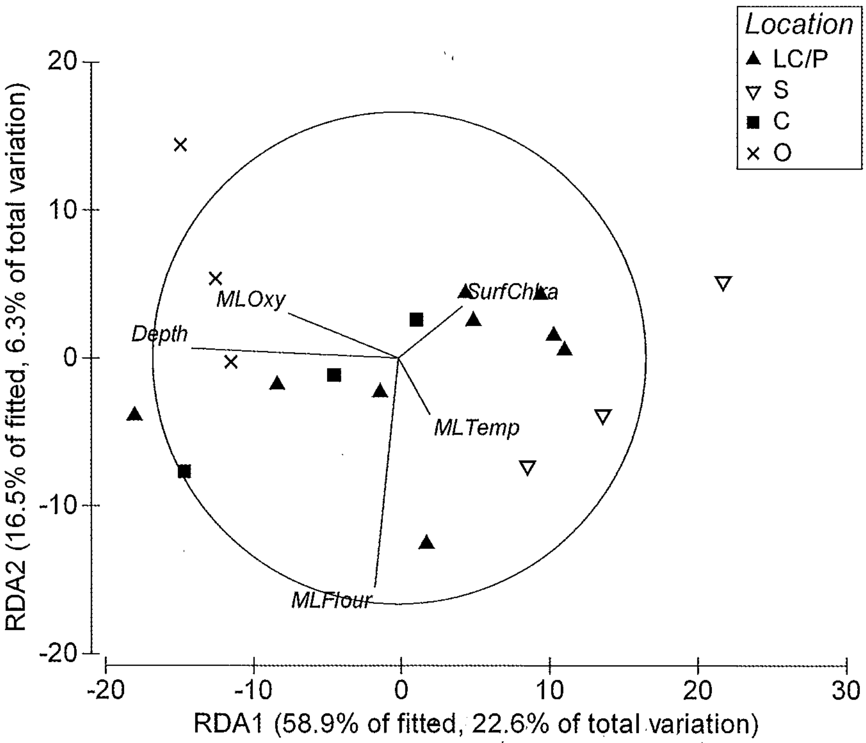

Figure 5. Explanation of the variation in euphausiid abundances across location using water column properties in a distance-based redundancy (dbRDA) biplot, including depth, mixed layer mean oxygen (MLOxy), mixed layer mean fluorescence (MLFlour), mixed layer mean temperature (MLTemp), and surface chlorophyll a (SurfChla).

Of the six water column properties used in the distance-based linear model, 29% of the total variance in euphausiid assemblages was accounted for, of which 19% was explained by depth (p = 0.001) (Fig. 5).

DISCUSSION

There have been few dedicated studies on euphausiids, or more broadly, zooplankton over the continental shelf and slope regions of the south-east Indian Ocean (Koslow *et al.* 2008). This study of the Leeuwin Current eddy field, encompassing shelf, slope and oceanic waters from 31°–34°S yielded 22 euphausiid species, including two new records for the south-east Indian Ocean and several new records for the Australian EEZ. Of the euphausiid species identified in this study, 17 have been previously identified along the 110°E meridian in oceanic waters about 200 km west of the study area (McWilliam 1977), and 12 previously identified off the north-west of Australia (Taniguchi 1974; Wilson *et al.* 2003). Of the numerically dominant species found in the eddy field, *E. recurva* is considered an oceanic species occurring in the subtropics of all ocean basins, and *S. carinatum* is typically epipelagic, occurring globally from 40°N to 40°S (Brinton 1975).

The third most numerically abundant euphausiid species, *P. latifrons,* is described as a neritic, tropical species with some records in the subtropics on the east and west coast of Australia (Brinton 1975; Brinton *et al.* 2000). Off the north-west shelf of Australia (21°–23°S), *P. latifrons* dominated euphausiid catches (> 98%) (Wilson *et al.* 2003) and the current study shows a high abundance of *P. latifrons* in shelf waters off temperate south-western Australia (30–34°S). Although not yet examined, it is suspected that the distribution of this typically tropical shelf species could extend along the entire temperate shelf region, in line with the southward flow of the Leeuwin Current. Indeed, *P. latifrons* has been recorded at 29°–32°S in the neritic zone off South Africa (Gibbons 1997), which is under the influence of the southward flowing Agulhas Current system.

Two species, *E. sanzoi* and *T. astylata,* although occurring in low numbers, are new records for the south-east Indian Ocean. Described as having a tropical/ sub-tropical distribution, *E. sanzoi* occurs in the western Indian Ocean, eastern Indonesian Archipelago, the Philippines and north-east Australia (Brinton 1975). *Thysanopoda astylata,* a tropical species, is distributed throughout the Pacific Ocean but is typically restricted to north of the equator in the Indian Ocean. In both cases, flow of Pacific waters through the Indonesian Archipelago (Indonesian Throughflow) and subsequent inclusion into the catchment of the Leeuwin Current (Domingues *et al.* 2007) would facilitate southward dispersal of these species.

Although occurring at oceanic and eddy stations, species such as *T. aequalis* and *Thysanoessa gregaria* Sars 1883, were not recorded from shelf or Leeuwin Current stations to the north (LC2 and LC3). The distribution of these two species, previously reported in oceanic waters along the 110°E meridian (McWilliam 1977), suggests their entrainment from the surrounding oceanic sub-tropical surface waters adjacent to the eddy.

Entrainment of shelf waters into the developing eddy, could aid in the offshore transport of euphausiids, as found for larvae of neritic fish species (Holliday *et al.* 2011, 2012) and the picoplankton *Synechococcus* spp. (Paterson *et al.* 2013). *Pseudeuphausia latifrons,* typically a coastal species (Brinton 1975), was found in higher concentrations on the shelf and in the eddy centre, with oceanic and Leeuwin Current stations having the lowest concentrations. The high concentrations of *P. latifrons* within the eddy were probably derived from the direct entrainment of shelf waters containing previously accrued *P. latifrons.*

Given that there was no significant variability in euphausiid assemblages amongst eddy centre, Leeuwin Current meander/ eddy perimeter and oceanic stations, and that Paterson *et al.* (2008) showed the water masses at the four locations had similar water column properties, the lack of significant explanation from environmental variables was not unexpected. With the inclusion of depth as an explanatory variable, 19% of the variation amongst euphausiid assemblages was low, but significantly explained. In the same eddy field, shelf assemblages of meroplankonic larval fishes were significantly different from those in the rest of the eddy field (Holliday *et al.* 2011) because of higher species richness, rather than lower species richness as found for holoplanktonic euphausiids.

Despite this being a short term study of a meso-scale feature of the Leeuwin Current system, 22 euphausiid species were identified. Bearing in mind survey effort, this equates to about half the number of species reported for other boundary current systems in the southern hemisphere. To date, forty species have been reported for the poleward flowing Agulhas Current in the south-west Indian Ocean within a similar latitudinal range to this study (Gibbons 1997; Gibbons *et al.* 1995). In total, 49 species have been recorded for the equatorward flowing Benguela Current system in the South Atlantic, of which 33 occurred within the same latitudinal range as this study. If indeed the number of euphausiid species is relatively low off temperate south-western Australia, this could be a reflection of the highly oligotrophic conditions when compared to other southern hemisphere boundary current systems (Pearce 1991). The pressure gradient driving the Leeuwin Current southwards (Cresswell & Golding 1980) is enough to suppress large scale and locally driven upwelling (Lourey *et al.* 2006; Twomey *et al.* 2007).

Euphausiid abundances throughout the Leeuwin Current eddy field during autumn did not indicate any evidence of swarming. These findings agree with Säwström *et al.* (2014) who investigated the prey field for phyllosoma larvae and reported relatively low concentrations of euphausiids within the Leeuwin Current between 28–32°S during July 2010. Euphausiids have been known to reach swarming concentrations of 10,000–500,000 individuals m^{-3} (O'Brien 1988; Murphy 2001; Guevara *et al.* 2008) and such swarms have been linked to reproduction (Mauchline & Fisher 1969; O'Brien 1988), temperature (Komaki 1967) and food (O'Brien 1988). However, aside from swarming events, euphausiids generally occur at much lower concentrations in the water column (Murphy 2001) although areas of upwelling can support substantially higher numbers of particular species.

For example, Pillar *et al.* (1989) recorded *Euphausia lucens* Hansen, 1905 in abundances of over 13,000 individuals under 1 m^2 down to 70 m in the Benguela upwelling system off South Africa. In the northern hemisphere, off Baja California within the California Current and using a bongo net tow from 210 m depth to the surface, Gomez-Gutierrez *et al.* (1995) found the dominant *Nyctiphanes simplex* Hansen 1911 at abundances of over 450 individuals under 1 m^2. Aside from *N. simplex*, all other species of euphausiids occurred at relatively low abundances, comparable to those observed for the Leeuwin Current eddy field. The Benguela and California Currents are both major upwelling areas and the studies indicated above were undertaken in autumn after the summer upwelling period.

As the Leeuwin Current is generally oligotrophic, primary production is low and typically dominated by smaller phytoplankton and microbes (Hanson *et al.* 2007). Interestingly, patches of chlorophyll *a* do occur in the south-east Indian Ocean, often within anticyclonic eddies where populations of coastal diatoms have been entrained (Thompson *et al.* 2007; Waite *et al.* 2007b; Moore *et al.* 2007). Likewise, these anticyclonic eddies have been observed to support greater abundances of meso-zooplankton such as chaetognaths, copepods and euphausiid larvae (Strzelecki *et al.* 2007). The developing anticyclonic eddy from this study contained higher chlorophyll *a* concentrations (Paterson *et al.* 2008) and higher abundances of the picoplankton *Synechococcus* spp. than the surrounding waters (Paterson *et al.* 2013). For the majority of euphausiid species in the eddy field, the eddy perimeter and eddy centre stations had greater abundances than the shelf and oceanic stations. As diatoms and microbes are known food sources for euphausiids (Quetin & Ross 1991; Cadee *et al.* 1992; Bargu & Silver 2003; Murphy *et al.* 2006), the higher abundances of euphausiids within the eddy may be linked to a greater abundance of such prey organisms.

Previous investigations of an eddy pair in the south-east Indian Ocean showed increased primary production and chlorophyll *a* in a Leeuwin Current warm core eddy compared to the cold core eddy (Thompson *et al.* 2007; Waite *et al.* 2007c). The increased productivity observed within Leeuwin Current warm core eddies is considered unusual given that cold core eddies are typically more productive as a result of the upwelling of nutrient rich waters (Falkowski *et al.* 1991; McGillicuddy & Robinson 1997; Bidigare *et al.* 2003). Similarly, the warm core Haida eddies formed in the North Pacific Ocean carry enhanced productivity and high levels of chlorophyll derived from coastal waters to surrounding offshore oceanic waters (Mackas & Galbraith 2002; Crawford *et al.* 2005). Warm core eddies are important meso-scale features and appear to provide a productive area in which entrained zooplankton, such as euphausiids, can accumulate and survive, particularly within an oligotrophic environment such as the south-east Indian Ocean.

CONCLUSIONS

Within the studied eddy field, 22 species of euphausiids were identified, which is more than double the number expected by Davie (2002). Several species have never before been recorded for Australian waters in the south-east Indian Ocean. These included species that have previously only been recorded for the north-west shelf of Australia, and point to the Leeuwin Current as a potential vector for southward dispersal. In general, euphausiid abundances were relatively low and this was ascribed to the oligotrophic conditions off the coast of Western Australia. This was the first study to investigate euphausiid distributions within an evolving anticyclonic eddy in the south-east Indian Ocean and revealed the influence of mixing processes associated with the meso-scale feature on holoplanktonic euphausiids.

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