Krill in the Leeuwin Current system: influence of oceanography and contribution to Indian Ocean zoogeography

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Declaration

I declare that this thesis is my own account of my research and contains as its main content work which has not previously been submitted for a degree at any tertiary education institution.

Alicia Louise Sutton

Abstract

Euphausiids (krill) are important in the food webs of pelagic ecosystems and constitute the prey of a range of species including fishes, whales and seabirds. However, knowledge about euphausiid diversity, distribution and abundance in the south-east Indian Ocean off Western Australia is limited. The influence of the Leeuwin Current system on horizontal and vertical structuring of euphausiid assemblages was investigated from a series of plankton surveys with concurrent oceanographic sampling along the west and north-west coasts of Australia. In total, 34 species of euphausiids were identified and assemblages were significantly structured across shelf, shelf break and oceanic waters, as well as alongshore. Further, vertical structuring of assemblages was evident from depth-stratified sampling across a thermohaline front between Leeuwin Current Water and Sub Tropical Surface Water. For all surveys, assemblages were related to a suite of environmental variables, and were significantly influenced by the physio-chemical properties of the prevailing water masses, as well as indicators of food availability, such as chlorophyll *a*. To ascertain the environmental variables driving euphausiid zoogeography in the Indian Ocean (20°N - 40°S and 20°E - 122°E), data on euphausiids from the Leeuwin Current system were combined with distribution records from the literature (spanning the past 50 years), to generate measures of species richness and taxonomic distinctness across the basin. Salinity and dissolved oxygen were found to be important drivers of euphausiid zoogeography, and were particularly significant with respect to the low numbers of species in the northern Indian Ocean. Finally, to understand the role of euphausiids in marine food webs off Western Australia, fatty acids and stable isotopes placed common euphausiid species from the Perth Canyon (32°S) as omnivorous but feeding primarily on dinfolagellates. Overall, this thesis expands on the knowledge of euphausiid diversity, distribution and

abundance in the south-east Indian Ocean and confirms the influence of boundary currents on euphausiid distributions.

Statement on the contribution of others

Supervision

Prof Lynnath Beckley, Murdoch University

Dr Patti Virtue, University of Tasmania and the Institute for Marine and Antarctic Studies

Contribution to data chapters

Chapter 1

Alicia Sutton reviewed the literature, wrote the introduction and formulated the aims. Lynnath Beckley provided editorial input on the structure and content of the chapter.

Chapter 2

Alicia Sutton formulated the research aim, sorted and identified all euphausiids from zooplankton samples, ran all statistical analyses and wrote the chapter. Lynnath Beckley collected zooplankton samples in the field prior to commencement of this PhD, and provided editorial input on the structure and content of the chapter.

Chapter 3

Alicia Sutton formulated the research aim, helped collect zooplankton samples in the field, sorted and identified all euphausiids from zooplankton samples, ran all statistical analyses and wrote the chapter. Lynnath Beckley collected zooplankton samples in the field, and provided editorial input on the structure and content of the chapter.

Chapter 4

Alicia Sutton formulated the research aim, sorted and identified all euphausiids from zooplankton samples, ran all statistical analyses and wrote the chapter. Lynnath Beckley collected zooplankton samples in the field, and provided editorial input on the structure and content of the chapter.

Chapter 5

Alicia Sutton formulated the research aim, reviewed the literature, collated euphausiid distribution records and environmental data sources, ran all statistical analyses and ArcGIS mapping, and wrote the chapter. Lynnath Beckley provided editorial input on

structure and content of the chapter. Dr Susan Wijffels provided guidance on the use of CSIRO environmental data (CSIRO Atlas of Regional Seas). Dr Fiona Valesini and Dr James Tweedley provided guidance on statistical analyses.

Chapter 6

Alicia Sutton formulated the research aim, collected samples in the field, analysed samples for lipids and fatty acids in the laboratory at CSIRO, Tasmania, ran all statistical analyses and wrote the chapter. Lynnath Beckley collected samples in the field and provided editorial input on structure and content of the chapter. Dr Patti Virtue and Dr Peter Nichols assisted with lipid and fatty acids analyses in the laboratory at CSIRO, Tasmania, provided guidance on the interpretation of results, provided editorial input on the structure and content of the chapter. The Centre for Whale Research assisted with sample collection in the field. Stable isotopes samples were analysed by the Western Australian Biogeochemistry Centre, and chlorophyll *a* samples were analysed by the Marine and Freshwater Research Laboratory, Murdoch University.

Chapter 7

Alicia Sutton reviewed the literature and wrote the general conclusions. Lynnath Beckley provided editorial input on structure and content of the chapter.

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Last, but by no means least, I express thanks to my family and friends. Thanks to Mum and Dad for their support over the years, and to Sam for his support and tolerance, and for listening to my complaints and celebrating my successes. To all my friends, thanks for your encouragement and good times, you help to form an important part of my life!

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Chapter 1: General Introduction

Biology and ecology and euphausiids

Euphausiids, or krill, are crustaceans of the order Euphausiacea and 86 species occur in the world's oceans (Mauchline & Fisher 1969; Baker et al. 1990). All species, but one, are distributed across ten genera from the family Euphausiidae. Euphausiids are an important component of the zooplankton in all oceans. They are generally regarded as macrozooplankton (2 - 20 mm in size) (Gibbons 1999), although, are sometimes considered to be micronekton as some species are > 20 mm (Mauchline & Fisher 1969).

Euphausiids are holoplanktonic, which means they spend their whole life cycle as part of the plankton (Gibbons 1999; Ritz et al. 2003). The seven developmental stages of euphausiids are the egg, nauplius, metanauplius, calyptopis, furcilia, juvenile and adult stages (Mauchline & Fisher 1969; Siegel 2000). Longevity estimates vary among species, and can range from less than one year (Brinton 1976; Gomez-Gutierrez et al. 2010) to a predicted 11 years (Ikeda 1985). As holoplankton, they have the ability to be transported in ocean currents, and larval euphausiids, in particular, are susceptible to ocean circulation because of reduced locomotive ability (Mauchline & Fisher 1969).

Euphausiids are particularly recognized for their importance in marine food webs by being the direct link between large predators and primary production. Their propensity to form dense swarms (10,000 - 500,000 individuals m^{-3}) (O'Brien 1988; Ladrón-de-Guevara et al. 2008) make them prey to a range of consumers, such as fishes, seabirds and whales. Swarming of euphausiids is hypothesised to be related to reproduction (Mauchline & Fisher 1969; O'Brien 1988), temperature (Komaki 1967) or food

availability (O'Brien 1988). Euphausiids are typically known to have high lipid content and, in particular, a high concentration of omega-3, which is of high nutritional value to consumers (Virtue et al. 1995, Phleger et al. 1998; Falk-Peterson et al. 2000; Virtue et al. 2000; Nicol et al. 2004; Schmidt et al. 2006; Ju et al. 2009).

On a biochemical level, euphausiids are also important in the transfer of carbon and other nutrients throughout the water column (Schnack-schiel & Isla 2005; Tarling & Johnson 2006). Euphausiids are generally omnivorous, with most species adapted for filter feeding, predation or a combination of both (Mauchline & Fisher 1969; Gibbons 1999; Ju et al. 2009). Euphausiids feed on phytoplankton, such as diatoms and dinoflagellates (Mauchline & Fisher 1969; Cadée et al. 1992; Gibbons 1999; Ju et al. 2009), zooplankton, e.g. copepods, chaetognaths, other euphausiids, as well as detritus (Mauchline & Fisher 1969). When euphausiids feed they can release nutrients, such as iron, into the water column, and can release faecal pellets at deeper depths when they undergo diel vertical migration (Tovar-Sanchez et al. 2007). This aids in carbon sequestration and the cycling of nutrients back into the water column where they can be utilised again in primary production.

Euphausiids are found in all oceanic and neritic environments of ocean basins, seas and fjords. A comprehensive record of the distribution of all euphausiids across the world's oceans was compiled by Brinton et al. (2000). Different species exhibit tropical, subtropical, temperate or polar distributions, while some are more cosmopolitan. However, not all species are found in all oceans. For example, over 80 species have been documented for the Pacific Ocean (Brinton 1962; Brinton et al. 2000; Letessier et al. 2011), while about 60 species have been found in the Atlantic (Gibbons et al. 1995; Gibbons 1997; Letessier et al. 2009), about 50 species in the Indian Ocean (Brinton et

al. 2000), and about 10 species throughout the colder Southern Ocean (Brinton et al. 2000). Euphausiids exhibit a similar latitudinal pattern to many other marine biota, whereby species richness declines with increasing latitude (Tittensor et al. 2010).

Diel vertical migration is a well-known behaviour of euphausiids, and zooplankton in general. Individuals migrate to deeper depths during the day to avoid predation in surface layers, and then migrate to the shallower waters during the night to feed (Brinton 1967; Youngbluth 1976; Gibbons 1999). Of the 86 species of euphausiids known worldwide, most exhibit some degree of vertical migration. Some species are considered large vertical migrators, e.g. *Meganyctiphanes norvegica*, over hundreds of metres, and others relatively short or non-migrators, e.g. *Nyctiphanes simplex* (Brinton 1962; Brinton 1967; Mauchline & Fisher 1969; Youngbluth 1976; Tarling et al. 1999; Brinton et al. 2000). The extent of diel vertical migration through the water column is influenced by environmental tolerances (Brinton 1967; Brinton 1979; Hirota 1987; Taki 2008), light intensity (Lewis 1954; Youngbluth 1976), food availability (Youngbluth 1975; Hu 1978; Gibbons 1993; Taki 2008), predator avoidance (Bollens et al. 1992), reproduction (Tarling et al. 1999) and the size class of species (Mauchline & Fisher 1969).

Oceanography plays a key role in influencing both the horizontal and vertical distribution of euphausiids. Species-specific tolerances to physio-chemical variables, such as temperature, salinity and dissolved oxygen, can link euphausiids to different water masses, such as those detailed in Brinton (1962) for euphausiids of the Pacific Ocean. Euphausiid assemblages have been used to define biogeographical provinces for the South Atlantic (Gibbons 1997), south-east Asian waters (Brinton 1975), and Pacific Ocean (Brinton 1962), while species richness has been used to identify

latitudinal patterns across ocean basins for the world (Tittensor et al. 2010), Pacific Ocean (Letessier et al. 2011) and Atlantic Ocean (Letessier et al. 2009). These broad biogeographical patterns were found to reflect the oceanographic environment, particularly major water masses and temperature gradients.

Euphausiids in the Indian Ocean

The Indian Ocean is unusual in comparison to the Pacific and Atlantic Oceans. The northern extent is blocked by a land boundary, i.e. Asia and the Middle East, and thus lacks subtropical and temperate zones. The northern Indian Ocean is subject to seasonal reversal of monsoonal winds and currents, such as the Somali Current (Schott & McCreary Jr 2001; Shanker et al. 2002; Schott et al. 2009). Further, Pacific Ocean waters can enter into the Indian Ocean via the Indonesian Throughflow, which plays a significant role in global climate by controlling the heat and fresh water budgets between the two oceans (Gordon & Fine 1996; Wijffels & Meyers 2004; McCreary et al. 2007; Xu 2014). Water from the Indonesian Throughflow also contributes to the source waters for the poleward flowing Leeuwin Current (LC) off the west coast of Australia (Meyers et al. 1995; Domingues et al. 2007). Together with the Agulhas Current off the south-east coast of Africa, the Indian Ocean is the only ocean to have both eastern and western boundary currents flowing poleward. These features are likely to influence distribution patterns of euphausiids in the Indian Ocean basin.

The first basin-wide investigation of euphausiids in the Indian Ocean was conducted during the first International Indian Ocean Expedition (IIOE) (1962 - 1965) (Brinton & Gopalakrishnan 1973). A suite of biological samples (including euphausiids) and environmental measurements were collected during the many research voyages of the expedition. Since then, most studies on euphausiids have focused around the

coastlines of the Indian Ocean (e.g. Fatima 1987; Gallienne et al. 2004; Gibbons et al. 1995), although, information for the south-east Indian Ocean, in particular, the LC system, was limited due to poor survey effort.

During the IIOE, 31 euphausiid species (McWilliam 1977) and total euphausiid concentrations (Tranter & Kerr 1977) were recorded along the 110°E meridian between 9°S - 32°S, and 11 species were recorded in the headwaters of the LC, between 20°S - 26°S and 105°E - 118°E (Taniguchi 1974). Off the coast of Western Australian, 11 species were also identified as part of the IIOE (Brinton & Gopalakrishnan 1973). Since the IIOE, *Pseudeuphausia latifrons*, *Euphausia hemigibba*, and *Thysanopoda tricuspidata* have been recorded off the coast of Ningaloo (20°S - 23°S, 113° - 115°E) (Wilson et al. 2003a), and *Euphausia recurva* was identified from the Perth Canyon (32°S, 115°E) (Rennie et al. 2009). A more detailed investigation into euphausiid assemblages from a voavge in May 2006 found 22 species within and around a mesoscale eddy of the LC (31°S - 34°S and 112°E - 115°E) (Sutton et al. 2015).

The Leeuwin Current system

The dominant ocean current in the south-east Indian Ocean is the poleward flowing LC, which follows the shelf break off the coast of Western Australia (Fig. 1.1) (Cresswell & Golding 1980; Meyers et al. 1996; Ridgway & Condie 2004). It is referred to as an anomalous current, as all other eastern boundary currents, such as the Benguela, California and Humboldt Currents, flow equatorward (Pearce 1991). It is a relatively narrow current at ~ 100 km wide, and shallow with a depth < 300 m (Feng et al. 2003; Rennie et al. 2007). The LC flows south from the North West Cape to Cape Leeuwin, and when the strength of the LC is intensified during the austral autumn/winter, the

current extends eastward across the Great Australian Bight towards Tasmania (Cresswell & Golding 1980; Meyers et al. 1996; Ridgway & Condie 2004).

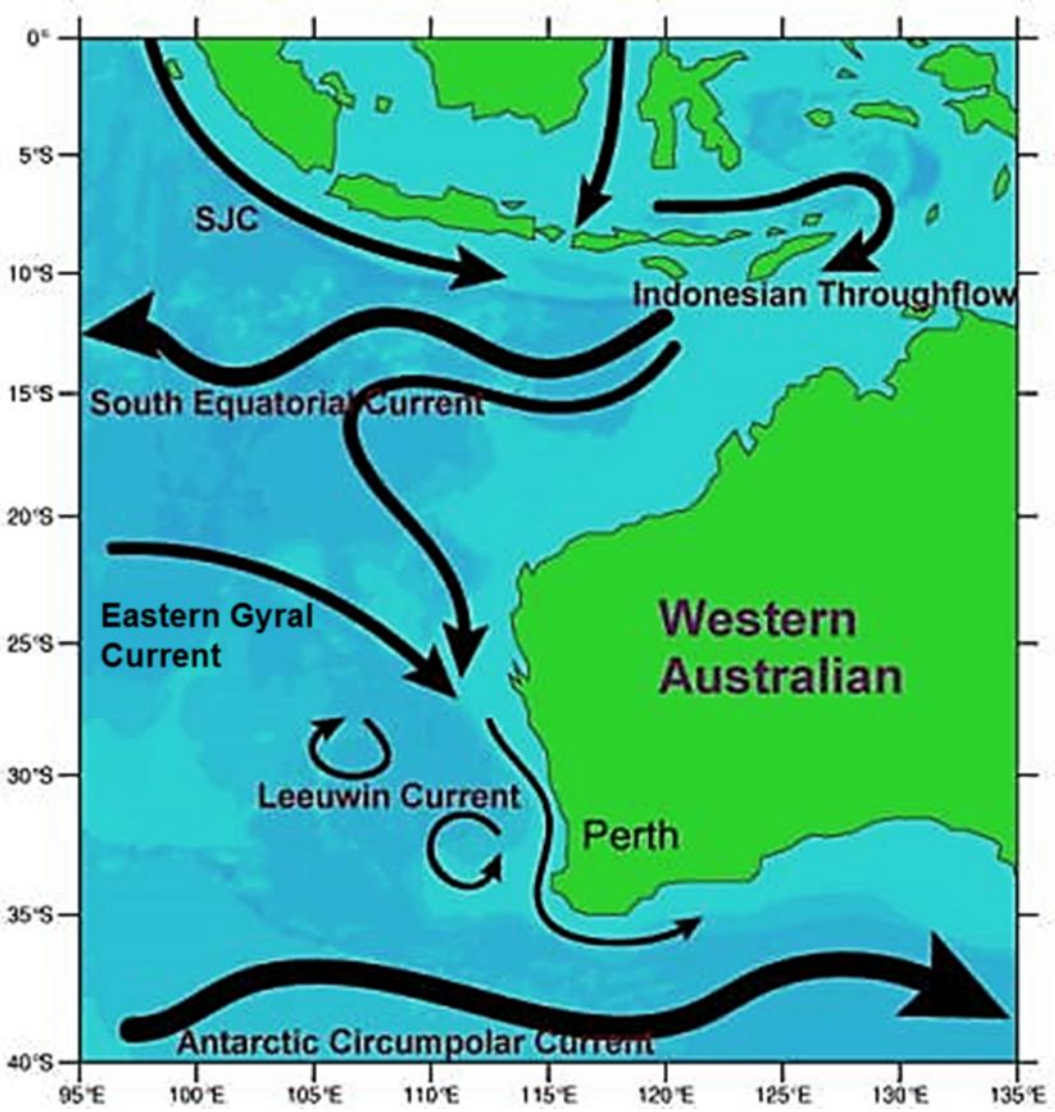


Figure 1.1 Schematic of the Leeuwin Current (LC) and major surface currents in the south-east Indian Ocean, sourced from Feng et al. (2003). SJC: South Java Current.

The LC comprises Tropical Surface Water (TSW) sourced from the Indo-Australian basin, with inputs from the Indonesian Throughflow, South Java Current, South Equatorial Current and the Eastern Gyral Current (Meyers et al. 1995; Feng & Wijffels 2002; Domingues et al. 2007; Menezes et al. 2014). TSW is a warm, low salinity and highly oxygenated water mass. As the LC carries these waters southward off the coast of Western Australia, the current becomes cooler and more saline due to evaporative

cooling and mixing with surrounding Sub Tropical Surface Water (STSW) and shelf waters (Woo et al. 2006a; Weller et al. 2011). This creates a longshore temperature and salinity (density) gradient in the LC along the extent of the Western Australian coast (Menezes et al. 2013; Menezes et al. 2014).

The LC becomes increasingly energetic and variable during the autumn/winter which frequently results in the generation of mesoscale features such as meanders and eddies (Feng et al. 2005; Weller et al. 2011; Holliday et al. 2012). Meanders can create thermohaline fronts between the LC and surrounding STSW. Oceanographic fronts can result from physical processes creating discontinuities in water properties across a sharp gradient (Franks 1992; Belkin et al. 2009), and can exhibit differences in sea-surface temperature and salinity of 2 - 5°C and 0.3 - 1.0 psu, respectively (Säwström et al. 2014). Often, these thermohaline fronts have associated sharp gradients in other biogeochemical properties such as nutrients and chlorophyll *a* concentrations (Belkin et al. 2009). LC meanders and fronts are a common occurrence off the WA coast, and particularly in the vicinity of the Abrolhos Islands (Meuleners et al 2008; Säwström et al. 2014). These meanders can develop into anticyclonic eddies, which are important for cross shelf transport of biota and nutrients from surrounding water masses (Gasca et al. 2001; Mackas & Galbraith 2002; Fieux et al. 2005; Feng et al. 2007; Muhling et al. 2007; Strzelecki et al. 2007; Paterson et al. 2008; Holliday et al. 2011).

A large meridional pressure gradient drives the LC which creates onshore geostrophic flow and downwelling along the coast (Godfrey & Ridgway 1985; Meyers et al. 1995; Feng & Wijffels 2002). As a result, upwelling of nutrient rich waters is suppressed, particularly with stronger current flow during the austral autumn/winter months (Cresswell & Golding 1980; Meyers et al. 1996; Ridgway & Condie 2004). The LC, and

south-east Indian Ocean in general, are typically low in nutrients and biological productivity (Hanson et al. 2005; Koslow et al. 2008; Thompson et al. 2011; Lourey et al. 2012). During the austral summer, the LC is weakened due to opposing southerly winds, which gives rise to limited upwelling and coastal currents like the seasonal equatorward flowing Ningaloo and Capes Currents (Pearce & Pattiaratchi 1999; Woo et al. 2006b; Rennie et al. 2007). Overall, the LC and south-east Indian Ocean are considered to be oligotrophic compared to the usual highly productive ecosystems of eastern ocean basins (Pearce 1991).

Nutrient rich waters usually generate a marine food web dominated by large phytoplankton (i.e. diatoms), whereas nutrient poor waters tend to be dominated by small autotrophic flagellates (i.e. dinoflagellates) and cyanobacteria (Ryther 1969; Cushing et al. 1989; Legendre & Rassoulzadegan 1995; Paterson et al. 2013). Oligotrophic waters of the LC system result in a microbial food web consisting of smaller celled phytoplankton (Hanson et al. 2007b). This is also reflected in the fisheries of the region, which are dominated by benthic invertebrate species, such as the western rock lobster, rather than the pelagic finfish typical of upwelling regions (Lenanton et al. 1991, Caputi et al. 1996).

Nevertheless, despite its low biological production, the LC and the waters off the coast of Western Australia play a role in the life cycles of commercially important finfish species and marine megafauna. For example, southern blue fin tuna are spawned in the eastern Indian Ocean waters between north-west Australia and Indonesia (Hobday et al. 2015) and juveniles use the LC to migrate south to the feeding grounds off South Australia and Tasmania in the Southern Ocean (Bestley et al. 2008). Euphausiids have been recorded in the stomachs of juvenile bluefin tuna caught from the southern coast

of Western Australia (Itoh et al. 2011). Blue whales also migrate along the Western Australian coast, from the Southern Ocean to the tropics, and have been observed to feed at hotspots along the way (Double et al. 2014). In particular, whales have been found to feed on euphausiids in the Perth Canyon (32°S, 115°E) (Rennie et al. 2009).

Thesis aims

The primary aim of this thesis was to examine the influence of oceanography on the euphausiid assemblages of the LC system, and to contribute to the knowledge of euphausiid zoogeography in the Indian Ocean. In doing so, this study firstly addresses the alongshore and cross-shelf structuring of epipelagic euphausiid assemblages off the west coast of Australia. The aim of Chapter 2 was to investigate the diversity, distribution and abundance of euphausiid assemblages along a 1,500 km stretch of the LC and to relate these assemblages to the abiotic and biotic oceanographic variables of the water masses of the south-east Indian Ocean. Waters of the LC are sourced from the north-west marine bioregion of Australia, with inputs from the Indonesian Throughflow and eastern Indian Ocean currents. The bioregion is oceanographically complex and its influence on marine biota, particularly zooplankton, is still relatively understudied. Thus, the aim of Chapter 3 was to characterise euphausiid assemblages and relate them to the physical and biological properties of the tropical waters that inundate the bioregion. Considering that water masses are known elsewhere to influence euphausiid assemblages, Chapter 4 aimed to examine the vertical structuring of euphausiid assemblages across a thermohaline front between Leeuwin Current Water and surrounding STSW.

The above mentioned chapters all involved the identification of euphausiid species and their distributions, and this information was collated with records for the rest of the

Indian Ocean to reveal a more complete picture of euphausiid zoogeography. Chapter 5 aimed to ascertain zoogeographic patterns of euphausiids in the Indian Ocean using species richness and taxonomic distinctness as measures of biodiversity, and to investigate the broad-scale environmental drivers of these patterns.

A large motivator behind understanding the ecology, distributions and environmental tolerances of euphausiids, is because of their importance in marine food webs. Little attention has been given to euphausiids and food webs in the LC, despite being a system that supports commercially important fishes, migratory baleen whale populations and globally important colonies of seabirds (Surman & Wooller 2003; Rennie et al. 2009, Itoh et al. 2011). The aim of Chapter 6 was to analyse the fatty acids and stable isotopes of common euphausiid species from the LC and relate this to a potential food source, phytoplankton, and a predator, the pygmy blue whale (*Balaenoptera musculus brevicauda*). This investigation took place in the Perth Canyon (32°S, 115°E), a known feeding area for blue whales (Rennie et al. 2009; Double et al. 2014).

The aim of the final chapter was to provide a general discussion based on the common themes arising from the results of Chapters 2-6.

Chapter 2: Influence of the Leeuwin Current on the epipelagic euphausiid assemblages of the south-east Indian Ocean

Abstract

The Leeuwin Current is an anomalous eastern boundary current which transports warm, low salinity water poleward off Western Australia. Epipelagic euphausiid assemblages along a 1,500 km stretch of the Leeuwin Current system (22°S - 34°S) off Western Australia were correlated with a suite of oceanographic variables to ascertain drivers of euphausiid distribution patterns. Twenty seven euphausiid species were recorded across the study area from 80 zooplankton samples, of which *Nyctiphanes australis*, *Stylocheiron indicum*, *Stylocheiron insulare* and *Stylocheiron robustum* were identified as new records for the south-east Indian Ocean. The Leeuwin Current also provided a suitable environment for tropical species to extend their distributions further south. *Pseudeuphausia latifrons* characterised assemblages in the Leeuwin Current with a Tropical Surface Water signature, *Euphausia recurva* characterised Sub Tropical Surface Water and the waters in the southern part of the Leeuwin Current, while *Stylocheiron carinatum* was distributed across the whole study area. Differences in assemblages occurred between shelf, shelf break and oceanic stations, as well as between the north and south of the study area, with a significant influence of diel variation. The Leeuwin Current exhibited an increase in seawater density and dissolved oxygen from north to south and, along with mesozooplankton settled volume, were identified as drivers of the distribution of euphausiid assemblages. 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.

Introduction

Euphausiids are holoplanktonic, vertically migrating crustaceans with distribution patterns that are strongly influenced by ocean currents (Mauchline & Fisher 1969; Pillar et al. 1989; Barange & Pillar 1992; Gibbons 1999). There are 86 species known from the world's oceans, and they are recognized for their important role in pelagic food webs, both as a food source for higher order consumers and for the distribution of organic matter and nutrients throughout the water column during vertical migration (Mauchline & Fisher 1969; Longhurst et al. 1989). Diel vertical migration involves species migrating to shallower waters during the night and descending to deeper waters during the day. The role of euphausiids in food webs is inherently linked with the physical and biological oceanographic processes that influence both their horizontal and vertical distributions.

The distribution of euphausiids in the world's oceans is well known (Brinton et al. 2000). Euphausiids generally have affinities with tropical, subtropical or temperate marine environments, although, some can be cosmopolitan. Euphausiids also follow the same global trend as many other marine biota, whereby the number of species decreases with increasing latitude (Letessier et al. 2009; Tittensor et al. 2010; Letessier et al. 2011). Boundary currents can, however, disrupt biogeographic boundaries, and in turn, the latitudinal gradient in species richness, by transporting waters with tropical characteristics towards temperate environments. For example, the dominant poleward flowing Leeuwin Current (LC), in the south-east Indian Ocean, has been attributed as providing a suitable environment for tropical corals, fishes and other taxa to exist as far south as the Houtman Abrolhos Islands (29°S) and Rottnest Island (32°S) off the

coastline of Western Australia (Maxwell & Cresswell 1981; Wilson & Allen 1987; Hutchins & Pearce 1994; Fox & Beckley 2005).

The LC comprises 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, cool, salty Sub Tropical Surface Water (STSW) is entrained into the current, and together with evaporative cooling, a longshore temperature and salinity gradient is created in the LC along the extent of the Western Australian coast (Woo et al. 2006a; Weller et al. 2011). The strength of the LC is intensified during the austral autumn/winter months when the current, after passing Cape Leeuwin, extends eastward across the Great Australian Bight towards Tasmania (Cresswell & Golding 1980; Meyers et al. 1996; Ridgway & Condie 2004).

Studies on the euphausiid assemblages within the LC system are few, particularly for a system that supports southern blue fin tuna, endangered 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, *Pseudeuphausia latifrons*, *Euphausia hemigibba*, *Euphausia recurva* and *Thysanopoda tricuspidata*, have been previously identified within the LC system during the austral spring and summer (Wilson et al. 2003a; Rennie et al. 2009), and during austral autumn 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). In waters neighbouring the LC system, 31 euphausiid species were recorded along the 110°E meridian between 9°S - 32°S during the 1962 - 1965 International

Indian Ocean Expedition (McWilliam 1977) and 11 species have been recorded in the headwaters of the LC, between 20°S - 26°S, 105°E - 118°E (Taniguchi 1974).

The primary aim of this study was to investigate the diversity, distribution and abundance of epipelagic euphausiid assemblages along a 1,500 km stretch of the LC system off the western seaboard of the Australian continent. Further, assemblages were related to abiotic and biotic oceanographic variables to ascertain potential environmental drivers of distribution patterns, with a particular focus on water masses. It was hypothesised that euphausiid assemblages would contain tropical species being transported south with the LC and that assemblages would acquire more subtropical/temperate species as the LC became more influenced by surrounding STSW in the south of the study area.

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. 2.1). The concurrent studies of oceanography (Weller et al. 2011), nutrients (Thompson et al. 2011), primary production (Lourey et al. 2012) and larval fish assemblages (Holliday et al. 2012) identified physical and biological structuring in a system with dynamic longshore and cross-shelf transport.

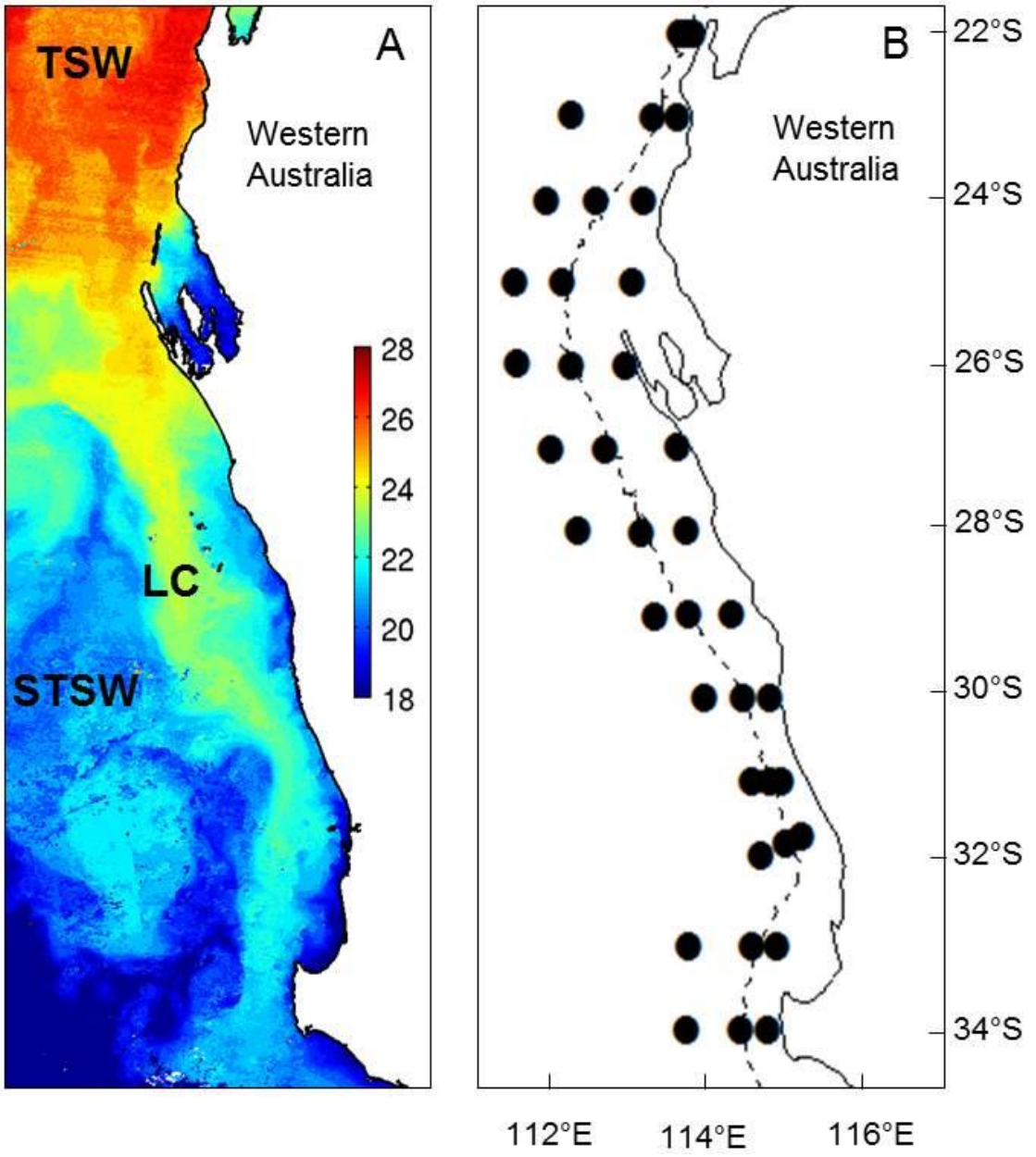


Figure 2.1 A) Sea surface temperature for the 5 June 2007, highlighting Tropical Surface Water (TSW), cooler Sub Tropical Surface Water (STSW), and the warm, southward flowing Leeuwin Current (LC) (adapted from Weller et al. 2011). B) Zooplankton sampling stations along shelf, shelf break and oceanic stations. The 200 m isobath is indicated by the dashed line.

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 to measure fluorescence. Chlorophyll *a* was determined from additional 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, expressed at sigma-t (σ_t). Stations were classified *a priori* as Tropical Surface Water (TSW; < 24.5 σ_t), Sub Tropical Surface Water (STSW; > 24.8 σ_t) or mixed, which refered to those stations with a mean seawater density in between that of TSW and STSW.

Zooplankton samples, from which euphausiids were identified, were collected using a bongo net (100 and 355 µm meshes, net diameters of 0.5 m) in two replicate oblique tows from a maximum depth of 150 m (or shallower on the shelf) to the surface at each station. Only the 355 µm net samples were used in this study. 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. During the voyage, zooplankton tows were taken after oceanographic measurements. Zooplankton samples were preserved in 5% buffered formaldehyde in seawater. Estimates of mesozooplankton volume were made by pouring the zooplankton sample through a 1 mm sieve and measuring the settled volume of remaining zooplankton in a graduated cylinder after a 24 h period (Gibbons 1999; Suthers & Rissik 2009); 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).

In some cases, small zooplankton samples needed no splitting, whereas, large zooplankton samples required splits ranging up to 1/32. Concentrations of euphausiids were expressed as the average number of individuals per 1000 m^{-3} ± standard error. It is recognised that such inflation of the volume might have some influence on statistical results. Damaged or indistinguishable immature and mature specimens were grouped as unidentified. The classification of species as tropical, subtropical or temperate throughout the text was based upon geographical distributions given by Brinton et al. (2000).

Statistical analyses

Due to the influence of diel vertical migration, stations were classified as day or night. *A priori* factors of day/night, isobath (shelf, shelf break, oceanic) and latitude (north or south of 29°S) were applied to the data to assess meaningful differences in euphausiid assemblages. Northern latitudes included 22°S - 28°S and southern stations included 29°S - 34°S. For univariate analyses on total euphausiid concentrations and dominant species, non-parametric Kruskal-Wallis tests for independent samples were conducted in IBM SPSS Statistics 21. For multivariate analyses of euphausiid assemblages, the PRIMER v6 PERMANOVA+ software package was used (Clarke & Gorley 2006, Anderson et al. 2008).

Prior to multivariate analyses, a fourth root transformation was applied to euphausiid concentrations to reduce the relative importance of abundant species. A Bray-Curtis resemblance matrix was constructed to quantify the dissimilarity in assemblages between two samples (Fig. 2.2). Non-metric multidimensional scaling ordinations were used to assess the spatial relationships among euphausiid assemblages at each station. A three-factor permutational multivariate analysis of variance (PERMANOVA) was used

to test the hypotheses that euphausiid assemblages did not differ across day/night, isobath and latitude, and that there were no significant interactions between these factors (Anderson 2005). Analysis of similarity (ANOSIM) and similarity percentage (SIMPER) routines were used for pair-wise testing and to identify which euphausiid species were driving the differences between assemblages (Clark & Warwick 2001).

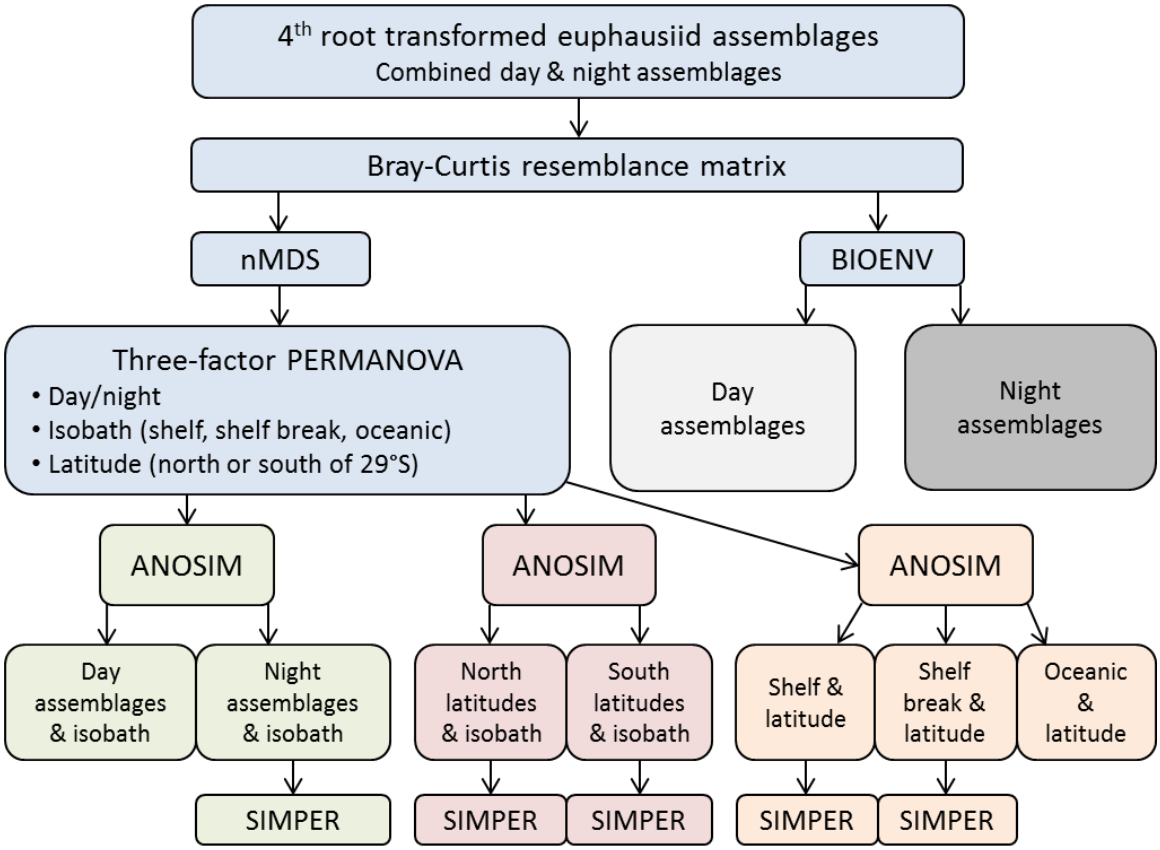


Figure 2.2 The sequence of multivariate statistical tests on euphausiid assemblages from the Leeuwin Current, across *a priori* factors of day/night, isobath and latitude. nMDS = non-metric multidimensional scaling, PERMANOVA = permutational MANOVA, ANOSIM = analysis of similarities, SIMPER = similarity percentage, BIOENV = Biota and Environment Matching.

Euphausiid assemblages were correlated with abiotic and biotic oceanographic variables using a Biota and Environment Matching (BIOENV) sub-routine (Clarke & Ainsworth 1993) (Fig. 2.2). This analysis determined the subset of environmental variables that best matched with euphausiid assemblages and tested whether this was significant or not. Although latitude was included in the PERMANOVA as a way to

compare warmer water euphausiid assemblages with cooler water assemblages, the LC confounds this as it transports the warmer TSW southwards. Thus, to investigate further the effect of water mass on euphausiid assemblages, mean seawater density was included as a variable in the BIOENV analysis. The environmental variables, mean seawater density, mean dissolved oxygen, surface chlorophyll *a*, depth integrated chlorophyll *a* (0 - 100 m) and mesozooplankton settled volume were correlated with euphausiid assemblages. Chlorophyll *a* and mesozooplankton settled volume were included as measures of food availability to euphausiids, and euphausiids can have differing tolerances to dissolved oxygen concentration. Square root transformations were applied to environmental data, and 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 led to the removal of mean dissolved oxygen due to its positive correlation with mean seawater density.

Results

The Leeuwin Current environment

The LC was the dominant feature in the south-eastern Indian Ocean during May - June 2007 (Fig. 2.1) and was most evident along the shelf break. For shelf, shelf break and oceanic 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 observed as the LC transported warm, lower salinity waters southwards from 22°S to 34°S (Fig. 2.3; Fig 2.4). Some stations had mean seawater densities in between the ranges for TSW and STSW, and were termed 'mixed'. Furthermore, intrusions of underlying STSW at oceanic stations as far north as 25°S, lead to oceanic stations having a more stratified

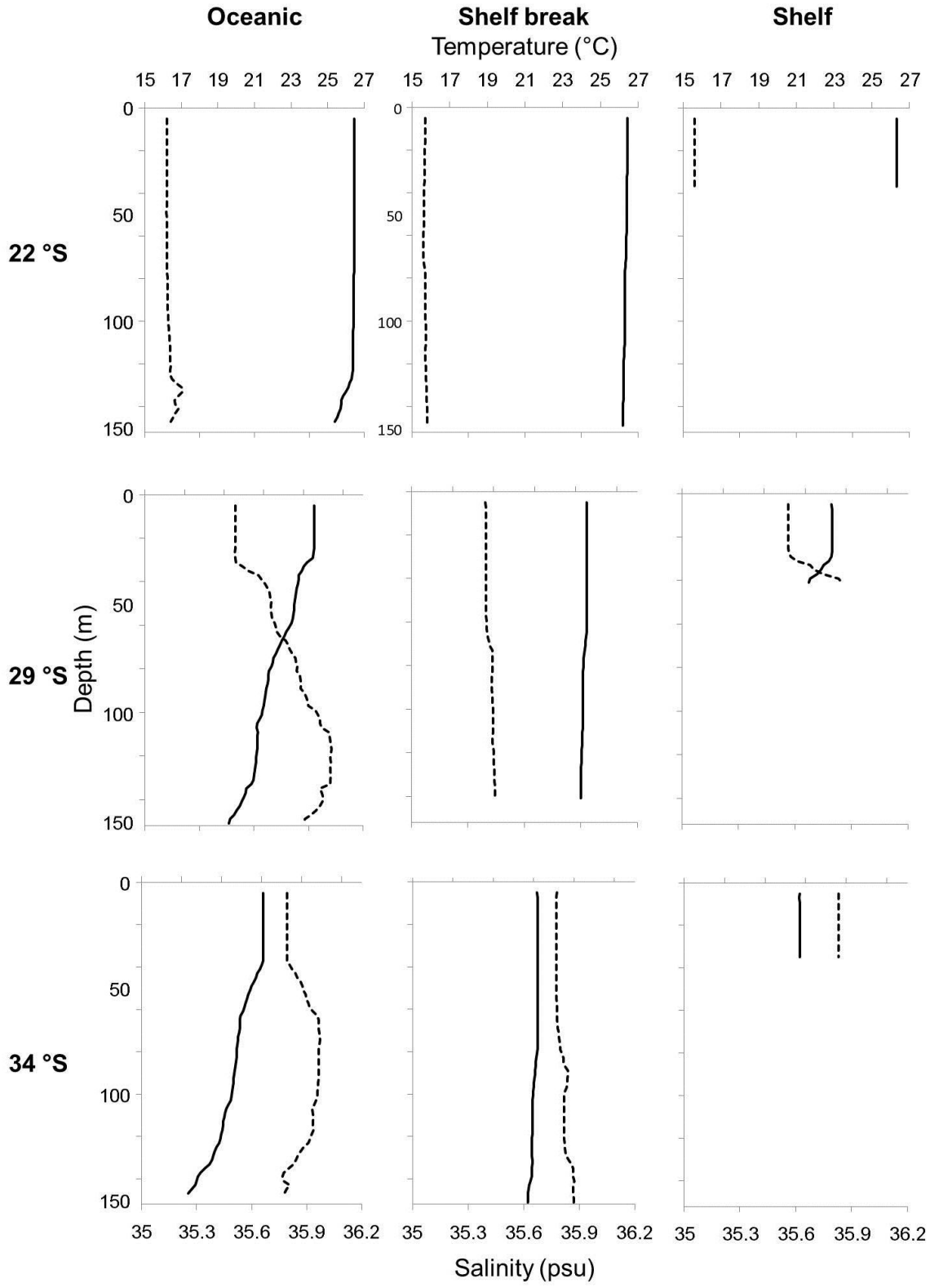


Figure 2.3 Temperature and salinity profiles (0 - 150 m) of shelf, shelf break and oceanic water columns at 22°S, 29°S and 34°S. Solid line indicates temperature (°C) and dashed line indicates salinity (psu).

water column and shallower mixed layers. Focusing on the top 150 m of the water column (to match the extent of epi-pelagic zooplankton sampling), a decrease in temperature corresponded to an increase in salinity, dissolved oxygen, and, in turn, seawater density (Fig. 2.4). In general, surface chlorophyll *a* (Fig. 2.5A) and depth-integrated chlorophyll *a* greater south of 29°S. Mesozooplankton settled volume decreased with increasing latitude for shelf stations, but showed no obvious patterns for shelf break and oceanic stations (Fig. 2.5B).

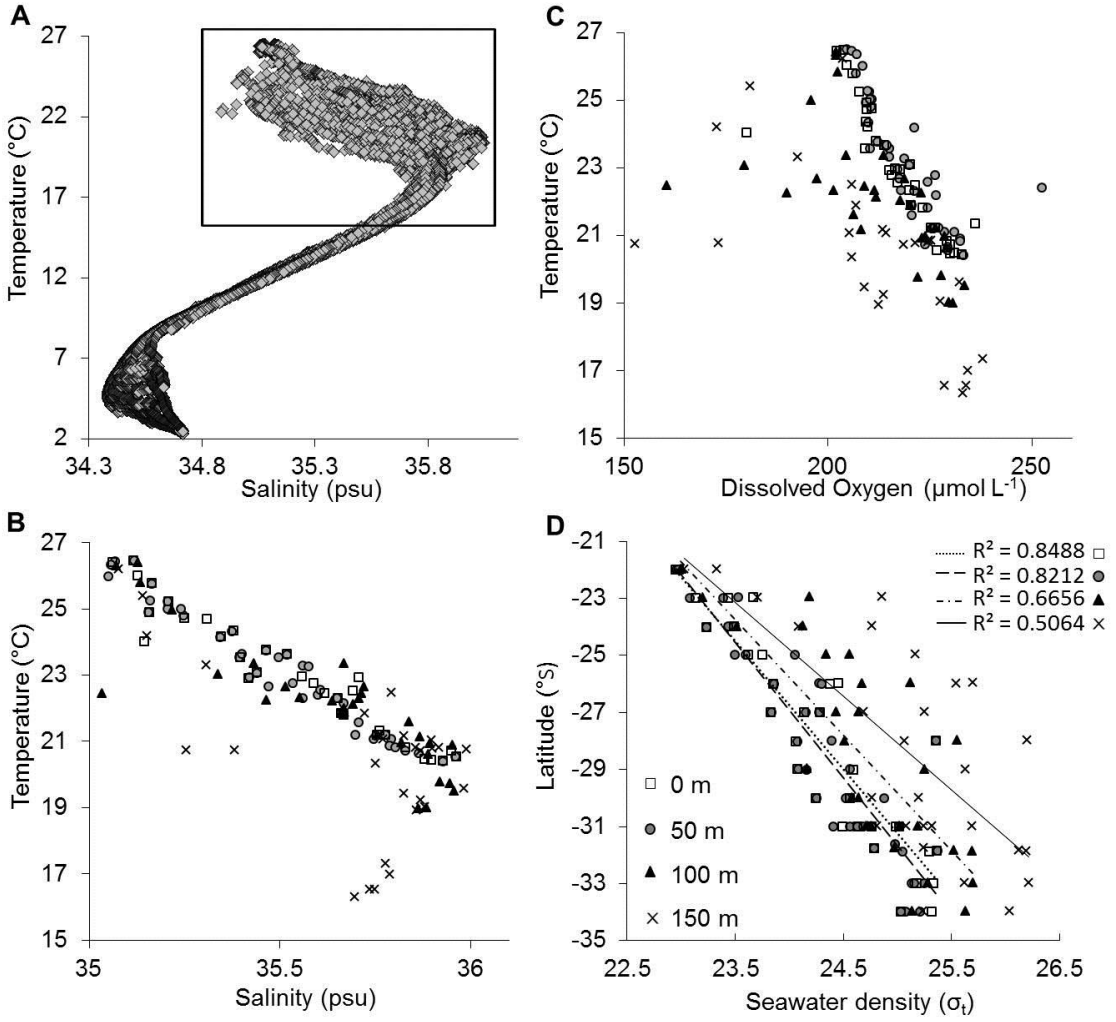


Figure 2.4(A) Temperature and salinity profile of the water column, to 2000 m depth, across the Leeuwin Current study area. Box indicates 0 - 150 m of the water column which is expanded to show the correlations between B) temperature and salinity C) temperature and dissolved oxygen and D) latitude and seawater density at four depths.

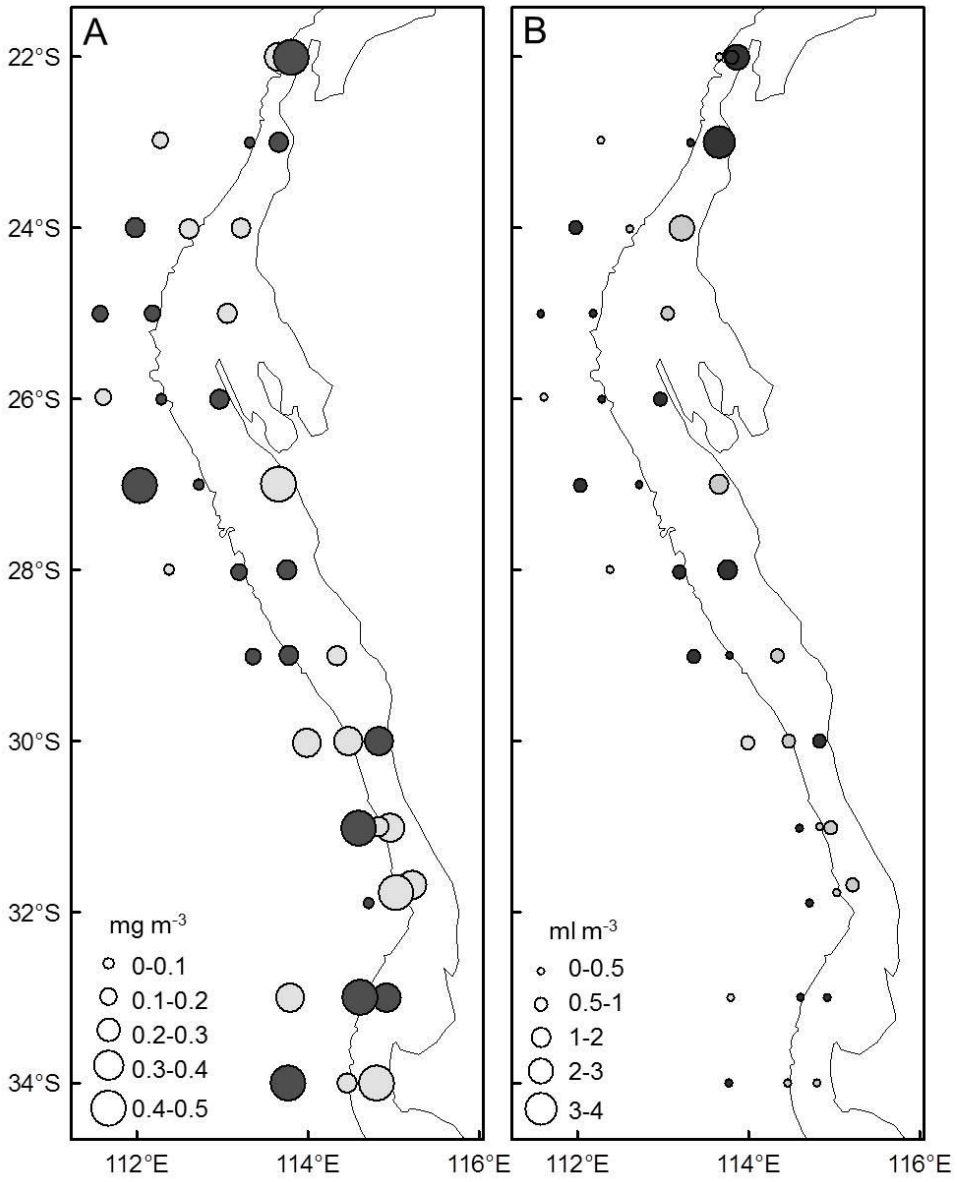


Figure 2.5 A) Surface chlorophyll *a* concentration and B) mesozooplankton settled volume for shelf, shelf break and oceanic stations across the Leeuwin Current study area. Grey and black circles distinguish stations sampled during the day and night, respectively.

Euphausiid assemblages of the Leeuwin Current

A total of 27 euphausiid species was identified from the LC study area (Fig. 2.6). They comprised eight tropical species, 15 with subtropical/ tropical affinities and four species with cooler subtropical/ temperate water affinities. The number of species recorded was highest for shelf break and oceanic stations (Fig. 2.7A). Oceanic stations yielded more species (25) than shelf stations (14). 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 27 species were recorded at night stations.

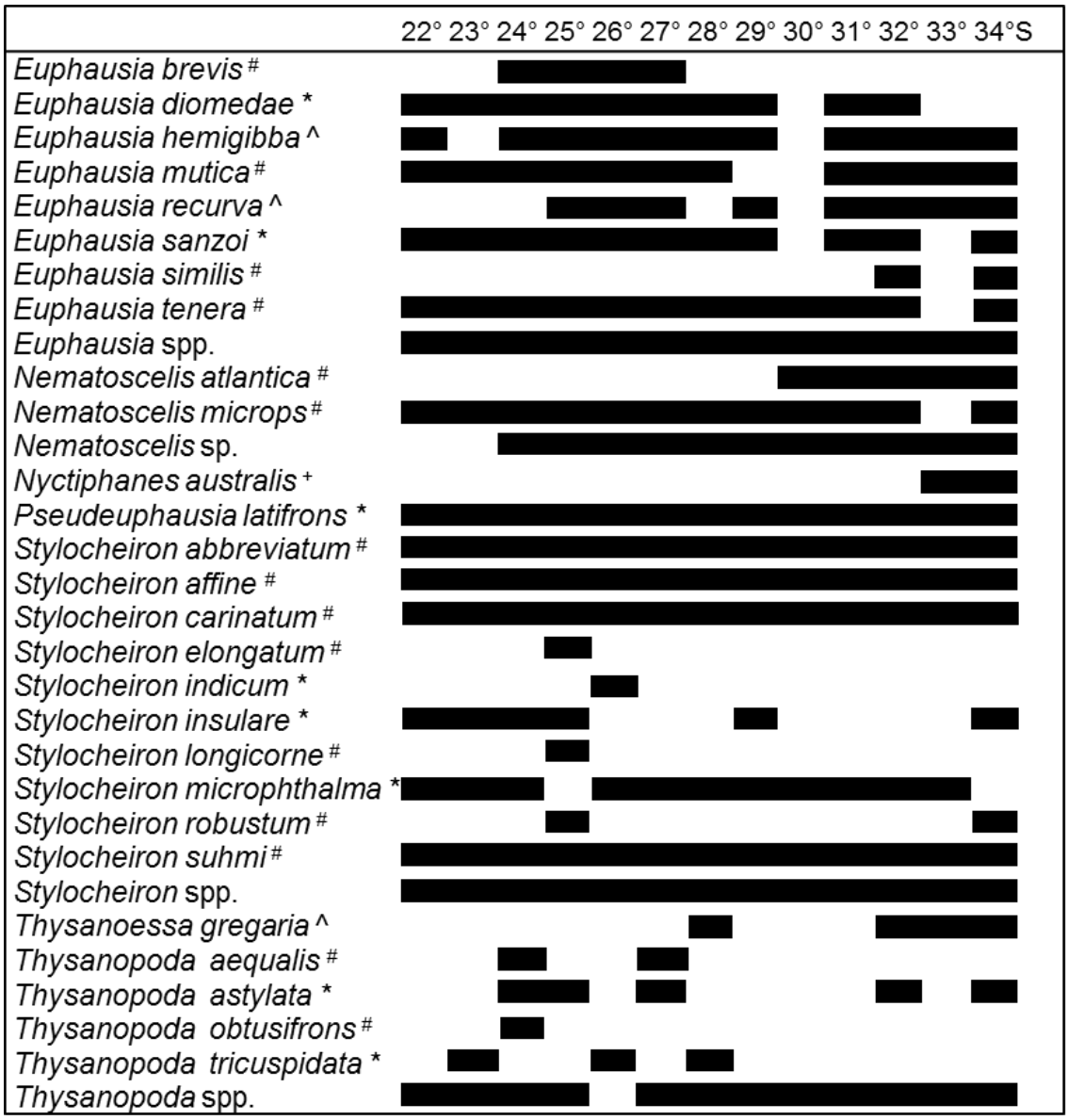


Figure 2.6 The euphausiid species and their respective latitudinal ranges (°S) recorded across the Leeuwin Current survey area in 2007. Previously known distribution ranges are given based on Brinton et al. (2000) and are indicated by * tropical, # tropical/subtropical, ^ subtropical/temperate and + temperate. Sp. refers to a species of a genus that could not be distinguished. Spp. refers to more than one species of the same genus that could not be distinguished.

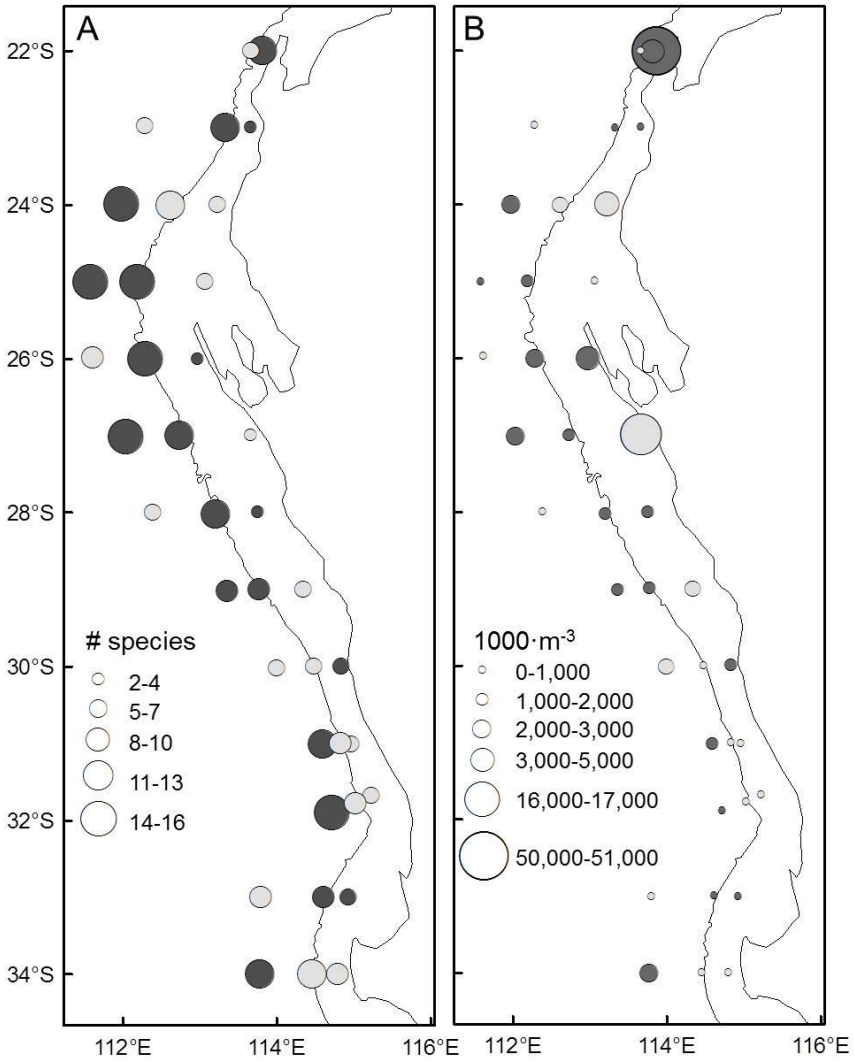


Figure 2.7 A) The number of euphausiid species identified and B) total euphausiid concentrations for all the shelf, shelf break and oceanic stations over the Leeuwin Current study area. Grey and black circles indicate stations sampled during the day and night, respectively.

Nyctiphanes australis, *Stylocheiron indicum*, *Stylocheiron insulare*, and *Stylocheiron robustum* were identified as new records for the LC and south-east Indian Ocean. *Nyctiphanes australis* was recorded between 33°S - 34°S, *S. indicum* only at 26°S, *S. insulare* between 22°S - 34°S (although not at every latitude), and *S. robustum* at 25°S and 34°S (Fig. 2.6). Of the eight tropical species identified in the study area, namely, *S. indicum*, *T. tricuspidata*, *Euphausia diomedeae*, *Euphausia sanzoi*, *P. latifrons*, *S. insulare*, *Stylocheiron microphthalma*, and *Thysanopoda astylata*, all except the first two species were also recorded south of 30°S.

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. 2.7B). Generally, though, total concentrations at all other stations ranged between 130 - 4191 inds·1000 m^{-3}, with more specimens 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). There were no significant differences in total concentration across isobath ($p = 0.676$, $n = 39$, Kruskal-Wallis) or latitude ($p = 0.067$, $n = 39$, Kruskal-Wallis).

Pseudeuphausia latifrons, *Stylocheiron carinatum* and *E. recurva* were the most common and abundant species throughout the study area. Together, they accounted for over 75% of the total numbers of euphausiids caught. *Pseudeuphausia latifrons*, a tropical neritic species, was identified from every station sampled, including oceanic stations and to the southernmost extent of the study area (34°S) (Fig. 2.8A). Concentrations of *P. latifrons* were significantly greater in the north (3914 ± 2468 inds·1000 m^{-3}) compared to the south (200 ± 74 inds·1000 m^{-3}) ($p = 0.021$, $n = 39$, Kruskal-Wallis). Concentrations were also significantly greater at shelf stations, having an average of 6018 ± 3925 inds·1000 m^{-3}, in comparison to shelf break (1392 ± 273 inds·1000 m^{-3}, $p = 0.033$, $n = 26$, Kruskal-Wallis) and oceanic stations (1190 ± 270 inds·1000 m^{-3}, $p = 0.002$, $n = 26$, Kruskal-Wallis). Concentrations of *P. latifrons* did not significantly differ across shelf break or oceanic stations ($p = 0.144$, $n = 26$, Kruskal-Wallis), and were not significantly influenced by day/night ($p = 0.592$, $n = 39$, Kruskal-Wallis). The large standard deviations was mostly due to the high concentration recorded at shelf stations at 22°S (50848 inds·1000 m^{-3}) and 27°S (16171 inds·1000 m^{-3}).

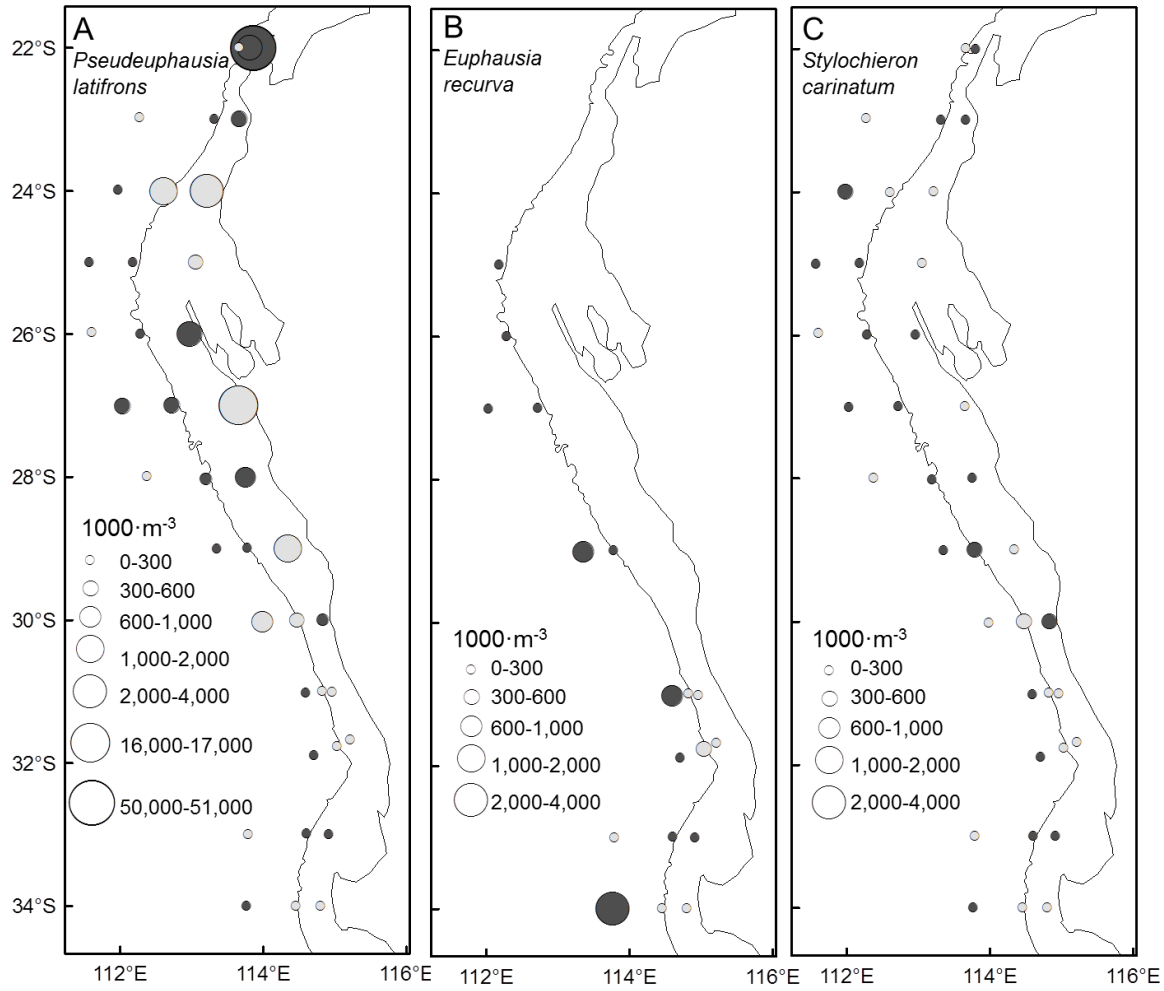


Figure 2.8 Concentrations (1000·m^{-3}) of the three dominant euphausiid species at shelf, shelf break and oceanic stations in the Leeuwin Current study area A) *Pseudeuphausia latifrons*, B) *Euphausia recurva* and C) *Stylocheiron carinatum* . Scales are the same for all three species and grey and black circles indicate stations sampled during the day and night, respectively.

The subtropical/temperate oceanic species, *E. recurva*, was mostly identified from stations in the southern region of the study area (29°S - 34°S), with some occurrences outside of its typical distribution between 25°S - 27°S (Fig. 2.8B). As such, there were significantly higher mean concentrations of *E. recurva* in the south of the study area ($p = 0.001$, $n = 39$, Kruskal-Wallis). *Euphausia recurva* was, on average, more abundant during the night (265 ± 144 inds·1000 m^{-3}) than the day (41 ± 27 inds·1000 m^{-3}), although, variation was high for night concentrations and the comparison between night and day was not significant ($p = 0.083$, $n = 30$, Kruskal-Wallis). While some specimens of *E. recurva* were caught in shelf waters (6 ± 4 inds·1000 m^{-3}; 32° - 34°S

only), this species was most abundant at shelf break stations (84 ± 39 inds·1000 m^{-3}, p = 0.007, n = 20, Kruskal-Wallis). Concentrations at oceanic stations were, on average, highest (394 ± 224 inds·1000 m^{-3}), however, large variation existed which resulted in no significant differences in concentrations between shelf break (p = 1.000, n = 20, Kruskal-Wallis) or shelf stations (p = 0.069, n = 20, Kruskal-Wallis). It should be noted that comparison of means across isobath and day/night were only conducted within the latitudinal range of *E. recurva* (25°S - 34°S), rather than the full extent of the study area, as this species is not tropical in its distribution.

Stylocheiron carinatum is typically cosmopolitan and it was collected at most stations throughout the study area (Fig. 2.8C). Concentrations were comparable across shelf (99 ± 30 inds·1000 m^{-3}), shelf break (172 ± 33 inds·1000 m^{-3}) and oceanic stations (129 ± 27 inds·1000 m^{-3}), and across latitude, 113 ± 18 inds·1000 m^{-3} and 157 ± 31 inds·1000 m^{-3} for north and south, respectively. Given this, there were no significant differences in concentration across isobath (p = 0.141, n = 26, Kruskal-Wallis), day/night (p = 0.630, n = 39, Kruskal-Wallis) or latitude (p = 0.414, n = 39, Kruskal-Wallis).

Multidimensional scaling ordination of euphausiid assemblages showed more variation amongst shelf stations, than shelf break or oceanic stations (Fig. 2.9A). Defined by water mass, assemblages in TSW were, for the most part, spatially separated from assemblages in STSW, with assemblages from mixed waters in between. The similar assemblages at shelf break stations at 25°S, 27°S, and 28°S and oceanic stations at 24°S, 25°S, and 27°S were in a stratified water column with STSW underlying TSW but, which overall, had a mean seawater density allocated to TSW. The influence of day and night on assemblages was also observed, with shelf break and oceanic stations sampled at night mostly separated from stations sampled during the day (Fig. 2.9B).

Shelf stations sampled at night had similar euphausiid assemblages to shelf stations sampled during the day.

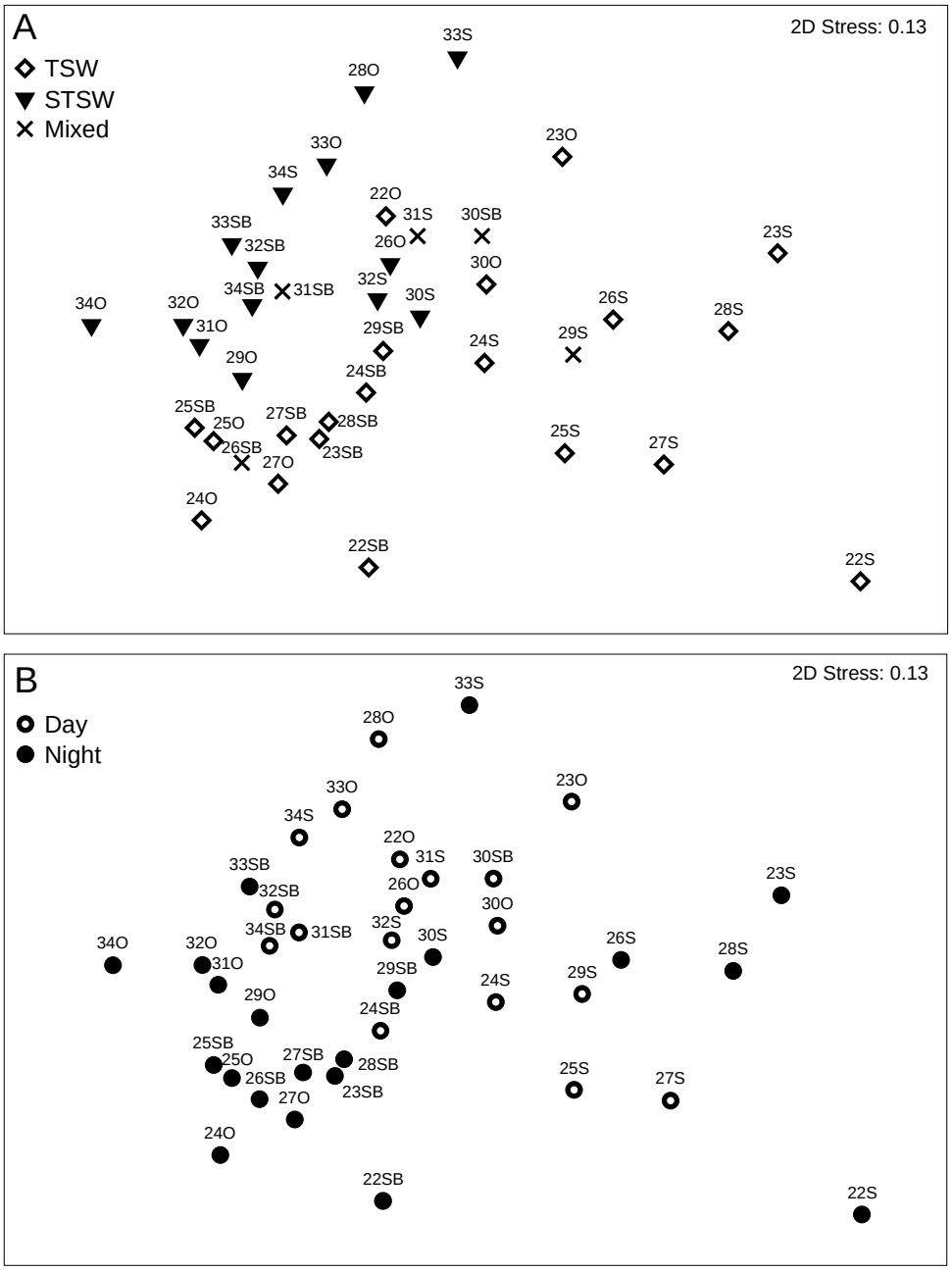


Figure 2.9 nMDS ordinations showing similarities in euphausiid assemblages, defined by A) water mass and station, and B) day/night and station. TSW = Tropical Surface Water and STSW = Sub Tropical Surface Water. Mixed refers to those stations with a mean seawater density in between that of TSW and STSW. Stations are labelled by latitude and isobath, S = shelf, SB = shelf break and O = oceanic.

PERMANOVA revealed significant differences in assemblages across day/night ($P = 0.004$, $n = 39$), isobath ($P < 0.001$, $n = 39$) and latitude ($P < 0.001$, $n = 39$), including a

significant interaction between day/night and isobath (P < 0.001, n = 39), and isobath and latitude (P = 0.024, n = 39) (Table 2.1). ANOSIM revealed shelf assemblages were only significantly different from shelf break ($\bar{R}$ = 0.73, P < 0.001, n = 14) and oceanic assemblages ($\bar{R}$ = 0.82, P < 0.001, n = 14) for stations sampled at night and not day (Table 2.2). SIMPER revealed this pattern was largely driven by the high concentrations of *P. latifrons* on the shelf (Table 2.2). Conversely, shelf break stations had higher concentrations of *Euphausia mutica*, *Euphausia tenera* and *E. sanzoi*, whereas oceanic stations had higher concentrations of *E. recurva*, *E. hemigibba*, and *E. tenera*. Shelf break and oceanic assemblages were relatively similar ($\bar{R}$ = 0.13, P = 0.072, n = 26), regardless of day/night.

Table 2.1 A three-factor PERMANOVA testing the effect of day/night, isobath (shelf, shelf break, oceanic) and latitude (north or south of 29°S) on the structuring of euphausiid assemblages of the Leeuwin Current system off Western Australia. Asterisks denote a significant difference.

Factor	df	MS	F	P
Day/night	1	2134.2	3.2	0.0039*
Isobath	2	3937.1	5.9	0.0001*
Latitude	1	3758	5.6	0.0002*
Day/night x Isobath	2	2449.1	3.6	0.0001*
Day/night x Latitude	1	698.4	1.0	0.4013
Isobath x Latitude	2	1369.3	2.0	0.0236*
Day/night x Isobath x Latitude	2	601.24	0.9	0.5590
Residual	27	669.29		
Total	38			

Differences related to isobath were further structured by latitude, and ANOSIM revealed all isobaths were significantly different from each other in the north (all $\bar{R}$ > 0.22, P < 0.035, n = 21), but not in the south (all $\bar{R}$ < 0.22, P > 0.076, n = 18). *Pseudeuphausia latifrons* and *E. recurva* characterised the northern and southern assemblages, respectively, according to SIMPER. With respect to latitude differences within each isobath, ANOSIM revealed northern assemblages were different from southern assemblages for stations sampled on the shelf ($\bar{R}$ = 0.39, P = 0.005, n = 13),

and shelf break ($\bar{R}$ = 0.56, P = 0.001, n = 13). For shelf stations, *Pseudeuphausia latifrons* and *S. suhmi* drove the differences in assemblages for the north and south, respectively. For the shelf break, *E. mutica* and *E. tenera* drove the northern assemblages and *E. recurva* the southern assemblage. ANOSIM found no significant differences between the northern and southern assemblages for oceanic stations ($\bar{R}$ = 0.10, P = 0.177, n = 13).

Table 2.2 One-way ANOSIM and SIMPER of euphausiid assemblages across isobath for stations sampled at night in the Leeuwin Current system. Shading indicates the assemblage typical for each isobath; un-shaded areas indicate comparisons between isobaths, with significant differences marked with an asterisk. The five species contributing the highest concentrations are listed for the isobath comparisons and superscript denotes the isobath at which each species was most abundant. Ave. diss. = average dissimilarity.

	Shelf (~ 50 m)	**Shelf break (~ 200 m)**	**Oceanic (1000 - 2000 m)**
Shelf	Ave. diss. = 50.6% *P. latifrons* *S. carinatum* *S. suhmi*		
Shelf break	*$\bar{R}$= 0.73, P < 0.001 Ave. Diss. = 62.4% *P. latifrons* (S) *E. mutica* (SB) *E. tenera* (SB) *E. sanzoi* (SB) *E. diomedeae* (SB)	Ave. diss. = 33.6% *S. carinatum* *P. latifrons* *S. suhmi* *E. tenera* *E. mutica*	
Oceanic	*$\bar{R}$= 0.82, P= 0.001 Ave. Diss.= 69.1% *P. latifrons* (S) *E. recurva* (O) *E. hemigibba* (O) *E. tenera* (O) *E. mutica* (O)	$\bar{R}$= 0.13, P= 0.720 Ave. Diss.= 36.2% No significant species	Ave. diss. = 32.8% *S. carinatum* *E. hemigibba* *S. suhmi* *P. latifrons* *E. recurva*

Influence of the Leeuwin Current on euphausiid assemblages

Due to obvious day/night differences in euphausiid assemblages, BIOENV analyses were run on day and night samples separately, as any differences may have been a result of diel variation rather than the environmental variables. Four environmental

variables were included in the analyses, namely, mean seawater density, surface chlorophyll *a*, depth integrated chlorophyll *a* and mesozooplankton settled volume.

For euphausiid assemblages sampled during the day, there were no significant correlations with environmental variables ($\rho = 0.28$ $P = 0.110$, $n = 18$) (Table 2.3). Conversely, mean seawater density (and mean dissolved oxygen) and mesozooplankton settled volume were most correlated with euphausiid assemblages sampled during the night ($\rho = 0.60$, $P < 0.001$, $n = 21$). Environmental variables were overlayed on nMDS ordinations of the euphausiid assemblages sampled at night using bubble plots (Fig. 2.10). An increase in mean seawater density correlated somewhat with a separation of euphausiid assemblages across latitude, and a higher mesozooplankton settled volume correlated with the separation of shelf euphausiid assemblages from shelf break and oceanic assemblages, which had lower settled volumes.

Pseudeuphausia latifrons, *E. recurva* and *S. carinatum* were correlated separately with the same environmental variables using BIOENV, but not separated into day and night samples, as this factor did not significantly affect the concentrations of these three species. Mean seawater density (and mean dissolved oxygen) and mesozooplankton settled volume returned the highest correlation for both *P. latifrons* ($\rho = 0.34$, $P < 0.001$, $n = 39$) and *E. recurva* ($\rho = 0.40$, $P < 0.001$, $n = 39$), whilst no environmental variables were significantly correlated with *S. carinatum* concentrations ($\rho = 0.16$, $P = 0.173$, $n = 39$) (Table 2.3).

Table 2.3 BIOENV correlations between environmental variables and euphausiid assemblages sampled during the day and night as well as for the three dominant species, *Pseudeuphausia latifrons*, *Euphausia recurva* and *Stylocheiron carinatum*. The highest correlation overall, and the two highest individual variable correlations for each analysis, are shown. Global $\bar{R}$ statistics and P values are provided. Asterisks denote a significant difference.

Assemblages sampled during the day	
$\bar{R}$ = 0.28, P = 0.11	Correlation
BEST: Surface chlorophyll *a*	0.28
Surface chlorophyll *a* & mesozooplankton settled volume	0.23
Mean seawater density & surface chlorophyll *a*	0.22
Assemblages sampled during the night	
$\bar{R}$ = 0.60, P < 0.001*	Correlation
BEST: Mean seawater density and mesozooplankton settled volume	0.60
Mesozooplankton settled volume	0.55
Mean seawater density, depth integrated chlorophyll *a* & mesozooplankton settled volume	0.46
Pseudeuphausia latifrons	
$\bar{R}$ = 0.34, P < 0.001*	Correlation
BEST: Mean seawater density & mesozooplankton settled volume	0.34
Mesozooplankton settled volume	0.27
Mean seawater density	0.26
Euphausia recurva	
$\bar{R}$ = 0.40, P < 0.001*	Correlation
BEST: Mean seawater density and mesozooplankton settled volume	0.40
Mesozooplankton settled volume	0.27
Mean seawater density, depth integrated chlorophyll *a* & mesozooplankton settled volume	0.27
Stylocheiron carinatum	
$\bar{R}$ = 0.16, P = 0.173	Correlation
BEST: Mean seawater density & mesozooplankton settled volume	0.16
Mesozooplankton settled volume	0.14
Mean seawater density, depth integrated chlorophyll *a* & mesozooplankton settled volume	0.12

Discussion

A major finding from this study was the identification of 27 euphausiid species, including four new records for the south-east Indian Ocean, along a 1,500 km stretch of the LC system. Of the 27 species identified in this study, 18 had been previously recorded in a LC eddy investigated in 2006 (31° - 34°S) (Sutton et al. 2015), resulting in nine additional species being recorded over the greater latitudinal extent of this LC survey.

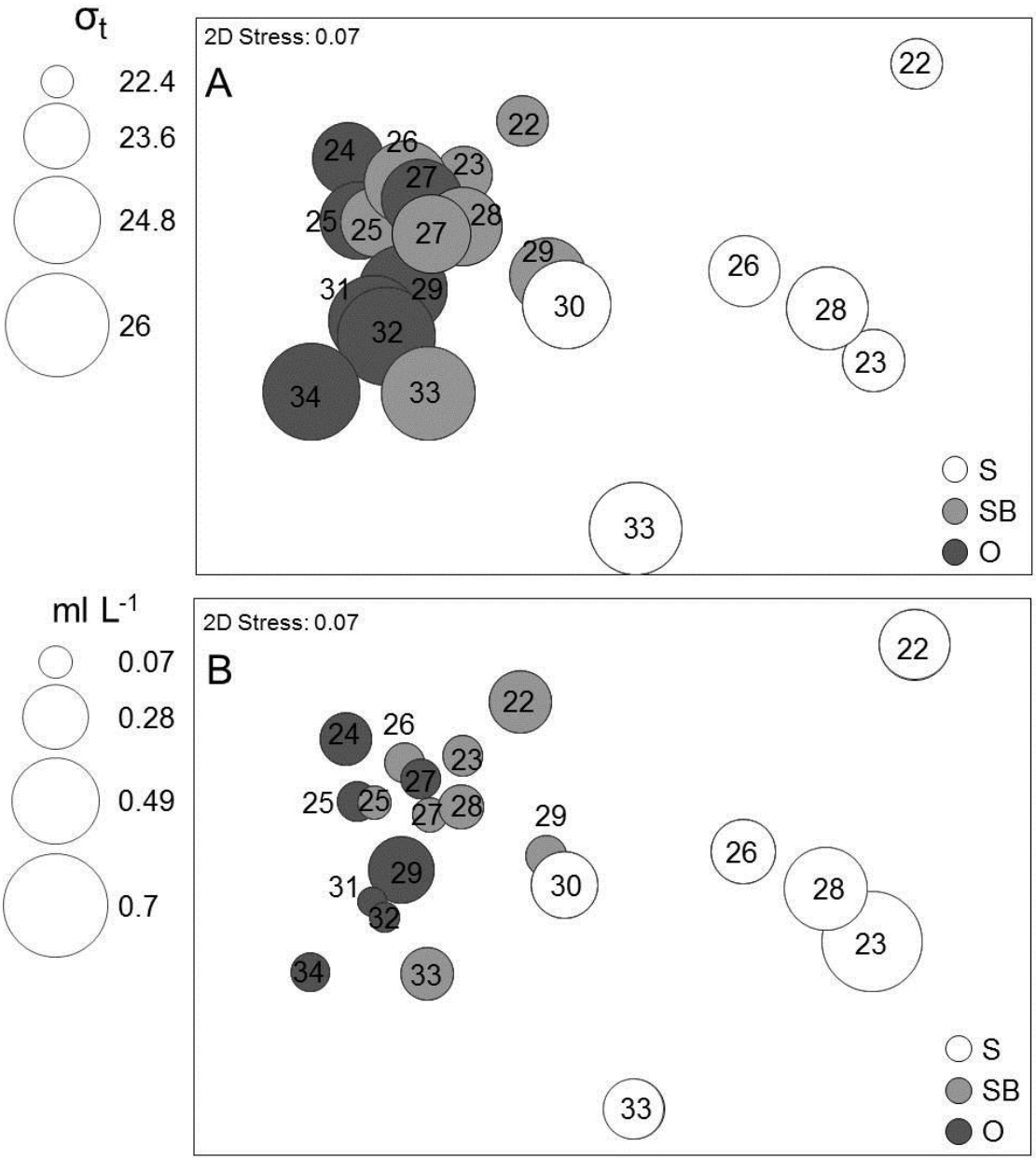


Figure 2.10 A bubble plot of environmental variables A) mean seawater density and B) mesozooplankton settled volume (0 - 150 m depth) overlaid on nMDS ordinations of euphausiid assemblages sampled during the night in the Leeuwin Current system between 22°S - 34°S. Bubbles are coded by isobath (S= shelf, SB = shelf break, O = oceanic) and each degree of latitude.

Differences in assemblages were found between shelf, shelf break and oceanic stations, as well as between northern and southern stations, and there was significant diel variation. Seawater density (and mean dissolved oxygen), mesozooplankton settled volume and depth-integrated chlorophyll *a* were identified as important drivers

of distribution for the euphausiid assemblages of the LC, as well as for two of the most dominant species *P. latifrons* and *E. recurva*.

The LC would be expected to contain a mixture of euphausiid species entrained from surrounding water masses and currents, i.e. Indonesian Throughflow, South Java Current and Eastern Gyral Current. *Stylocheiron insulare*, *Euphausia fallax*, and *E. sanzoi*, all considered Indo-Australian endemics (Brinton 1975), were found south of 22°S in this study. Likewise, *Euphausia diomedeae*, an Indo-Pacific equatorial species, has been recorded to be transported north to the western Pacific by the Kuroshio Current, (Brinton et al. 2000) so transport polewards by the LC is the likely explanation for its occurrence as far south as 32°S off Western Australia. *Stylocheiron robustum*, which has a distribution across the middle of the 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*, *E. similis*, *N. australis*, and *T. gregaria* (Brinton et al. 2000), were all present 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*, *S. insulare*, *S. microphthalma*, *T. astylata* and, particularly, *P. latifrons*, at the southern stations indicates that the LC affords an extension of suitable environment for tropical euphausiid species to extend their typical distributions. Euphausiid biogeography is relatively well known across the oceans (Brinton 1962; Brinton & Gopalakrishnan 1973; Brinton 1975; Brinton 2000; Letessier et al. 2009; Letessier et al. 2011), and Brinton (1962) highlights the role of current systems in transporting and adapting euphausiids to new environments that are within their physiological tolerances. Whether or not

tropical populations of euphausiids are sustained within the LC would require seasonal sampling and an examination of whether tropical species are reproducing within the LC. Although not reported on in this study, many *P. latifrons* specimens were observed to have brood pouches full of eggs in these samples collected during austral autumn/winter (unpublished data).

Mean seawater density (and mean dissolved oxygen), which was the variable used to represent TSW, STSW and the changes in LC water properties as the current flowed from 22° - 34°S, had a significant correlation with euphausiid assemblages sampled during the night. Distributions of euphausiid species are well-known to be linked with water masses (Brinton 1975; Dadon & Boltovsky 1982; Gibbons et al. 1995; Tarling et al. 1995). Youngbluth (1976) explained the changes in the euphausiid assemblage and dominant species throughout the California Current were, in part, due to the mixing of species from the different water masses in the region. In this LC study, the tropical species, *P. latifrons*, was dominant in the warmer TSW in the north, but was also mixed with more subtropical assemblages as the LC transported warm water southwards, where maximum poleward geostrophic transport can reach 5 Sv (Feng et al. 2003). Southern assemblages were generally under the influence of cooler STSW, which resulted in the subtropical/temperate species, *E. recurva*, becoming the dominant species. *Pseudeuphausia latifrons* and *E. recurva* were the main species driving the differences in assemblages observed across latitude.

The separation of northern and southern euphausiid assemblages was further structured by isobath and revealed significant differences in assemblages across shelf, shelf break and oceanic stations in the north, but not in the south. As diel variation occurred in both the north and the south, the greater range in seawater density in the

north may, in part, explain why there were significant differences in assemblages across the isobaths. Intrusions of underlying cooler STSW occurred as far north as 25°S, resulting in stratification and thus a greater variation in seawater density and assemblages across isobath. In the south, seawater density was not as varied given the evaporative cooling, the STSW inundating oceanic stations, and the LC becoming cooler and more saline because of the entrainment of STSW and shelf water (Weller et al. 2011). Overall, the water column profile down to 2000 m was similar to that shown in the two austral summer LC surveys (2000 and 2003) conducted by Woo & Pattiaratchi (2008), albeit with some minor summer and autumn differences.

A number of studies have highlighted, not only the longshore transport of marine biota by the LC, but also cross-shelf transport to the offshore environment through meanders and eddies (Waite et al. 2007a; Waite et al. 2007b; Holliday et al. 2011a; Weller et al. 2011; Holliday et al. 2012; Paterson et al. 2013). *Nyctiphanes simplex* 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), and it is proposed here that *P. latifrons* could be similarly used as a tracer of longshore and cross-shelf transport of LC waters. Classified as a tropical coastal species, the distribution of *P. latifrons* has previously included the neritic waters of the north-west Indian Ocean through to the Indonesian Archipelago and tropical western Pacific (Brinton et al. 2000). However, in the Pacific Ocean, distribution extensions of *P. latifrons* include southwards to 34°S with the East Australian Current, northward of 35°N with the Kuroshio Current, and in Indian Ocean neritic waters to 30°S adjacent to the Agulhas Current (Wang & Chen 1963; Griffiths 1979; Gibbons et al. 1995). *Pseudeuphausia latifrons* was found at every degree of latitude in the LC survey area, highlighting the longshore transport of

tropical epi-pelagic biota by the current. *Pseudeuphausia latifrons* was also found at every station in shelf break and oceanic waters, which for a coastal species, could be achieved by cross-shelf transport of shelf waters via meanders and eddies.

As expected for a species known to have a strong coastal affinity, *P. latifrons* was the species that distinguished the shelf assemblages in this study. Fewer species were found in shelf waters and, as most euphausiid species tend to be oceanic (Brinton et al. 2000), this would be anticipated and has also been shown for the Benguela upwelling system (Barange et al. 1992) and Agulhas Current (Gibbons et al. 1995). Shelf break and oceanic euphausiid assemblages sampled at night were significantly different from shelf assemblages. During the night, at these deeper stations, some species would have migrated vertically through the water column and been captured in the upper 150 m thereby increasing the number of species and euphausiid concentrations and resulting in prominent differences from the shelf assemblage.

Diel variation in euphausiid assemblages was apparent for the study area. Euphausiids undergo pronounced diel vertical migration which is largely driven by predator avoidance (Bollens et al. 1992) and food availability (Youngbluth 1975; Hu 1978; Gibbons 1993; Taki 2008). Although this migration behaviour is likely to have caused the large diel differences in euphausiid assemblages in this study, depth stratified sampling was not conducted and it can only be inferred. Euphausiids are also known to form patchy aggregations and exhibit net avoidance (particularly during the day) (Brinton 1967; Wiebe et al. 1982), so by using bongo nets, there could be potential underestimation of euphausiid concentrations.

Euphusiid behaviour causes variation in their distribution and abundance, as do ecosystem effects such as oceanography, primary productivity, competition and predation. The environmental variables used in this study explained some of the variation in euphausiid assemablges, but not all. The influence of predators and competitors on assemblages was not examined, but it could be speculated that competition for food may significantly influence the distribution of euphausiids, particularly in an environment low in nutrients (Hanson et al. 2005; Rossi et al. 2013b).

This investigation has shown that in the south-east Indian Ocean, TSW, STSW, the LC, and their associated abiotic and biotic properties, influenced euphausiid assemblages within the epipelagic environment. In particular, the north was characterised by the tropical species, *P. latifrons*, and the south was characterised by the subtropical/temperate species, *E. recurva*, which reflected the predominant water masses. The LC provided a suitable environment for tropical species to extend their typical biogeographical ranges, and explains new records of species for the south-east Indian Ocean in general. This study expands the knowledge of distribution patterns of euphausiids in the LC system and enhances the understanding of biological and physical oceanographic relationships within the south-east Indian Ocean.

Chapter 3: Euphausiid assemblages of the oceanographically complex north-west marine bioregion of Australia

Abstract

The epipelagic euphausiid assemblages of the north-west marine bioregion of Australia were investigated during the austral autumn of 2010, and related to properties of the water column and food availability for the Kimberley and Ningaloo environments. Twenty five euphausiid species were identified from the bioregion, equating to 29% of the world's euphausiid species, and included three new records for Australian waters. *Pseudeuphausia latifrons* was the most abundant euphausiid across both study areas, dominating the shelf waters. *Stylocheiron carinatum* replaced *P. latifrons* in deeper waters, where species richness was greater. Ningaloo harboured greater total concentrations of euphausiids than the Kimberley, and this may be linked to the physical oceanography and narrowness of the shelf at Ningaloo. Mean seawater density and mean fluorescence correlated significantly with euphausiid assemblages, and isobath (depth) significantly structured assemblages along a gradient from the inner shelf to oceanic stations. This study has shown that the euphausiid assemblages of the north-west marine bioregion are reflective of the connection between the Pacific and Indian Oceans via the Indonesian Throughflow, and physical properties of the water column and food availability are recurrent drivers of euphausiid assemblage variation in the eastern Indian Ocean.

Introduction

The tropical north-west marine bioregion of Australia boasts a marine environment with a diverse array of habitats and biota (Wilson 2013). The bioregion encompasses Commonwealth waters from the state boundary between Western Australia and the Northern Territory, south to Kalbarri (28°S). It is a bioregion of the Indian Ocean that is directly influenced by the intrusion of Pacific Ocean water via the Indonesian Throughflow (Meyers et al. 1995; Susanto et al. 2012) and has been referred to as a sink for tropical species (Wilson 2013). Although some studies have investigated the zooplankton communities of the north-west marine bioregion (Tranter 1962; Wilson et al. 2003a; Wilson et al. 2003b; McKinnon et al. 2008; Holliday et al. 2011b; McKinnon et al. 2015), little emphasis has been placed on euphausiid assemblages.

The one million km^2 of ocean encompassed by the north-west marine bioregion is influenced by the Indonesian Throughflow, South Indian Countercurrent and the Eastern Gyral Current, which form the source waters for the Leeuwin Current (LC), the anomalous eastern boundary current of the Indian Ocean (Feng et al. 2003; Domingues et al. 2007; Menezes et al. 2014). It is a dynamic oceanographic environment with strong currents, large tidal fluctuations, seasonal monsoons, and tropical cyclones strongly influenced by the El Niño Southern Oscillation and Indian Ocean Dipole (Holloway 1983; Godfrey & Ridgeway 1985; Meyers 1996; Lough 1998; Feng et al. 2001; Ridgeway & Condie 2004; Brink et al. 2007; Condie & Andrewartha 2008). The Kimberley has a broad shelf, extending out for > 150 km and experiences semi-diurnal tides of up to 10 m. Monsoonal rains can also influence the oceanography of the region by diluting coastal salinity. Conversely, Ningaloo has the narrowest continental

shelf, of ~ 10 km, for the whole Australian coastline, and experiences semi-diurnal tides of < 2 m.

During the autumn and winter months, the seasonal Holloway Current flows south-westwards along the shelf and shelf break of the north-west marine bioregion (Condie & Andrewartha 2008; D'Adamo et al. 2009). This produces a deeper thermocline in offshore waters (Holloway & Nye 1985), and the surface waters along the shelf margin are often nutrient poor. However, seasonal blooms in primary production are observed during autumn (Thompson & Bonham 2011; Rousseaux et al. 2012; Rossi et al. 2013b). During summer, the thermocline is shallower (Church & Craig 1998), mixing is intensified, and cooler, nutrient rich waters often upwell and intrude onto the shelf. As holoplanktonic organisms, euphausiid assemblages would be influenced by the oceanographic conditions of the bioregion, and assemblages may contain species entrained from the Indonesian Throughflow, South Indian Countercurrent and Eastern Gyral Current.

Investigations on euphausiids off Western Australia in the eastern Indian Ocean have, so far, focused on the LC system south of 22°S (Sutton et al. 2015; Chapter 2). For the north-west marine bioregion, investigations by Brinton & Gopalakrishnan (1973), Taniguchi (1974), Wilson et al. (2003a) and Chapter 2 of this thesis collectively found 21 species to occur off Ningaloo between 20°S and 23°S. Further north, off the Kimberley, preliminary results on the macro-zooplankton from Holliday et al. (2011) noted two euphausiid species, *Pseudeuphausia latifrons* and *Stylocheiron carinatum*, as the most commonly occurring species for the bioregion. Early investigations from the International Indian Ocean Expedition also found *P. latifrons* and six other euphausiid species in the deeper waters off the Kimberley coast (Brinton &

Gopalakrishnan 1973). Outside of the north-west marine bioregion and the LC, euphausiids have been investigated in south-east Asian waters (Taniguchi 1974; Brinton 1975), and along the 110°E meridian in the Indian Ocean from 9° - 32°S (McWilliam 1977).

The aim of this chapter is to characterise the epipelagic euphausiid assemblages of the north-west marine bioregion during the austral autumn. Environmental drivers of euphausiid assemblages are poorly understood in the bioregion and this study aims to identify which environmental variables are causing assemblage differences. This is of particular importance given the role of euphausiids in marine food webs (Chittleborough 1965; Wilson et al. 2001a; Jarman & Wilson 2004), and that the north-west marine bioregion is faced with growing anthropogenic disturbances, e.g. oil and gas, and fishing.

Methods

Study area and sampling procedure

During the austral autumn of 2010, investigations aboard the R.V. *Southern Surveyor* (voyages SS03/2010 and SS04/2010) were conducted in the north-west marine bioregion of Australia, off the Kimberley and Ningaloo coasts (Fig. 3.1). Five cross-shelf transects were surveyed off the Kimberley between 13°S - 17°S and 120°E - 124°E (14th April - 5th May), sampling inner shelf (50 m depth), mid shelf (100 m), shelf break (200 m), shelf slope (500 m) and oceanic stations (1000 m and 2000 m) (Fig. 3.1). Two of these transects, namely A and C, sampled the same locations across a spring and neap tidal cycle, respectively, to assess any influence of the tidal cycle on zooplankton assemablages. The 50 m, 200 m and 1000 m isobaths were sampled during both the day and night, at the start and end of a 12 h period.

Seven cross-shelf transects were surveyed off Ningaloo between 21° - 23°S and 113° - 115°E (10th - 20th May 2010), at inner shelf (50 m), shelf break (200 m) and oceanic (1000 m) stations (Fig. 3.1). Additional stations were also sampled near Barrow Island (~20.8°S, 115.1°E), and at the 50 m and 200 m isobaths at Sandy Bay (~ 22.4°S, 113.7°E).

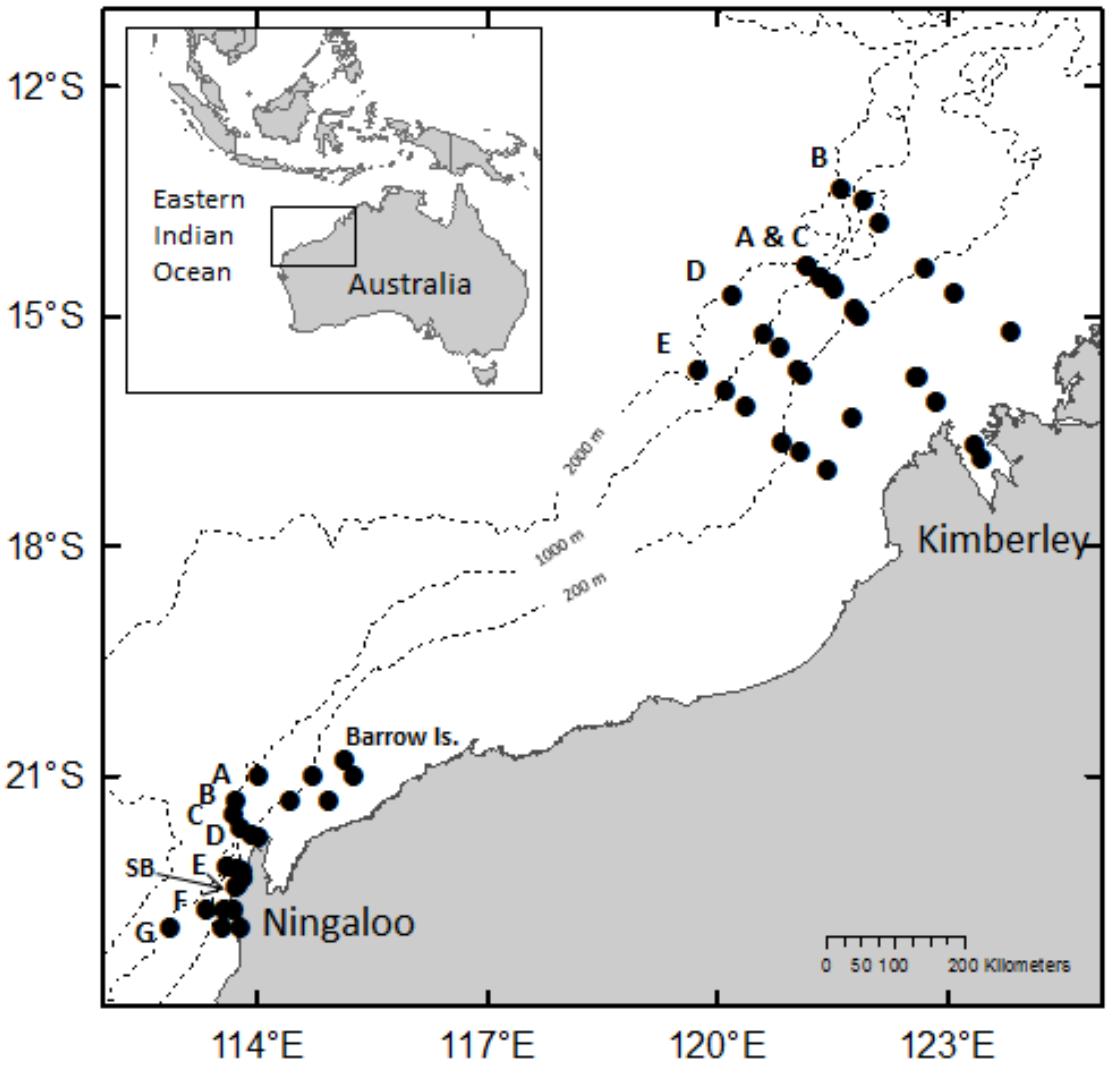


Figure 3.1 The north-west marine bioregion of Australia indicating sampling stations for each transect in the Kimberley and Ningaloo study areas. SB = Sandy Bay and letters indicate transect lines.

Hydrographic measurements from the surface to 1000 m depth (or 10 m above shallower sea floors) were taken using a Seabird SBE 19+ conductivity-temperature-depth-oxygen (CTD-O_2) instrument, equipped with dual temperature and conductivity

sensors, and additionally fitted with a SBE43 oxygen sensor and a Chelsea TGI fluorometer. Mixed layer depth was determined as the depth at which temperature was 0.4°C less than that measured at 10 m, or the salinity was 0.03 psu greater than that measured at 10 m (Condie & Dunn 2006). Measurements are expressed as the mean ± standard deviation.

At both study areas, replicate depth-integrated zooplankton samples for each station were collected during the day and night using bongo nets (diameter 0.5 m), of which the 355 µm mesh net samples were analysed for euphausiid specimens. Nets were obliquely towed from a depth of 150 m to the surface, or 10 m from the bottom in shallower water, for 15 minutes at a ship's speed of 2 knots. General Oceanics Flowmeters were attached to the mouth of the nets to quantify the volume of seawater filtered through the nets. Zooplankton samples were preserved in 5% buffered formaldehyde in seawater solution. Estimates of mesozooplankton volume were made by pouring the zooplankton samples through a 1 mm sieve and measuring the settled volume of remaining zooplankton in a graduated cylinder after a 24 h settling period (Gibbons 1999; Suthers & Rissik 2009); volumes were expressed in mL m^{-3} as the mean ± standard deviation.

Euphausiid identification

Immature and mature euphausiids were identified and counted using a dissecting microscope and relevant literature (Baker et al. 1990, Brinton et al. 2000). With the aid of a Folsom plankton splitter, zooplankton samples were sub-sampled and a minimum of 50 euphausiids (immature and mature, collectively) were counted from sub-samples before estimates were made of the total concentration (Gibbons 1999; Suthers & Rissik, 2009). Concentrations of euphausiids were expressed as the number of

individuals per 1000 m^{-3} of filtered seawater ± standard error. Damaged, or indistinguishable, immature and mature specimens were grouped as unidentified. The classification of species as tropical, subtropical or temperate was based upon geographical distributions given by Brinton et al. (2000).

Statistical analysis

Univariate analyses were conducted using non-parametric Kruskal-Wallis tests for independent samples in IBM SPSS Statistics 21. Multivariate analyses were carried out using the PRIMER v6 PERMANOVA+ software package (Anderson et al. 2008; Clarke & Gorley 2015). Differences in euphausiid assemblages within each study area were analysed based on *a priori* factors of day/night, due to diel vertical migration, and isobath (Fig. 3.2). To compare euphausiid assemblages between the Kimberley and Ningaloo study areas, only inner shelf, shelf break and oceanic (1000 m) stations sampled during the night were selected for consistency in multivariate analyses (n = 24). *A priori* factors of study area (two levels) and isobath (three levels) were applied to these data.

Prior to multivariate analysis, shade plots were used to determine the appropriateness of a fourth root transformation on euphausiid data to reduce the relative importance of abundant species (Clarke et al. 2014). A Bray-Curtis resemblance matrix was constructed to quantify the dissimilarity in assemblages between the samples (Fig. 3.2). Shade plots were also used to visualise the relative concentration of euphausiid species across the *a priori* factors of day/night and isobath, where a white space indicates that the species was not present, and the grey to black shading was linearly proportional to the concentration. Within each study area, a two-factor permutational

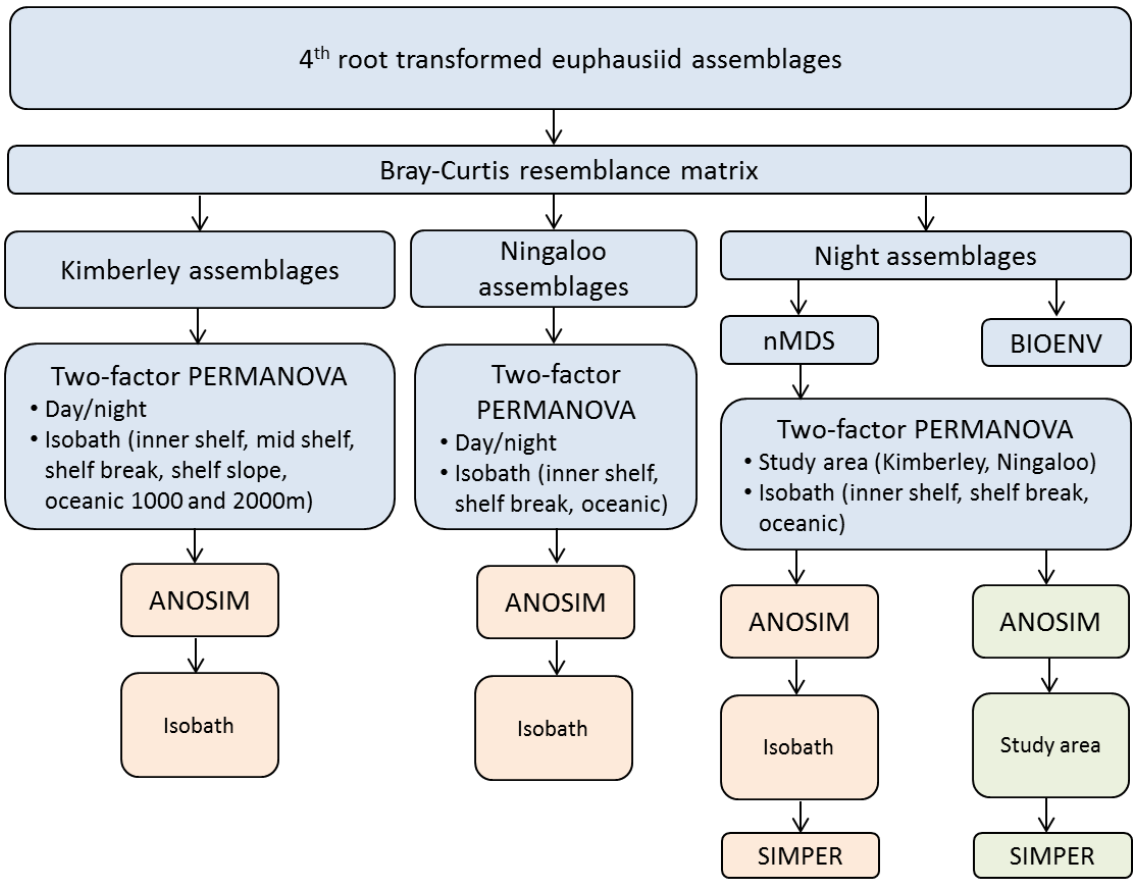


Figure 3.2 The sequence of multivariate statistical tests on euphausiid assemblages from the Kimberley and Ningaloo study areas, and between study areas using night assemblages only. nMDS = non-metric multidimensional scaling, PERMANOVA = permutational MANOVA, ANOSIM = analysis of similarities, SIMPER = similarity percentage, BIOENV = Biota and Environment Matching.

multivariate analysis of variance (PERMANOVA) was used to test the hypothesis that euphausiid assemblages did not differ across day and night stations or isobath and that there were no significant interactions between these two factors (Anderson 2005). Between study areas, a two-factor PERMANOVA was used to test the hypothesis that euphausiid assemblages did not differ across study area or isobath, and that there were no significant interactions between these two factors. Analysis of Similarity (ANOSIM) and Similarity Percentage (SIMPER) routines were used for pair-wise testing and to identify the euphausiid species driving any differences between assemblages (Clark & Warwick 2001).

Euphausiid assemblages were correlated with abiotic and biotic oceanographic variables using a Biota and Environment Matching (BIOENV) sub-routine (Clarke & Ainsworth 1993) (Fig. 3.2). This analysis determined the subset of environmental variables that best matched with euphausiid assemblages, and included mean seawater density, mean dissolved oxygen, mean mesozooplankton settled volume and mean fluorescence across the 150 m water column sampled. Prior to analysis, draftsman plots revealed which environmental variables required transformation and which were strongly correlated with each other ($r^2 > 0.7$) and subsequently omitted from the analyses. No transformations were applied, but distance to coast and surface fluorescence were omitted from the analysis due to co-correlation with mean dissolved oxygen ($r^2 = -0.83$) and average fluorescence ($r^2 = 0.85$), respectively.

Results

Kimberley marine environment

During the austral autumn, most stations were characterised by a low salinity (< 34.7 psu) water mass, likely to be Indonesian Throughflow Water (Menezes et al. 2013) (Fig. 3.3). A warmer and more saline shallow surface layer was also detected. Mean seawater density averaged 22.3 ± 0.2 σ_t for the Kimberley study area, with density increasing from shelf (21.6 ± 0.1 σ_t) to oceanic stations (22.7 ± 0.2 σ_t) (Table 3.1). Mean dissolved oxygen was highest for inner shelf stations (186.0 ± 2.5 µmol L^{-1}) and lowest for oceanic (1000 m) stations (171.6 ± 2.3 µmol L^{-1}). Mixed layer depths ranged from 12 - 66 m, with inner shelf stations being relatively well mixed (42 ± 4 m) and shelf break stations being the most stratified (26 ± 4 m). Mean fluorescence was highest for inner shelf stations (27.2 ± 1.3 RFU), and lowest for oceanic (1000 m) stations (20.4 ± 0.4 RFU). Mean mesozooplankton settled volume was highest for inner shelf stations

(0.50 ± 2.0 ml m^{-3}), and similar for shelf break (0.1 ± 0.03 ml m^{-3}) and oceanic (1000 m) stations (0.1 ± 0.03 ml m^{-3}).

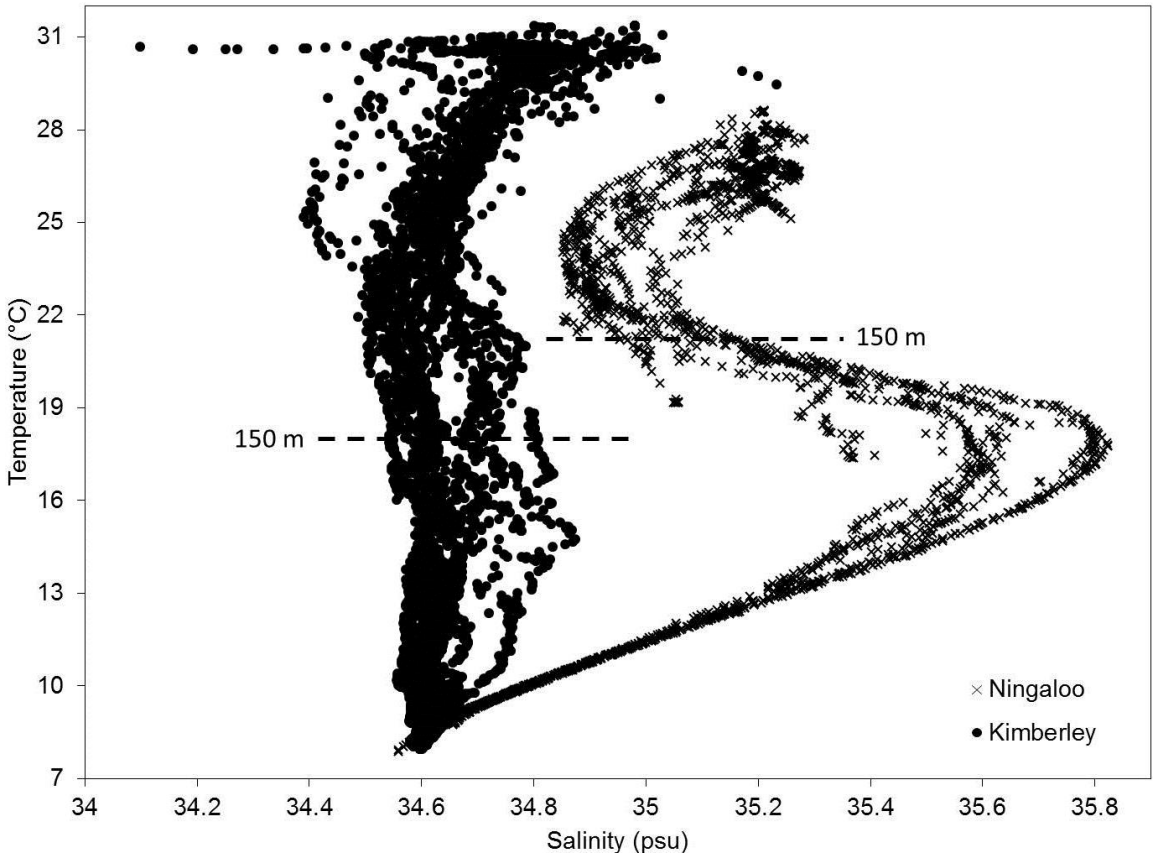


Figure 3.3 A temperature - salinity plot, of the upper 500 m of the water column, for the Kimberley and Ningaloo study areas off north-western Australia. The 150 m water column depth is indicated.

Table 3.1 A comparison of environmental variables for the Kimberley and Ningaloo marine environment from 0 - 150 m depth. Mean and ranges are calculated from all stations sampled for the Kimberley and Ningaloo study areas.

	Kimberley	**Ningaloo**
Mean temperature (°C)	26.8 (17.3 - 31.2)	26.2 (20.7 - 28.6)
Mean salinity (psu)	34.7 (33.2 - 35.2)	35.1 (34.8 - 35.3)
Mean seawater density (σ_t)	22.4 (21.3 - 22.9)	23.0 (22.6 - 23.4)
Mean dissolved oxygen (µmol L^{-1})	201.5 (179.4 - 300.7)	194.5 (18.5 - 204.5)
Mean fluorescence (RFU)	23.3 (19.6 - 33.4)	25.5 (19.4 - 31.6)
Mixed layer depth (m)	36.6 (12 - 66)	80 (34 - 150)

Ningaloo marine environment

The 0 - 150 m water column off Ningaloo was mainly dominated by Tropical Surface Water (> 25°C, 34.8 - 35.2 psu) (Fig. 3.3), overlaying a low dissolved oxygen, relatively high nitrate layer at ~110 m. Below this, South Indian Central Water (150 - 350 m) and Sub-Antarctic Mode Water (350 - 500 m) also occupied the water column. Seawater of the top 150 m was denser, on average, for the Ningaloo study area (23.0 ± 0.1 σ_t) compared to the Kimberley, and exhibited a similar trend to the Kimberley of increasing density from inner shelf stations (22.7 ± 0.1 σ_t) to oceanic (1000 m) stations (23.1 ± 0.1 σ_t) (Table 3.1). Mean dissolved oxygen was highest at inner shelf stations (196.8 ± 1.9 µmol L^{-1}), and decreased to 188.9 ± 1.5 µmol L^{-1} at oceanic (1000 m) stations. All inner shelf stations were well mixed throughout the water column, and the shelf break stations had, on average, the deepest mixed layers (92 ± 17.4 m). Mean fluorescence was highest for inner shelf stations (27.8 ± 1.3 RFU), and lowest for oceanic (1000 m) stations (22.4 ± 0.5 RFU). Mesozooplankton settled volume was also highest for shelf stations (0.2 ± 0.1 ml m^{-3}), and decreased slightly for shelf break (0.1 ± 0.04 ml m^{-3}) and oceanic stations 0.2 ± 0.1 ml m^{-3}).

Euphausiid assemblages off the Kimberley

Twenty euphausiid species were identified off the Kimberley study area (Fig. 3.4). Nine species had tropical affinities and 11 had tropical/subtropical affinities. *Pseudeuphausia latifrons* was the most abundant species across the shelf to shelf break, and *S. carinatum* dominated in deeper waters at shelf slope and oceanic stations. The presence of tropical species, *Euphausia fallax*, *Euphausia sibogae* and *Nematoscelis gracilis*, represent new records for the Kimberley study area. Species richness increased from a single species, *P. latifrons*, on the inner shelf, to 17 species at

oceanic stations; in general, the number of species recorded at each station increased towards oceanic stations.

The abundance of *P. latifrons* resulted in the inner shelf having the highest concentrations for the study area of 1862 ± 713 inds·1000 m^{-3}. Inner shelf stations for transects D and E were anomalous, however, in having very low concentrations of *P. latifrons* at transect D (< 6 inds·1000 m^{-3}), and low concentrations of unidentified and damaged euphausiids were collected at transect E.

Total euphausiid concentrations declined from the inner shelf to the shelf slope (328 ± 67 inds·1000 m^{-3}), but then increased to 996 ± 172 inds·1000 m^{-3} at oceanic stations (2000 m). *Stylocheiron carinatum* and *Euphausia mutica* dominated these deeper oceanic stations and all members of the genus *Thysanopoda*, excluding *Thysanopoda tricuspidata*, were also greater in concentration at these deeper stations (Fig. 3.4).

Total concentrations sampled during the night (1388 ± 268 inds·1000 m^{-3}) were significantly higher than those sampled during the day (476 ± 193 inds·1000 m^{-3}) ($p < 0.001$, $n = 44$, Kruskal-Wallis).

PERMANOVA revealed significant differences in Kimberley euphausiid assemblages between the factors of isobath ($P < 0.001$) and day/night ($P = 0.0156$), with no significant interaction between the two factors ($P = 0.070$). ANOSIM pairwise comparisons of assemblages revealed that inner shelf and mid shelf assemblages significantly differed from all other isobaths ($R > 0.31$, $P < 0.032$). Shelf break assemblages significantly differed from oceanic assemblages ($R > 0.20$, $P < 0.036$), but not shelf slope assemblages ($R = -0.09$, $P = 0.757$). Shelf slope assemblages were similar to 1000 m oceanic assemblages ($R = -0.12$, $P = 0.917$), but not 2000 m oceanic

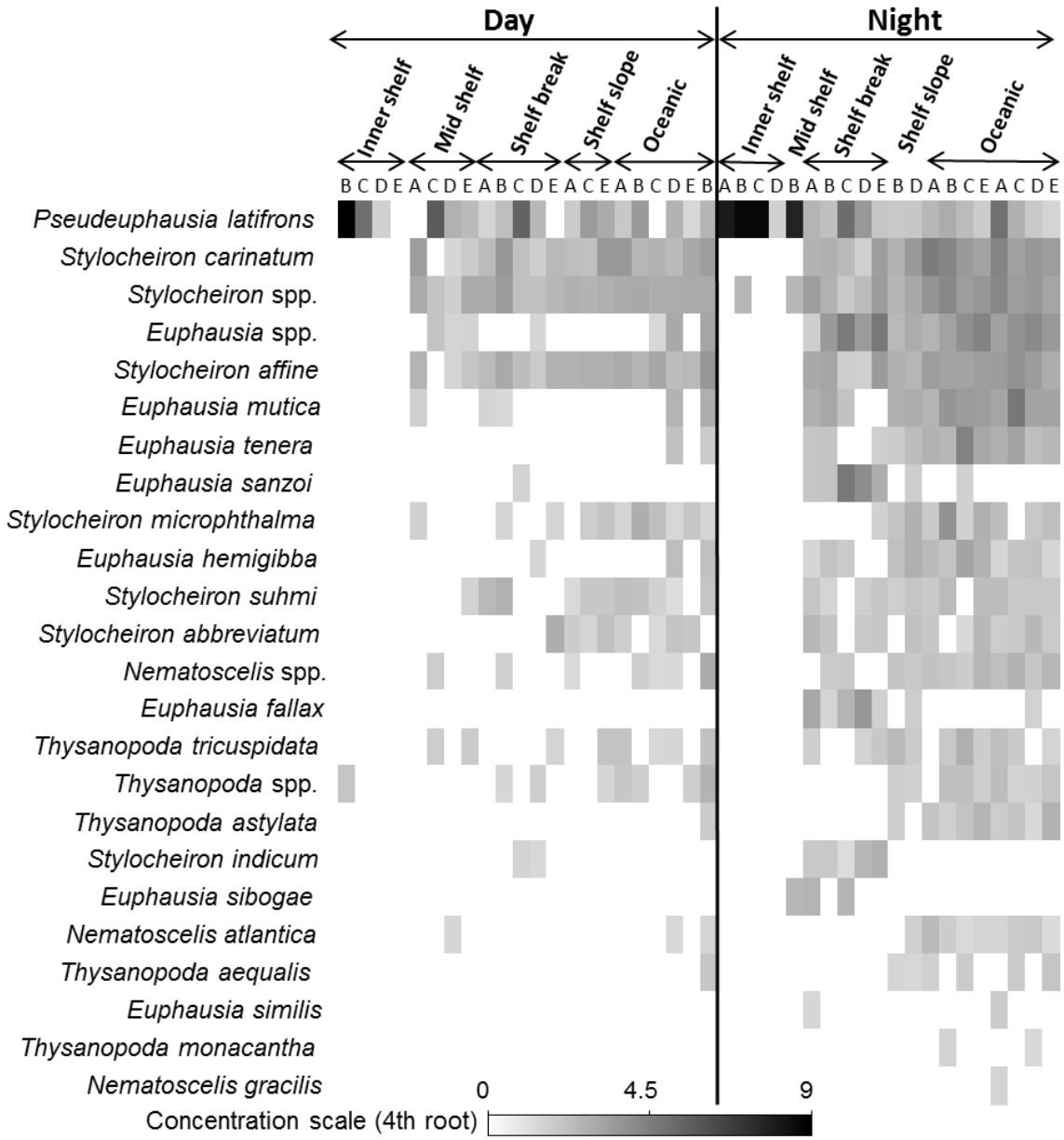


Figure 3.4 Shade plot of fourth-root transformed euphausiid assemblages of the Kimberley study area, ordered by day and night, isobath, and transect (A, B, C, D, E). Shading is linearly proportional to the concentration of the euphausiid species, and white space indicates the species was not collected. Ordering of species is based on total concentrations, from highest to lowest.

assemblages (R = 0.41, P = 0.016), and 1000 m and 2000 m oceanic assemblages did not significantly differ (R = -0.08, P = 0.728).

There was no significant difference in euphausiid assemblages between samples taken on the spring tide (transect A) and neap tide (transect C) (R= 0.00, P= 0.403), or

between total euphausiid concentrations for transects A and C (p = 0.620, Kruskal-Wallis).

Euphausiid assemblages off Ningaloo

Nineteen euphausiid species were identified from the Ningaloo transects (Fig. 3.5). The assemblage included a mix of seven tropical species, 11 tropical/subtropical species and *Euphausia recurva*, a species that occupies both subtropical and temperate waters. *Pseudeuphausia latifrons* was the most abundant species across the Ningaloo study area, followed by *S. carinatum*, *Stylocheiron abbreviatum*, *Euphausia sanzoi* and *E. mutica*. *Euphausia fallax* was also identified off Ningaloo and is recognized as a new record for the area. Eleven euphausiid species were identified across inner shelf stations and 16 for both shelf break and oceanic stations. The mean number of species recorded at each station was higher for shelf break and oceanic stations than shelf stations.

Total euphausiid concentrations were greatest at stations sampled on the inner shelf, 3900 ± 1171 inds·1000 m^{-3}, and were mostly *P. latifrons* (3851 ± 1176 inds·1000 m^{-3}). Stations sampled at the shelf break were similarly high, 3210 ± 2058 inds·1000 m^{-3}, however, this was, in part, due to very high concentrations of *P. latifrons* at Transect E (1627 inds·1000 m^{-3}), in comparison to total euphausiid concentrations at other shelf break stations (< 861 inds·1000 m^{-3}). *Euphausia sanzoi*, *Euphausia diomedeae*, *T. tricuspidata*, *E. recurva*, and *S. abbreviatum* appeared to peak in abundance over the shelf break (Fig. 3.5). Stations sampled in oceanic waters had a relatively lower total euphausiid concentration of 870 ± 207 inds·1000 m^{-3}, and were largely comprised of *S. carinatum* (159 ± 51 inds·1000 m^{-3}), *P. latifrons* (156 ± 98 inds·1000 m^{-3}) and *E. mutica*

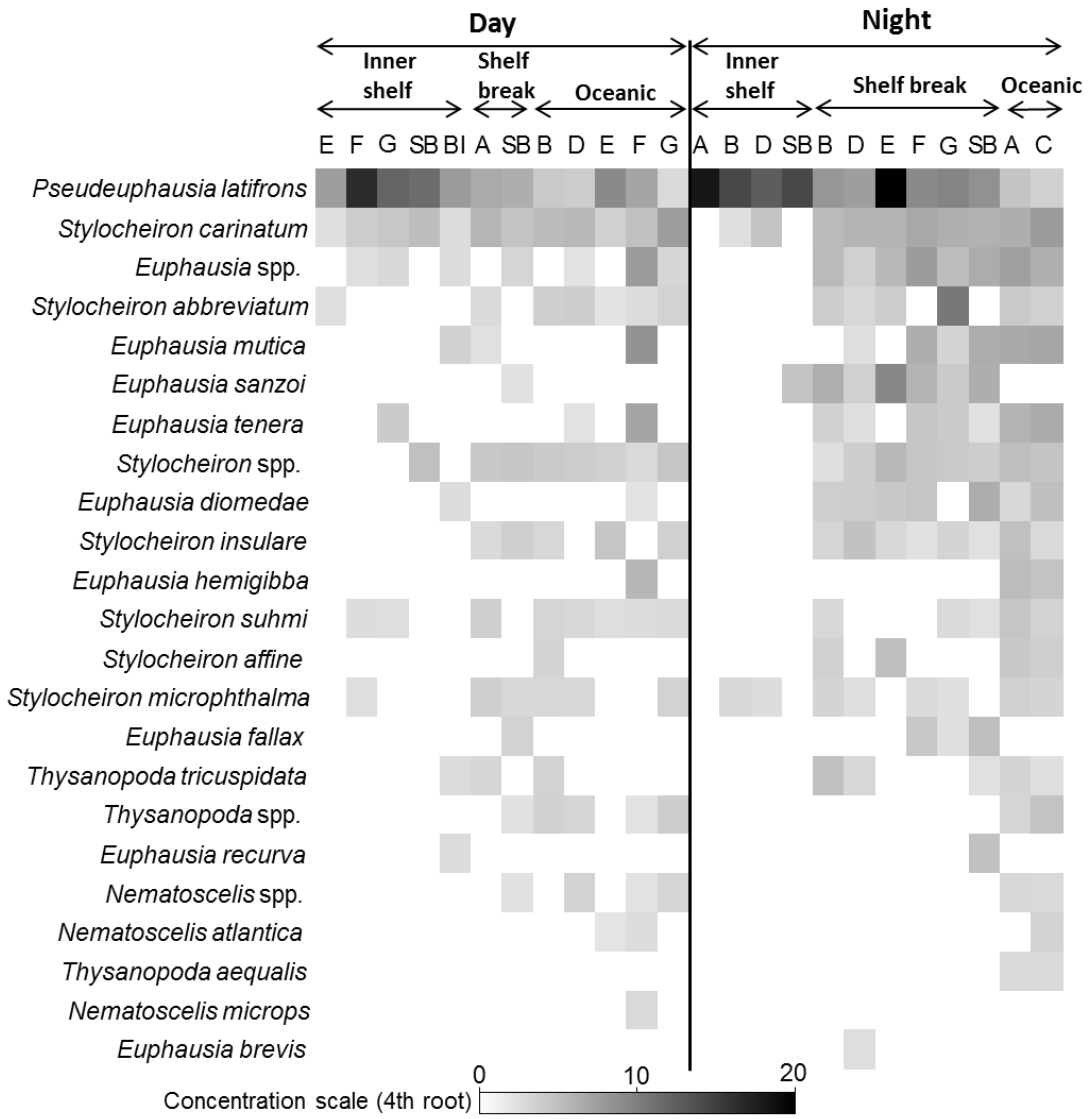


Figure 3.5 Shade plot of fourth-root transformed euphausiid assemblages of the Ningaloo study area, ordered by day and night, isobath, and transect (A, B, C, D, E, F, G, SB, BI). Shading is linearly proportional to the concentration of the euphausiid species, and white space indicates the species was not collected. SB = Sandy Bay and BI = Barrow Island. Ordering of species is based on total concentrations, from highest to lowest. Note the change in scale when compared with Figure 3.4.

(138 ± 75 inds·1000 m^{-3}). *Euphausia tenera*, *Stylocheiron microphthalma*, and *Stylocheiron suhmi* showed a pattern of increasing abundance with increasing isobath. *Nematoscelis microps, Nematoscelis atlantica*, *Euphausia hemigibba* and *Thysanopoda aequalis* were only identified from stations in oceanic waters. Total concentrations sampled during the night (4159 ± 1460 inds·1000 m^{-3}) were significantly higher than

those samples during the day (1414 ± 611 inds·1000 m^{-3}) (p = 0.008, n = 24, Kruskal-Wallis).

PERMANOVA revealed significant differences in Ningaloo euphausiid assemblages between the factors of isobath (P < 0.001) and day/night (P = 0.006), with no significant interaction between the two factors (P = 0.053). ANOSIM pairwise comparisons revealed significantly different assemblages at all three isobaths (R > 0.44; P < 0.002).

Comparison of euphausiid assemblages of the north-west marine bioregion

The Kimberley and Ningaloo study areas had 14 species in common out of the 25 species identified in total. *Pseudeuphausia latifrons* was the most abundant species for both study areas. Total euphausiid concentration was significantly greater for Ningaloo (2786 ± 825 inds·1000 m^{-3}) than for the Kimberley (891 ± 174 inds·1000 m^{-3}) based on all sampled stations during the day and night (p = 0.001, n = 68).

A nMDS ordination on euphausiid assemblages sampled during the night revealed a separation of shelf assemblages from shelf break and oceanic assemblages (Fig. 3.6). Inner shelf assemblages for both study areas were relatively similar, except for Kimberley transect E, where no euphausiids were recorded. Shelf break assemblages were relatively similar, but did have some separation between the study areas. Oceanic assemblages were also relatively similar for both study areas. A PERMANOVA revealed euphausiid assemblages sampled during the night differed significantly across study area (P = 0.002) and isobath (P < 0.001), and there was no significant interaction between the two factors (P = 0.108) (Table 3.2). Isobath was more important than study area in structuring the assemblages.

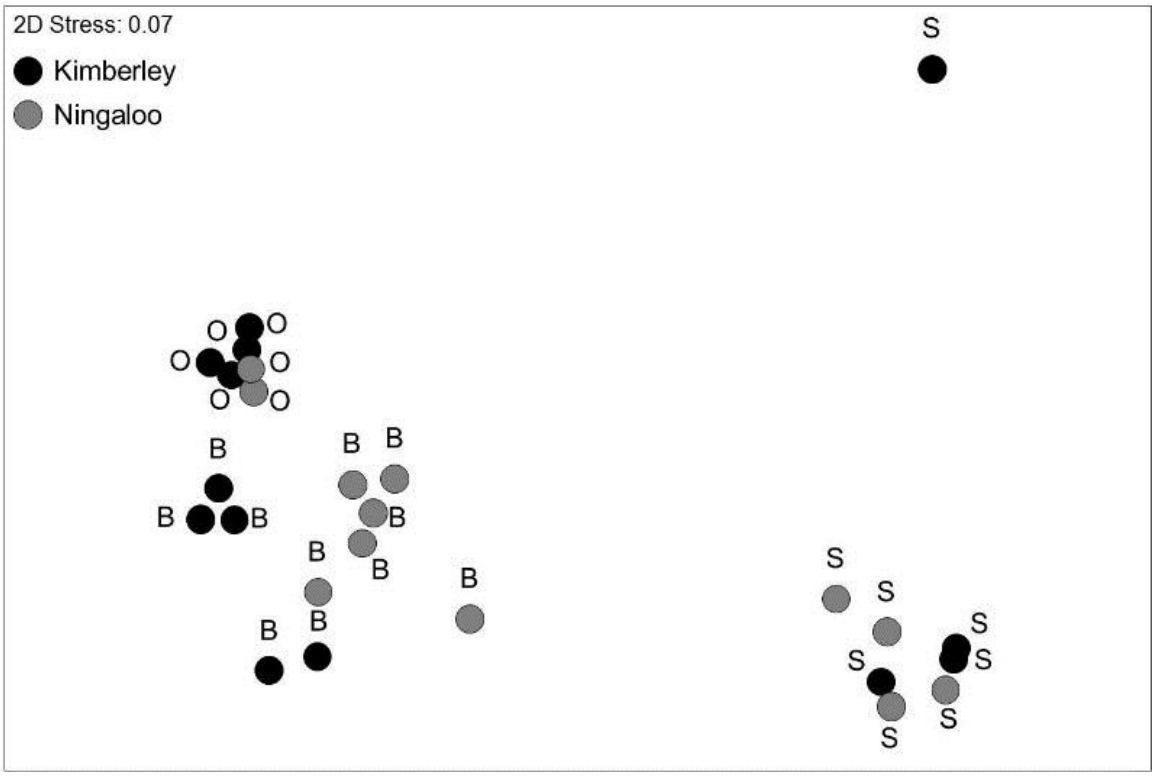


Figure 3.6 A nMDS ordination showing similarities in euphausiid assemblages of the north-west marine bioregion of Australia. Assemblages are defined by study area and isobath (S = inner shelf, B = shelf break, O = oceanic).

Table 3.2 A two-factor PERMANOVA testing the effect of study area (Kimberley and Ningaloo) and isobath (inner shelf, shelf break, oceanic) on the structuring of euphausiid assemblages of the north-west bioregion of Australia. Asterisks denote a significant difference.

Factor	df	MS	F	P
Study area	1	2098.7	4.00	0.002*
Isobath	2	15338.0	29.26	0.000*
Study area x isobath	2	812.4	1.55	0.108
Residual	19	524.2		
Total	24			

ANOSIM revealed that inner shelf assemblages differed significantly from shelf break ($R = 0.93$, $P < 0.001$) and oceanic assemblages ($R = 0.99$, $P < 0.001$), and shelf break assemblages differed significantly from oceanic assemblages ($R = 0.62$, $P < 0.001$). *Pseudeuphausia latifrons* was the most important species on the inner shelf driving the differences between shelf break and oceanic assemblages. *Euphausia sanzoi* and *P. latifrons* were greater in abundance for the shelf break and were the most important species driving the differences with oceanic assemblages (Table 3.3). Oceanic

assemblages were distinguished by higher concentrations of *E. hemigibba*, *E. mutica* and *E. tenera*.

Table 3.3 One-way ANOSIM and SIMPER of euphausiid assemblages compared across isobath (inner shelf, shelf break and oceanic) for all stations sampled across the north-west marine bioregion of Australia. Shading indicates the assemblage typical for each isobath; un-shaded areas indicate comparisons between isobaths, with significant differences marked with an asterisk. The five species contributing the greatest concentrations are listed for the isobath comparisons and superscript denotes the isobath at which each species was most abundant (S = inner shelf, B = shelf break, O = oceanic). Ave. diss. = average dissimilarity.

	Inner shelf (50 m)	**Shelf break (200 m)**	**Oceanic (1000 m)**
Inner shelf (50 m)	Ave. diss. = 66.0% *P. latifrons*		
Shelf break (200 m)	*$\bar{R}$= 0.93, P = 0.0001 Ave. Diss. = 75.3% *P. latifrons* (S) *E. sanzoi* (B) *S. carinatum* (B) *S. abbreviatum* (B) *E. fallax* (B)	Ave. diss. = 62.7% *P. latifrons* *S. carinatum* *E. sanzoi* *S. abbreviatum*	
Oceanic (1000 m)	*$\bar{R}$= 0.99, P = 0.0003 Ave. Diss. = 86.6% *P. latifrons* (S) *E. mutica* (O) *S. carinatum* (O) *E. tenera* (O) *S. affine* (O)	*$\bar{R}$= 0.62, P = 0.0001 Ave. Diss. = 45.75% *E. sanzoi* (B) *P. latifrons* (B) *E. hemigibba* (O) *E. mutica* (O) *E. tenera* (O)	Ave. diss. = 79.7% *S. carinatum* *E. mutica* *E. tenera* *S. affine* *E. hemigibba*

Environmental variables driving assemblage variation

Euphausiid assemblages for the north-west marine bioregion were correlated with mean seawater density, mean dissolved oxygen, mean mesozooplankton settled volume and mean fluorescence of the 150 m water column. Euphausiid assemblages had the highest correlation with mean seawater density, mean fluorescence, and mesozooplankton settled volume ($\rho = 0.54$, $P < 0.001$). Mean fluorescence and mesozooplankton settled volume were the most significant variables in the model. All four variables combined returned a slightly lower $\rho = 0.52$. Environmental variables were overlayed on nMDS ordinations of the euphausiid assemblages using bubble plots (Fig. 3.7). A decrease in mean fluorescence from shelf to oceanic stations

correlated with a separation of euphausiid assemblages into shelf, shelf break and oceanic groupings (Fig. 3.7A). High mesozooplankton settled volume distinguished shelf stations from shelf break and oceanic stations (Fig. 3.7B), however, these high volumes on the shelf were for Kimberley stations, and not Ningaloo shelf stations. This indicates a low influence of mesozooplankton settled volume on euphausiid assemblages on the shelf, as assemblages from both study areas were relatively similar regardless.

The similarities in euphausiid assemblages across study areas for shelf break and oceanic stations correlated with relatively high mean seawater density (Fig. 3.7C). Despite Kimberley shelf stations having a lower mean seawater density in comparison to Ningaloo shelf stations, euphausiid assemblages were relatively similar, which indicates that differences in mean seawater density did not have a strong influence on shelf assemblages. Mean dissolved oxygen was similar across most stations of the bioregion (Fig. 3.7D), however, the lower oxygen concentrations at some Kimberley shelf break stations may have accounted for some of the difference observed in shelf break euphausiid assemblages across the two study areas.

Discussion

The north-west marine bioregion of Australia was found to harbour 29% of the world's euphausiid species. The euphausiid assemblages were characterised largely by relatively high concentrations of the tropical, neritic species, *P. latifrons*, across the shelf, whereas deeper waters had more species with *S. carinatum* the most abundant. Ningaloo harboured greater total concentrations of euphausiids than the Kimberley,

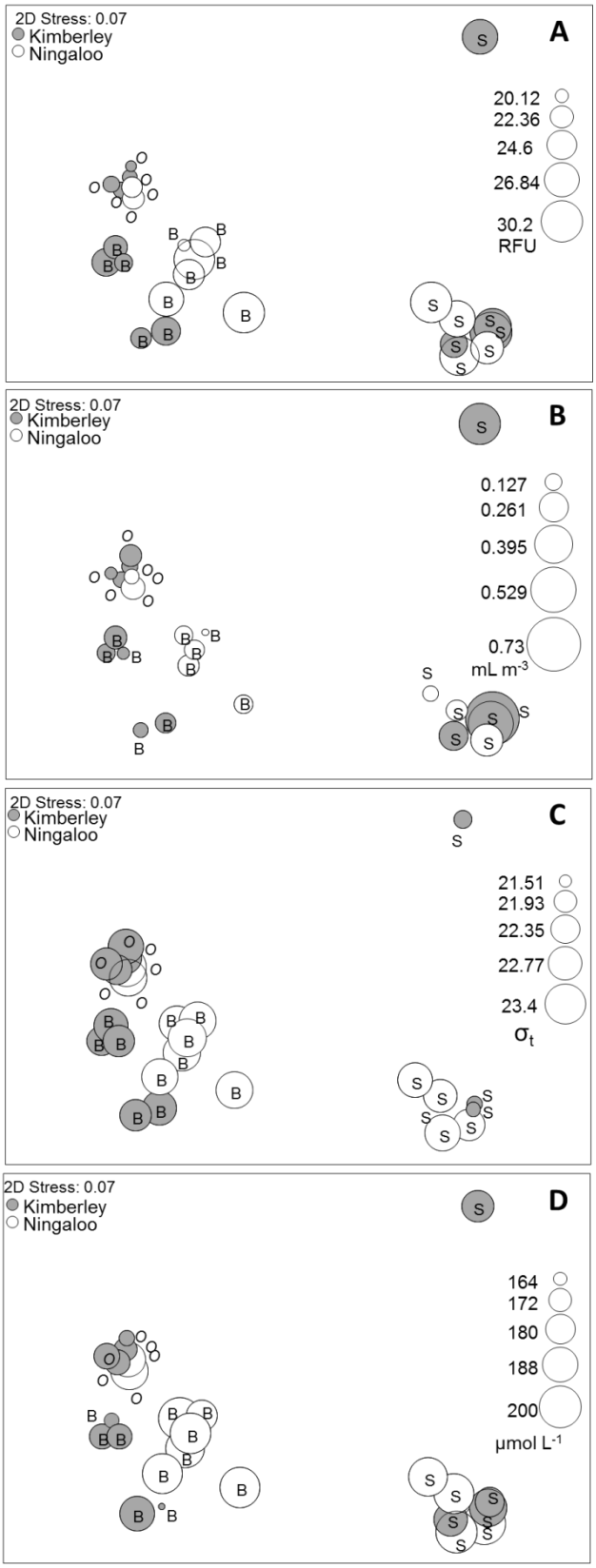


Figure 3.7 A bubble plot of environmental variables A) mean fluorescence, B) mesozooplankton settled volume, C) mean seawater density and D) mean dissolved oxygen (0-150 m depth) overlaid on nMDS ordinations of euphausiid assemblages of the north-west marine bioregion of Australia. Bubbles are coded by study area and isobath (S = inner shelf, B = shelf break, O = oceanic).

and this may be linked to the physical oceanography and narrowness of the shelf at Ningaloo. Mean seawater density and mean fluorescence correlated significantly with euphausiid assemblages, and isobath (depth) significantly structured assemblages along a gradient from the inner shelf to oceanic stations.

An earlier, localised study investigating shelf waters showed *P. latifrons* to constitute 98.5% of the euphausiid catch off Ningaloo (Wilson et al. 2003a). This pattern is not unlike that observed across south-east Asian waters. The South China Sea is dominated by *P. latifrons* on the shelf and 25 species were found in deeper waters. *Pseudeuphausia latifrons* was the only species found throughout the Gulf of Thailand, with the occasional presence of *S. carinatum* (Brinton 1975).

All of the euphausiid species identified from the north-west marine bioregion have previously recorded distributions throughout the Indo-Australian Archipelago (Brinton 1975) and the Pacific Ocean (Brinton 1962), and reflect the connection between the two oceans via the Indonesian Throughflow (Cresswell et al. 1993; Meyers et al. 1995). The euphausiid assemblage mix may have also been influenced by the transport of species via the Eastern Gyral Current and the South Indian Countercurrent (Menezes et al. 2014). Eight of the species identified in this study have distributions spanning the Indian Ocean basin (Brinton 2000), and may have been transported towards the north-west marine bioregion via eastward flowing currents. For example, *E. mutica* is rare throughout the Indo-Australian Archipelago (Brinton 1975), but it has a wide distribution across the Indian Ocean basin.

The Ningaloo study area had an average total euphausiid concentration almost three times greater than that found in the Kimberley study area. This difference was largely

driven by the higher concentration of *P. latifrons* on the shelf at Ningaloo, particularly at transect A (~ 11,000 ind.m^{-3}). Fluorescence concentrations were similar for both Kimberley and Ningaloo shelf stations, and chlorophyll *a* concentrations had a significant proportion of larger phytoplankton cells, such as diatoms, across the shelf at both locations (Thompson & Bonham 2011; Rossi et al. 2013a). Of the environmental variables included in this study, mean dissolved oxygen and mean seawater density were higher at Ningaloo shelf stations, and shelf stations were closer to the coast due to the narrow continental shelf. Rossi et al. (2013a) also noted the presence of "trapped" sub-mesoscale eddies off Ningaloo during the time of this study and speculated that their occurrence may be important for retention and promoting primary production. It appears that the physical oceanography and narrowness of the shelf at Ningaloo could be influencing the higher concentrations of *P. latifrons*. Although the measures of food availability did not relate to the high concentrations in this study, it should not be ruled out as a significant variable influencing euphausiid assemblages in the north-west bioregion of Australia.

Attempting to explain the variation in euphausiid assemblages of the north-west marine bioregion using environmental variables returned a significant, but not a strong, relationship with mean seawater density and mean fluorescence. These environmental variables have also been noted throughout the literature as being potential drivers of euphausiid distributions (Brinton 1962; Hirota 1987; Gibbons 1997; Ashjian et al. 2008; Antezana 2009). Seawater density, dissolved oxygen and mesozooplankton settled volume were identified as drivers of differences in euphausiid assemblages across Tropical Surface Water and Sub Tropical Surface Water between 22° - 34°S of the LC (Chapter 2). It appears that the physical properties of the

water column, along with determinants for food availability, play a role in structuring euphausiid assemblages in this part of the eastern Indian Ocean. To account for the remaining variation not explained by environmental variables, many other factors should be considered, such as the distributions of each euphausiid species. For example, certain species (*S. carinatum*) are cosmopolitan in their distribution and may tolerate environments differing in oceanographic properties (Brinton 2000; Sutton et al. 2015).

The Kimberley and Ningaloo study areas had relatively similar euphausiid assemblages, and there was a gradient from inner shelf to oceanic stations. While mean fluorescence was on average low for oceanic stations and high for inner shelf stations, it did not fully explain the differences in assemblages delineated by isobath. Isobath, or depth, significantly structured assemblages cross-shelf, and this was particularly evident given most euphausiid species are oceanic (Mauchline & Fisher 1969; Brinton et al. 2000). *Pseudeuphausia latifrons* is typically found in less than 100 m of water, which would explain its common occurrence and suitability to shelf waters.

In conclusion, the euphausiid assemblages of the north-west marine bioregion were characterised by 25 euphausiid species with high concentrations of *P. latifrons* in inner shelf waters. The assemblages appear to reflect the connection between the Indian and Pacific Oceans provided by the Indonesian Throughflow, and may have also been influenced by the surrounding eastern Indian Ocean circulation. Physical properties of the water column and food availability are recurrent drivers of euphausiid assemblage variation in the eastern Indian Ocean.

Chapter 4: Vertical structuring of epipelagic euphausiid assemblages across a thermohaline front in the south-east Indian Ocean

Abstract

The epipelagic vertical structuring of euphausiid life stages and species assemblages was investigated across a thermohaline front between Leeuwin Current Water (LCW) and Sub Tropical Surface Water (STSW) in the south-east Indian Ocean (29°S - 31°S, 111.5°E - 115°E). Twenty five species of euphausiids were identified across the front; 16 of these were shared by both water masses, of which most exhibited a preference for LCW. Differences in euphausiid assemblages between LCW and STSW were mostly driven by the numerical abundance of shared species, rather than the presence or absence of species in either water mass. Diel vertical migration was evident in both water masses, and the dominant euphausiid species, *Stylocheiron carinatum* and *Euphausia recurva*, were most abundant during the night. Significant structuring of assemblages across depth was only observed in STSW, both during the day and at night. This was likely a result of stratification of temperature, salinity and dissolved oxygen to 200 m depth. LCW had a more uniform water column, and no significant structuring was observed for euphausiid assemblages during the day or night. Mean mesozooplankton settled volume and mean chlorophyll *a* concentration appeared to be driving the euphausiid assemblage variation in LCW and in the upper 100 m of STSW. Mean temperature drove the variation in assemblages located at > 100 m depth in STSW. This is the first study to examine vertical structuring and environmental drivers of euphausiid life stages and species assemblages in oceanic waters in the south-east Indian Ocean.

Introduction

Euphausiids occupy the vertical and horizontal extent of most of the world's oceans. They ascend to shallower depths during the night, and descend to deeper depths during the day (diel vertical migration) (Brinton 1967; Mauchline & Fisher 1969; Youngbluth 1976). The deepest record for a euphausiid species was *Thysanopoda minyops*, captured at 5800 m (Brinton et al. 1987; Brinton et al. 2000). Some species are considered to be large vertical migrators, up to the order of 1000 m, and others relatively short or non-migrators (Brinton 1962; Youngbluth 1976; Tarling et al. 1999; Brinton et al. 2000). Ontogenetic layering also occurs, where early life history stages inhabit shallower waters, and mature specimens, with increased mobility, inhabit deeper depth strata, particularly during the day (Mauchline 1980; Pillar et al. 1989). The extent of diel vertical migration of euphausiid species through the water column is influenced by environmental tolerance (Brinton 1967; Brinton 1979; Hirota 1987; Sameoto et al. 1987; Barange 1990; Taki 2008), along with light intensity (Lewis 1954; Youngbluth 1976), food availability (Youngbluth 1975; Hu 1978; Gibbons 1993; Taki 2008), predator avoidance (Bollens et al. 1992), and reproductive strategy (Barange 1990; Tarling et al. 1999).

In the south-east Indian Ocean, 31 euphausiid species were recorded along the 110°E meridian between 9°S - 32°S during the first International Indian Ocean Expedition (1962-1965) (McWilliam 1977). Further east, within the Leeuwin Current (LC) system off Western Australia, 32 species of euphausiids have been recorded (Wilson et al. 2003a; Rennie et al. 2009; Sutton et al. 2015). The physical and chemical properties of the water column were found to be significant drivers of variation in euphausiid assemblage structure in the Leeuwin Current (Chapter 2). It is not uncommon for

euphausiid species to be affiliated with particular water masses (Brinton 1975; Dadon & Boltovsky 1982; Gibbons et al. 1995; Tarling et al. 1995).

The anomalous, southward flowing LC comprises warm, less saline water 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; Menezes et al. 2014). As the LC flows south, temperature decreases and salinity increases as a result surface air-sea heat fluxes, eddy advection, geostrophic inflow and mixing with surrounding Sub Tropical Surface Water (STSW) and shelf waters (Pearce et al. 2006; Paterson et al. 2008; Weller et al. 2011; Menezes et al. 2014). The south-east Indian Ocean is usually considered an oligotrophic region, with low chlorophyll *a* concentrations, as a result of the less productive STSW and the suppression of upwelling by the LC (Lenanton et al. 1991; Pearce et al. 2000; Hanson et al. 2005; Rossi et al. 2013b). Oceanographic fronts can often occur between Leeuwin Current Water (LCW) and STSW when the LC meanders from its southwards trajectory to form eddies (Feng et al. 2007; Paterson et al. 2008; Holliday et al. 2012; Paterson et al. 2013; Säwström et al. 2014). Meanders and eddies of the LC are a regular occurrence in the south-east Indian Ocean, particularly during the austral autumn/winter months (Feng et al. 2003)

Oceanographic fronts typically experience differences in sea-surface temperature and salinity of 2 - 5°C and 0.3 - 1.0 psu, respectively, and result from physical processes creating discontinuities in water properties across a sharp gradient (Franks 1992; Belkin et al. 2009). Such fronts allow for in situ comparison of the vertical structuring of biota across depths within different water masses. Often, these thermohaline fronts have associated sharp gradients in other biogeochemical properties such as nutrient

and chlorophyll *a* concentrations (Belkin et al. 2009). As a result, fronts can attract feeding aggregations of higher order consumers, such as fishes (Fiedler & Bernard 1987), seabirds and mammals (Bost et al. 2009).

In the south-east Indian Ocean, attention to date has only been given to the horizontal structuring, rather than the vertical structuring of euphausiids. In July 2010, a large meander of the LC resulted in a strong front between LCW and STSW at about 30°S in the south-east Indian Ocean (Säwström et al. 2014). The aim of this study was to examine the vertical structuring of epipelagic euphausiid assemblages in two distinct water masses, LCW and STSW, separated by this thermohaline front, and to investigate which physical and biotic factors were driving any differences in the assemblages. It is hypothesised that differences in euphausiid assemblages would occur across the two distinct water masses and that vertical structuring of assemblages would be more evident for those sampled during the night than the day.

Methods

Study area

A LC frontal feature between 29°S - 31°S in the south-east Indian Ocean was investigated aboard the R.V. *Southern Surveyor* (voyage 05/2010) during the austral winter (6 - 27 July 2010). Stations were sampled at 0.5° longitudinal intervals across shelf break and oceanic waters between 111.5°E - 115°E (Fig. 4.1) at each of the three latitudes. All stations had a water column depth > 1000 m. In total, 13 stations form the focus of this study, four in LCW and nine in STSW. Water masses were classified based on temperature and salinity, with LCW being warmer (> 20°C) and less saline (<35.6 psu) than STSW (18° - 20°C, >35.6 psu). One LCW station (station 27) was excluded from analyses due to a problem with sampling equipment.

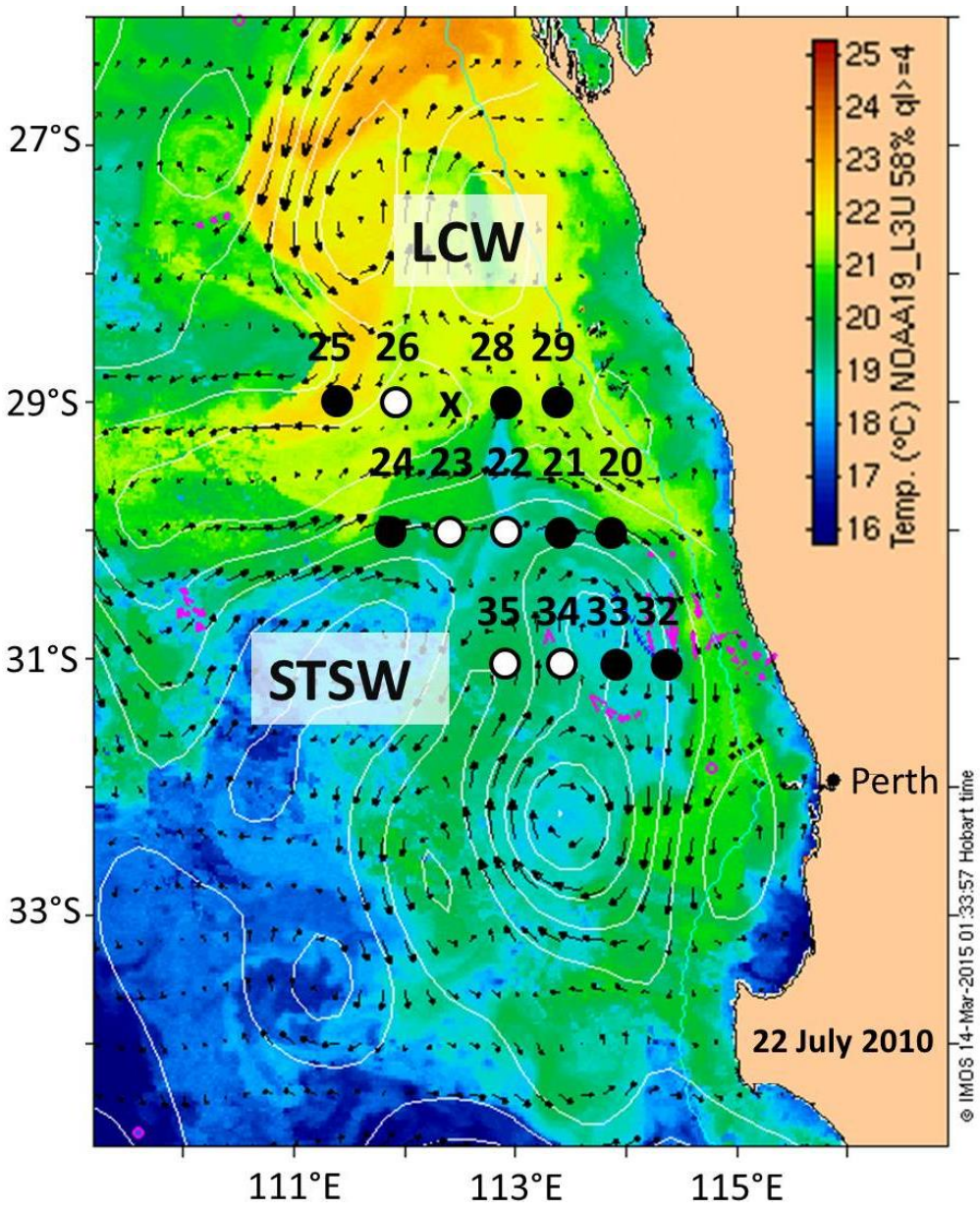


Figure 4.1 Sea surface temperature for the south-east Indian Ocean, 22 July 2010, highlighting the front between Leeuwin Current Water (LCW) and Sub Tropical Surface Water (STSW) and geostrophic flow (IMOS 2015), with zooplankton sampling stations overlayed. White circles indicate stations sampled during the day, and black circles indicate stations sampled during the night. Note the large Leeuwin Current meander in the study area (29°S - 31°S) creating a front between LCW and STSW. Station X was excluded from analyses due to a problem with sampling equipment.

Field and laboratory sampling

The distinction of the frontal feature in the field was obtained by continuous underway measurements of sea surface temperature using a SBE 3T Seabird thermosalinograph and remote sensing (sourced from http://oceancurrent.imos.org.au). Horizontal current velocity and direction were continuously measured using a vessel mounted RDI

75 kHz ocean Surveyor Acoustic Doppler Current Profiler (ADCP). The ADCP measured the current between 10 - 300 m and data were averaged in 8 m depth bins.

Hydrographic measurements from 0 - 1000 m depth were taken using a Sea-bird SBE911 conductivity-temperature-depth (CTD) instrument fitted with a SBE43 oxygen sensor and mounted in a 24 - Niskin bottle rosette. The CTD was further equipped with a Chelsea Aquatracker fluorometer and Biospherical Photosynthetically Active Radiation sensor. Chlorophyll *a* was derived from Niskin bottle water samples and fluorescence measurements, using a linear regression and a detection limit of 0.04 µg L^{-1} (Säwström et al. 2014). For depth strata with chlorophyll *a* values less than the detection limit, an arbitrary value of 0.005 µg L^{-1} was assigned for statistical purposes. Chlorophyll *a* concentrations are expressed as the mean ± standard deviation.

Depth-stratified zooplankton samples were taken using an opening-closing EZ net (mesh size 355 µm; mouth area 1 m^2) at each of the 13 stations regardless of day or night. Four depth strata were targeted at each station; 0 - 50 m, 50 - 100 m, 100 - 150 m and 150 - 200 m. The net was equipped with a flow meter and was controlled using an electronic interface to achieve a tow time of ~ 15 minutes per depth stratum at a vessel speed of 2 knots.

Upon net retrieval, zooplankton samples were preserved in 5% buffered formaldehyde in seawater solution. Estimates of mesozooplankton volume were made by pouring the zooplankton samples through a 1 mm sieve and measuring the settled volume of remaining zooplankton in a graduated cylinder after a 24 h settling period (Gibbons 1999; Suthers & Rissik 2009); volumes were expressed in mL m^{-3} as the mean ± standard deviation. Only mesozooplankton settled volumes for stations sampled

during the night are discussed because of the influence of diel vertical migration. Mature and immature euphausiids were counted and identified to species level with the use of relevant taxonomic keys (Baker et al. 1990; Brinton et al. 2000). Calyptopis and furcilia euphausiid larval stages were enumerated, but not identified to genus or species level. Where necessary, large zooplankton samples were split using a Folsom splitter, and a minimum of 100 specimens, for each of the four life stages, were counted from sub-samples before estimates could be made of the total abundance in a whole sample (Gibbons 1999). Concentrations of euphausiids were represented as the number of individuals per 1000 m^{-3} ± standard error of the mean.

Data analysis

Univariate analyses were conducted using non-parametric Kruskal-Wallis tests for independent samples in IBM SPSS Statistics 21. Univariate analyses were used to test for significant differences between mesozooplankton settled volume and chlorophyll *a* across depth strata and for significant differences in total concentrations of each life history stage for evidence of ontogenetic layering across depth within water masses.

All multivariate analyses were carried out using the PRIMER v7 PERMANOVA+ software package (Anderson et al. 2008; Clarke & Gorley 2015). Prior to analysis, a square root transformation was applied to euphausiid assemblage data to reduce the relative importance of abundant species. A Bray-Curtis resemblance matrix was constructed to quantify the dissimilarity in assemblages amongst samples (Fig. 4.2). Similarities in euphausiid assemblages (mature and immature specimens combined) for each station and depth were visualised using a non-metric Multidimensional Scaling (nMDS) ordination. A 3-way permutational multivariate analysis of variance (PERMANOVA) was used to test the hypotheses that euphausiid assemblages were the same across the

factors of day/night, water mass (LCW and STSW) and depth stratum (0 - 50 m, 50 - 100 m, 100 - 150 m and 150 - 200 m) and that there were no interactions between factors. Analysis of Similarity (ANOSIM) and Similarity Percentage (SIMPER) routines were used for pair-wise testing and to identify the euphausiid species driving the differences between assemblages (Clark & Warwick 2001).

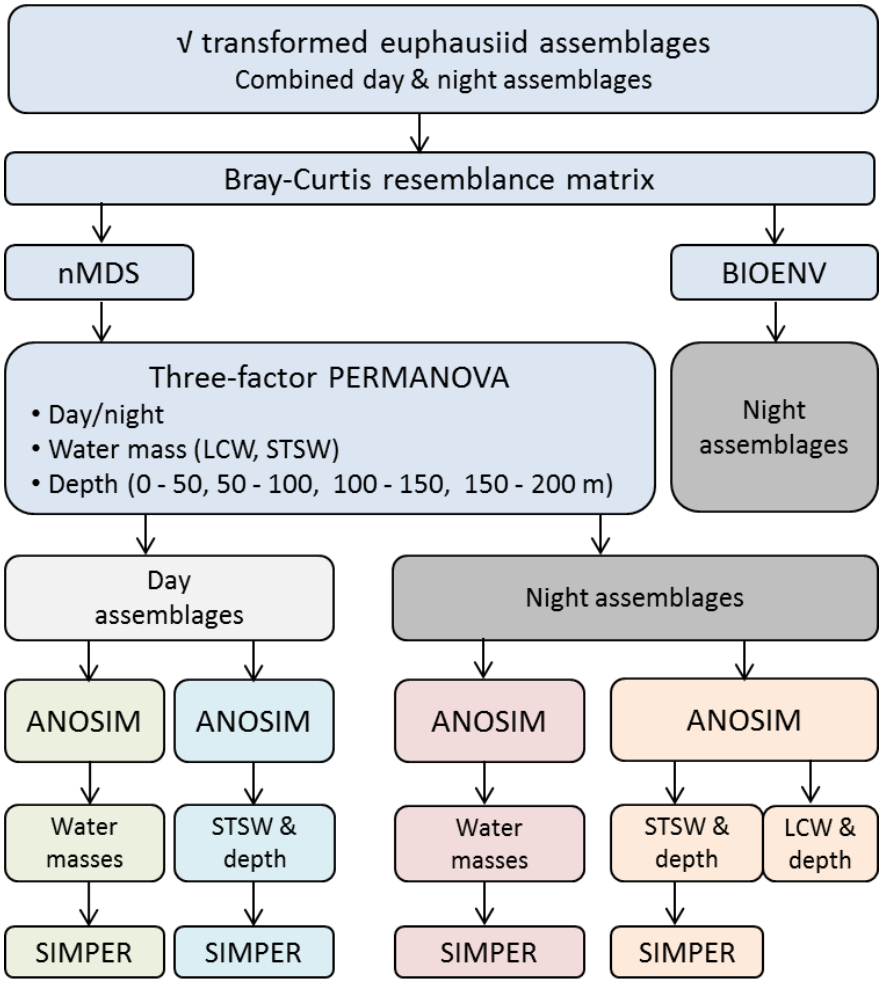


Figure 4.2 The sequence of multivariate statistical tests on euphausiid assemblage across a thermohaline front using *a priori* factors of day/night, water mass (LCW = Leeuwin Current Water, STSW = Sub Tropical Surface Water) and depth (0 - 50, 50 - 100, 100 - 150, 150 - 200 m). nMDS = non-metric multidimensional scaling, PERMANOVA = permutational MANOVA, ANOSIM = analysis of similarities, SIMPER = similarity percentage, BIOENV = Biota and Environment Matching.

Because of diel vertical migration, only euphausiid assemblages from stations sampled during the night (n = 32) were used to investigate the influence of environmental variables on euphausiid assemblage variation. Principal Components Analysis (PCA)

was performed to evaluate the structuring of stations based on environmental variables (mean temperature, mean salinity, mean dissolved oxygen, mean chlorophyll *a* and mesozooplankton settled volume for each depth stratum). Euphausiid assemblages were correlated with abiotic and biotic oceanographic variables using a Biota and Environment Matching (BIOENV) sub-routine (Clarke & Ainsworth 1993) (Fig. 4.2). This analysis determined the subset of environmental variables that best matched with euphausiid assemblages and whether this was significant or not. Prior to analysis, square root transformations were applied to environmental data. Draftsman plots revealed that mean temperature was negatively correlated with mean dissolved oxygen (r^2 = -0.82), and because of this co-correlate, mean dissolved oxygen was removed from analyses.

Results

Oceanographic environment

Remotely-sensed sea surface temperature imagery (sourced from http://oceancurrent.imos.org.au) showed that the oceanographic front separating the LCW and STSW persisted throughout the duration of the study. Around 29°S, a large meander of the LC extended offshore to 109°E in the north and returned towards the shelf break near 30°S, with a strong eastward surface flow (Fig. 4.1). The four stations sampled along 29°S were in LCW, with temperatures throughout the water column (0 - 200 m) ranging from 19.7 - 21.5°C and salinity from 35.4 - 35.8 psu (Table 4.1). To the south, along 30°S and 31°S, cooler STSW with lower water column temperatures and higher salinity of 13.2 - 19.9°C and 35.3 - 35.9 psu, respectively, occurred. The LCW meander did, however, cross the 30°S transect close to station 22 (113°E) (Fig. 4.3B).

Table 4.1 A comparison of environmental variables for Leeuwin Current Water (LCW) and Sub Tropical Surface Water (STSW) for each depth stratum between 0 - 200 m. Mean ± standard deviations are shown.

	LCW			
	0-50 m	**50-100 m**	**100-150 m**	**150-200 m**
Temperature (°C)	21.32 ± 0.10	21.32 ± 0.11	21.25 ± 0.03	20.97 ± 0.35
Salinity (psu)	35.40 ± 0.01	35.40 ± 0.01	35.43 ± 0.02	35.52 ± 0.10
Dissolved oxygen (µmol L^{-1})	222.20 ± 0.90	221.30 ± 1.25	219.27 ± 1.72	216.31 ± 1.74
Chlorophyll *a* (µg L^{-1})	0.42 ± 0.05	0.38 ± 0.06	0.23 ± 0.14	0.07 ± 0.09
Mesozooplankton (mL L^{-1})	0.08 ± 0.04	0.09 ± 0.01	0.07 ± 0.02	0.05 ± 0.03
	STSW			
	0-50 m	**50-100 m**	**100-150 m**	**150-200 m**
Temperature (°C)	18.91 ± 0.57	18.49 ± 0.47	17.36 ± 0.92	15.18 ± 1.17
Salinity (psu)	35.79 ± 0.09	35.83 ± 0.08	35.76 ± 0.08	35.54 ± 0.10
Dissolved oxygen (µmol L^{-1})	233.97 ± 3.85	234.29 ± 3.17	234.24 ± 3.77	235.65 ± 2.42
Chlorophyll *a* (µg L^{-1})	0.35 ± 0.14	0.29 ± 0.11	0.11 ± 0.10	0.03 ± 0.04
Mesozooplankton (mL L^{-1})	0.05 ± 0.01	0.05 ± 0.01	0.03 ± 0.01	0.03 ± 0.00

The thermocline was deeper at all four LCW stations (> 150 m), compared with the average depth of the thermocline for STSW of 80 m (34 - 130 m) (Fig. 4.3). The halocline for both LCW and STSW was always situated at, or slightly above, the thermocline at each station. Concentrations of dissolved oxygen were greater in STSW than LCW, averaging 234.5 µmol L^{-1} (217.1 - 241.7) and 219.7 µmol L^{-1} (212.1 - 223.4), respectively (Fig. 4.3).

Both chlorophyll *a* concentration and mesozooplankton settled volumes were, on average, greater in LCW than STSW. The surface 50 m of the LCW column harboured the most chlorophyll *a* (0.4 ± 0.1 µg L^{-1}) (Table 4.1), followed by the 50 - 100 m stratum (0.4 ± 0.1 µg L^{-1}), and this was mirrored by mesozooplankton settled volume (0.1 ± 0.04 and 0.1 ± 0.01 mL m^{-3}, respectively). The STSW generally had lower mean chlorophyll *a* concentrations than LCW for 0 - 50 m (0.3 ± 0.1 µg L^{-1}) and 50 - 100 m (0.3 ± 0.1 µg L^{-1}), although this difference was not significant ($p = 0.191$). A high concentration of 0.6 µg L^{-1} was, however, recorded in 0 - 50 m at STSW station 24. As with LCW, chlorophyll

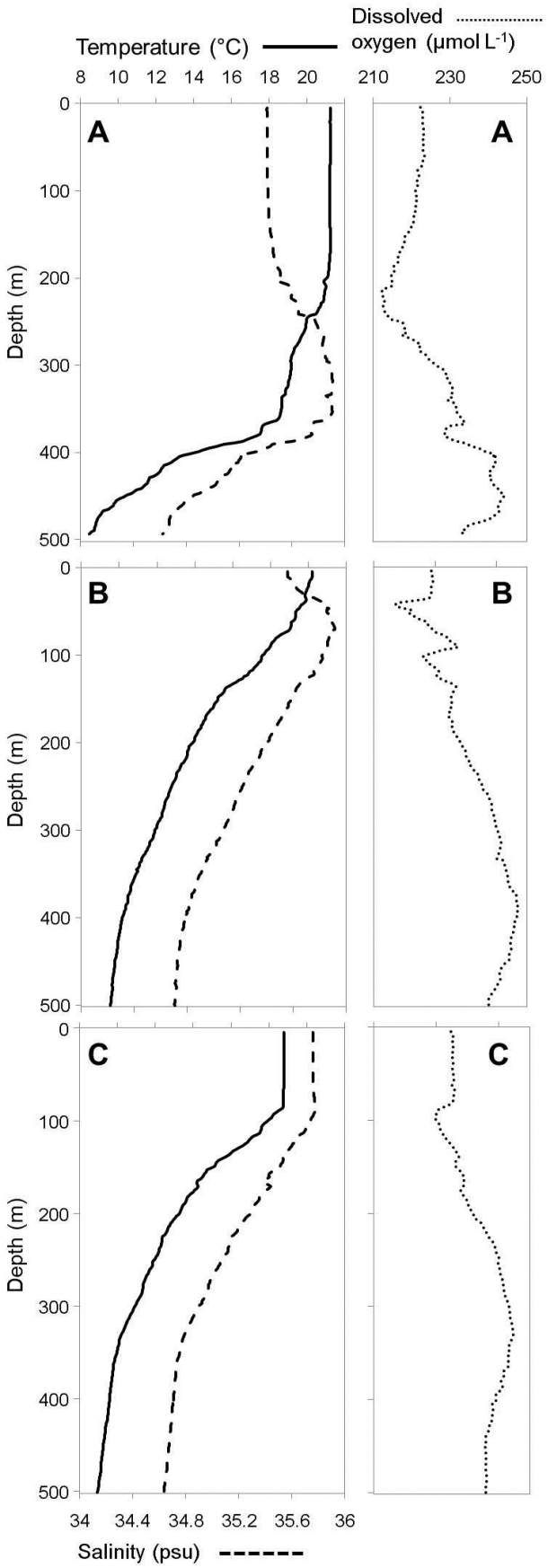


Figure 4.3 Representative temperature-salinity-oxygen profiles to a depth of 500 m for A) station 28 (29°S), B) station 22 (30°S), and C) station 33 (31°S).

a was most concentrated in the surface 100 m of STSW (p = 0.004). Mesozooplankton settled volume, on the other hand, was highest within the surface 0 - 50 m (0.05 ± 0.01 mL m^{-3}), and decreased steadily to 0.03 ± 0.00 mL m^{-3} at 150 - 200 m depth (p = 0.014) for STSW.

In the PCA of environmental variables, PC1 explained 55% of the total variance across depth strata. Mesozooplankton settled volume, mean temperature and mean chlorophyll *a* were the largest contributors to explaining the variation along PC1, and increased in value from left to right, which delineated all LCW depth strata from the deeper depth strata of STSW (Fig. 4.4). PC2 explained 29% of the variance across depth strata and mean salinity was the major contributor to the variation along this axis, followed by chlorophyll *a*. Higher mean salinity and chlorophyll *a* delineated the shallower STSW depth strata from the deeper STSW depth strata and all LCW depth strata.

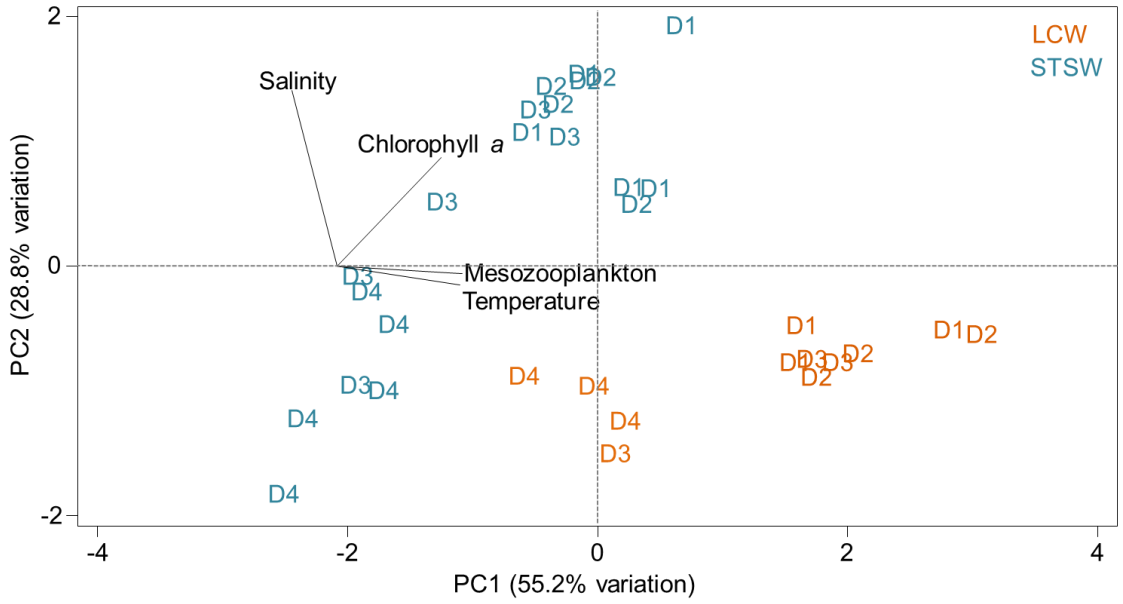


Figure 4.4 PCA ordination of all Leeuwin Current Water (LCW) and Sub Tropical Surface Water (STSW) stations based on their environmental variables (mean temperature, mean salinity, mesozooplankton settled volume and mean chlorophyll a). Stations are coded by water mass

and depth stratum (D1= 0 - 50 m, D2 = 50 - 100 m, D3 = 100 - 150 m, D4 = 150 - 200 m). Vectors for all four environmental variables are shown.

Euphausiid assemblages

Twenty five euphausiid species were identified across the study area, 18 of which occurred in LCW, and 23 in STSW (Appendix 1). In LCW, all species were identified from the stations sampled during the night, whereas only nine were recorded from the stations sampled during the day. Similarly for STSW, 22 species were identified from the stations sampled during the night and only 13 from the stations sampled during the day. *Stylocheiron elongatum* and *Thysanopoda monacantha* were only found in LCW, and *Euphausia similis* var. *armata*, *Euphausia similis*, *Nematobrachion flexipes*, *Stylocheiron longicorne*, *Thysanopoda aequalis* and *Thysanopoda orientalis* were only found in STSW. *Stylocheiron carinatum* was the most abundant species in LCW during the day (169 ± 133 inds·1000 m^{-3}) and night (528 ± 121 inds·1000 m^{-3}), and in STSW during the day (109 ± 49 inds·1000 m^{-3}) (Fig. 4.5). However, in STSW during the night, *Euphausia recurva* was dominant (266 ± 73 inds·1000 m^{-3}).

Vertical structuring of euphausiid assemblages

The nMDS ordination showed clear separation between assemblages sampled during the day and night (Fig. 4.6A). Within each day and night grouping, there was also a trend across depth, from shallow to deep, but more so for night assemblages (Fig. 4.6B). A PERMANOVA routine revealed significant differences across day/night ($P < 0.001$), water mass ($P < 0.001$) and depth ($P < 0.001$), with significant interactions between day/night and depth ($P < 0.001$) and water mass and depth ($P = 0.010$) (Table 4.2). Therefore, separate ANOSIM and SIMPER routines were conducted for assemblages sampled during the day and night.

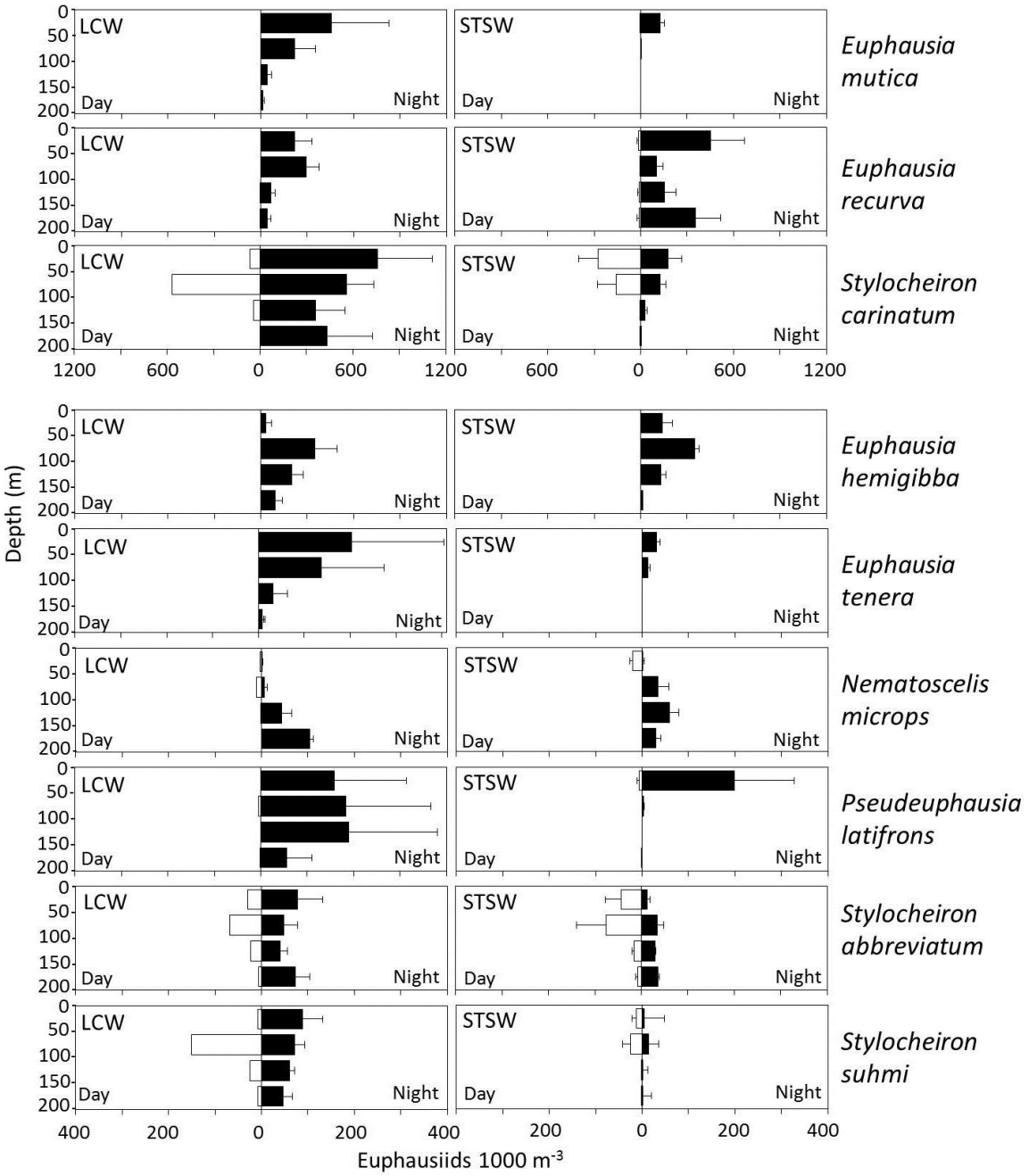


Figure 4.5 Mean concentrations (per 1000 m^{-3}) of the dominant euphausiid species for each depth stratum in Leeuwin Current Water (LCW) and Sub Tropical Surface Water (STSW), in the south-east Indian Ocean. Concentrations from night samples are shown in black and concentrations from day samples are shown in white. Standard error bars are shown.

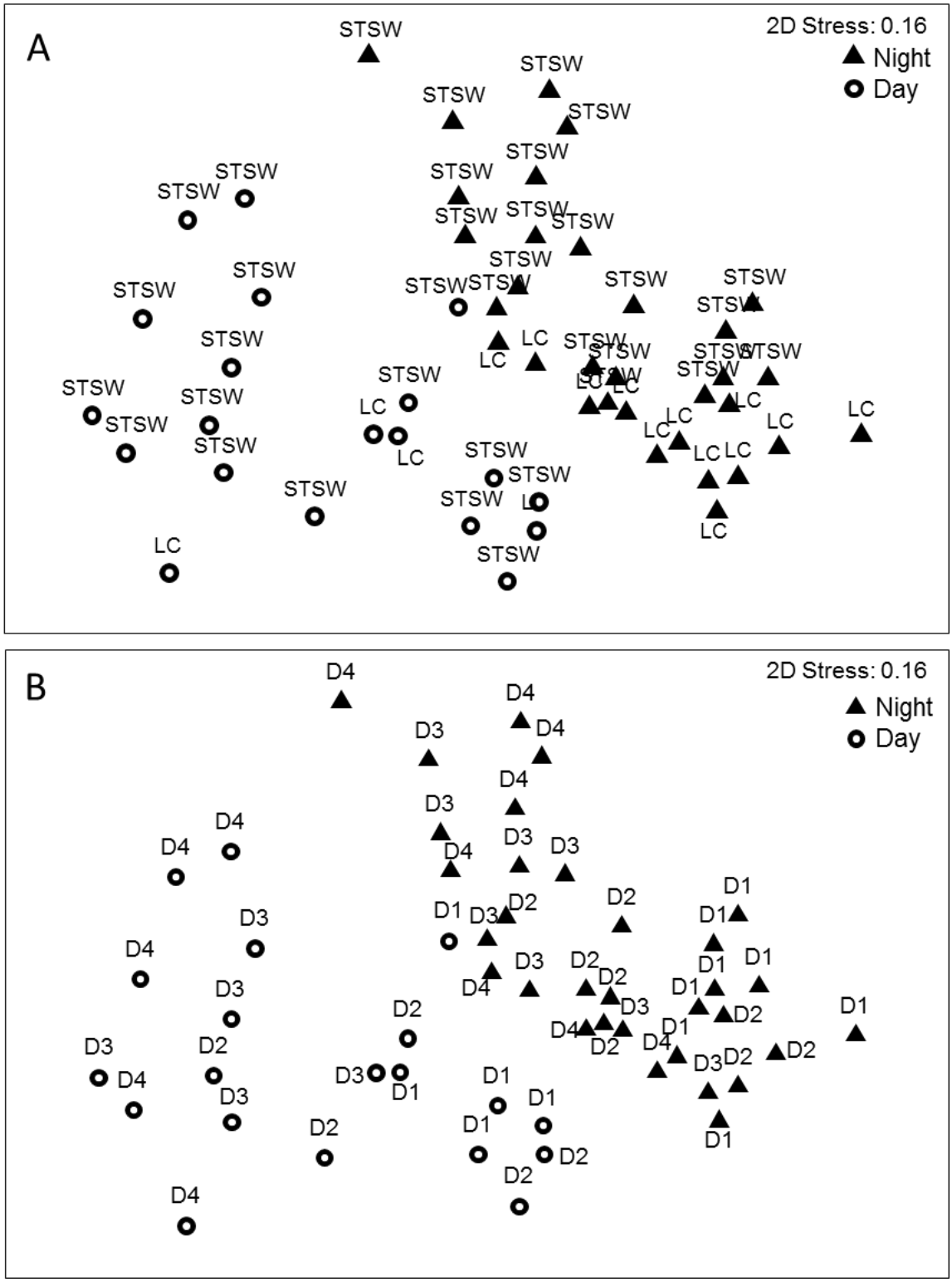


Figure 4.6 nMDS ordination plots, constructed from Bray-Curtis similarity matrices, showing the similarities in euphausiid assemblages across A) water mass and B) depth stratum for all stations sampled. LCW = Leeuwin Current Water, STSW = Sub Tropical Surface Water. D1 = 0 - 50 m, D2 = 50 - 100 m, D3 = 100 - 150 m, D4 = 150 - 200 m.

Table 4.2 A three-factor PERMANOVA testing the effect of day/night, water mass (Leeuwin Current Water and Sub Tropical Surface Water) and depth strata (0 - 50 m, 50 - 100 m, 100 - 150 m, 150 - 200 m) on the structuring of euphausiid assemblages in the south-east Indian Ocean. Asterisks denote a significant difference.

Factor	df	MS	F	P
Day/night	1	18760	17.7	0.000*
Water mass	1	5762.6	5.4	0.000*
Depth	3	3939.3	3.7	0.000*
Day/night x water mass	1	1979.3	1.9	0.058
Day/night x depth	3	2858.4	2.7	0.000*
Water mass x depth	3	1931.6	1.8	0.010*
Day/night x water mass x depth	3	1259.4	1.2	0.243
Residual	36	1056.8		
Total	51			

For euphausiid assemblages sampled during the night (Fig. 4.5), there were significant differences between LCW and STSW ($\overline{R}$ = 0.22, P = 0.006) (Table 4.3) and this was most attributable to the higher concentrations of *S. carinatum*, *E. mutica*, *S. suhmi* and *P. latifrons* in LCW, and the higher concentrations of *E. recurva* in STSW. There was significant structuring of assemblages across depth within STSW ($\overline{R}$ = 0.72, P < 0.001) (Table 4.4), but not LCW ($\overline{R}$ = 0.04, P = 0.364). All depth strata within STSW were

Table 4.3 One-way ANOSIM and SIMPER of euphausiid assemblages according to water mass for both day and night samples from the 0 - 200 m water column. Shading indicates the assemblage typical for each water mass; un-shaded are comparisons between water masses, with significant differences marked with an asterisk. The five species contributing the greatest concentrations are listed for the water mass comparisons and superscript denotes the water mass in which each species was most abundant. LCW = Leeuwin Current Water, STSW = Sub Tropical Surface Water, Ave. dis. = average dissimilarity.

	Night		**Day**	
	LCW	**STSW**	**LCW**	**STSW**
LCW	Ave. dis. = 44.3% *S. carinatum* *E. recurva* *S. suhmi* *S. abbreviatum* *E. hemigibba*		Ave. dis. = 47.6% *S. abbreviatum* *S. suhmi* *S. carinatum* *S. affine*	
STSW	*$\overline{R}$= 0.19, P= 0.008 Ave. dis. = 57.7 % *S. carinatum* (LCW) *E. recurva* (STSW) *E. mutica* (LCW) *P. latifrons* (LCW) *S. suhmi* (LCW)	Ave. dis. = 53.5% *E. recurva* *E. hemigibba* *S. abbreviatum* *S. carinatum* *N. microps*	$\overline{R}$= -0.08, P= 0.754 Ave. dis. = 50.7% No significant species	Ave. dis. = 53.4% *S. abbreviatum* *S. carinatum*

Table 4.4 One-way ANOSIM and SIMPER on euphausiid assemblages sampled in Sub Tropical Surface Water at night, stratified by depth. Shading indicates the assemblage typical for each depth stratum; un-shaded are comparisons between depth strata, with significant differences marked with an asterisk. The five species contributing the greatest concentrations are listed for the depth comparisons and superscript denotes the depth in which each species was most common and abundant. Ave. dis. = average dissimilarity.

	0 - 50 m (D1)	**50 - 100 m (D2)**	**100 - 150 m (D3)**	**150 - 200 m (D4)**
0 - 50 m	Ave. dis. = 34.2% *E. recurva* *E. mutica* *P. latifrons* *S. carinatum*			
50 - 100 m	*$\bar{R}$= 0.67, P= 0.008 Ave. dis.= 49.3% *E. mutica* (D1) *P. latifrons* (D1) *E. recurva* (D1) *S. carinatum* (D1) *E. hemigibba* (D2)	Ave. dis.= 37.4% *E. hemigibba* *S. carinatum* *E. recurva*		
100 - 150 m	*$\bar{R}$=0.94, P= 0.008 Ave. dis.= 65.9% *P. latifrons* (D1) *E. mutica* (D1) *E. recurva* (D1) *S. carinatum* (D1) *N. microps* (D3)	*$\bar{R}$=0.54, P= 0.008 Ave. dis.= 49.9% *E. recurva* (D3) *S. carinatum* (D2) *E. hemigibba* (D2) *N. microps* (D3) *N. atlantica* (D3)	Ave. dis.= 39.6% *N. microps* *E. hemigibba* *S. abbreviatum* *E. recurva* *N. atlantica*	
150 - 200 m	*$\bar{R}$=0.98, P= 0.008 Ave. dis.= 72.8% *P. latifrons* (D1) *E. mutica* (D1) *E. recurva* (D1) *S. carinatum* (D1) *N. atlantica* (D4)	*$\bar{R}$=0.94, P= 0.008 Ave. dis.= 65.0% *E. recurva* (D4) *S. carinatum* (D2) *E. hemigibba* (D2) *N. atlantica* (D4) *T. gregaria* (D4)	$\bar{R}$=0.17, P= 0.079 Ave. dis.= 43.4% No significant species	Ave. dis.= 39.2% *E. recurva* *N. atlantica* *S. abbreviatum* *S. longicorne*

significantly different in their assemblages, except the 100 - 150 m & 150 - 200 m pairwise comparison ($\overline{R}$ = 0.17, P = 0.079). The surface 0 - 50 m stratum was characterised by *E. recurva*, *E. mutica* and *P. latifrons*; 50 - 100 m by *E. hemigibba*, *S. carinatum* and *E. recurva*; 100 - 150 m by *Nematoscelis microps*, *E. hemigibba* and *S. abbreviatum*; and the 150 - 200 m stratum by *E. recurva*, *Nematoscelis atlantica*, *S. abbreviatum* (Fig. 4.5; Table 4.4). The species driving the differences between depth strata are shown in Table 4.4. Comparison of each depth stratum across water mass (Table 4.5) showed that the two water masses differed in euphausiid assemblages for all depth strata; 0 - 50 m ($\overline{R}$ = 0.44, P = 0.036), 50 - 100 m ($\overline{R}$ = 0.68, P = 0.018), 100 –

Table 4.5 One-way ANOSIM and SIMPER of night euphausiid assemblages for each depth stratum, according to water mass (Leeuwin Current Water and Sub Tropical Surface Water). Shading indicates the assemblage typical for each water mass; un-shaded are comparisons between water masses, with significant differences marked with an asterisk. The five species contributing the greatest concentrations are listed for the water mass comparisons and superscript denotes the water mass in which each species was most abundant. Ave. dis. = average dissimilarity.

	LCW	**STSW**
LCW	Ave. dis. = 46.4% *S. carinatum* *E. recurva* *E. mutica*	**0 - 50 m (D1)**
STSW	*$\bar{R}$= 0.44, P= 0.036, Ave. dis. = 43.3% *S. carinatum* (LCW) *P. latifrons* (STSW) *E. mutica* (LCW) *E. recurva* (STSW) *E. tenera* (LCW)	Ave. dis. = 34.2% *E. recurva* *E. mutica* *P. latifrons* *S. carinatum*
LCW	Ave. dis. = 38.2% *S. carinatum* *E. recurva* *E. tenera* *E. mutica*	**50 - 100 m (D2)**
STSW	*$\bar{R}$= 0.7, P= 0.018, Ave. dis. = 50.8% *S. carinatum* (LCW) *E. mutica* (LCW) *P. latifrons* (LCW) *E. tenera* (LCW) *E. recurva* (LCW)	Ave. dis. = 37.4% *E. hemigibba* *S. carinatum* *E. recurva*
LCW	Ave. dis. = 44.2% *S. carinatum* *S. suhmi* *E. hemigibba* *E. recurva* *S. abbreviatum*	**100 - 150 m (D3)**
STSW	*$\bar{R}$= 0.63, P= 0.018, Ave. dis. = 57.4% *S. carinatum* (LCW) *S. suhmi* (LCW) *E. recurva* (STSW) *P. latifrons* (LCW) *E. tenera* (LCW)	Ave. dis. = 39.6% *N. microps* *E. hemigibba* *S. abbreviatum* *E. recurva* *N. atlantica*
LCW	Ave. dis. = 42.9% *N. microps* *S. carinatum* *S. abbreviatum* *S. suhmi* *E. hemigibba*	**150 - 200 m (D4)**
STSW	*$\bar{R}$= 0.92, P= 0.018, Ave. dis. = 64.9% *S. carinatum* (LCW) *E. recurva* (STSW) *N. microps* (LCW) *S. suhmi* (LCW) *T. gregaria* (STSW)	Ave. dis. = 39.2% *E. recurva* *N. atlantica* *S. abbreviatum* *S. longicorne*

150 m ($\overline{R}$ = 0.63, P = 0.018) and 150 - 200 m ($\overline{R}$ = 0.92, P = 0.018). The species driving the difference between water masses for each depth stratum are indicated in Table 4.5.

For assemblages sampled during the day (Table 4.3), there were no discernible differences across water mass, albeit it that only a single daytime LCW station (4 strata) was included in the test ($\overline{R}$ = -0.08, P = 0.754). Structuring of assemblages across depth within LCW could not be ascertained as there was no replication. However, replicated STSW stations revealed significant structuring across depth ($\overline{R}$ = 0.43, P = 0.002). Assemblages were similar between 0 - 50 m and 50 - 100 m ($\overline{R}$ = 0.37, P = 0.057), 50 - 100 m and 100 - 150 m ($\overline{R}$ = 0.26, P = 0.114), and 100 - 150 m and 150 - 200 m ($\overline{R}$ = -0.30, P = 0.914). All other comparisons of depth strata were significantly different from each other (all $\overline{R}$ > 0.45, P = 0.029). The 0 - 50 m stratum was characterised by *S. carinatum*, and *N. microps*, 50 - 100 m by *S. carinatum*, *S. abbreviatum*, and *S. suhmi*, 100 - 150 m by *S. abbreviatum* and *Stylocheiron affine*, and 150 - 200 m by *S. abbreviatum* and *S. longicorne*. There were no significant differences when comparing each depth stratum across water mass during the day (P > 0.050).

Environmental correlations

Of the four environmental variables tested, mean temperature and mean chlorophyll *a* returned the highest correlation, ρ = 0.62, with euphausiid assemblages (P < 0.001). Temperature (and dissolved oxygen), was the most significant correlating variable (ρ = 0.59, P < 0.001). All four variables combined gave a lower ρ = 0.53 (P < 0.001). Environmental variables were overlayed on nMDS ordinations of the euphausiid assemblages using bubble plots (Fig. 4.7). Euphausiid assemblages across all LCW depth strata were similar (P = 0.364), and

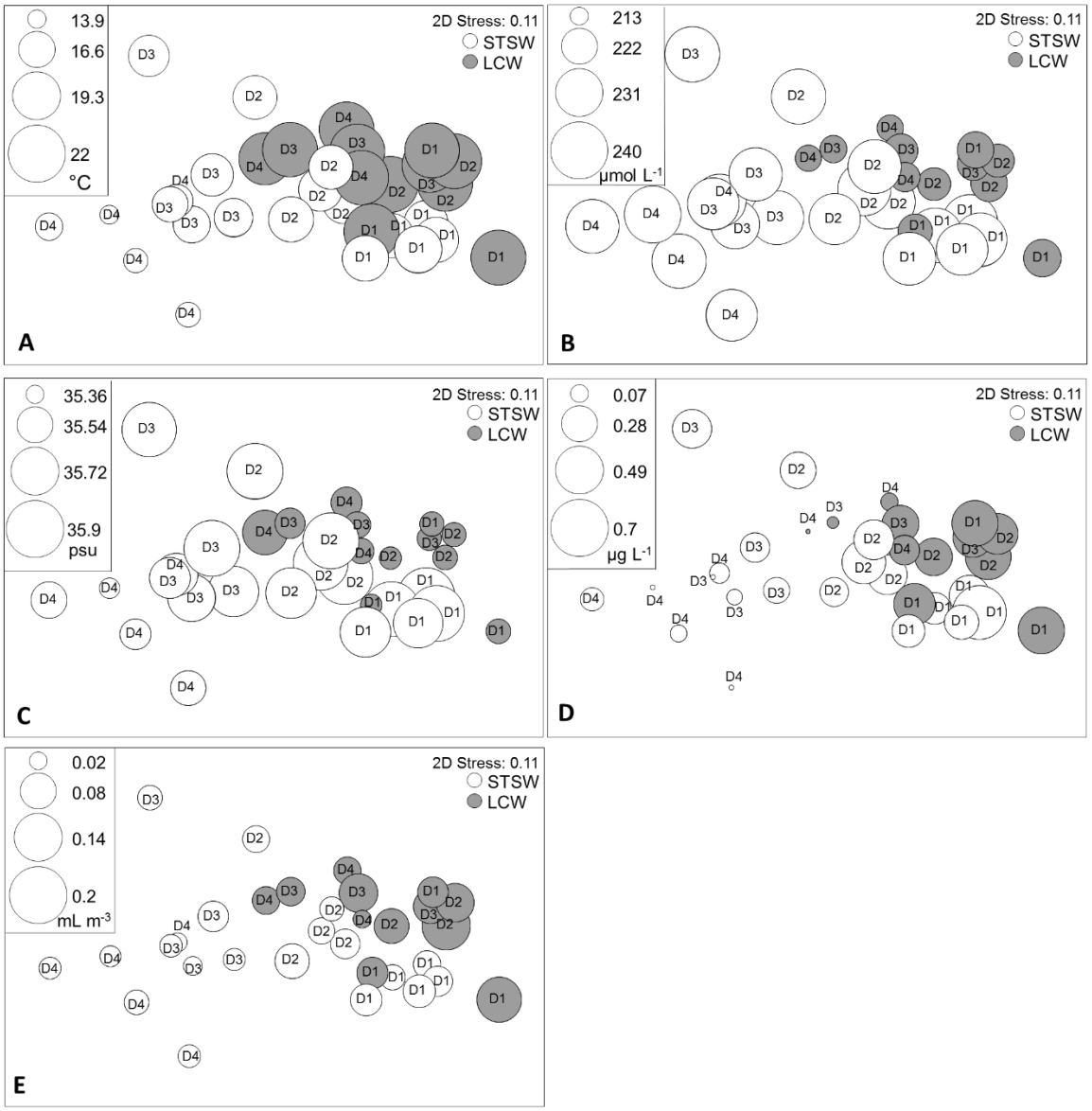


Figure 4.7 Bubble plots of environmental variables overlayed on nMDS ordinations of euphausiid assemblages sampled at night from Leeuwin Current Water (LCW) and Sub Tropical Surface Water (STSW) for A) mean temperature, B) mean dissolved oxygen, C) mean salinity, D) mean chlorophyll *a* and E) mesozooplankton settled volume. Assemblages are coded by depth strata (D1 = 0 - 50 m, D2 = 50 - 100 m, D3 = 100 - 150 m, D4 = 150 - 200 m).

this correlated with relatively uniform values of high mean temperature, chlorophyll *a*, and mesozooplankton settled volume and low dissolved oxygen and salinity, across all depth strata. Euphausiid assemblages were significantly structured along a gradient from shallow to deep strata in STSW ($P < 0.001$). This shallow to deep gradient in assemblages correlated with a decrease in mean temperature, mean salinity, and

chlorophyll *a*, and a slight decrease in mesozooplankton settled volume. Dissolved oxygen was relatively uniform across depth strata.

Life stages and ontogenetic layering

Calyptopis larvae had a significantly higher average concentration in LCW (4462 ± 1766 inds·1000 m^{-3}) than STSW (1202 ± 457 inds·1000 m^{-3}) ($p < 0.001$, n = 52, Kruskal-Wallis) (Fig. 4.8A). Calyptopis larvae were also significantly structured across depth ($p = 0.004$, n = 52, Kruskal-Wallis), with concentrations tending to be greater in the 0 - 50 m

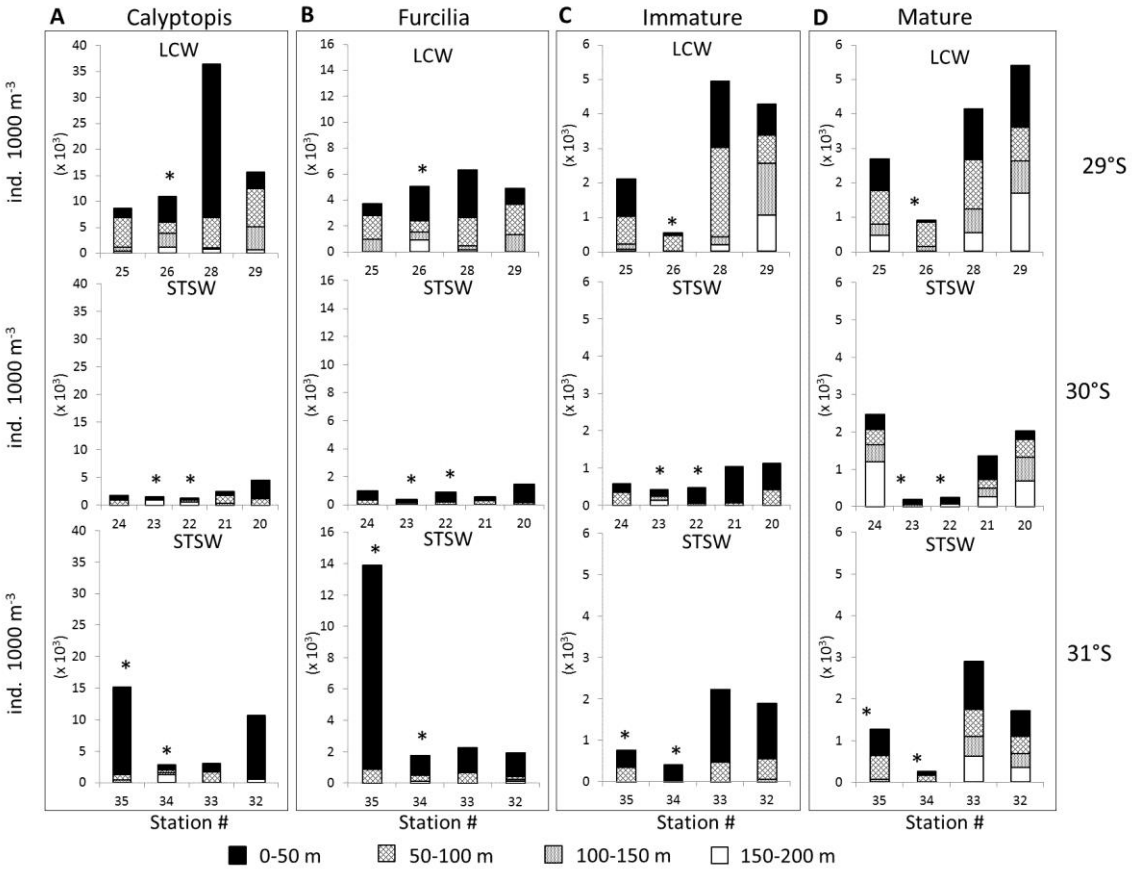


Figure 4.8 Concentrations (individuals 1000 m^{-3}) of A) calyptopis larvae, B) furcilia larvae, C) immature euphausiids and D) mature euphausiids for each depth stratum at each station sampled in Leeuwin Current Water (LCW) and Sub Tropical Surface Water (STSW). Asterisks denotes those stations sampled during the day. Note different y axis scales.

stratum for both LCW (9860 ± 6599 inds·1000 m^{-3}) and STSW (3473 ± 1650 inds·1000 m^{-3}). Furcilia larvae exhibited similar structuring to calyptopis larvae in being more concentrated on average in LCW (1247 ± 255 inds·1000 m^{-3}) than STSW (671 ± 361 inds·1000 m^{-3}) ($p < 0.001$, $n = 52$, Kruskal-Wallis) (Fig. 4.8B). Furcilia concentrations also decreased with increasing depth ($p < 0.001$, $n = 52$, Kruskal-Wallis) and were most concentrated in the 0 - 50 m stratum for both LCW (2121 ± 632 ind·1000 m^{-3}) and STSW (2287 ± 1356 inds·1000 m^{-3}). There was no effect of day/night on calyptopis or furcilia concentrations in either water mass ($p > 0.050$, Kruskal-Wallis).

Immature euphausiid concentrations were significantly greater in LCW (737 ± 190 inds·1000 m^{-3}) compared to STSW (249 ± 66 inds·1000 m^{-3}) ($p = 0.006$, $n = 52$, Kruskal-Wallis) (Fig. 4.8C), and concentrations were greater during the night than the day in LCW ($p = 0.021$, $n = 16$, Kruskal-Wallis), but not STSW ($p = 0.553$, $n = 36$, Kruskal-Wallis). Immature euphausiids generally decreased in concentration with increasing depth, but there was only significant structuring across depth for STSW during the day ($p = 0.038$, $n = 15$, Kruskal-Wallis) and night ($p = 0.001$, $n = 21$, Kruskal-Wallis), not LCW ($p > 0.319$, Kruskal-Wallis). Concentrations in STSW were greater within the 0 - 50 m stratum during the day (326 ± 64 inds·1000 m^{-3}) and night (999 ± 260 inds·1000 m^{-3}) ($p < 0.050$, Kruskal-Wallis).

Mature euphausiids were significantly greater in concentration in LCW (817 ± 141 inds·1000 m^{-3}) than STSW (344 ± 51 inds·1000 m^{-3}) ($p = 0.002$, $n = 52$, Kruskal-Wallis) (Fig. 4.8D), and were higher in concentration for stations sampled during the night than the day, for both water masses ($p < 0.015$, Kruskal-Wallis). Structuring of mature euphausiids was also observed across depth strata, but only for STSW stations sampled during the day ($p = 0.041$, $n = 15$, Kruskal-Wallis). Concentrations were only

significantly greater in the 0 - 50 m and 50 - 100 m depth stratum in comparison to the 150 - 200 m depth stratum ($p < 0.049$, Kruskal-Wallis).

Discussion

The structuring of euphausiid assemblages in LCW and STSW in the south-east Indian Ocean was mostly driven by the numerical abundance of shared species, rather than the presence or absence of species in either water mass. Most euphausiid species were shared across the two water masses and across depths, and most were considered to be subtropical species (Brinton et al. 2000). Species did, however, exhibit a greater preference for a particular water mass or depth, and this is consistent with the nature of many euphausiid species in that they can exist over a great vertical range, but aggregate most where the conditions are most favourable (Brinton 1967; Youngbluth 1975; Hirota 1987). Gibbons (1997) also recognized that the differences observed in euphausiid assemblages across neighbouring water masses in the south-west Indian Ocean, i.e. the Agulhas Current, was due to numerical abundance, rather than different species. In this south-east Indian Ocean study, most of the shared species were in LCW, and within that, were in shallower depth strata, particularly at night.

Chlorophyll *a* and mesozooplankton abundance were considered important drivers of euphausiid assemblage variation sampled during the night, and both variables were higher in the LCW. This correlated with higher concentrations of euphausiids in these waters, including both calyptopis and furcilia larval stages. Spikes in calyptopis concentrations in the 0 - 50 m depth stratum at station 28 and station 35, and in furcilia concentrations at station 35 coincided with relatively high chlorophyll *a* concentrations. Station 35 was also on the perimeter of a warm core eddy which, for

the south-east Indian Ocean, are typically found to contain higher chlorophyll *a* concentrations and primary productivity (Moore et al. 2007; Thompson et al. 2007; Waite et al. 2007a; Dufois et al. 2014). Chlorophyll *a* concentrations are comparable to other studies concerning the LC (Hanson et al. 2005; Pearce et al. 2006; Lourey et al. 2012, Chapter 2). Without direct visual observations of euphausiid behaviour, it is difficult to discern whether food availability alone was a key driver, or whether the physical conditions of the LCW resulted in the accumulation of both euphausiids and their prey (Price 1989). More support for the former comes from chlorophyll *a* driving assemblages in the surface 100 m of STSW, where physical conditions were significantly different to LCW.

There was no structuring of euphausiid assemblages across depth in LCW, but there was in STSW. LCW had more chlorophyll *a* and greater mesozooplankton settled volumes across the water column, as well as a deeper thermocline (> 150 m). This may have meant that for most euphausiids, the conditions were ideal throughout most of the water column, and that little accumulation or partitioning across depth for resources was necessary. Youngbluth (1976) found juvenile *Euphausia pacifica* populations to be greater, and more widely distributed across depth, in waters with higher turbidity and more phytoplankton. The inverse was true for oligotrophic and less turbid waters, where specimens accumulated in narrower depth bands and vertical migrations were more pronounced. STSW was found to be less turbid and relatively lower in nutrients (Säwström et al. 2014), and these waters also had lower concentrations of chlorophyll *a* and lower mesozooplankton settled volumes, as well as variable thermocline depths from station to station. Temperature, salinity and dissolved oxygen measurements were wider ranging across the 200 m sampled in

STSW, and were significant in driving some of the variation in euphausiid assemblages. The above measured environmental variables have been noted throughout the literature as being potential drivers of euphausiid distributions (Brinton 1962; Hirota 1987; Gibbons 1997; Ashjian et al. 2008; Antezana 2009).

Ontogenetic structuring across depth was evident in this study. Calyptopis and furcilia larvae were most abundant in the 0 - 50 m stratum, which is a typical pattern for euphausiid larvae (Mauchline & Fisher 1969; Mauchline 1980; Hirota et al. 1987). Mature and immature euphausiids, on average, showed the usual pattern of joining the larval stages during the night, then descending during the day to deeper waters (Mauchline & Fisher 1969). Total mature and immature euphausiid concentrations sampled during the day were consistently lower than those recorded at night, which indicated that the majority of specimens had migrated deeper than the 200 m of water column sampled. Most of the species identified in this study have typical day time distributions of > 200 m (Brinton 1962; Mauchline & Fisher 1969; Hirota 1987). The specimens that remained in the upper 200 m during the day largely consisted of *S. carinatum*, a species that has a typical epipelagic distribution, particularly around the 100 m during both the day and night (Lewis 1954; Brinton 1967; Youngbluth 1975; Hirota 1987). Members of the *Nematoscelis*, *Thysanopoda*, and *Stylocheiron* genera, particularly *S. abbreviatum* and *S. suhmi*, contributed a small proportion to day time assemblages. *Stylocheiron abbreviatum* has been labelled a non-migrator, occupying waters between 100 - 400 m and *S. suhmi* as a short or non-migrator, typically being found in the top 100 m during the day (Brinton 1962; Youngbluth 1975; Hirota 1987). These two species exhibited similar vertical distributions in this study, although, *S. abbreviatum* was just as abundant in waters < 100m.

In STSW, from stations sampled at night, both the 0 - 50 m and 150 - 200 m depth strata had similar high concentrations of mature euphausiids. *Euphausia recurva* was present across the whole depth range sampled, but was greater in concentration at 0 - 50 m and 150 - 200 m, and was the greatest contributor to the assemblages at these depths. These findings are in agreement with earlier studies that found *E. recurva* to be most concentrated in the surface 50 m (Brinton 1967; Youngbluth 1976; Griffiths 1979). However, these studies did not mention a second maximum at 150 - 200 m, as observed for this study. One possible explanation for the additional accumulation of *E. recurva* between 150 - 200 m, is the higher dissolved oxygen concentrations within this depth range. Brinton (1962) included *E. recurva* in the Pacific Central Water group, which typically occurred in more oxygen rich waters. Due to the lower concentrations of *E. recurva* found during the day in STSW, this suggests that *E. recurva* migrated below 200 m, which would support *E. recurva* as a long distance vertical migrator, unlike that reported in Griffiths (1979) for the east coast of Australia.

Euphausia recurva, *S. carinatum*, *E*. *mutica* and *P. latifrons* were the most dominant species across the front. These results concur with previous studies on euphausiid assemblages and dominant species within the LC system (Sutton et al. 2015; Chapter 2). *Stylocheiron carinatum* is a cosmopolitan species and, as such, has been noted as one of the most common species found in the eastern Indian Ocean and western Pacific Ocean (Hirota 1987) as well as throughout the eastern South Pacific (Youngbluth 1975). Adjacent to the LC, along 110°E in the south-east Indian Ocean, *S. carinatum*, along with *E. mutica* were found to be the most abundant euphausiid species (McWilliam 1977). *Euphausia recurva* is more adapted to cooler subtropical/ temperate waters and was the most dominant species in the STSW in this study. In the

Pacific Ocean, *E. recurva* was often abundant at the front between water masses, particularly bordering cooler, productive eastern boundary currents (Brinton 1962). This species was also the most dominant in cooler waters south of 30°S in a latitudinal survey of the LC from 22°S - 34°S (Chapter 2) and within a warm core LC eddy between 31°S - 34°S (Sutton et al. 2015). In contrast, the coastal, and typically tropical, species, *P. latifrons*, usually dominated the warm LCW. This species was found in concentrations lower than previously recorded for LC studies (Sutton et al. 2015, Chapter 2), and may be reflective of the oceanic waters of greater depths sampled in this study.

In conclusion, this study has identified a difference in euphausiid assemblages across two dominant water masses in the south-east Indian Ocean, as well as significant vertical structuring in the more variable water column of STSW. Assemblage differences were mainly driven by numerical abundance of species shared across the water masses. Ontogenetic layering of life stages and diel vertical migration amongst immature and mature euphausiids was evident. Similar to previous studies involving the LC system, and elsewhere, temperature, mean mesozooplankton settled volume and mean chlorophyll *a* concentration were significant drivers of variation in assemblages.

Chapter 5: Species richness and taxonomic distinctness as measures to assess environmental drivers of euphausiid zoogeography in the Indian Ocean

Abstract

Two thirds of the world's euphausiid species exist in the Indian Ocean and the environmental drivers of euphausiid diversity in this ocean are yet to be ascertained. Most euphausiid records for the Indian Ocean originated from the International Indian Ocean Expedition (1962 - 1965), and together with other available records, spatially-explicit data on species richness and taxonomic distinctness were produced for the 56 species occurring in the Indian Ocean (20°N - 40°S, 20°E - 122°E). Average taxonomic distinctness (AveTD) and variation in taxonomic distinctness (VarTD) are measures calculated from the taxonomic separation of species in a classification tree, and both measures can be applied to presence/absence data and are robust to differences in sampling effort. Most of the Indian Ocean was comparable in euphausiid species richness, AveTD and VarTD, and had relatively similar assemblages, which reflects the ocean connectivity across the basin and, in turn, the transport of holoplanktonic euphausiids. Opposite perspectives of euphausiid diversity were seen for the northern Indian Ocean where species richness was lowest, but AveTD and VarTD were highest. Areas of high AveTD and VarTD were largely attributable to the occurrence of *Bentheuphausia amblyops* from the monotypic family Bentheuphausiidae. Surface salinity was an important explanatory variable for all three diversity measures, where low salinity from large river run-off correlated with low species richness, but high AveTD and VarTD in the Bay of Bengal. Oxygen was also a significant variable for all three measures and again, the northern IO that was an area of interest due to the

Oxygen Minimum Zone (OMZ). This study presents broad-scale patterns of euphausiid species richness and taxonomic distinctness for the Indian Ocean, and has identified environmental drivers of euphausiid diversity and distribution.

Introduction

Euphausiids are holoplanktonic, pelagic crustaceans inhabiting the world's oceans from the surface waters to deeper than the bathypelagic realm (4000 m) (Brinton 1962; Mauchline & Fisher 1969). Globally, there are 86 species of euphausiids and they fill an important role in the pelagic food web by consuming other plankton and by being a food source for higher order consumers, such as fishes, seabirds, and whales (Kawamura 1980; Hipfner 2009; Itoh et al. 2011). Euphausiids also play a role in carbon sequestration and the transfer of organic material and iron throughout the water column during feeding and diel vertical migration (Longhurst 1989; Schnack-Schiel & Isla 2005; Nicol et al. 2010).

Euphausiids have been the subject of broad scale plankton zoogeographical studies as most extant species are expected to have been identified, and their distributions are relatively well known across the world's oceans (Baker et al. 1990; Brinton et al. 2000). Euphausiid assemblages have been used to define biogeographical provinces for the South Atlantic (Gibbons 1997), south-east Asia (Brinton 1975), and Pacific Ocean (Brinton 1962), while species richness has been used to identify latitudinal patterns across ocean basins for the world (Tittensor et al. 2010), Pacific Ocean (Letessier et al. 2011) and Atlantic Ocean (Letessier et al. 2009). These broad biogeographical patterns were found to reflect the oceanographic environment, particularly major water masses and temperature gradients.

Oceanography plays a key role in influencing the distribution of euphausiids (Brinton 1979; Taki 2008 Letessier et al. 2009; Letessier et al. 2011; Sutton et al. 2015). Species possess different tolerances to environmental variables such as temperature, salinity and dissolved oxygen, and this can link their distributions with tropical, subtropical or temperate water masses and geographic areas (Brinton 1975; Gibbons et al. 1995; Tarling et al. 1995). Environmental drivers of euphausiid species richness have been investigated for the Pacific Ocean (Letessier et al. 2011) and Atlantic Ocean (Letessier et al. 2009); sea surface temperature and salinity were the main drivers of species richness for the Pacific, and sea surface temperature was the main environmental driver for the Atlantic Ocean. A broader scale examination of euphausiids for all oceans, including the Indian Ocean, identified sea surface temperature and primary productivity to be important predictors of species richness (Tittensor et al. 2010). Environmental drivers of euphausiid zoogeography specifically in the Indian Ocean have yet to be investigated.

Two thirds of the world's euphausiid species live in the Indian Ocean (Brinton et al. 2000) and the features of the ocean make it very different to the Pacific and Atlantic Oceans. The northern extent of the Indian Ocean is landlocked by Asia and the Middle East, thereby lacking subtropical and temperate zones. The northern Indian Ocean experiences a seasonal reversal of currents as a result of monsoonal winds, which is also linked to large changes in upwelling and downwelling circulation (Schott & McCreary 2001; Shanker et al. 2002; Schott et al. 2009). The seasonal reversals and associated changes in upwelling intensity also have significant influences on nutrient (Wiggert et al. 2006) and oxygen concentrations in the northern Indian Ocean (Naqvi et al. 2006), which can have impacts throughout trophic levels. In particular, the

northern Indian Ocean is a major open-ocean oxygen minimum zone, where oxygen concentrations can decline to nearly zero between 100 - 800 m depth (Morrison et al. 1999; Naqvi et al. 2009). Pacific Ocean waters intrude into the Indian Ocean via the Indonesian Throughflow at a flow rate of 10 - 15 Sv, and that plays a significant role in global climate by controlling the heat and fresh water budgets between the two oceans (Gordon & Fine 1996; Wijffels & Meyers 2004; McCreary et al. 2007; Xu 2014). Water from the Indonesian Throughflow also helps form the source waters for the poleward flowing Leeuwin Current (Meyers et al. 1995; Domingues et al. 2007). Together with the Agulhas Current along the south-east coast of Africa, the Indian Ocean is the only ocean to have poleward flowing boundary currents along both eastern and western margins.

The first Indian Ocean wide investigation of euphausiid distributions was conducted during 1962 - 1965 as part of the first International Indian Ocean Expedition (IIOE) (Brinton & Gopalakrishnan 1973). More recent studies examining euphausiids have since been conducted in the eastern Indian Ocean (e.g. Wilson et al. 2003a; Sutton et al. 2015), western Indian Ocean (e.g. Galliene et al. 2004), northern Indian Ocean (e.g. Jayalakshmi et al. 2011) and southern Africa (e.g. Gibbons et al. 1995). Accurately representing euphausiid species richness (i.e. the number of species) in the Indian Ocean from these collated studies is confounded by differences in survey effort and sampling methods, as well as the behaviour of euphausiids themselves i.e. net avoidance and diel vertical migration (Brinton 1967; Wiebe et al. 1982). Traditional measures like species richness fail to capture the full extent of true biodiversity and give an equal weighting to all species in their contribution to diversity, i.e. five species

from one genus are considered as diverse as five species from five families (Gotelli & Colwell 2001).

Taxonomic distinctness is a measure of the taxonomic relatedness of species comprising the assemblage in a sample, based on the level of separation through the classification tree (Warwick & Clarke 1995). It is a diversity measure that is growing in application and has been applied to communities in estuaries and ocean current systems (e.g. Tolimieri & Anderson 2010, Tweedley et al. 2012). Average taxonomic distinctness (AveTD) calculates an average of all the path lengths between pairs of species, which gives an indication of the taxonomic breadth of a sample (Clarke & Warwick 1998). The variation in taxonomic distinctness (VarTD) measures the variation in branch lengths and reflects the unevenness of the taxonomic tree (Clarke & Warwick 2001). These measures of biodiversity can be applied to presence/absence data and are not affected by sampling effort or the number of species because they are averages (Clarke & Warwick 1998), and are different from conventional diversity measures as they include the degree to which species are taxonomically related to each other. This means that historical data sets, such as those from the International Indian Ocean Expedition, can be included in analyses.

This study has three main aims, namely, 1) to determine zoogeographic patterns of euphausiids in the Indian Ocean using species richness and assemblage structure, 2) to use taxonomic distinctness as an additional measure to assess the biodiversity of euphausiids in the Indian Ocean, and 3) to use generalised additive modelling to determine environmental drivers of euphausiid species richness and taxonomic distinctness in the Indian Ocean.

Methods

Study area and euphausiid distributions

Using ArcGIS 10.2.1, a sampling cell design of 2° latitude x 3° longitude was applied to the Indian Ocean basin from 30°N - 40°S and from 20°E - 122°E, giving a total of 708 sampling cells. The size of the sampling cells was a trade off between a manageable data set and a biological meaningful resolution for euphausiids.

Presence/absence data for individual euphausiid species throughout the Indian Ocean were collated from a number of data sources (Table 5.1). A large proportion of distribution data, which encompassed the middle basin, was taken from the International Indian Ocean Expedition during 1962 - 1965 (Brinton & Gopalakrishnan 1973; McWilliam 1977). Brinton et al. (2000) provides euphausiid distribution maps that encompasses the International Indian Ocean Expedition and additional records from other studies. Subsequent studies documenting euphausiid presence that were not included in Brinton et al. (2000), and those that have been published since 2000, are also included in this study, and these are listed in Table 5.1. To the best of the author's knowledge, this is an extensive and comprehensive collection of the published studies available on euphausiids in the Indian Ocean.

Measures of biodiversity

Spatial cells across the Indian Ocean were populated with species richness values from summed species layers. Those that only contained a single species (n = 5) were excluded from further analyses as taxonomic path lengths could not be calculated for average taxonomic distinctness (AveTD) and variation in taxonomic distinctness (VarTD).

Table 5.1 Published records of euphausiid occurrence and distribution used to produce a species richness map for the Indian Ocean. Note that euphausiid distributions from many studies are represented in Brinton et al. (2000). The studies listed in this table provided additional and more recent distributional information on euphausiid species that was not included in Brinton et al. (2000).

Published source	Indian Ocean region	Sampling net; mesh size	Depth range (m)	# samples
Taniguchi 1974	Indo-Australian Basin	Indian Ocean standard net* ($1m^2$); 0.33mm Norpac net- 50cm & 56cm	0 - 2976	164
Casanova 1980	Western Indian Ocean	Indian Ocean standard net* ($1m^2$); 0.33mm 200 cm Net (44 - 48.5cm diamter); 300um	0 - 4000	
Nair et al. 1981	Bay of Bengal	Indian Ocean standard net* ($1m^2$); 0.33mm	0 - 200	22
Mathew 1985	Arabian Sea	Indian Ocean standard net* ($1m^2$); 0.33mm	0 - 150	182
Silas & Mathew 1986	Arabian Sea	Indian Ocean standard net* ($1m^2$); 0.33mm Isaacs Kidd Mid-water Trawl	0 - 1300	312
Fatima 1987	Somalia, Gulf of Aden	Indian Ocean standard net* ($1m^2$); 0.33mm	-	9
Hirota 1987	Eastern Indian Ocean	Multi-depth sampling MTD- 0.56m; 0.10mm, 0.33mm, 0.68mm	0 - 1000	52
Gibbons et al. 1995[#]	Southern Africa	Various	Various	Various
Brinton et al. 2000	Whole basin	Indian Ocean standard net* ($1m^2$); 0.33mm Various	0 - 200 most Various	1231
Hitchcock et al. 2002	Arabian Sea	MOCNESS $1m^2$; 153um	0 - 1200	
Mathew et al. 2003	Arabian Sea	Bongo net- 60cm diameter net; 0.33mm	0 - 150	493
Wilson et al. 2003a	Eastern Indian Ocean, NW shelf Australia	Light traps	0 - 75	426
Galliene et al. 2004	South-west Indian Ocean	Conical net (0.4m diameter); 125um	0 - 50	36
Holliday et al. 2011b	Kimberley, eastern Indian Ocean	Bongo net ($.196m^2$); 355um	0 - 150	72
Jayalakshmi et al. 2011	Arabian Sea	Multiple Plankton Net Sampler $0.25m^2$; 200um	Wind-mixed layer and thermocline	9
Sutton et al. 2015	South-east Indian Ocean	EZ net $1m^2$; 335um	0 - 200	36
Chapter 2	South-east Indian Ocean	Bongo net- 50 cm; 355um	0 - 150	26
Chapter 3	Indo-Australian Basin	Bongo net- 50 cm; 355um	0 - 150	108

*most samples collected used Indian Ocean standard net

[#] presented data from a collection of published studies

PRIMER-7 was used to calculate AveTD and VarTD for each cell based on species richness information (Clarke & Warwick 2001; Clarke & Gorley 2015). AveTD calculates the average path length distance between pairs of species in a cell, based on a classification tree (Clarke & Warwick 1998). It is defined as:

$$AveTD = [\sum \sum_{i<j} \omega_{ij}] / [s(s-1)/2]$$

where ω is the branch length between species pairs *i* and *j*, and *s* is the number of species in the sample. A Linnaean classification tree was used with four taxonomic levels, species, genus, family, order. Taxonomic branches were unweighted and equal step lengths were given to each taxonomic level, so that the maximum distance through the tree was ω = 100.

VarTD calculates the variance of the pairwise path lengths and determines the unevenness of the taxonomic tree (Clarke & Warwick 2001), where:

$$VarTD = [\sum \sum_{i<j} (\omega_{ij} - AveTD)^2] / [s(s-1)/2]$$

A master list of all euphausiid species in the Indian Ocean was used in a randomisation test to detect significant departures in AveTD and VarTD from the expected AveTD and VarTD for the Indian Ocean using funnel plots and 95% probability limits.

nMDS and cluster analyses

Euphausiid assemblage structure based on presence/absence data was investigated using the PRIMER-7 software package (Clarke & Gorley 2015). A cluster analysis was performed on group-average linkages using a Bray-Curtis similarity matrix to quantify the dissimilarity in assemblages between two cells. A non-metric multi-dimensional scaling (nMDS) ordination was used to display the similarities among cell assemblages,

at the 65% level of similarity. Groupings at the 65% level of similarity were further justified using an Analysis of Similarity (ANOSIM) between cluster groupings.

Environmental explanatory variables and data exploration

Environmental data were obtained from a number of online databases (Table 5.2). As euphausiid records span back to the International Indian Ocean Expedition of the 1960s, long term climatologies and data sets were sourced. In total, 42 environmental explanatory variables, that were potentially relevant in explaining variation in euphausiid species richness, AveTD and VarTD, were collated. Data exploration was carried out using R v3.1.1 software and was inspected for independence, outliers, normality and collinearity of variables, following Zuur et al. (2010). Outliers were assessed using Cleveland dot plots and, where necessary, log transformations were applied to explanatory variables to improve normality and homoscedasticity. Normality was assessed using histograms and collinearity was assessed using multi-panel scatterplots. If a correlation of > 0.7 occurred between two explanatory variables, one explanatory variable would be dropped based on the minimisation of the Akaike Information Criterion (AIC, Burnham & Anderson 2004) while also ensuring the explanatory variable kept was biologically meaningful to euphausiids.

A generalised additive model (GAM) was used to investigate environmental drivers of euphausiid species richness, AveTD and VarTD. A GAM was chosen for its ability to describe non-linear data (Austin 2002). Models were constructed using the mgcv package in R v3.1.1 (Wood 2006) and a Gaussian distribution with identity link to improve residuals was chosen for AveTD and VarTD, and a Poisson distribution with a log link was chosen for species richness. Thin plate regression spline smoothers were

Table 5.2 The explanatory environmental variables sourced from online databases to investigate environmental drivers of euphausiid species richness and taxonomic distinctness in the Indian Ocean using generalised additive models. Chlorophyll *a* measurements divided by season represent the respective months of that season from the northern and southern hemispheres.

Environmental variable	Unit	Source	Temporal range	Resolution/average over
Temperature (0, 50, 100, 150, 200, 300 m)	°C	CSIRO Atlas of Regional Seas http://www.marine.csiro.au/atlas/	1950-2008	0.5° x 0.5°/ annually
Salinity (0 m, 50 m, 100 m, 150 m, 200 m, 300 m)	psu	http://www.marine.csiro.au/atlas/	1950-2008	0.5° x 0.5°/ annually
Oxygen (0 m, 50 m, 100 m, 150 m, 200 m, 300 m)	ml L^{-1}	http://www.marine.csiro.au/atlas/	2011-2015	0.5° x 0.5°/ annually
Silicate (0 m, 50 m, 100 m, 150 m, 200 m, 300 m)	µmol L^{-1}	http://www.marine.csiro.au/atlas/	2011-2015	0.5° x 0.5°/ annually
Nitrate (0 m, 50 m, 100 m, 150 m, 200 m, 300 m)	µmol L^{-1}	http://www.marine.csiro.au/atlas/	2011-2015	0.5° x 0.5°/ annually
Phosphate (0 m, 50 m, 100 m, 150 m, 200 m, 300 m)	µmol L^{-1}	http://www.marine.csiro.au/atlas/	2011-2015	0.5° x 0.5°/ annually
Mixed layer depth	m	http://www.marine.csiro.au/atlas/	1950-2008	0.5° x 0.5°/ annually
Seafloor depth	m	GEBCO http://www.gebco.net/		1-arc minute
Winter surface chlorophyll *a*	mg m^{-3}	OceanColour http://oceancolor.gsfc.nasa.gov/cms/	2002-2013	1°/Seasonally
Summer surface chlorophyll *a*	mg m^{-3}	http://oceancolor.gsfc.nasa.gov/cms/	2002-2013	1°/Seasonally
Autumn surface chlorophyll *a*	mg m^{-3}	http://oceancolor.gsfc.nasa.gov/cms/	2002-2013	1°/Seasonally
Spring surface chlorophyll *a*	mg m^{-3}	http://oceancolor.gsfc.nasa.gov/cms/	2002-2013	1°/Seasonally

applied to all non-linear variables included in the GAM model, as justified by the estimated degrees of freedom being > 1 (Zuur 2012).

Prior to running the GAM, a classification and regression tree (CART) was used to identify which explanatory variables had a significant correlation with the response variables, and could be used to create the most parsimonious model. CART is a non-parametric analysis and explanatory variables are transformed to rank scores prior to analysis (Breiman et al. 1984). Manual forward and backward stepwise selection after the GAM procedure was also performed to validate this selection based on minimisation of the Akaike Information Criteria (AIC) (Burnham & Anderson 2004). Model appropriateness was assessed by examining diagnostic plots (e.g. fitted vs residuals and histograms) and r^2 values, which is the fraction of variance explained by the model. The deviance explained is expressed as a percentage. The importance of each explanatory variable in the models was determined by calculating the pseudo-R^2 and sequentially removing one explanatory variable at a time from the model and comparing the change in the residual deviance from the full model. Residuals showed no strong structure for all three models, however, normality and homogeneity of variance were improved with the use of transformations and the Gaussian distribution with identity link.

Results

Euphausiid species richness and biogeographic assemblages in the Indian Ocean

Fifty six species of euphausiids have distributions within the Indian Ocean study area. This includes species from two families, Bentheuphausiidae and Euphausiidae, and nine genera, *Bentheuphausia*, *Euphausia*, *Nematoscelis*, *Nematobrachion*, *Nyctiphanes*, *Pseudeuphausia*, *Stylocheiron*, *Thysanoessa* and *Thysanopoda*.

Euphausia, *Stylocheiron* and *Thysanopoda* are the most speciose genera of euphausiids, and these were well represented in the Indian Ocean, together accounting for 77% of the species recorded.

Species richness ranged between 2 and 34 species per cell (Fig. 5.1). Overall, there was a general decrease in species richness with increasing latitude (Fig. 5.2), although there was an extension of high species richness in the southern hemisphere boundary currents i.e. Agulhas and Leeuwin Currents (Fig. 5.1). Species richness declined more rapidly with increasing latitude in the northern Indian Ocean, compared with the southern Indian Ocean. Areas with the highest species richness occurred within the Agulhas Current, Leeuwin Current, Indo-Australian basin and between the Mascarene Plateau and Chagos Archipelago. Areas of low species richness occurred in the northern Indian Ocean, most notably in the Arabian Sea, Bay of Bengal, Red Sea and the Persian Gulf. Relatively lower richness also occurred off the southern coast of Australia.

The Indian Ocean was divided into seven biogeographic assemblage groups based on a Bray-Curtis similarity matrix of the presence/absence euphausiid assemblage data, and 65% level of similarity (Fig. 5.3). One of these groups consisted of a single cell, off the north-west shelf of Australia (120.5°E, 19°S), and could not be statistically compared to other groups, which were all significantly different from each other ($P < 0.010$, $R > 0.70$). The largest assemblage group spanned the entire tropics and subtropics of the Indian Ocean between the 14°N and 34°S, and encompassed the most species rich In the northern Indian Ocean, the Bay of Bengal, Arabian Sea, and Red Sea were grouped into a northern Indian Ocean assemblage (Fig. 5.3). However, some coastal

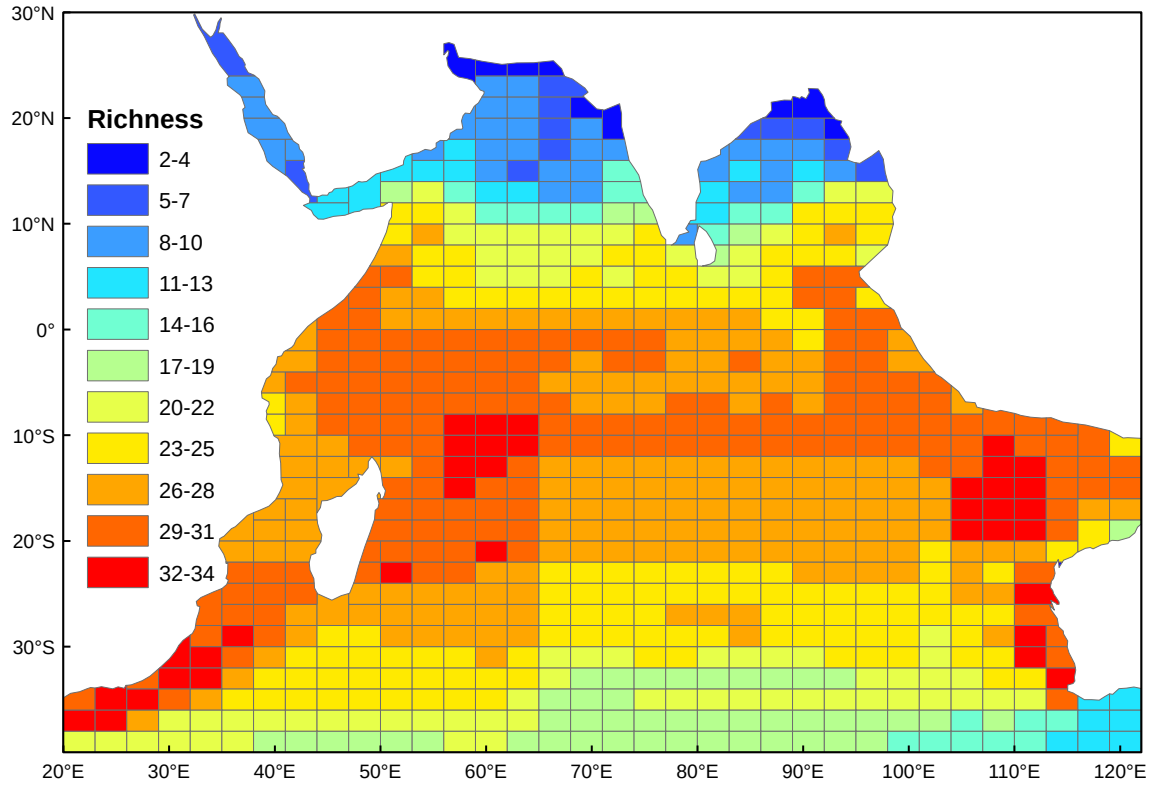


Figure 5.1 Euphausiid species richness for each sampling cell in the Indian Ocean, collated from published euphausiid records. Red cells indicate high species richness and dark blue cells indicate low species richness.

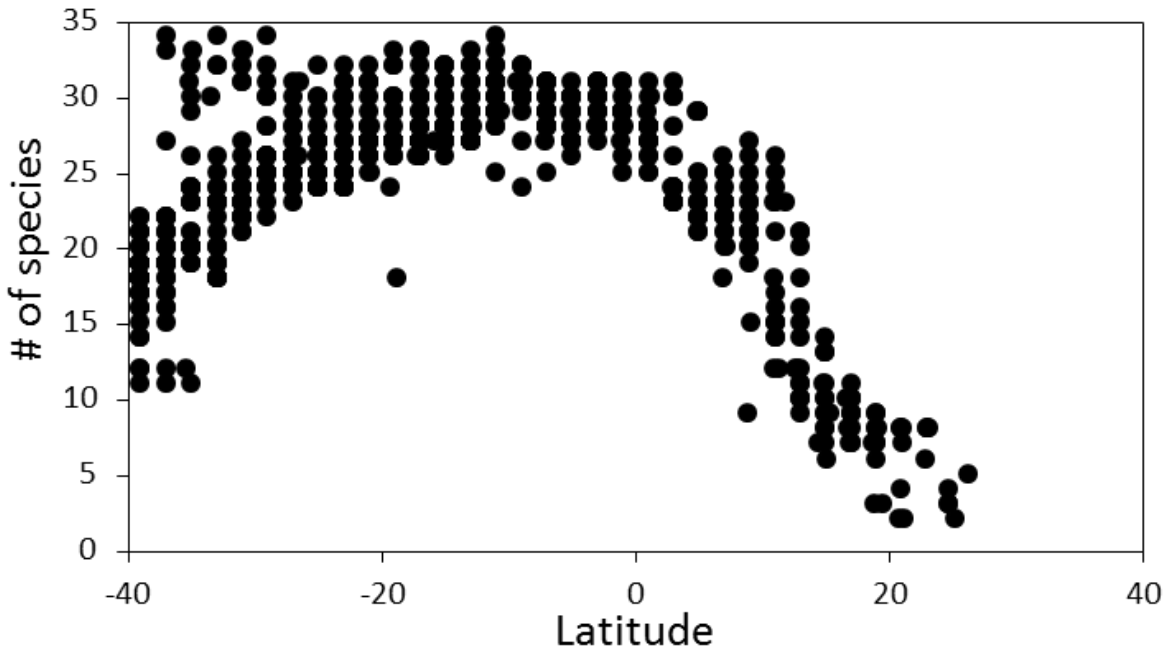


Figure 5.2 Euphausiid species richness versus latitude in the Indian Ocean between 40°N and 40°S.

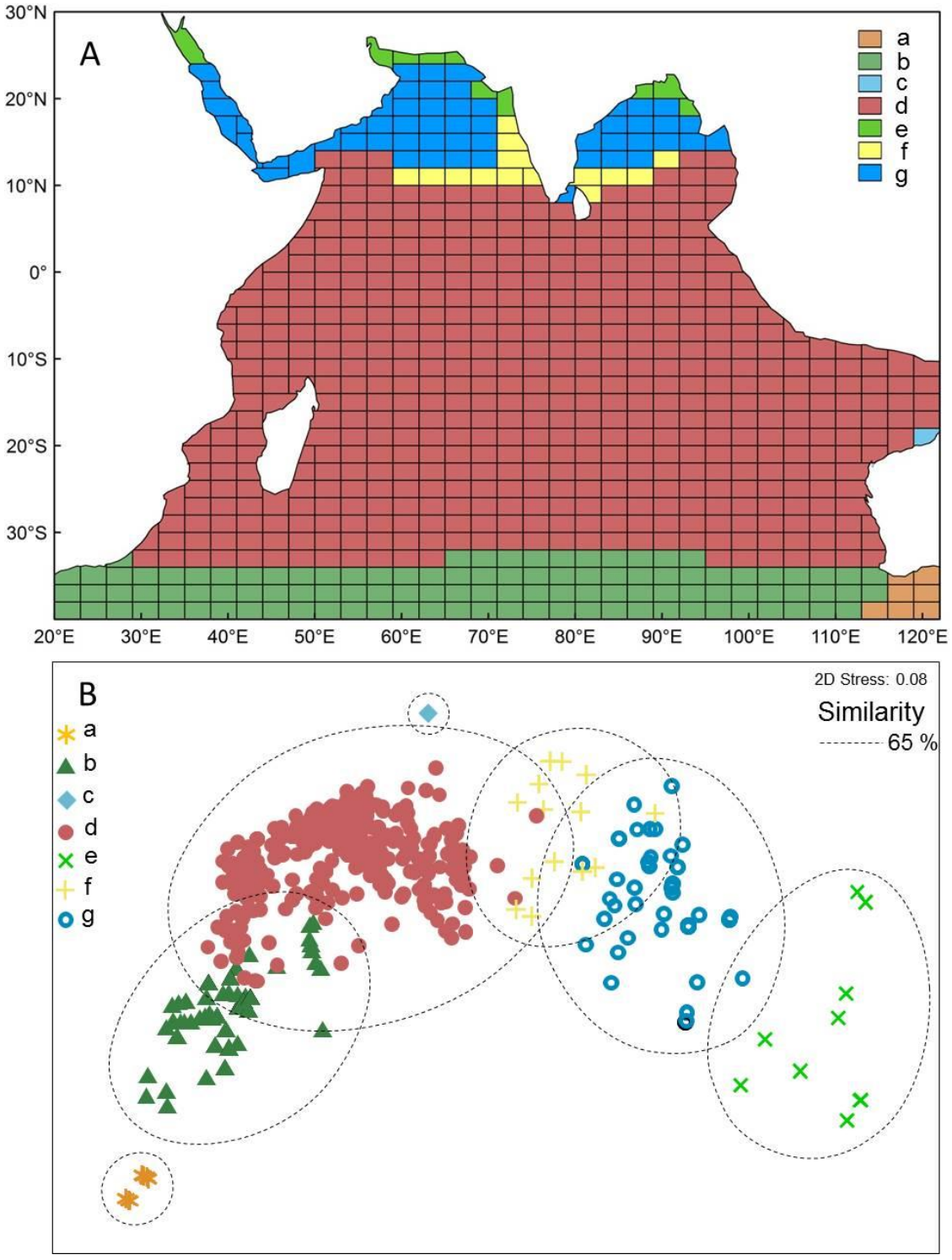


Figure 5.3 A) The Indian Ocean divided into seven biogeographic assemblage groups (a-g), based on B) a Bray-Curtis similarity matrix, and represented by the nMDS, of the presence/absence euphausiid assemblage data. Assemblage groups were separated based on a 65% level of assemblage similarity.

cells were further distinguished because of species richness values from 2 - 5 species per cell (Fig. 5.1). There was also an assemblage group south of the Bay of Bengal and Arabian Sea and bordering the large tropical/subtropical assemblage; this grouping may be indicative of a transition zone (Fig. 5.3).

Taxonomic distinctness of euphausiids in the Indian Ocean

AveTD was remarkably similar across most of the Indian Ocean (Fig. 5.4). A relatively uniform distinctness of 59 - 61 occurred across the middle ocean basin and in line with the boundary currents on both the eastern and western sides of the ocean. The highest AveTD of euphausiids occurred where there was lowest species richness. The centre of the Bay of Bengal attained a value of 70 from the presence of 10 species per

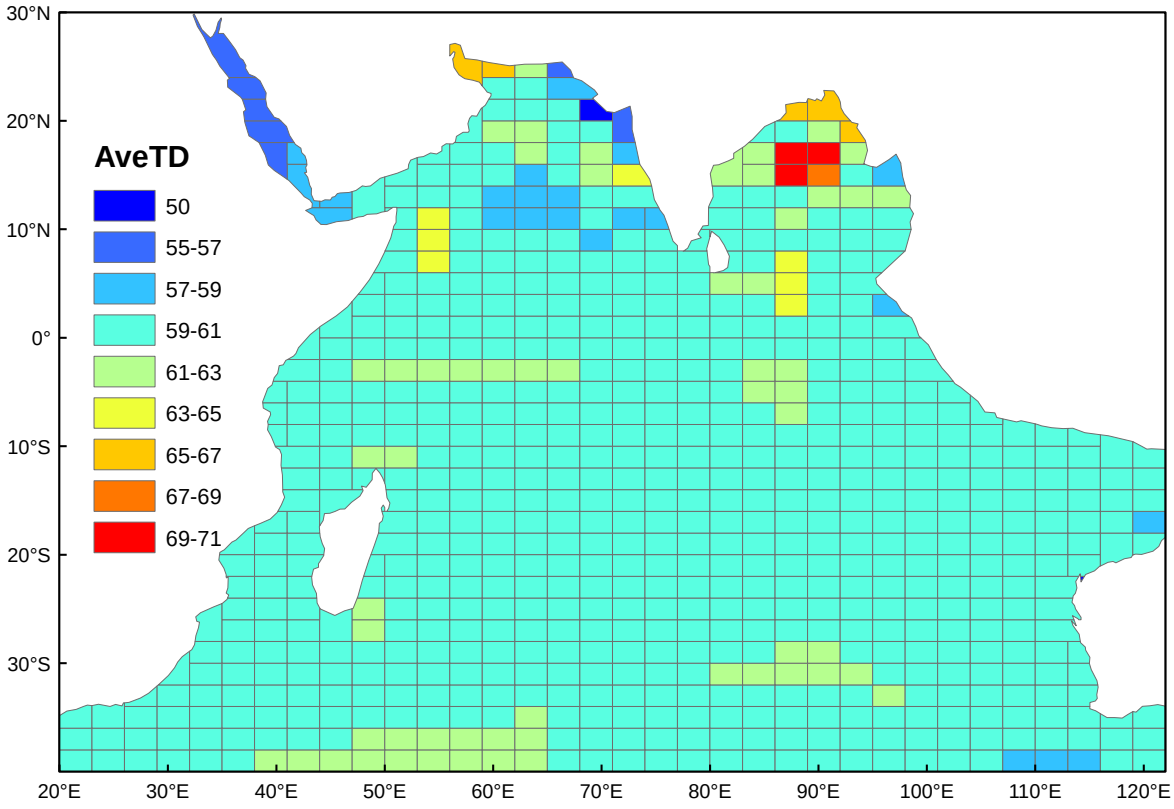


Figure 5.4 Average taxonomic distinctness of euphausiids for each sampling cell in the Indian Ocean. Red cells indicate high average taxonomic distinctness and dark blue cells indicate low average taxonomic distinctness.

cell, and was largely due to the presence of *B. amblyops*, from the monotypic family Bentheuphausiidae, and *P. latifrons*, which is the only species of the *Pseudeuphausia* genus found in the Indian Ocean. Additional areas of higher distinctness occurred in the Gulf of Oman and the northern extent of the Bay of Bengal. These localities were somewhat of an anomaly as only *P. latifrons* and *E. sibogae* were recorded there, and the path length between these two species returned a relatively higher AveTD. Areas of low AveTD occurred in the Red Sea (~ 57), and to the north-east of the Arabian Sea (~55 - 58).

A randomisation test showed that all values of AveTD fell within the 95% probability limits of the expected mean for AveTD, which indicated that the euphausiid species sampled were representative of the Indian Ocean species pool (Fig. 5.5a).

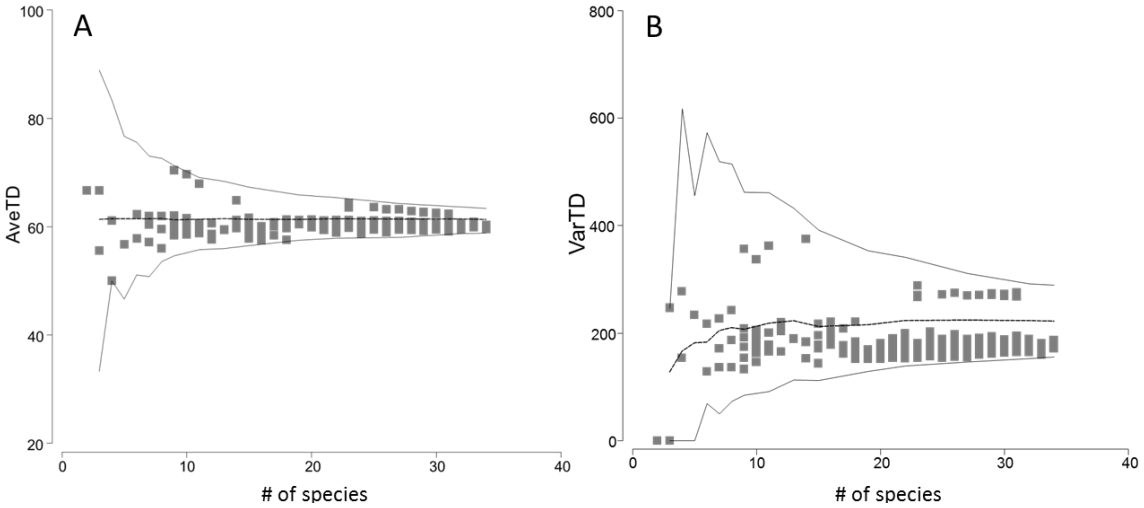


Figure 5.5 Funnel plots showing the expected mean value (dashed line) for A) average taxonomic distinctness (AveTD) and B) variation in taxonomic distinctness (VarTD) for euphausiids in the Indian Ocean. The expected mean value is derived from random subsamples of the 56 species of euphausiids recorded from the 708 sampling cells, and the upper and lower 95% probability limits are shown (solid lines).

Most of the southern Indian Ocean and much of the northern Indian Ocean had a relatively low VarTD (Fig. 5.6). VarTD was highest at the centre of the Bay of Bengal (~356) and off the coast of Goa, India (375). Other areas of higher VarTD occurred in

the Red Sea, north-east Arabian Sea, and at points either side of the equator. The Gulf of Oman and the northern Bay of Bengal had a VarTD of 0 due to the presence of only two species.

A randomisation test showed that there were no under or over-estimates of VarTD, as all values fell within the 95% probability limits of the expected mean for VarTD (Fig. 5.5b).

Environmental drivers of euphausiid zoogeography

The explanatory variables used in the final GAMs can be seen in Fig. 5.7. All other explanatory variables used in the CART but not in the final GAMs can be found in Appendix 2.

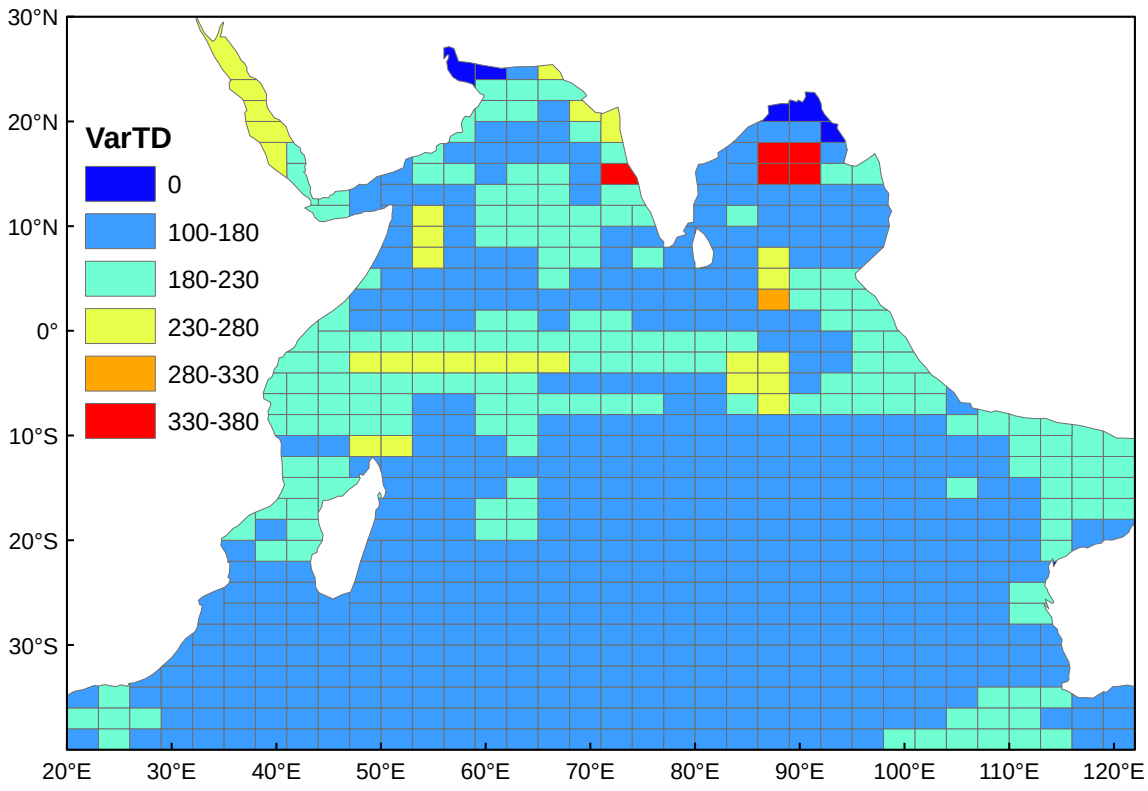


Figure 5.6 Variation in taxonomic distinctness (VarTD) of euphausiid for each sampling cell in the Indian Ocean. Red cells indicate high variation in taxonomic distinctness and dark blue cells indicate low variation in taxonomic distinctness

Species richness

A CART analysis revealed surface salinity, oxygen at 300 m, winter chlorophyll and temperature at 150 m to be most correlated with species richness across the Indian Ocean. These variables were included in the GAM for species richness and, after further model selection, the final model included all but temperature at 150 m.

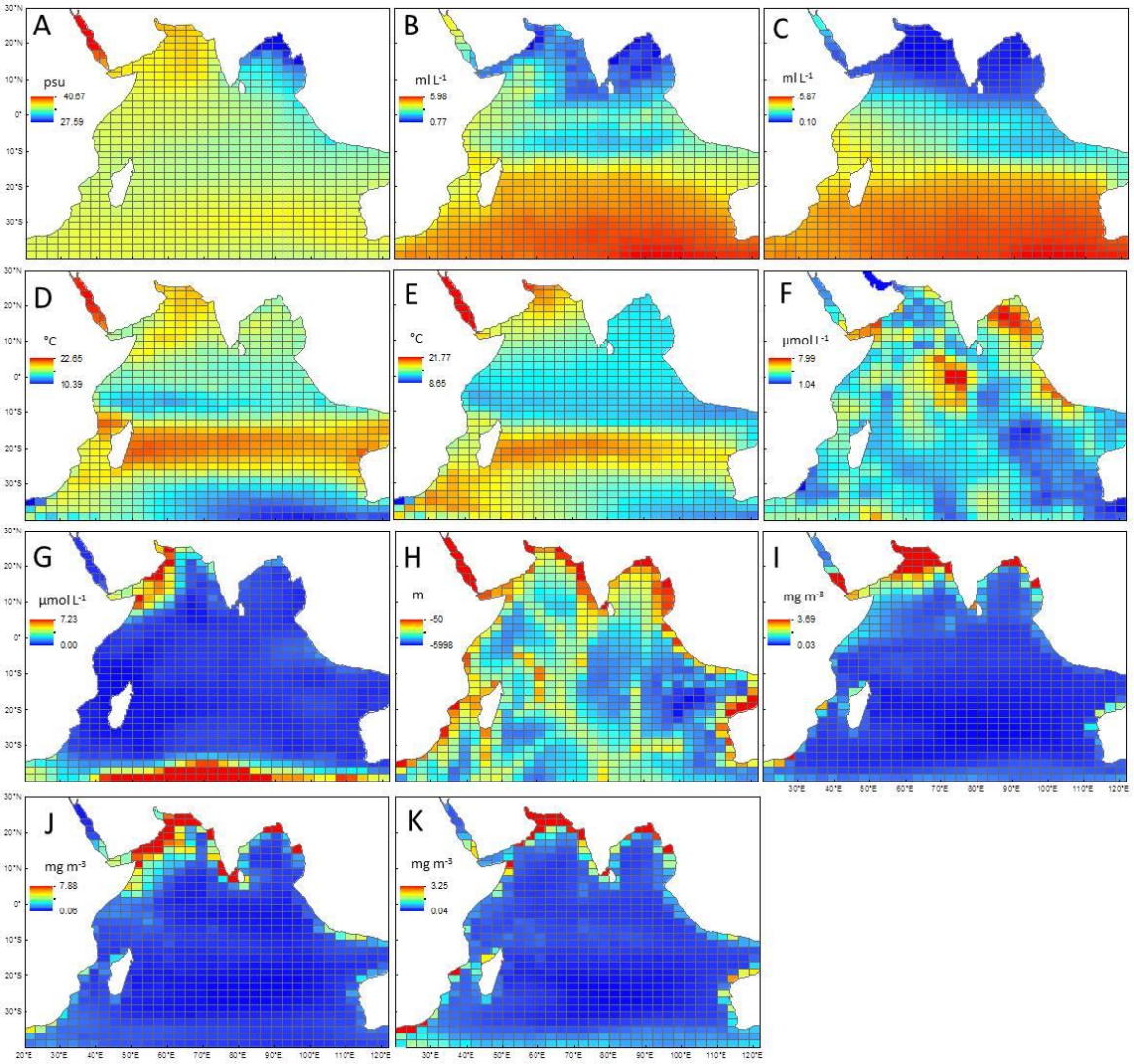


Figure 5.7 Derived environmental variables, used in generalised additive models for species richness, average taxonomic distinctness and variation in taxonomic distinctness, extracted to each sampling cell for the Indian Ocean. A) surface salinity, B) oxygen at 100m depth, C) oxygen at 300 m, D) temperature at 150 m depth, E) temperature at 300 m depth , F) surface silicate, G) surface nitrate, H) depth, I) winter chlorophyll, J) summer chlorophyll and K) spring chlorophyll.

The GAM explained 85% of the variation in species richness (r^2 = 0.82, $p < 0.001$, n= 708) (Table 5.3), and all three variables were significant in the model ($p < 0.001$) (Table 5.4). Oxygen at 300 m was the most important variable in terms of the amount of variance explained, followed by surface salinity (log). Species richness increased with increasing oxygen at 300 m until ~ 2.5 ml L^{-1} (Fig. 5.8A), where richness remained high until reaching ~ 4.5 ml L^{-1}. Species richness then declined as oxygen at 300 m increased. Species richness showed an increase with increasing surface salinity (log) to ~ 1.52 (~33.5 psu) (Fig. 5.8B), but then decreased with increasing surface salinity (log) thereafter. Species richness varied slightly with increasing winter chlorophyll (log) (Fig. 5.8C), but then decreased when winter chlorophyll (log) was greater than 0.2 (~ 1.7 mg m^{-3}).

Table 5.3 The generalised additive models used to explain euphausiid species richness, average taxonomic distinctness (AveTD) and variation in taxonomic distinctness (VarTD) in the Indian Ocean. The most parsimonious model is shown for each diversity measure along with the deviance explained, the significance of the model (p value) and the number of sampling cells included in the analysis. The *s* before parentheses indicates a smoothing term was used.

GAM model	**% deviance explained**	**p value**	**n**
Species richness ~ s(surface salinity (log)) + s(winter chlorophyll (log)) + s(oxygen at 300 m)	85%	< 0.001	708
AveTD ~ s(oxygen at 100 m) + s(surface salinity (log)) + s(surface nitrate (log)) + s(surface silicate (log)) + s(depth) + s(summer chlorophyll (log)) + s(temperature at 300 m (log))	53%	< 0.001	708
VarTD ~ s(depth) + s(oxygen at 100 m) + s(surface salinity (log)) + s(surface silicate (log)) + s(spring chlorophyll (log)) + s(temperature at 300 m (log))	39%	< 0.001	708

Table 5.4 The significance (estimated p-value) of each environmental explanatory variable in the GAMs for species richness, average taxonomic distinctness and variation in taxonomic distinctness of euphausiids in the Indian Ocean. Estimated degrees of freedom, chi-squared value and F statistic are also shown for each variable.

Model	Variable	edf	Chi- squared	p-value
Species richness	Surface salinity (log)	6.37	103.47	< 0.001
	Oxygen at 300 m	8.15	264.30	< 0.001
	Winter chlorophyll (log)	8.43	28.86	0.001
Model	**Variable**	**edf**	**F statistic**	**p-value**
AveTD	Oxygen at 100 m	4.79	4.27	< 0.001
	Surface salinity (log)	8.41	16.07	< 0.001
	Surface nitrate (log)	7.39	2.30	0.018
	Surface silicate	5.04	6.21	< 0.001
	Depth	2.72	7.70	< 0.001
	Summer chlorophyll (log)	6.25	4.72	< 0.001
	Temperature at 300 m (log)	8.35	4.60	< 0.001
VarTD	Depth	6.38	2.32	0.021
	Oxygen at 100 m	7.35	3.40	< 0.001
	Surface salinity (log)	4.26	16.54	< 0.001
	Surface silicate	5.29	7.85	< 0.001
	Soring chlorophyll (log)	7.56	2.60	0.007
	Temperature at 300 m	8.18	2.73	0.004

Average taxonomic distinctness

The CART analysis identified oxygen at 100 m, surface salinity, surface nitrate, surface silicate, temperature at 300 m, depth of water and summer chlorophyll to correlate most with AveTD of euphausiids. All of these variables were included in the GAM.

The GAM explained 53% of the variation in AveTD of euphausiids ($r^2 = 0.50$, $p < 0.001$, $n = 708$) (Table 5.3). All variables in the model were significant ($p < 0.010$) (Table 5.4). Surface salinity (log) was the most important variable in terms of the amount of variance explained. Although, no clear pattern was observed for AveTD with increasing surface salinity (log) (Fig. 5.9A), and the low surface salinity and low species richness in the Bay of Bengal was largely attributed for this variation. AveTD initially decreased

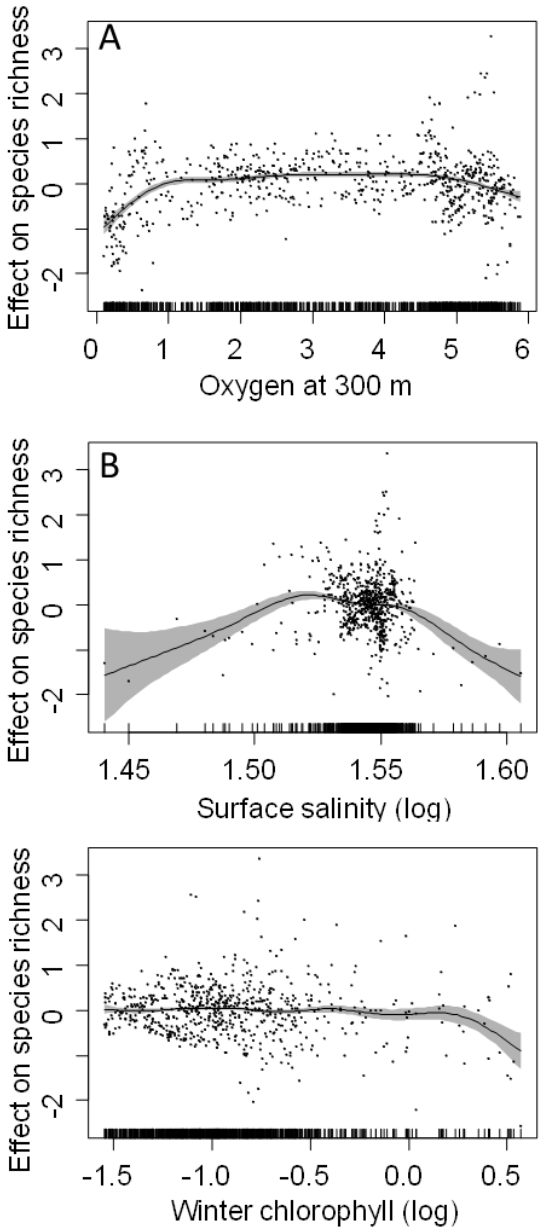


Figure 5.8 Smoothed additive effects of A) oxygen at 300 m depth, B) surface salinity (log) and C) winter chlorophyll (log) on euphausiid species richness in the Indian Ocean, as estimated by a three variable generalised additive model. Zero on the vertical axes corresponds to no effect of the explanatory variable. Grey bands indicate the 95% confidence limits and the vertical dashes at the bottom of the plots show the distribution of points included in the model. Log scales are indicated.

with increasing temperature at 300 m (log) (Fig. 5.9B), but then increased with increasing temperature at 300 m (log) until 1.24 (~ 17.3°C). AveTD declined thereafter. AveTD varied slightly with the remaining variables, although, higher AveTD occurred where oxygen at 100 m was lowest (Fig. 5.9C) and surface silicate was highest (Fig.

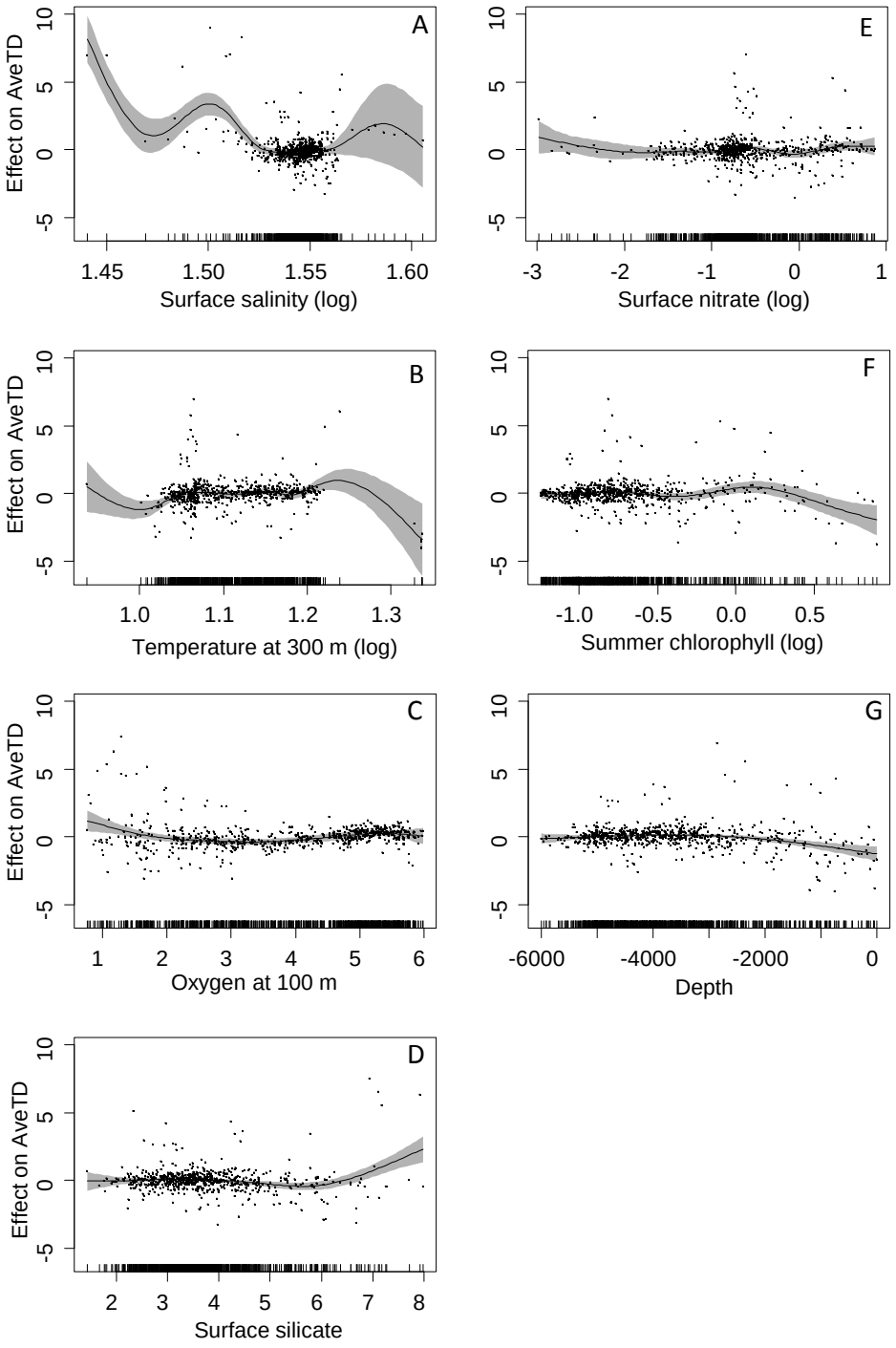


Figure 5.9 Smoothed additive effects of A) surface salinity (log), B) temperature at 300 m depth (log), C) oxygen at 100 m depth, D) surface silicate, E) surface nitrate (log), F) summer chlorophyll (log) and G) depth on the average taxonomic distinctness of euphausiids in the Indian Ocean, as estimated by a seven variable generalised additive model. Zero on the vertical axes corresponds to no effect of the explanatory variable. Grey bands indicate the 95% confidence limits and the vertical dashes at the bottom of the plots show the distribution of points included in the model. Log scales are indicated.

5.9D). This was largely attributable to the low oxygen, high silicate, and low species richness of the northern Indian Ocean. Lower AveTD occurred where summer chlorophyll was highest (Fig. 5.9F) and depths were shallower (Fig. 5.9G).

Variation in average taxonomic distinctness

A CART analysis revealed depth, oxygen at 100 m, surface salinity (log), surface silicate(log), temperature at 300 m (log), and spring chlorophyll (log) to correlate most with VarTD of euphausiids, and all variables were included in the GAM.

The GAM explained 39% of the variation in VarTD of euphausiids ($r^2 = 0.35$, $p < 0.001$, $n = 708$) (Table 5.3). All variable were significant in the model ($p < 0.010$) (Table 5.4). Surface salinity (log) was the most important variable in terms of the amount of variance explained. VarTD increased with increasing surface salinity (log) until reaching ~ 1.53 (~ 33.9 psu) (Fig. 5.10A), and then remained relatively stable with a further increase in surface salinity (log). VarTD varied slightly with increasing temperature at 300 m (log) (Fig. 5.10B), and then increased when temperature at 300 m (log) exceeded ~ 1.25 (~ 17.3°C). VarTD varied slightly with increases in the remaining variables, but showed an increase where depths were shallower than 1500 m (Fig. 5.10C), oxygen at 100 m was lowest (Fig. 5.10D), and where spring chlorophyll (Fig. 5.10E) and surface silicate (Fig. 5.10F) were highest.

Discussion

Species richness and taxonomic distinctness provided different, almost opposite, perspectives on euphausiid biodiversity across the Indian Ocean and can offer complementary information when considering biodiversity patterns. The unique

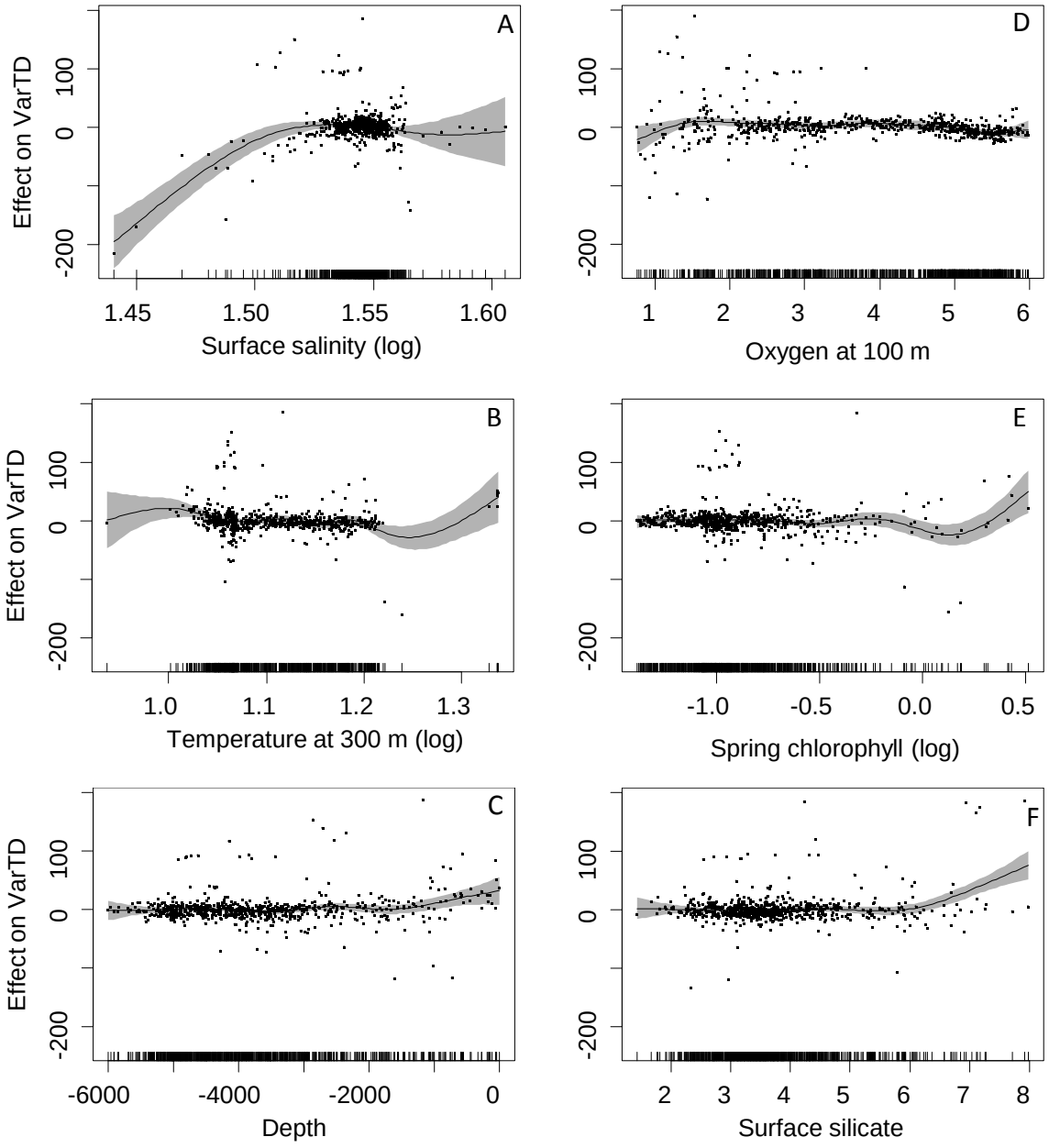


Figure 5.10 Smoothed additive effects of A) surface salinity (log), B) temperature at 300 m depth (log), C) depth, D) oxygen at 100 m depth E) spring chlorophyll (log) and F) surface silicate on the variation in taxonomic distinctness of euphausiids in the Indian Ocean, as estimated by a six variable generalised additive model. Zero on the vertical axes corresponds to no effect of the explanatory variable. Grey bands indicate the 95% confidence limits and the vertical dashes at the bottom of the plots show the distribution of points included in the model. Log scales are indicated.

environment of the northern Indian Ocean, most notably the low dissolved oxygen and low salinity, were dominant drivers of the patterns observed for species richness, species assemblages and taxonomic distinctness in the Indian Ocean. Most of the Indian Ocean was relatively uniform in species richness and taxonomic distinctness of

euphausiids, and the euphausiid assemblage was largely similar across the ocean basin, which may reflect the ocean circulation and ability of euphausiids to be transported via currents (Swartzman et al. 2005; Nicol 2006; Chapter 2).

Biodiversity of euphausiids in the Indian Ocean

The number of species occurring in the Indian Ocean (56) is less compared to values for the Atlantic Ocean (> 60) and Pacific Ocean (~ 81) (Brinton 1962; Gibbons 1997; Brinton et al. 2000; Letessier et al. 2009; Letessier et al. 2011). Letessier et al. (2011) speculated that the high number of euphausiid species in the Pacific may be attributable to the older age and larger area encompassed by this ocean, some 32% of the earth's surface. The Indian Ocean contains about 65% of the world's species of euphausiids and this may be attributable, in part, to species entering the Indian Ocean from the speciose Pacific Ocean via the Indonesian Throughflow (Brinton 1962; Brinton 1975).

Euphausiids are relatively low in diversity, in terms of total known species (86), compared to other orders from the class Malacostraca, such as Decapoda (e.g. crabs, shrimps) and Mysida (e.g. mysids). Most euphausiid species and their distributions are known (Brinton 1962; Brinton & Gopalakrishnan 1973; Brinton 1975; Brinton 2000; Letessier et al. 2009; Letessier et al. 2011), which would lessen the issue of sampling effort in comparison to more speciose taxa that are relatively unknown. While future genetic differentiation of euphausiids may increase the number of species currently known (Bucklin et al. 2007), differentiation at the family level seems less likely, and taxonomic distinctness of euphausiids would thus remain similar. All but one species of euphausiid are attributed to the family Euphausiidae (Baker et al. 1990). *Bentheuphausia amblyops* is from the monotypic family Bentheuphausiidae, and

although AveTD converges on an average of all species pairs in the sample, the presence of *B. amblyops* in a sample will increase the AveTD due to a longer path length through the taxonomic tree. *Bentheuphausia amblyops* has a wide distribution throughout the Pacific and Atlantic Oceans, and thus, it is likely that this species occurs widely in the Indian Ocean. However, due to its deep vertical distribution range (500 - 2000+ m) (Brinton et al. 2000), the collection of this euphausiid may prove more difficult.

Environmental drivers of euphausiid biodiversity

Salinity at the surface, which was strongly correlated with salinity in waters down to 300 m, was the most important variable, overall, driving variation in all three euphausiid biodiversity indices from this study. The lowest salinity was recorded from the Bay of Bengal, which receives a large freshwater influx from the rivers draining the Indian subcontinent and south-east Asia (Vinayachandran & Kurian 2007), and it also had the lowest species richness and highest euphausiid AveTD and VarTD. Euphausiid species richness modelling from the Pacific Ocean also found salinity to be a significant variable explaining the variation in euphausiid richness, where high salinity correlated with high euphausiid richness, particularly in the subtropical gyres (Letessier et al. 2011). In this Indian Ocean study, low salinity was associated with low species richness and high AveTD and VarTD, but only for the Bay of Bengal.

The Arabian Sea and Bay of Bengal were anomalies for the Indian Ocean in terms of euphausiid biodiversity and environmental variables. Species richness was the lowest recorded here for the Indian Ocean, whilst, somewhat surprisingly, AveTD was the highest. Higher AveTD was largely attributed to the presence of *B. amblyops* in its separate family Bentheuphausiidae. The Arabian Sea and Bay of Bengal also have

oxygen minimum zones (Morrison et al. 1999; Naqvi et al. 2009), which is a likely contributor to the low species richness for the area. Dissolved oxygen at 300 m, using GAM, was one of the most important variables to explain the variance in species richness. The few species that do occur there, however, are taxonomically separate from each other at the family level and spread across six different genera. *Bentheuphausia amblyops* is usually found below 500 m (Brinton et al. 2000), and has been found from the lower oxyclines in the Costa Rica Dome (Maas et al. 2004). *Euphausia sibogae* migrates to the surface waters at night, but descends into the oxygen minimum zone to around 300 – 400 m during the day (Brinton et al. 2000). These euphausiids, along with other species adapted to living in an OMZ, dwell in the cooler, hypoxic waters during the day and migrate up to consume food in the oxygenated photic zone during the night (Wishner et al. 1995). This behaviour is likely in response to such factors as predator avoidance, metabolic advantage and/or niche partitioning (Morrison et al. 1999; Antezana 2009).

The latitudinal gradient in species richness is a widely observed pattern for a number of marine taxa (Willig et al. 2003; Hillebrand 2004), and is often strongly correlated with sea surface temperature (Fuhrman et al. 2008; Tittensor et al. 2010). Further, peaks in species richness in mid latitudinal bands are found for a range of marine taxa (Tittensor et al. 2010), including zooplankton such as foraminiferans (Rutherford et al. 1999) and euphausiids (Gibbons 1997, Letessier et al. 2009; Letessier et al. 2011). This Indian Ocean study also found a latitudinal gradient in euphausiids. High species richness was extended further south towards the poles from transport in the Agulhas and Leeuwin Currents. However, sea surface temperature, and temperature at 300 m depth were not significantly contributing explanatory variables in the model. The

strength of the temperature and species richness relationship was likely inhibited by the confounding effect of the OMZ in the northern Indian Ocean creating lower species richness than would usually occur at mid-latitudes, due to low oxygen intolerance of many species (Sameoto et al. 1987). Despite this, it is highly likely, based on previous euphausiid studies, that temperature does play a significant role for euphausiids in the Indian Ocean, but due to the unique situation in the northern Indian Ocean, this relationship is not as clear. It is also likely, that if the study area was extended to 60°S, as in Letessier et al. (2009, 2011), a further decrease in species richness would occur, and may have generated a stronger temperature relationship.

The division of the Indian Ocean into euphausiid assemblage groupings based on a 65% level of similarity was investigated to see if they reflected environmental patterns, but also to observe the congruence with the biogeochemical provinces proposed by Longhurst (2007). Longhurst's provinces related to the pelagic environment in all oceans and were based on the influences of oceanographic factors on remotely sensed chlorophyll data. A total of nine biogeographical provinces has been defined within the boundaries of this Indian Ocean study. Overall, there was a mismatch in euphausiid assemblage groups with these nine provinces, particularly, the lack of division in euphausiid assemblages, as well as the three biodiversity measures, between the Indian Monsoon Gyre and Indian South Subtropical Gyre, as defined by Longhurst (2007). Although the assemblage groups did not match well with the static boundaries of the northern Indian Ocean provinces (Longhurst, 2007), they did match better with the dynamic and shifting boundaries calculated by Reygondeau et al. (2013). Reygondeau et al. (2013) analysed the provinces established by Longhurst (2007) with sea surface temperature, bathymetry, sea surface salinity and chlorophyll to establish

new dynamic boundaries that would reflect seasonal and interannual variability. For example, the South Subtropical Convergence province varied seasonally in Reygondeau et al. (2013), and the southern temperate euphausiid assemblage from this study coincided with this province more so during May – October. The assemblage boundaries in the northern Indian Ocean also matched the boundaries of the Northwest Arabian Sea upwelling, Western Indian Ocean and Eastern Indian Ocean for the February – April province distributions (Reygondeau et al. 2013), which is under the influence of the north-east monsoon (Schott & McCreary 2001).

Sea surface salinity was used by Reygondeau et al. (2013) to discriminate subtropical gyres from areas influenced by draining rivers. The Eastern India Coast province from Reygondeau et al. (2013) encompassed more of the Bay of Bengal than previously defined by Longhurst (2007), where salinity is low and attributed to river run off (Vinayachandran & Kurian 2007). Surface salinity was the most important variable explaining euphausiid biodiversity in the current study, and the boundaries of the northern Indian Ocean assemblage and the salinity boundary of the Bay of Bengal from this study were similar to the Eastern India Coast province (Reygondeau et al. 2013).

Ocean connectivity

Species richness and taxonomic distinctness of euphausiids displayed relatively uniform patterns across a large proportion of the Indian Ocean, and the euphausiid assemblage was largely similar across much of the ocean basin. This could be a reflection of ocean connectivity and the holoplanktonic nature of euphausiids where their distribution is assisted via transport in currents (Swartzman et al. 2005; Nicol 2006; Chapter 2). Population connectivity via dispersal in currents can be important for maintaining genetic diversity, isolated populations, and re-establishment of disturbed

locations (Treml et al. 2008; White et al. 2010). For euphausiids, currents can facilitate mixing of populations and genetic exchange. For example, *Euphausia superba* is considered to have a weak genetic differentiation in the large-scale context of the Southern Ocean due to the mixing of Antarctic waters in circum-Antarctic currents (Zane & Patarnello 2000). Conversely, *Meganyctiphanes norvegica* populations in the North Atlantic Ocean have been found to have more discrete genetic differences attributed to oceanographic patterns that may act as a barrier between western – eastern Atlantic and Atlantic - Mediterranean exchange (Zane & Patarnello 2000). In this study, Indian Ocean circulation may result in less distinct euphausiid populations, particularly for species that are found across the middle of the ocean basin and in boundary currents, e.g. *Stylocheiron carinatum*, *Euphausia mutica*, *Nematobrachion flexipes* and *Thysanopoda tricuspidata*.

Another case where high euphausiid species richness was not similarly reflected in AveTD was for the boundary currents of the Indian Ocean. The Indonesian Throughflow, South Indian Countercurrent and the Eastern Gyral Current form the source waters for the Leeuwin Current in the eastern Indian Ocean (Meyers et al. 1995; Domingues et al. 2007). The Leeuwin Current attained richness values of up to 34 species in some cells and harbours 37% of the world's euphausiid species (Sutton et al. 2015; Chapter 2, Chapter 3). Tropical species are also found as far south as 34°S, highlighting the Leeuwin Current as an effective transport route for euphausiids. This is similar for the Agulhas Current, which contains ~ 45% of the world's species. The species found in both current systems span eight genera from the Euphausiidae family, and most species are from the *Euphausia*, *Stylocheiron* and *Thysanopoda* genera. Given this, AveTD is not high, and is similar to the rest of the Indian Ocean.

In conclusion, this study has updated information of species richness for euphausiids in the Indian Ocean, and it is the first study to apply taxonomic distinctness as a biodiversity measure to euphausiids. The results of this study suggest that salinity and oxygen are the driving environmental variables for euphausiid species richness and taxonomic distinctness in the Indian Ocean, which links to the unique environment of the northern Indian Ocean. The influence of boundary currents on euphausiid distributions in the southern Indian Ocean was also evident.

Chapter 6: Trophodynamics of euphausiids in the marine food web of the Perth Canyon, south-east Indian Ocean

Abstract

The Perth Canyon is a known hotspot for pygmy blue whales (*Balaenoptera musculus brevicauda*) feeding on euphausiids in the south-east Indian Ocean. Fatty acids and stable isotopes in phytoplankton and the common euphausiids were analysed to ascertain the trophic structure in this oligotrophic environment, and to examine the potential biochemical link with pygmy blue whales. Stable isotope data placed *E. recurva* as a first order consumer. All euphausiids analysed (*E. recurva*, *Euphausia diomedeae*, *Stylocheiron carinatum*, *Pseudeuphausia latifrons*) were high in the nutritionally important docosahexaenoic acid (DHA, 22:6ω3) and 18:1ω9c, suggesting they are omnivorous and feeding largely on dinoflagellates typical of an oligotrophic environment. The fatty acids profiles of phytoplankton/detrital material from surface, 50 and 100 m depth suggests euphausiids were probably not feeding in these surface layers. *Balaenoptera musculus brevicauda* outer blubber layer fatty acid composition did not accurately reflect a diet of euphausiids. Blubber samples were, however, high in DHA which suggests a diet originating from dinoflagellates, similar to that of euphausiids. This study is the first to describe the fatty acid composition of *E. recurva*, *E. diomedeae*, S *carinatum*, *P. latifrons* and *B. musculus brevicauda*, and the comparative biochemical analyses performed provide new insights into the food web involving euphausiids of the Perth Canyon and south-east Indian Ocean.

Introduction

The importance of euphausiids in marine food webs has led to a number of trophodynamic studies investigating prey/consumer pathways inferred by fatty acid (FA) and stable isotope analyses (e.g. Mayzaud et al. 1999; Falk-Petersen et al. 2000; Schmidt et al. 2003; Schmidt et al. 2006). Some FA attained from prey can be synthesised by consumers, but usually, many FA assimilate intact, such as long-chain (LC, $\geq C_{20}$) polyunsaturated FA (LC-PUFA), resulting in the FA signature of the consumer reflecting that of its prey (Iverson 2004; Iverson 2009). Stable isotopes of carbon ($\delta^{13}C$) are often used to identify the primary producer (Fry and Sherr 1984; France and Peters 1997), and nitrogen ($\delta^{15}N$), the trophic position of a consumer based on the stepwise enrichment of $\delta^{15}N$ (Peterson and Fry 1987; Davenport and Bax; 2002; Post 2002). Most investigations on euphausiid trophodynamics have focused on temperate and Southern Ocean species, in particular, Antarctic krill, *Euphausia superba* (e.g. Saether et al. 1986; Virtue et al. 1996; Phleger et al. 1998; Mayzaud et al. 1999; Nicol et al. 2004; Ju et al. 2009; Yoshida et al. 2011). However, there are 86 known species of euphausiids worldwide that are adapted to a range of feeding behaviours (Mauchline & Fisher 1987), and few trophodynamic studies exist for species in tropical and subtropical environments.

Over a third of the world's euphausiid species have been identified within the Leeuwin Current system in the south-east Indian Ocean (Wilson et al. 2003a; Sutton et al. 2015; Chapter 2; Chapter 3). The Leeuwin Current system also supports southern blue fin tuna, migratory baleen whale and whale shark populations, and globally important colonies of seabirds, all of which are consumers of euphausiids (Wilson et al. 2001b; Surman & Wooler 2003; Rennie et al. 2009; Itoh et al. 2011). The trophodynamics of

euphausiids have not yet been investigated within the Leeuwin Current system, nor the south-east Indian Ocean. In particular, the subtropical/temperate species, *Euphausia recurva*, tends to dominate euphausiid assemblages between 30°S - 34°S (McWilliam 1977; Sutton et al. 2015), and is considered an important food source for pygmy blue whales (*Balaenoptera musculus brevicauda*) as they migrate north along the coast of Western Australia (Rennie et al. 2009). The Perth Canyon has also been identified as one of three distinct feeding grounds for *B. musculus brevicauda* in waters off Australia (Double et al. 2014).

Nutrient rich waters usually generate a marine food web dominated by large phytoplankton (i.e. diatoms), whereas nutrient poor waters tend to be dominated by small autotrophic flagellates (i.e. dinoflagellates) and cyanobacteria (Ryther 1969; Cushing 1989; Legendre & Rassoulzadegan 1995). Off Western Australia, the suppression of upwelling by the dominant Leeuwin Current results in relatively oligotrophic waters (Lenanton et al. 1991; Pearce 1991; Hanson et al. 2005, Koslow et al. 2008; Lourey et al. 2013). However, the high eddy kinetic energy of the Leeuwin Current leads to the generation of anticyclonic eddies containing elevated nutrients and diatom populations (Thompson et al. 2007; Waite et al. 2007a; Waite et al. 2007b).

The aim of this study is to investigate the FA and stable isotope composition of the common euphausiid species, in particular *E. recurva*, in the south-east Indian Ocean. Biochemical data of euphausiids were related to their potential food source, phytoplankton, and their potential consumer, *B. musculus brevicauda*, sampled in the Perth Canyon.

Methods

Sample collection

Zooplankton samples were collected during the day and night in proximity to *B. musculus brevicauda* sightings in surface waters of the Perth Canyon (32°S, 115°E) between April 24 - 27, 2014 and April 2 - 4, 2015 (Fig. 6.1). A surface zooplankton net (500 µm, 50 cm diameter) was towed repeatedly at a speed of two knots for 15 minutes until sufficient specimens were caught. Onboard R.V. *Whale Song*, four euphausiid species, *E. recurva*, *Euphausia diomedeae*, *Stylocheiron carinatum* and *Pseudeuphausia latifrons* were separated from zooplankton samples and identified

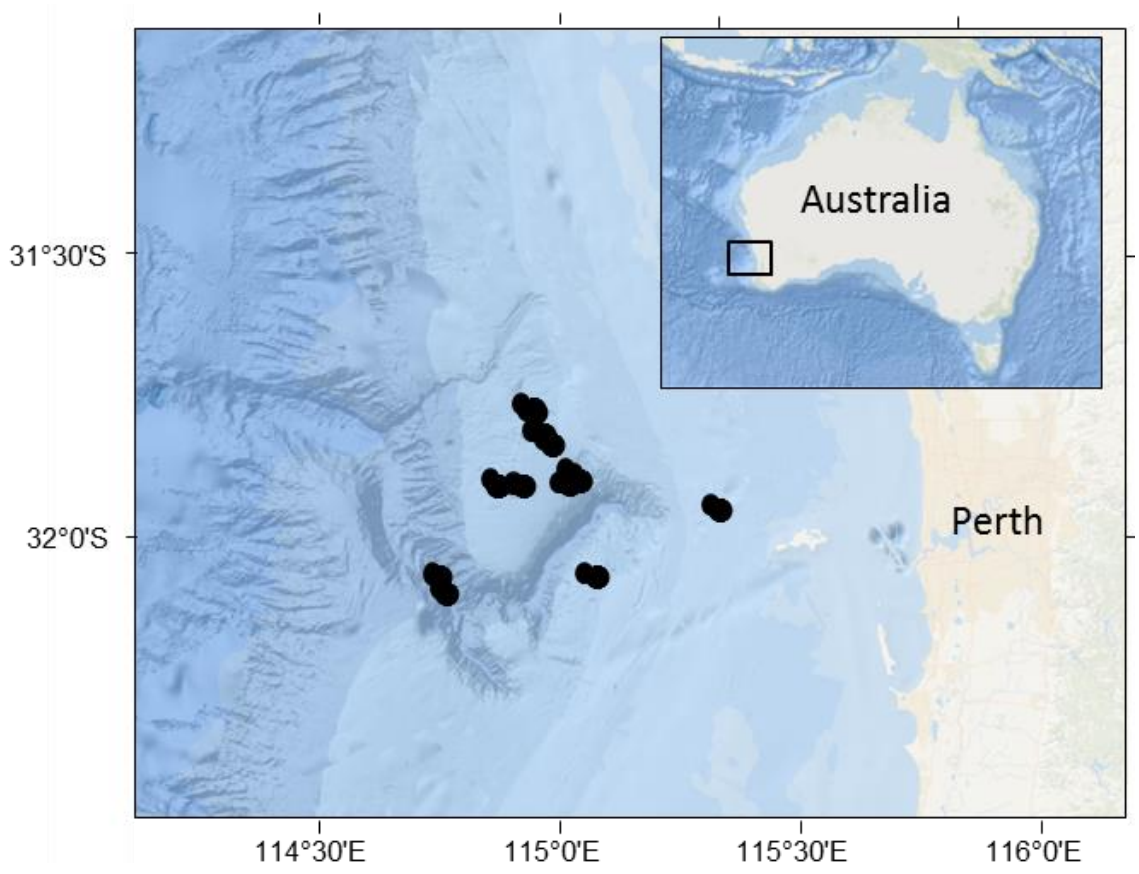


Figure 6.1 Sampling stations where euphausiids, phytoplankton and the pygmy blue whale (*Balaenoptera musculus brevicauda*) outer blubber layer samples were collected across the Perth Canyon, off Western Australia, during April 2014 and 2015 (Base map credit: ArcGIS World Ocean Base).

using a light microscope. Specimens were immediately frozen in liquid nitrogen. All *E. recurva* (n = 39), *E. diomedeae* (n = 6), *S. carinatum* (n = 3) and *P. latifrons* (n = 1) samples were analysed for fatty acids. *Euphausia recurva* (n = 26) specimens were also analysed for stable isotopes.

Concurrently with zooplankton sampling, sea water was filtered to obtain phytoplankton samples (2 - 5 L). Surface phytoplankton samples were obtained during 2014 and 2015, and additionally, phytoplankton samples were collected at 50 m and 100 m depths during 2015. All samples were immediately frozen in liquid nitrogen. Eight surface, two 100 m and one 50 m phytoplankton sample were analysed for chlorophyll *a*. Frozen glass fibre GF/C filter papers (pore size 1.2µm, Whatman Ltd. England) containing chlorophyll *a* were ground in 90% acetone and kept for 24 hours in the dark at 4°C. Chlorophyll *a* was then measured spectrophotometrically (Varian Cary 50 Spectrophotometer; Greenberg et al. 1992). Further, 13 surface phytoplankton samples and 50 m and 100 m phytoplankton sample were analysed for FA composition. Surface, 50 m and 100 m phytoplankton samples collected during 2015 were also analysed for stable isotopes (n = 5).

In addition to euphausiids and phytoplankton collection, samples of the outer blubber layer from individual *B. musculus brevicauda* animals were obtained using a biopsy probe from both sampling years (n = 1 in each year sampled). The outer blubber layer samples were immediately frozen in liquid nitrogen for lipid and FA analyses.

Stable isotope analysis

Whole *E. recurva* specimens were rinsed in deionised water for 15 minutes and oven-dried at 55°C for 24 - 48 hrs. Phytoplankton samples were rinsed with HCL then water

to remove calcium carbonate residue ($CaCO_3$), before drying at 55°C for 24 - 48 hrs. Samples were analysed for stable isotopes, $\delta^{15}N$ and $\delta^{13}C$, using a continuous flow system consisting of a Delta V Plus mass spectrometer connected with a Thermo Flush 1112 via Conflo IV (Thermo-Finnigan/Germany). Sample analysis was undertaken following the methods of Skrzypek and Paul (2006). Samples were weighed into tin capsules and were oxidised in a combustion reactor maintained at 102°C. The resulting gas mixture of CO_2, N_2 and H_2O was passed through a reduction reactor under the continuous flow of Helium at 65°C. CO_2 and N_2 were separated using a gas chromatography (GC) column maintained at 55°C and carried to a ConFlo III interface. Helium flow rates were lowered to ~ 0.3 mL/min before samples were introduced into the stable isotope ratio mass spectrometer (IRMS).

$\delta^{13}C$ and $\delta^{15}N$ were expressed as the relative difference in parts per thousand (‰) between the isotope ratio of the sample and the reference standards of Vienna PeeDee Belemnite and air, respectively, using the following equation:

$$\delta(\text{sample}) = \left(\frac{Rsample}{Rstandard} - 1\right) \times 1000\ ‰$$

where R is the concentration ratio of heavy to light isotope i.e. ^{13}C: ^{12}C and ^{15}N: ^{14}N.

Lipid and fatty acid analysis

Euphausiid specimens were sized, sexed and weighed prior to analysis. Samples of euphausiids, phytoplankton and *B. musculus brevicauda* outer blubber layer were quantitatively extracted overnight using the modified Bligh and Dyer (1959) method consisting of a methanol:dichloromethane:water ($MeOH/CH_2Cl_2/H_2O$) solvent mixture (20:10:8 mL). Phase separation was achieved the next day by adding 10 mL CH_2Cl_2 and 10 mL H_2O, giving a final methanol:dichloromethane:water solvent ratio of 1:1:0.9. The

lower layer was drained and the total solvent extract was concentrated using rotary evaporation. The extract was transferred into a pre-weighed 2 mL vial and the solvent was blown down under nitrogen gas to ascertain a total lipid extract weight. Solvent was added until further procedures were carried out to avoid oxidation.

The lipid class composition for *B. musculus brevicauda* outer blubber layer samples were determined from a portion of the total lipid extract using an Iatroscan MK-5 TLC/FID Analyser. A standard solution of known quantities of wax ester (WE), triacylglycerol (TAG), free fatty acid (FFA), sterol (ST) and phospholipid (also termed polar lipids, PL) was used to calibrate the flame ionisation detector. Aliquots of the total lipid extract was spotted on chromarods and developed for 30 minutes in a solvent system of hexane:diethyl-ether:acetic acid (70:10:0.1 mL). Rods were then oven dried at 100°C for 10 minutes prior to analysis in the Iatroscan. Lipid class peaks were labelled using SIC-480II Iatroscan Integrating Software v.7.0-E and quantified to mass per µl spotted using predetermined linear regressions. Total lipid content for *B. musculus brevicauda* outer blubber layer was expressed as mg g^{-1}.

For fatty acid methyl ester (FAME) preparation, a subsample of the total lipid extract was treated with 3 mL of methylating solution (methanol:dichloromethane: hydrochloric acid, 10:1:1) and heated at 100°C for one hour. Samples were cooled and 1 mL of H_2O and 1.5 mL of hexane:dichloromethane solution was added to extract FAME after vortexing. Centrifuging took place for 5 minutes and the upper layer containing FAME was transferred to a vial. This process was repeated twice using 1.5 mL of hexane:dichloromethane and samples were blown down using nitrogen gas. Samples were made to the desired concentration using an internal injection standard (19:0 FAME) and analysed via gas chromatography using an Agilent Technologies

7890A GC System (Palo Alto, California USA) equipped with a non-polar Equity™-1 fused silica capillary column (15 m x 0.1 mm internal diameter and 0.1 µm film thickness. Samples (0.2 µl) were injected at an oven temperature of 120°C with helium as the carrier gas. The oven temperature was raised to 270°C at a rate of 10°C per minute, then to 310°C at 5°C per minute. Peaks were quantified using Agilent Technologies ChemStation software, with initial identification based on comparison of retention times with known and laboratory standards. FA peaks were expressed as a percentage of the total FA area. Confirmation of component identification was performed by GC-MS of selected samples and was carried out on a ThermoScientific 1310 GC coupled with a TSQ triple quadruple. Samples were injected using a Tripleplus RSH auto sampler using a non polar HP-5 Ultra 2 bonded-phase column (50 m x 0.32 mm i.d. x 0.17 µm film thickness). The HP-5 column was of similar polarity to the column used for GC analyses. The initial oven temperature of 45°C was held for 1 min, followed by temperature programming at 30°C per minute to 140°C, then at 3°C per minute to 310°C, where it was held for 12 minutes. Helium was used as the carrier gas. Mass spectrometer operating conditions were: electron impact energy 70 eV; emission current 250 µamp, transfer line 310°C; source temperature 240°C; scan rate 0.8 scan/sec and mass range 40 - 650 Da. Mass spectra were acquired and processed with Thermo Scientific XcaliburTM software (Waltham, MA, USA).

Data analyses

In IBM SPSS Statistics 22, non-parametric Mann-Whitney U tests for independent samples were used to test for significant differences in stable isotopes, $\delta^{13}C$ and $\delta^{15}N$, between *E. recurva* specimens sampled during 2014 and 2015. Significant difference in

$\delta^{13}C$ and $\delta^{15}N$ values between *E. recurva* specimens and phytoplankton samples was also tested.

FA were included in analyses if they accounted for ≥ 0.5% of the total FA in at least one sample. FA were categorised as saturated (SFA), monounsaturated (MUFA) and polyunsaturated (PUFA), and each FA was expressed as a percentage of the total FA. Mean percentages and standard deviations are shown.

Multivariate analyses of FA compositions were carried out using the Primer-7 package (Clarke & Gorley 2015). An analysis of similarity (ANOSIM) was used to detect for any significant difference in FA composition between *E. recurva* specimens from 2014 and 2015. This interannual analysis was not carried out on phytoplankton or *B. musculus brevicauda* outer blubber layer samples due to the limited sample size. A principal component analysis (PCA) was used to visualise the similarity in FA composition across groups (phytoplankton, euphausiids and *B. musculus brevicauda*) based on Euclidean distance. Euphausiids included all species sampled, and phytoplankton included all surface, 50 m and 100 m samples for this analysis. The most important FA with a correlation > 0.15 were indicated on the PCA plot. ANOSIM routines tested for significant differences in FA composition between groups and a similarity percentage (SIMPER) routine was used to identify which FA were driving the differences between groups. Prior to analysis, a square root transformation was applied to the data to reduce the relative importance of abundant fatty acids. A Bray-Curtis resemblance matrix was constructed to quantify the dissimilarity in fatty acid composition between samples.

Results

Perth Canyon environment

Sea surface temperature of the Perth Canyon clearly showed the presence of the Leeuwin Current (> 22°C) (Fig. 6.2) during the time of sampling in April of 2014 and 2015 (sourced from http://oceancurrent.imos.org.au). The temperature signature of the Leeuwin Current was evident throughout the well mixed water column down to ~ 115 m for both years (Fig. 6.3). During 2015, a small anticyclonic eddy was observed near the sampling stations between 31.4°S - 31.9°S and 114.8°E - 115.4°E (Fig. 6.2). Chlorophyll *a* concentrations of surface phytoplankton samples collected in 2014 measured 0.4 µg/L, while those surface samples collected in 2015 all measured 0.3 µg/L. Phytoplankton collected at 50 m and 100 m depth in 2015 also showed low chlorophyll *a* concentrations, which ranged between 0.2 to 0.3 µg/L.

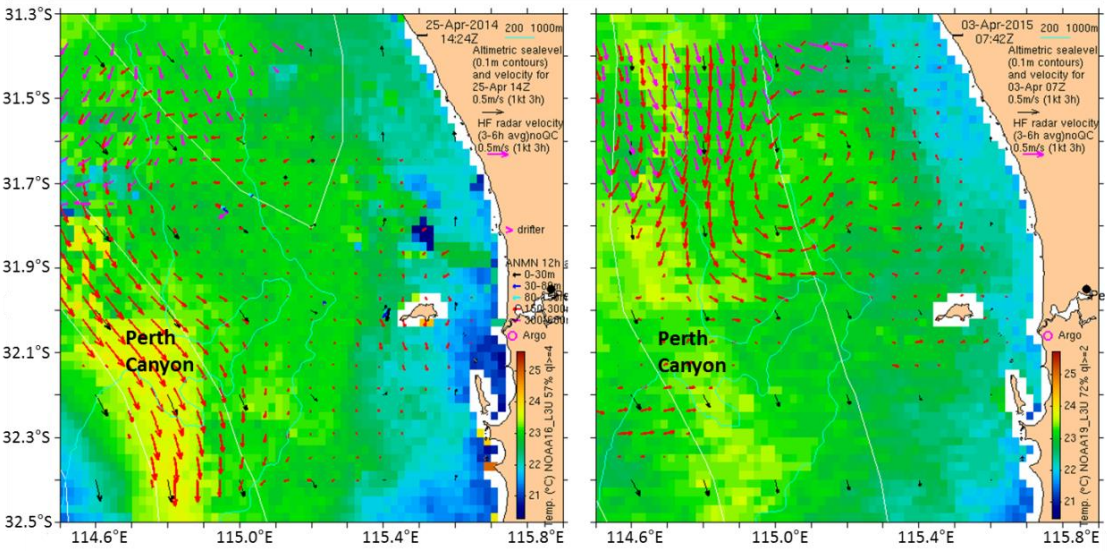


Figure 6.2 Sea surface temperature, current direction and velocity of the Leeuwin Current in the Perth Canyon study area for April 25, 2014 and April 3, 2015. An anticyclonic eddy was present in 2015. Images were sourced from the Integrated Marine Observing System (http://oceancurrent.imos.org.au/).

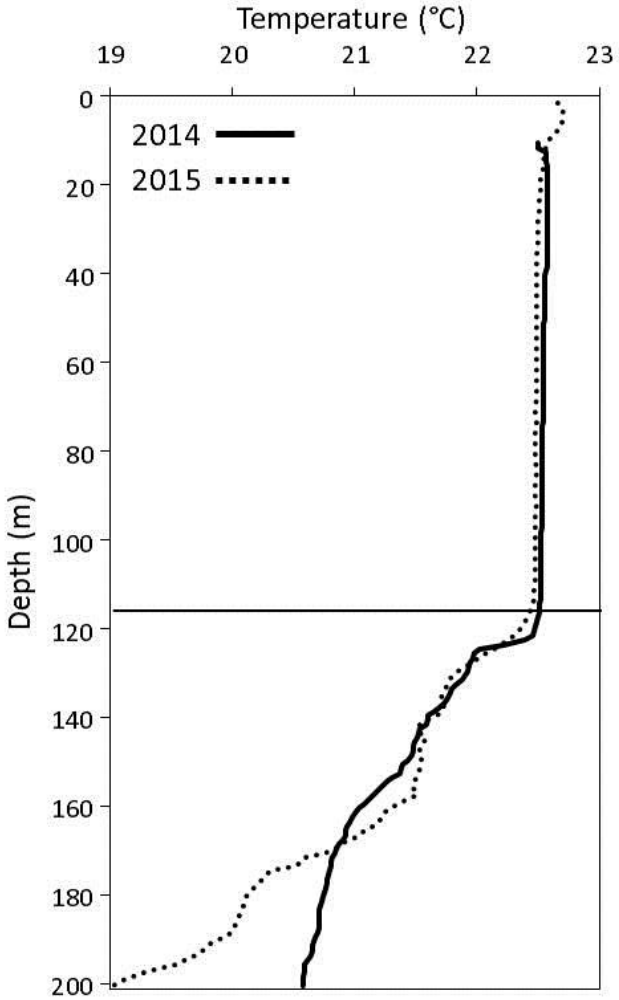


Figure 6.3 Temperature profiles through the water column (0 - 200 m) in the Perth Canyon during April 2014 and 2015. The mixed layer depth is indicated at ~ 115 m.

Stable isotopes of *Euphausia recurva*

$\delta^{13}C$ values of *E. recurva* ranged from -22.1 to -25.4 ‰, and $\delta^{15}N$ values from 4.8 to 8.4 ‰ (Fig. 6.4). The $\delta^{13}C$: $\delta^{15}N$ ratio for all samples ranged from 3.1 to 5.5. ANOVA revealed a significant difference in $\delta^{13}C$ ($p = 0.030$, $n = 26$, Mann-Whitney U) and $\delta^{15}N$ ($p = 0.003$, $n = 26$, Mann-Whitney U) values for *E. recurva* specimens sampled in 2014 and 2015.

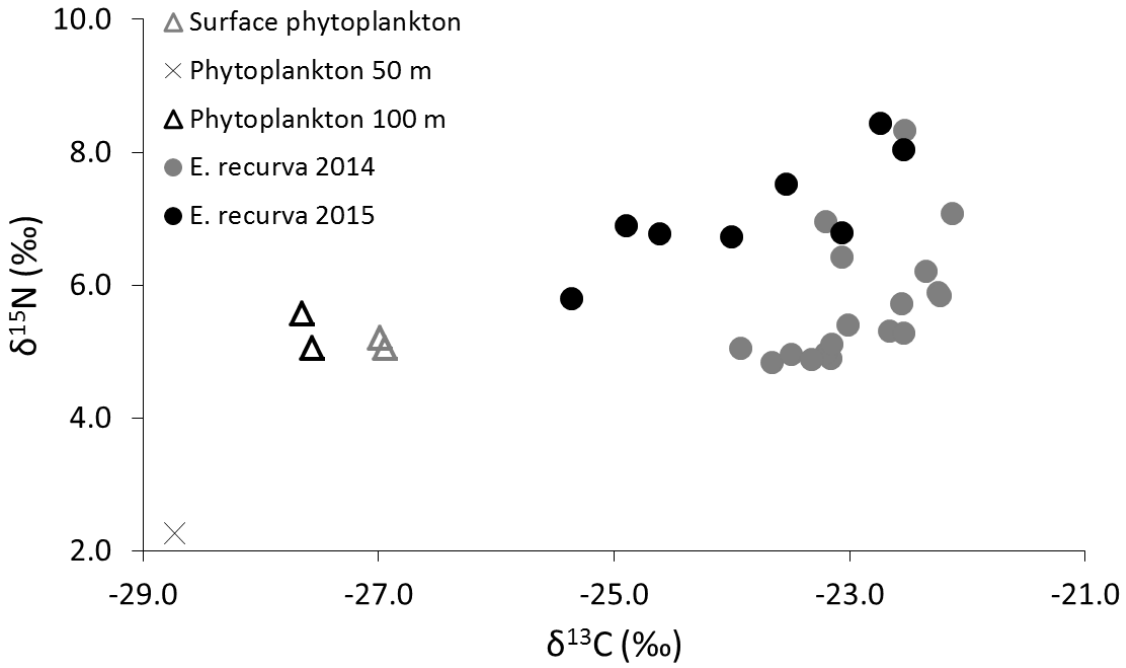


Figure 6.4 Stable isotopes, $\delta^{15}N$ plotted against $\delta^{13}C$, for *Euphausia recurva* specimens collected in April 2014 and April 2015, and phytoplankton samples collected at the surface and > 50 m depth in April 2015.

Stable isotopes of phytoplankton

Surface phytoplankton samples, and those taken at 100 m depth, had $\delta^{13}C$ ranging between -27.0 to -27.6 ‰, and $\delta^{15}N$ ranging from 5.0 to 5.6 ‰ (Fig. 6.4). Surface phytoplankton had a slightly higher $\delta^{13}C$ than phytoplankton sampled at 100 m depth. The single phytoplankton sample from 50 m depth had a lower $\delta^{13}C$ of -28.7 ‰ and a lower $\delta^{15}N$ of 2.3 ‰. ANOVA revealed a significant difference in $\delta^{13}C$ ($p < 0.001$, $n = 31$, Mann-Whitney U) and $\delta^{15}N$ ($p = 0.041$, $n = 31$, Mann-Whitney U) between all phytoplankton samples and *E. recurva* specimens.

Fatty acids of euphausiids

Of the 62 FA identified from all *E. recurva* specimens, 35 and 21 FA were detected at > 0.5 % for 2014 (Table 6.1) and 2015 (Table 6.2) samples, respectively. Docosahexaenoic acid (DHA, 22:6ω3), eicosapentaenoic acid (EPA, 20:5ω3), palmitic acid (16:0) and oleic acid (18:1ω9c) were the dominant FA across all *E. recurva*

Table 6.1 Fatty acid percentage composition for phytoplankton; the euphausiids *Euphausia recurva*, *Stylocheiron carinatum*, *Pseudeuphausia latifrons* and the pygmy blue whale *Balaenoptera musculus brevicauda* outer blubber layer sampled in the Perth Canyon during April 2014. Mean and standard deviations are shown for fatty acids > 0.5% of the total fatty acid composition.

	E. recurva	***S. carinatum***	***P. latifrons***	**Phytoplankton (surface)**	***B. musculus brevicauda***
	n = 27	n = 3	n = 1	n = 10	n = 1
14:0	2.2 ± 1.3	1.4 ± 0.5	0.0	4.5 ± 2.0	3.8
i15:0	0.2 ± 0.1	0.1 ± 0.1	0.0	0.5 ± 0.1	0.2
a15:0	0.1 ± 0.1	0.1 ± 0.1	0.0	1.1 ± 0.3	0.1
15:0	0.9 ± 0.4	0.7 ± 0.2	0.0	2.3 ± 0.5	0.6
16:0	16.4 ± 2.8	18.9 ± 2.7	11.6	28.3 ± 2.1	14.8
16:0FALD	0.6 ± 0.2	1.5 ± 0.3	0.0	0.6 ± 0.3	0.3
i17:0	0.2 ± 0.1	0.2 ± 0.1	0.0	0.4 ± 0.2	0.3
17:0	1.4 ± 0.2	1.6 ± 0.0	1.7	1.2 ± 0.2	1.0
i18:0	0.4 ± 0.1	0.3 ± 0.1	0.4	0.1 ± 0.1	0.1
18:0	3.6 ± 1.5	6.1 ± 1.7	15.7	10.5 ± 1.2	3.9
18:FALD	0.2 ± 0.1	0.2 ± 0.1	0.4	0.3 ± 0.1	0.2
20:0	0.8 ± 2.6	0.2 ± 0.0	0.8	1.1 ± 0.2	0.4
21:0	0.2 ± 0.1	0.2 ± 0.1	0.4	0.3 ± 0.1	0.1
22:0	0.3 ± 0.1	0.3 ± 0.0	0.5	1.3 ± 0.9	0.2
23:0	0.2 ± 0.2	1.0 ± 1.4	0.3	0.3 ± 0.1	0.1
24:0	0.2 ± 0.1	0.2 ± 0.0	0.6	1.7 ± 0.4	0.1
∑ SFA	**27.9 ± 2.5**	**32.9 ± 5.6**	**32.4**	**54.3 ± 4.6**	**26.2**
16:1w9c	0.2 ± 0.1	0.1 ± 0.1	0.0	6.4 ± 2.4	0.3
16:1w7c	2.7 ± 0.8	1.8 ± 0.5	0.8	2.2 ± 1.7	6.1
16:1w13t	0.1 ± 0.0	0.0 ± 0.0	0.0	0.5 ± 0.1	0.0
17:1w8c+a17:0	0.8 ± 0.2	0.4 ± 0.0	0.2	1.3 ± 0.1	1.4
18:1w9c	11.2 ± 2.0	7.6 ± 1.1	12.6	20.7 ± 3.3	41.2
18:1w7c	2.9 ± 0.4	1.5 ± 0.2	3.0	1.7 ± 0.5	4.7
18:1w7t	0.1 ± 0.1	0.1 ± 0.1	0.2	0.3 ± 0.2	0.1
18:1w5c	0.1 ± 0.0	0.2 ± 0.2	0.0	0.6 ± 0.5	0.2
20:1w11c	0.2 ± 0.4	0.1 ± 0.1	0.0	0.1 ± 0.2	0.1
20:1w9c	0.9 ± 0.6	0.6 ± 0.2	2.1	0.7 ± 0.4	2.3
20:1w7c	0.1 ± 0.2	0.0 ± 0.0	0.0	0.0 ± 0.1	0.3
20:1w5c	0.1 ± 0.2	0.3 ± 0.3	0.7	0.1 ± 0.1	0.0
22:1w11c	0.2 ± 0.9	0.0 ± 0.0	0.0	0.3 ± 0.1	0.1
22:1w9c	0.1 ± 0.1	0.1 ± 0.0	0.5	1.2 ± 0.6	0.2
22:1w7c	0.1 ± 0.1	0.0 ± 0.0	0.0	0.0 ± 0.0	0.1
24:1w9c	0.3 ± 0.1	0.6 ± 0.2	0.2	0.0 ± 0.1	0.2
∑ MUFA	**20.0 ± 3.4**	**13.6 ± 1.4**	**20.3**	**36.4 ± 3.4**	**57.3**
18:4w3	0.9 ± 0.3	0.5 ± 0.2	0.6	0.5 ± 0.2	0.4
18:2w6	3.3 ± 0.9	1.9 ± 0.2	3.5	3.9 ± 0.9	2.2
18:3w3	2.2 ± 0.6	1.3 ± 0.1	2.3	1.7 ± 0.3	1.4
20:4w6	3.4 ± 0.8	1.8 ± 0.7	2.4	0.1 ± 0.1	1.1
20:5w3 EPA	12.1 ± 1.7	11.0 ± 1.3	15.4	0.5 ± 0.4	1.5
20:4w3	0.4 ± 0.1	0.2 ± 0.2	0.7	0.2 ± 0.1	0.4
20:2w6	0.4 ± 0.1	0.2 ± 0.2	0.6	0.4 ± 0.1	0.3
22:5w6	1.1 ± 0.3	1.0 ± 0.1	0.9	0.1 ± 0.1	0.6
22:6w3 DHA	26.1 ± 2.6	34.0 ± 4.0	20.0	0.9 ± 0.8	5.0
22:4w6	0.2 ± 0.5	0.2 ± 0.1	0.2	0.0 ± 0.0	0.5
22:5w3	0.9 ± 0.7	0.6 ± 0.1	0.5	0.1 ± 0.2	1.7
∑ PUFA	**50.9 ± 3.4**	**52.8 ± 6.7**	**47.1**	**8.3 ± 2.6**	**14.9**
Other	**1.1 ± 0.1**	**0.7 ± 0.2**	**0.2**	**0.9 ± 0.2**	**1.6**
sum w3	**42.5 ± 3.4**	**47.7 ± 5.5**	**39.5**	**3.8 ± 1.6**	**10.3**
sum w6	**8.3 ± 1.0**	**5.1 ± 1.2**	**7.6**	**4.5 ± 1.0**	**4.6**
w3/w6	**5.2 ± 0.8**	**9.6 ± 1.3**	**5.2**	**0.8 ± 0.2**	**2.3**
DHA/EPA	**2.2 ± 0.4**	**3.1 ± 0.0**	**1.3**	**1.2 ± 0.8**	**3.2**
18:1w9/18:1w7	**3.9 ± 0.7**	**4.7 ± 0.1**	**3.9**	**10.2 ± 0.9**	**8.6**

SFA = saturated fatty acids, MUFA = monounsaturated fatty acids, PUFA = polyunsaturated fatty acids. Other = 14:1, i16:0, 16:1ω7t, 17:1, 18:3ω6, 18:1FALD, 19:1a, 19:1b, 20:3ω6, 21:5ω3, 24:1ω11c.

Table 6.2 Fatty acid percentage composition for phytoplankton; the euphausiids *Euphausia recurva* and *Euphausia diomedeae*, and the pygmy blue whale *Balaenoptera musculus brevicauda* outer blubber layer sampled in the Perth Canyon during April 2015. Mean and standard deviations are shown for fatty acids > 0.5% of the total fatty acid composition.

	E. recurva	***E. diomedeae***	**Phytoplankton (surface)**	**Phytoplankton (> 50 m)**	***B. musculus brevicauda***
	n = 13	n = 6	n = 3	n = 2	n = 1
i14:0	0.1 ± 0.1	0.0 ± 0.0	0.2 ± 0.1	0.4 ± 0.6	0.2
14:0	3.5 ± 0.9	3.6 ± 1.6	3.1 ± 0.7	3.3 ± 1.7	3.8
a15:0	0.1 ± 0.0	0.1 ± 0.1	0.5 ± 0.2	0.5 ± 0.4	0.1
15:0	1.2 ± 0.2	1.2 ± 0.3	1.3 ± 0.6	1.5 ± 0.8	0.5
i16:0	0.1 ± 0.1	0.1 ± 0.1	0.5 ± 0.2	0.5 ± 0.3	0.1
16:0	17.6 ± 0.9	18.4 ± 1.1	27.5 ± 8.9	29.5 ± 1.0	11.4
16:0FALD	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.2	0.4 ± 0.6	0.0
i17:0	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.3
17:0	1.6 ± 0.2	1.5 ± 0.1	0.8 ± 0.4	1.1 ± 0.2	0.6
i18:0	0.4 ± 0.1	0.5 ± 0.1	0.1 ± 0.1	0.0 ± 0.0	0.1
18:0	3.4 ± 0.3	3.3 ± 0.2	13.3 ± 9.0	21.3 ± 7.1	3.2
20:0	0.2 ± 0.0	0.2 ± 0.1	1.1 ± 0.5	1.5 ± 0.5	0.5
22:0	0.3 ± 0.0	0.3 ± 0.1	4.6 ± 3.9	10.7 ± 7.5	0.1
24:0	0.1 ± 0.0	0.1 ± 0.0	1.0 ± 0.6	1.1 ± 0.3	0.1
∑ SFA	**28.9 ± 1.8**	**29.5 ± 3.2**	**54.5 ± 24.1**	**72.3 ± 9.0**	**21.2**
14:1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.2
16:1ω9c	0.2 ± 0.1	0.1 ± 0.1	2.0 ± 1.2	2.5 ± 3.5	0.4
16:1ω7c	3.5 ± 0.6	3.5 ± 0.8	2.7 ± 0.8	2.0 ± 0.8	14.3
17:1ω8c+a17:0	0.7 ± 0.1	0.8 ± 0.1	0.7 ± 0.2	0.7 ± 0.4	1.6
18:1ω9c	11.5 ± 5.1	10.5 ± 1.1	21.0 ± 13.5	9.8 ± 5.5	38.8
18:1ω7c	2.9 ± 0.4	2.8 ± 0.2	2.2 ± 1.8	1.2 ± 0.0	5.0
18:1ω5c	0.1 ± 0.0	0.1 ± 0.1	0.2 ± 0.3	0.1 ± 0.1	0.2
20:1ω11c	0.2 ± 0.1	0.3 ± 0.1	0.4 ± 0.4	0.6 ± 0.0	0.1
20:1ω9c	0.7 ± 0.3	0.6 ± 0.1	0.8 ± 1.2	0.1 ± 0.1	1.6
20:1ω5c	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.4	0.3 ± 0.4	0.0
∑ MUFA	**19.8 ± 5.8**	**18.7 ± 1.0**	**30.5 ± 16.0**	**17.2 ± 8.3**	**63.3**
16:4	0.7 ± 0.4	0.8 ± 0.3	1.2 ± 1.0	1.9 ± 0.6	0.2
18:4ω3	0.9 ± 0.3	1.0 ± 0.3	0.4 ± 0.0	0.3 ± 0.1	0.1
18:2ω6	2.5 ± 1.4	2.5 ± 0.3	4.9 ± 3.3	2.8 ± 0.4	1.7
CLA a	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.3	0.0 ± 0.0	1.1
18:3ω3	1.6 ± 0.2	1.6 ± 0.3	1.5 ± 0.6	1.7 ± 0.3	0.5
20:4ω6	2.7 ± 0.6	3.3 ± 0.5	0.2 ± 0.3	0.0 ± 0.0	1.4
20:5ω3 EPA	12.1 ± 2.1	11.9 ± 2.4	0.7 ± 0.5	0.3 ± 0.0	1.7
20:4ω3	0.5 ± 0.1	0.6 ± 0.1	0.1 ± 0.2	0.6 ± 0.8	0.3
20:2ω6	0.3 ± 0.0	0.4 ± 0.1	0.4 ± 0.2	0.1 ± 0.2	0.2
22:5ω6	0.8 ± 0.2	0.8 ± 0.2	0.2 ± 0.3	0.0 ± 0.0	0.5
22:6ω3 DHA	25.7 ± 4.1	25.8 ± 1.9	1.8 ± 2.3	0.4 ± 0.1	3.4
22:5ω3	0.7 ± 0.2	0.7 ± 0.1	0.6 ± 1.0	0.0 ± 0.0	1.3
∑ PUFA	**48.6 ± 5.2**	**49.3 ± 3.9**	**11.9 ± 7.6**	**8.2 ± 0.3**	**11.2**
Other	**2.6 ± 0.5**	**2.3 ± 0.9**	**2.8 ± 0.3**	**2.3 ± 0.4**	**3.2**
∑ω3	**41.6 ± 5.9**	**41.5 ± 2.9**	**5.1 ± 4.0**	**3.3 ± 0.3**	**7.2**
∑ω6	**6.3 ± 1.1**	**7.0 ± 0.8**	**5.6 ± 3.9**	**2.9 ± 0.6**	**3.9**
ω3/ω6	**6.8 ± 1.6**	**5.9 ± 0.3**	**0.9 ± 0.2**	**1.2 ± 0.1**	**1.9**
DHA/EPA	**2.1 ± 0.2**	**2.3 ± 0.7**	**2.0 ± 1.3**	**1.2 ± 0.2**	**2.0**
18:1ω9/ω7	**3.8 ± 1.2**	**3.6 ± 0.3**	**9.4 ± 1.7**	**8.4 ± 4.5**	**7.8**

SFA = saturated fatty acids, MUFA = monounsaturated fatty acids, PUFA = polyunsaturated fatty acids. Other = i15:0, 15:1ω6, 16:3, 16:1ω7t, 16:1ω5c, 16:1ω13t, 17:1, 18:3ω6, 18:1ω7t, 18:1, 18:1FALD, CLAc, 18:0FALD, 19:1a, 19:1b, 20:3ω6, 20:1ω7c, 21:5ω3, 22:4ω6, 22:1ω11c, 22:1ω9c, 22:1ω7c, 23:0, 24:1ω11c, 24:1ω9c

specimens for 2014 (Table 6.1) and 2015 (Table 6.2). Despite the 89.5 % similarity in FA composition of *E. recurva* samples collected in 2014 and 2015, differences in 16:4,

16:0FALD and 14:0, (amongst other FA) resulted in significantly different FA compositions ($R = 0.49$, $P < 0.01$). PUFA dominated the FA composition for *E. recurva* during both 2014 (50.9 ± 3.4 %; Table 6.1) and 2015 (48.6 ± 5.2 %; Table 6.2). In particular, the long-chain (LC, ≥ C20) PUFA (LC-PUFA), DHA, was the dominant omega-3 PUFA, followed by EPA. The DHA/EPA ratio averaged 2.2 ± 0.4 for 2014 samples, and 2.1 ± 0.2 for 2015 samples. 18:1ω9c was the most abundant MUFA for all *E. recurva* specimens, and the average 18:1ω9c/ω7c ratio was very similar for 2014 (3.9 ± 0.7) and 2015 (3.8 ± 1.2).

The FA profiles of *S. carinatum*, *P. latifrons* and *E. diomedeae* were also dominated by PUFA, 52.8 ± 6.7 %, 47.1 % (Table 6.1) and 49.3 ± 3.9 % (Table 6.2), respectively. There was a dominance of DHA in all species, with DHA/EPA ratios ranging between averages of 1.3 - 3.1. 18:1ω9c was, again, the dominant MUFA for all species and the 18:1ω9c/ω7c ratio ranged between averages of 3.6 to 4.7.

Fatty acids of phytoplankton

Phytoplankton samples contained 59 FA, of which 28 and 30 FA were detected at above 0.5% for 2014 (Table 6.1) and 2015 (Table 6.2), respectively. FA were dominated by SFA, more so in phytoplankton samples from > 50 m depth (50 m and 100 m) (72.3 ± 9.0 %), than surface phytoplankton sampled in 2014 (54.3 ± 4.6 %) and 2015 (54.5 ± 24.1 %). 16:0 was the most dominant SFA for all plankton samples. Stearic acid (18:0) was also common, but attained a higher proportion in > 50 m samples (21.3 ± 7.1 %) than surface samples for 2014 (10.5 ± 1.2 %) and 2015 (13.3 ± 9.0 %). MUFA composed a larger proportion of the surface phytoplankton FA composition in both 2014 (36.4 ± 3.4 %) and 2015 (30.5 ± 16.0 %) compared to samples from > 50 m (17.2 ± 8.3 %). 18:1ω9c was the major MUFA for all phytoplankton samples, but was considerably

higher in surface samples. Total PUFA was low across all phytoplankton samples (Table 6.1; Table 6.2).

Lipids and fatty acids of blue whale outer blubber layer

Total lipid content for the two *B. musculus brevicauda* outer blubber layer samples were 47.3 mg g^{-1} (2014) and 77.1 mg g^{-1} (2015) (Table 6.3). TAG was the dominant lipid class for both samples, 86.6 % (2014) and 73.6 % (2015). PL was greater for the 2015 sample (22.1 %), than the 2014 sample (2.6 %). WE was detected in 2014 (10.7 %) but not 2015.

Table 6.3 Lipid class composition on pygmy blue whale (*Balaenoptera musculus brevicauda*) outer blubber layer collected in the Perth Canyon during April 2014 an April 2015. Lipid classes are expressed as a percentage of the total lipid. Total lipid is expressed as mg g-1 of tissue wet weight. WE = wax ester, FFA = free fatty acid, ST = sterol, TAG = triacylglycerol, PL = phospholipid.

Lipid Class	2014 (n = 1)	2015 (n = 1)
WE*	10.7	-
FFA	-	2.8
ST	-	1.5
TAG	86.6	73.6
PL	2.7	22.1
Total lipid (mg g-1)	47.3	77.1

*may contain hydrocarbons or steryl ester

Of the 60 FA in the two *B. musculus brevicauda* outer blubber samples, 17 and 18 FA were detected at above 0.5 % in 2014 (Table 6.1) and 2015 (Table 6.2), respectively. The FA composition of the *B. musculus brevicauda* outer blubber layer was dominated by MUFA in both years (60.3 ± 4.2 %). 18:1ω9c was the dominant MUFA in 2014 (41.2 %) and 2015 (38.8 %), and the 18:1ω9c/ω7c ratio was similar for both years (8.6 and 7.8, respectively). A greater percentage of DHA was found in both outer blubber layer samples and the DHA/EPA ratio was 3.2 for 2014 and 2.0 for 2015.

Perth Canyon food web

The PCA revealed separation between phytoplankton, euphausiids and *B. musculus brevicauda* FA compositions (Fig. 6.5). The first principal component explained 65.9 % of the variation in FA composition, which was largely attributed to DHA and EPA. The second principal component explained another 8.9 % and was driven mostly by 18:1ω9c, 18:0, and 22:0. Euphausiid samples were characterised by high relative levels of the LC-PUFA, DHA, EPA and 20:4ω6. Phytoplankton were characterised by higher relative levels of SFA (16:0, 18:0, 20:0) and 16:1ω9c. *Balaenoptera musculus brevicauda* outer blubber layer was characterised by higher proportions of 18:1ω9c, 16:1ω9c and 14:0.

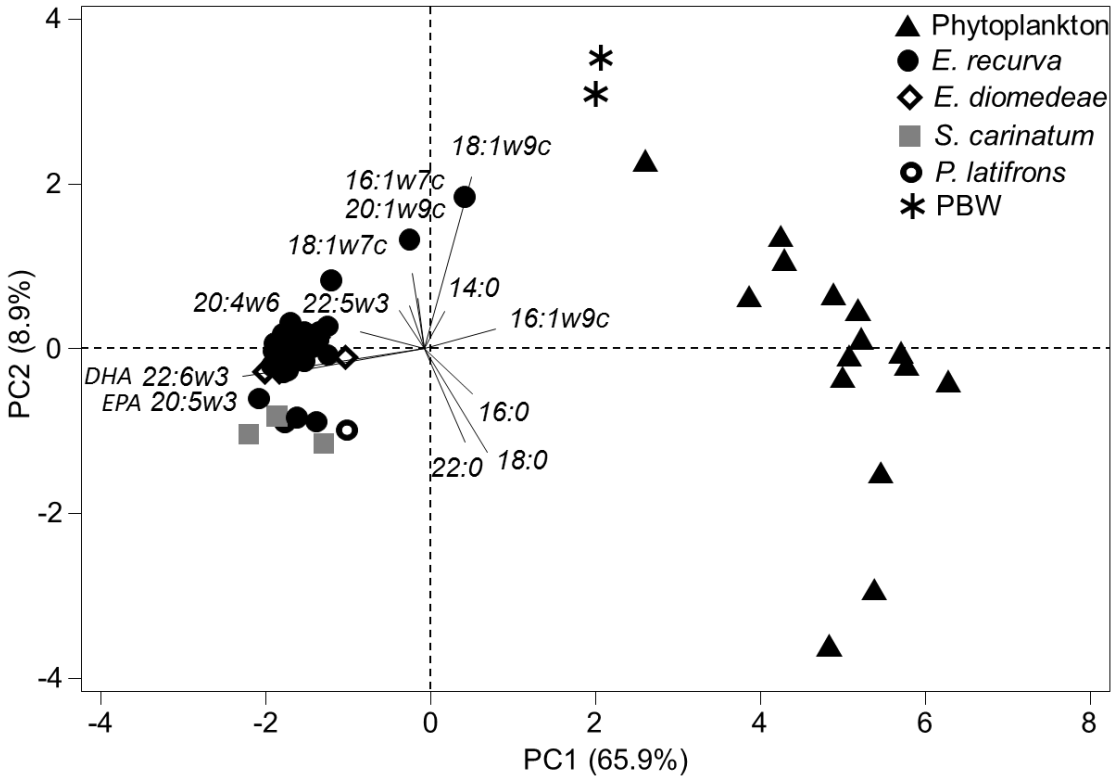


Figure 6.5 PCA plot of fatty acid compositions from phytoplankton; the euphausiids, *Euphausia recurva*, *Euphausia diomedeae*, *Stylocheiron carinatum*, *Pseudeuphausia latifrons* and the pygmy blue whale *Balaenoptera musculus brevicauda* (PBW) outer blubber layer. Dominant fatty acid eigenvectors are shown (> 0.15). PC1 explained 65.9 % of the variation in fatty acid composition, and PC2 explained 8.9 %. Only fatty acids > 0.5 % of the total fatty acid were included in analysis.

ANOSIM revealed an overall significant difference in FA composition between the groups, phytoplankton, euphausiids and *B. musculus brevicauda* outer blubber layer ($P < 0.01$, $R = 0.96$). Euphausiids and phytoplankton were the most significantly different ($P < 0.01$, $R = 0.97$). While the sample size of *B. musculus brevicauda* outer blubber layer ($n = 2$) was small, the ANOSIM R values did indicate a difference in FA composition when compared to phytoplankton ($R = 0.75$) and euphausiid ($R = 0.90$) FA compositions. There was high similarity of FA composition within each group of euphausiids (88.4 %), phytoplankton (80.1 %) and *B. musculus brevicauda* outer blubber layer (87.5 %). Phytoplankton and euphausiid FA composition were 64.3 % similar, and SIMPER revealed DHA and EPA distinguished euphausiid samples, while a higher proportion of 16:1ω9c and 18:0 distinguished phytoplankton samples. Phytoplankton and *B. musculus brevicauda* outer blubber layer FA compositions were 66.5 % similar, *B. musculus brevicauda* outer blubber layer had a higher proportion of 18:1ω9c and 16:1ω7c and phytoplankton had a higher proportion of SFA (16:0 and 18:0). Euphausiids and *B. musculus brevicauda* outer blubber layer FA compositions were more similar (74.1 %), however, euphausiid samples had higher proportions of DHA and EPA, and blubber samples had higher proportions of 18:1ω9c and 16:1ω7c.

Discussion

This study presents new insights into the diet of common euphausiid species off the south-west coast of Australia, particularly, the dominant subtropical/temperate species, *E. recurva*. Evidence suggests that the common euphausiid species in these waters, *E. recurva*, *E. diomedeae*, *S. carinatum* and *P. latifrons*, are feeding in an oligotrophic, dinoflagellate driven food web. Higher levels of DHA are typically reflective of a dinoflagellate driven diet (Harrington et al. 1970; Mayzaud et al. 1976;

Skerratt et al. 1995; Reuss & Poulsen 2002), rather than a diatom diet, which would otherwise see higher levels of EPA (Dunstan et al. 1994). The ratio of 18:1ω9c/ω7c was high for all euphausiid species indicating an omnivorous diet, which is typical of zooplankton in an oligotrophic environment (Phleger et al. 1998). The food web off the south-west of Australia is largely oligotrophic and dominated by microbial species (Hanson et al. 2007b). The diet of euphausiids observed from this study is similar to the dietary markers observed in western rock lobster phyllosoma larvae, which were found to have a diet originating from general flagellates and bacteria, (Phillips et al. 2006; Saunders et al. 2012) as well as dinoflagellates and general flagellates in cyclonic eddies (Wang et al. 2014).

While the south-west of Australia is largely considered oligotrophic, oceanographic features, such as anticyclonic eddies, are known to support higher levels of nutrients and primary productivity and, in turn, higher abundances of large diatoms (Thompson et al. 2007; Waite et al. 2007a; Waite et al. 2015). Anticyclonic eddies in the region of the Perth Canyon are frequent during the austral autumn/winter months, and euphausiids have been found in higher abundances inside these anticyclonic eddies (Sutton et al. 2015). Euphausiids can switch feeding strategies to adapt to changes in productivity, as is seen for *Meganyctiphanes norvegica* having a carnivorous or phytoplanktonic diet in the north-east Atlantic, Kattegat and Ligurian Sea (Virtue et al. 2000). While the euphausiids collected in this study indicated an oligotrophic diet, the dynamic oceanography of the Leeuwin Current and associated eddies create pulses of higher productivity, which may see a switch to a diatom diet if the opportunity arises.

The FA composition of the euphausiid species sampled in this study are characteristic of euphausiids in general (Virtue et al. 1995; Mayzaud et al. 1999; Phleger et al. 2002).

The most dominant FA found in this study were the omega-3 LC-PUFA, DHA and EPA, 16:0 and 18:1ω9c. Aside from the differing proportions based on diet, these FA are also prominent in euphausiid species sampled from both the northern and southern hemispheres (Virtue et al. 1995, Phleger et al. 1998; Falk-Peterson et al. 2000; Virtue et al. 2000; Nicol et al. 2004; Schmidt et al. 2006; Ju et al. 2009). High levels of omega-3 LC-PUFA, in particular, result in euphausiids being of high nutritional value for a range of consumers, and they are also used as a source of food in aquaculture (Virtue et al. 1995; Yoshitomi et al. 2007). Off the west coast of Australia, a number of potential consumers of euphausiids occur, including commercially important fishes, seabirds and whales (Surman & Wooler 2003; Rennie et al. 2009; Itoh et al. 2011), and the high proportion of omega-3 LC-PUFA found in the common euphausiid species off the south-west would clearly be of nutritional benefit for these consumers.

While FA composition was 74 % similar for euphausiids and *B. musculus brevicauda* outer blubber layer, the FA composition of the blubber did not accurately reflect a diet of euphausiids, due to lower relative levels of PUFA in the blubber. However, the DHA/EPA ratio of *B. musculus brevicauda* outer blubber layer samples suggested a diet originating from dinoflagellates, similar to that found for euphausiids. *Balaenoptera musculus brevicauda* feed on euphausiids in the Perth Canyon and *E. recurva* specimens have been collected from the mouth stream of a surfacing whale (Rennie et al. 2009). The trophodynamic link between *E. recurva* and *B. musculus brevicauda* was likely not observed in this study due to the samples being extracted from the outer layer of the blubber. Of most cetaceans studied, stratification in FA composition is evident across the depth of the blubber layer (Koopman et al. 1996; Hooker et al. 2001; Olsen & Grahl-Nielsen 2003). The inner blubber layer is more metabolically

active than the outer blubber layer and is understood to be a better indicator of prey FA composition. *Balaenoptera musculus brevicauda* also only spend a brief period of time in the Perth Canyon in comparison to the Southern Ocean (Double et al. 2014).

The phytoplankton sampled in the surface layers in this study did not reflect the diet of the euphausiid species analysed. Phytoplankton were relatively low in PUFA, and had low levels of EPA and DHA, whereas PUFA accounted for half of the total FA in euphausiids. The phytoplankton samples had a detrital and degraded FA composition and chlorophyll *a* concentrations were relatively low for the region. Euphausiids are vertical migrators and can move up and down the water column in response to a number of influences, such as food availability (Youngbluth 1975; Hu 1978; Gibbons 1993; Taki 2008). The deep chlorophyll maximum off Western Australia is typically between 70 - 100 m in the austral autumn/winter months and phytoplankton are often found in higher abundances at this maximum (Hanson et al. 2007a). Previous studies off Western Australia, examining deeper water columns, have found phytoplankton samples to be dominated by smaller plankton typical of a microbial food web (Hanson et al. 2007b; Twomey et al. 2007). This is more reflective of the diet of the euphausiids sampled in this study, and suggests that euphausiids could be feeding at the deep chlorophyll maximum, rather than on surface phytoplankton of lower quality. Based on this knowledge, phytoplankton samples were taken from 50 m and 100 m depth in 2015 in an attempt to capture the deep chlorophyll maximum layer. However, chlorophyll *a* was similarly low at these depths and the FA composition also did not closely reflect the diet of euphausiids, suggesting that the deep chlorophyll maximum was not actually sampled.

The stable isotopes results place *E. recurva* as a first order consumer (4.5 to 9‰ $\delta^{15}N$), and that the source of carbon for its diet likely originates from phytoplankton (-18 to -24 ‰ $\delta^{13}C$) (Fry & Sherr 1984). Typically, consumers will have a $\delta^{13}C$ close to their diet, with an enrichment of ~ 1 ‰ (DeNiro & Epstein 1978; Fry & Sherr 1984). *Euphausia recurva* samples were more than ~2 ‰ enriched in $\delta^{13}C$ than the phytoplankton samples, suggesting that these particular phytoplankton were not what *E. recurva* were feeding on, which is also supported by the differences in FA composition (France & Peters 1997). Stable isotopes were examined in organic matter and a range of zooplankton taxa, including euphausiids, in two counter-rotating eddies in the vicinity of the Perth Canyon during winter 2003 (Waite et al. 2007c). While *E. recurva* had a similar trophic position ($\delta^{15}N$) to the euphausiids sampled from the anticyclonic eddy in 2003, *E. recurva* had a lower $\delta^{13}C$ which was closer to that of salps and phyllosoma larvae sampled from the cyclonic eddy. Differences observed between the $\delta^{13}C$ of *E. recurva* from this study and the euphausiids from the anticyclonic eddy may be due to the large population of diatoms occurring in that eddy, which may have served as the primary food source for those euphausiids rather than dinoflagellates. Also, there were probably more than one species of euphausiid included in the 2013 anticyclonic eddy analyses, which may have caused some variation in $\delta^{13}C$.

Interannually, *Euphausia recurva* stable isotope and FA compositions significantly differed and this may simply be a result of variation in relation to food availability and oceanographic conditions. Phleger et al. (2002) found interannual differences in the presence of some FA in Antarctic euphausiids across 1997/1998 at Elephant Island, and attributed this difference to a greater importance of dinoflagellates in the diet of euphausiids in 1998. During 2015, an anticyclonic eddy occurred in the Perth Canyon in

proximity to the stations sampled. Although, the DHA/EPA ratio remained relatively similar, differences did occur for some fatty acids, such as 16:4, 16:0FALD and 14:0, of which several are derived from diatoms. For example, diatoms can synthesise 16:4ω1 in large amounts and this FA can be used as a biomarker for diatoms when identified in a consumer (Ackman et al. 1968; Budge et al. 2008). The changes in FA composition for *E. recurva* across years may have been influenced by the presence of the anticyclonic eddy nearby and an associated higher diatom population (Waite et al. 2007c).

In conclusion, this study found common euphausiid species off the south-west of Australia to reflect a diet of dinoflagellates, typical of an oligotrophic environment. This study is the first to describe the FA composition of E. recurva, E. diomedeae, S. carinatum, P. latifrons and B. musculus brevicauda. Investigation of phytoplankton from various depths could further describe trophic linkages in this region by ascertaining the depths at which euphausiids are feeding. Additionally, to determine consumers of euphausiids, it is imperative to obtain tissues most reflective of a relatively recent or sustained diet.

Chapter 7: General discussion and conclusions

This thesis has made a significant contribution to knowledge about euphausiid diversity, distribution and abundance in the south-east Indian Ocean, and confirms the influence of boundary currents on euphausiid distributions. In total, 34 species of euphausiids were identified from the Leeuwin Current (LC) system and assemblages were found to be structured both alongshore and cross-shelf. Vertical structuring of assemblages was evident from depth-stratified sampling across a thermohaline front between Leeuwin Current Water (LCW) and Sub Tropical Surface Water (STSW). Findings from these LC system studies contributed to an analysis of the environmental drivers of euphausiid zoogeography patterns in Indian Ocean, and boundary currents and the unusual features of the northern Indian Ocean influenced biodiversity patterns. Finally, to understand the role of euphausiids in marine food webs off Western Australia, fatty acids and stable isotopes placed common euphausiid species from the Perth Canyon (32°S) as omnivores and feeding primarily on dinfolagellates. This final chapter discusses some common themes from the findings of Chapters 2 – 6.

High species richness in the Leeuwin Current system

Euphausiid species richness in the Indian Ocean was found to decrease with increasing latitude, which is a trend observed in both the Pacific and Atlantic Oceans (Letessier et al. 2009; Tittensor et al. 2010; Letessier et al. 2011). Boundary currents can distort this latitudinal pattern and this study has highlighted the extension of high species richness in the LC, the eastern boundary current in the south-east Indian Ocean. The influence of boundary currents on euphausiid distribution, and in turn species richness, is more prominent for the Indian Ocean given that both of the southern hemisphere boundary

currents flow towards the poles, in contrast to typical eastern boundary currents which flow towards the equator (Pearce 1991).

Prior to the detailed surveys of the LC presented in this thesis, the euphausiid species documented for the LC reflected few species. This study found, however, that the LC has a similar species richness (34 species) as the tropical/subtropical regions of the Indian Ocean and the Agulhas Current (40 species) (Gibbons et al. 1995; Brinton et al. 2000). In comparison to the other eastern boundary current systems in the southern hemisphere, the southern Benguela Current has ~ 44 euphausiid species (Gibbons et al. 1995; Brinton et al. 2000) and the Humboldt/Peru Current has ~ 28 species (Ayon et al. 2008; Gibbons et al. 2000; Antezana 2009).

A proportion of the relatively high species richness in the LC system is attributed to euphausiid species with tropical affinities (Brinton et al. 2000). Several tropical species identified in the north-west marine bioregion of Australia were found south of 22°S in the LC. The current provides an extension of suitable environment for tropical marine species to survive (Maxwell & Cresswell 1981, Wilson & Allen 1987, Hutchins & Pearce 1994, Fox & Beckley 2005), and transport within boundary currents is an important mechanism for distribution of holoplanktonic organisms, such as euphausiids.

While high euphausiid species richness is reflected in the LC system, as well as the tropical/subtropical regions of the Indian Ocean and Agulhas Current, the opposite pattern is observed for average taxonomic distinctness. The boundary currents help to maintain the relatively low and uniform average taxonomic distinctness of euphausiids on par with most of the Indian Ocean. This is largely an artefact of the order Euphausiacea not being very taxonomically rich at higher taxon levels (Mauchline &

Fisher 1969, Brinton et al. 2000). Most species found in the Indian Ocean and boundary currents, belong to the speciose genera, *Euphausia*, *Stylocheiron* and *Thysanopoda*, of the same family, Euphausiidae.

Water masses influencing euphausiid assemblages in the three-dimensional environment

The alongshore structuring of euphausiid assemblages from the south-east Indian Ocean was largely driven by changes in the characteristics of the LC as it flowed polewards. From the north-west shelf (13°S) to south-west Australia (34°S), the marine environment experiences a gradual decrease in temperature, and an increase in salinity and dissolved oxygen (Woo & Pattiaratchi 2006; Weller et al. 2011). As a result of euphausiids being influenced by physio-chemical properties of the water column, the changes in euphausiid assemblages were also gradual, with subtropical/ temperate species contributing more to assemblages as the LC becomes increasingly influenced by STSW in the south.

The most prominent cross-shelf pattern observed for euphausiid assemblages in the south-east Indian Ocean was the increase in species richness and decrease in concentration from shelf to oceanic waters. As most euphausiid species are oceanic (Mauchline & Fisher 1969; Brinton et al. 2000), an increase in species richness in oceanic waters was expected, and this trend has been seen for the Agulhas Current and Benguela Current around southern Africa (Gibbons et al. 1995) and off southern Chile (Riquelme-Bugueño et al. 2012). The high total concentration in shelf waters off Western Australia was largely attributed to the neritic, tropical species, *Pseudeuphausia latifrons*. The dominance of shelf regions by a single neritic euphausiid species is also a trend observed around the world, such as for *Nyctiphanes simplex* off

the west coast of Baja California (Gomez 1995), *Nyctiphanes capensis* in the northern Benguela upwelling system (Barange & Stuart 1991) and *Euphausia mucronata* off southern Chile (Riquelme-Bugueño et al. 2012). The high abundance of neritic species on the shelf is likely due to a shorter lifespan (< 1 year), earlier maturation and faster egg growth in more productive shelf waters, in comparison to species in oceanic waters (Barange & Stuart 1991; Gomez 1995; Ross & Quetin 2000).

The vertical structuring, and the extent of diel vertical migration, of each euphausiid species in the water column is influenced by factors such as environmental tolerance (Brinton 1967; Brinton 1979; Hirota 1987; Taki 2008), food availability (Youngbluth 1975; Hu 1978; Gibbons 1993; Taki 2008), predator avoidance (Bollens et al. 1992), and reproductive strategy (Tarling et al. 1999). This study focused on assemblage structuring in relation to environmental variables and food availability, and found that the vertical structuring of species in the south-east Indian Ocean was influenced by water masses.

Depth stratified sampling across a thermohaline front allowed for an examination of how the physical and biological properties at each depth stratum related to species distributions. The uniform water column of LCW during the austral autumn resulted in no significant structuring of euphausiid assemblages over the upper 200 m depth sampled. The inverse was true for STSW, which had a more stratified water column with different physical and biological properties for each depth stratum. Antezana (2009) found vertical stratification within the Humboldt Current in relation to the oxygen minimum zone, but also found that species differed in the timing of their migrations, and suggested this was a form of habitat partitioning to avoid co-occurrence with other species. Further investigation into the timing of migrations of

species, and an examination of the feeding strategies and diet of the species that showed structuring, would considerably improve knowledge about habitat partitioning within the LC system.

Physical properties of the water column also influenced euphausiids on a wider scale across the Indian Ocean basin. Low salinity in the Bay of Bengal, and the presence of an oxygen minimum zone spanning most of the northern Indian Ocean, created an environment that was not occupied by many euphausiid species. Similarly, euphausiid species richness has been found to be relatively low in the eastern South Pacific Ocean (Letessier et al. 2011), which is also a known oxygen minimum zone (Paulmier et al. 2006; Fuenzalida et al. 2009).

Dominant species of the Leeuwin Current system and their role in structuring assemblages

Three euphausiid species dominated in the 0 - 200 m water column of the south-east Indian Ocean; the neritic, tropical species *P. latifrons*, the oceanic, subtropical/ temperate species *Euphausia recurva,* and the cosmopolitan species *Stylocheiron carinatum* (Brinton et al. 2000). *Pseudeuphausia latifrons* was the most abundant species for the north-west shelf of Western Australia, and continued to be abundant in shelf and offshore waters along the entire Western Australian coastline to 34°S. However, *E. recurva* replaced *P. latifrons* as the most dominant species in the south as the LC became cooler and more saline due to the influence of surrounding STSW. *Stylocheiron carinatum* was abundant all throughout the Leeuwin Current system. While the three species were found in both Tropical Surface Water (TSW) and STSW, *E. recurva* was higher in abundance in STSW and *P. latifrons* in TSW. This is consistent with the nature of many euphausiid species in that they can exist over a large

horizontal or vertical ranges, but aggregate most where the conditions are ideal (Brinton 1967; Youngbluth 1975; Hirota 1987).

It appears to be a common finding that current systems and coastlines 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*, *Euphausia hanseni* and *Nyctiphanes capensis* dominate in the Benguela Current (Pillar et al. 1992), *Euphausia mucronata* dominates in the Humboldt Current system (Antezana 2010) and *Euphausia pacifica* is very abundant in the Oyashio and Kuroshio Currents (Taki 1998; Taki 2008).

Behavioural factors influencing euphausiid assemblages

Diel vertical migration is well documented for euphausiids and plays an important role in their vertical structuring in the water column (Brinton 1967; Youngbluth 1975; Mauchline 1980; Barange 1990; Anderson & Sardou 1992). Vertical migration is likely to have caused the large diel differences in euphausiid assemblages observed in this study. This was evident across the thermohaline front of the LC, and diel variation was inferred for the rest of the LC and north-west shelf marine bioregion. Total concentrations of euphausiids and species richness were consistently higher for stations sampled during the night, within the 0 - 200 m water column. While some species were found during both day and night, many species appeared to have migrated below 200 m depth during the day, presumably to avoid predation within the photic zone. Diel vertical migration is a major consideration when making comparisons of euphausiid assemblages across stations, locations, or between separate studies in various parts of the world.

Euphausiids are also known to form dense patchy aggregations and swarms (Watkins et al. 1990; Cotté & Simard 2005; Guevara et al. 2008), and this introduces another source of sampling variability. For example, within the LC survey (22°S - 34°S) two stations had total concentrations reaching 16,000 and 51,000 ind. 1000 m^{-3}, while the rest of the net catches were < 4100 ind. 1000 m^{-3} with the lowest being 130 ind. 1000 m^{-3}. Variation in euphausiid concentrations found in this study have been discussed in terms of environmental influences rather than euphausiid behaviour, as behaviour was not directly measured and can only be inferred as a potential source of variability. The use of sonar and acoustic techniques have been used in several studies to detect deep scattering layers or patchy aggregations of euphausiids, sometimes in conjunction with net sampling (Green et al. 1992; Ressler et al. 2005; Tarling & Thorpe 2014).

Another behaviour exhibited by some euphausiids is net avoidance, particularly during the day (Brinton 1967). For example, evidence suggests that *Nematoscelis megalops* visually detects and avoids approaching nets (Wiebe et al. 1982), and *Euphausia superba* has been shown to move out of the way of a midwater trawl (Everson & Bone 1986). Comparative studies on *Meganyctiphanes norvegica* using nets, video/photography and acoustics found net density estimates to be orders of magnitude lower (Nicol 1986; Sameoto et al. 1993). While not directly measured, it is likely that there was some degree of net avoidance in this study, and the degree of net avoidance will also vary depending on the net used, and it can also be species biased (Watkins & Macauley 2008).

Two types of scientific plankton nets were used in this study, a bongo net (0.5 m diameter) and an opening-closing stratified EZ net (1 m^2), both with a mesh size of 355 µm. One of the recommended characteristics of nets to sample euphausiids is a large

mouth area (Clutter & Anraku 1968). However, comparing concentrations for oceanic stations from the two net types in this study revealed that euphausiid concentrations were comparable and of the same order of magnitude. In fact, bongo nets captured slightly higher average concentrations of euphausiids during the day and night than the larger EZ net. It is, however, still recognised that there could be potential underestimation of euphausiid concentrations using these net collection methods. Further, combining species richness data from these net types with data from the rest of the Indian Ocean could also generate variation in species richness estimates, particularly given most Indian Ocean euphausiid data were collected with an Indian Ocean Standard Net, which has a large mouth area (Brinton et al. 2000). While a standardised collection of euphausiid samples would allow more accurate comparisons across locations and years, it is difficult to ascertain which zooplankton net is most effective at catching euphausiids, and which would fit best for multidisciplinary research. Despite the combination of nets types used in this study, 34 euphausiid species, including new records, were captured by the nets and has provided considerable insight into the euphausiids occupying the waters of the LC system.

Implications of an oligotrophic environment on euphausiids

Productivity is generally lower in the south-east Indian Ocean under the influence of the LC when compared to eutrophic upwelling regions in other boundary currents (Hanson et al. 2005; Koslow et al. 2008; Thompson et al. 2011). Zooplankton biomass is reputed to be less than half that found for the Benguela and Humboldt currents (Pearce 1991). Nutrient rich environments typically have a short food chain based on large phytoplankton that can support large stocks of fish, whereas, nutrient poor environments have a longer food chain based on small phytoplankton and bacteria

(Ryther 1969; Cushing 1989; Legendre & Rassoulzadegan 1995). The fatty acids of the dominant euphausiid species examined in this study reflected a diet of dinoflagellates, typical of a nutrient poor environment.

Euphausiids occur in both eutrophic and oligotrophic environments, but concentrations could be expected to be lower in less productive waters. In the north-east tropical Atlantic, euphausiid density was found to decrease from 563 ind.m^{-2} in eutrophic waters to 79 ind.m^{-2} in oligotrophic waters (Anderson et al. 1997). While the oligotrophic conditions of the LC system and south-east Indian Ocean may allow many euphausiid species to exist, the low productivity of the waters may not be conducive for large aggregations or swarming. Upwelling can occur at some localised areas off Western Australia, and this may support higher concentrations and swarming that can, in turn, support predators, such as blue whales feeding on euphausiids in the Perth Canyon (Rennie et al. 2009).

Further, the weakened LC during the spring and summer months allows the occurrence of seasonal currents (Pearce & Pattiaratchi 1999; Woo et al. 2006b), which are associated with localised upwelling of nutrient rich waters on the shelf. This may not only influence the extent of euphausiid distributions, but it may also lead to higher concentrations of euphausiids. Diatoms have shown an increase in abundance during the summer upwelling months in the LC system (Hanson et al. 2005), and may become a more dominant component of the diet of euphausiids during these months. This study did not investigate euphausiid assemblages during the spring and summer months, but doing so would increase our understanding of the natural variability in euphausiid assemblages from the LC system.

Strengths, shortcomings and future work

Zooplankton datasets are often heterogeneous and not normally distributed, due to the nature of zooplankton and the sampling challenges within the marine environment. Applying a non-parametric statistical approach, such as PRIMER and PERMANOVA, is robust to assumptions of normality and homogeny, which is a better fit to this dataset, rather than using parametric methods and strongly transforming the data to the point where information is lost about assemblages (Clarke & Gorley 2016). If, however, the data are truely normal and analysed using non-parametric tests, then it is considered less powerful than parametric tests. The datasets collected for this thesis do not meet the assumptions for parametric analyses. The datasets are also multivariate, and the research questions were generated to assess changes in assemblages, rather than single species, or single metric univariate data. PRIMER has been used widely to investigate such marine assemblages and communities, and is a tried and tested statistical tool for multivariate data (Holliday et al. 2011b; Holliday et al. 2012; Tweedley et al. 2012; Clarke et al. 2014).

Similarly, the use of GAMs, as in Chapter 5, is a commonly used model for data that is not normally distributed and requires fewer assumptions (Austin 2002; Zuur et al. 2010). While the GAMs did not perform the best for measures of AveTD and VarTD, the amount of variation explained was still informative. Despite using CART, and forward and backwards selection procedures, to try and reduce the number of terms in the models, the models were complicated, which resulted in the model explaining wiggles, rather than trends in the data set. Further constraints on the effective degrees of freedom and choosing a simpler model of the most environmental variables may have produced a better fit for AveTD and VarTD of euphausiids in the Indian Ocean.

Using metrics of taxonomic distinctness to provide a different perspective on biodiversity is still a relatively new technique. It is a useful metric because it represents the relatedness of species based on the taxonomic tree, and thus gives a better estimate of true biodiversity and uniqueness by analysing whether species are spread across a number of families, rather than just one genus (Warwick & Clarke 1995). However, for euphausiids, there are only two families, and all but one species belong to one family. Mathew et al. (2003) is the only other study to use taxonomic distinctness solely on euphausiids, and AveTD and VarTD were found to be relatively low and uniform for the west coast of India, as was observed for the whole Indian Ocean in this study. The use of taxonomic distinctness was useful for highlighting the presence of the deep water species, *Bentheuphuasia amblyops* from the monotypic family, Bentheuphausiidae, which would have otherwise been counted as a non-descript single species in traditional measures of species richness. However, for euphausiids, the lack of spread across more than one family meant that any geographic or environmental influences on euphausiid taxonomic distinctness were not evident. Therefore, applying taxonomic distinctness to euphausiid data sets may not be most effective for representing differences.

Assessing differences and changes in euphausiids on a regional and global scale in relation to their environment is important for understanding the effects of future environmental changes on them. Euphausiids are important in marine food webs (Mauchline & Fisher 1969; Tarling & Johnson 2006), and changes in their distribution, abundance and diversity would have significant influences on their consumers and prey. The importance of euphausiids in the marine environment is still being investigated in our oceans, but it is a relatively slow progress given how difficult it is to

comprehensively sample euphausiids (due to natural behaviours and variation in sampling procedures) and obtain concurrently sampled environmental variables (Brinton 1967; Guevara et al. 2008; Watkins & Macauley 2008). This study has greatly improved on the knowledge of euphausiids, and has placed more importance on them given they are significantly influenced by the Leeuwin Current. The results provide important information on the relationship between euphausiids and the Leeuwin Current environment, but also provide baseline information of the species present and their distributions. This can significantly benefit future studies investigating changes with environment over time, as well as scope for food web analyses involving euphausiids in an oligotrophic environment.

A snapshot of the diet of common euphausiids during late autumn in the Perth Canyon found a diet typical of an oligotrophic environment (Phleger et al. 1998). Further studies on euphausiid trophodynamics are needed, however, as sporadic upwelling occurs along the coast, and in mesoscale features, which could alter the food available to euphausiids. This could, in turn, influence such factors as distribution, abundance and reproduction which could have flow on effects throughout the food web. Euphausiids have a range of feeding behaviours (Mauchline & Fisher 1969) and the degree of herbivory or carnivory off the coast of Western Australia is unknown. Further, an assessment of the consumers of euphausiids off the coast is also severely lacking in the current published literature, and these studies are needed in order to ascertain a complete picture of the role of euphausiids in the food web of the Leeuwin Current.

Concluding statements

The LC system was found to provide a suitable environment for 34 euphausiid species and includes new records for Australian waters as well as the broader south-east Indian Ocean. Euphausiid assemblages were significantly structured alongshore in relation to prevailing water masses. TSW contained more tropical species and the dominant *P. latifrons*, and STSW contained higher concentrations of subtropical/temperate species, such as *E. recurva*. Cross-shelf structuring of assemblages was also evident with species richness increasing and concentrations decreasing offshore. Vertical structuring of euphausiids occurred in the more stratified STSW water column than the uniform LCW, and many shared species across the two water masses had higher concentrations in the warmer and slightly more productive LCW. The influence of boundary currents on extending high euphausiid species richness and maintaining a low uniform average taxonomic distinctness was evident for the southern Indian Ocean. In contrast, the low salinity and oxygen minimum zone of the northern Indian Ocean drove the decline in species richness, although, this area was more taxonomically distinct. The oligotrophic environment of the south-east Indian Ocean was reflected in the diet of common euphausiids collected from the Perth Canyon, which were found to be omnivorous and feeding largely on dinoflagellates typical of an oligotrophic environment.

Appendix 1

Table 1. Mean concentrations of euphausiid species (individuals·1000 m^{-3}) identified from samples taken during the day and night within Leeuwin Current Water (LCW) and Sub Tropical Surface Water (STSW) (0 - 200 m water column). Standard errors are included.

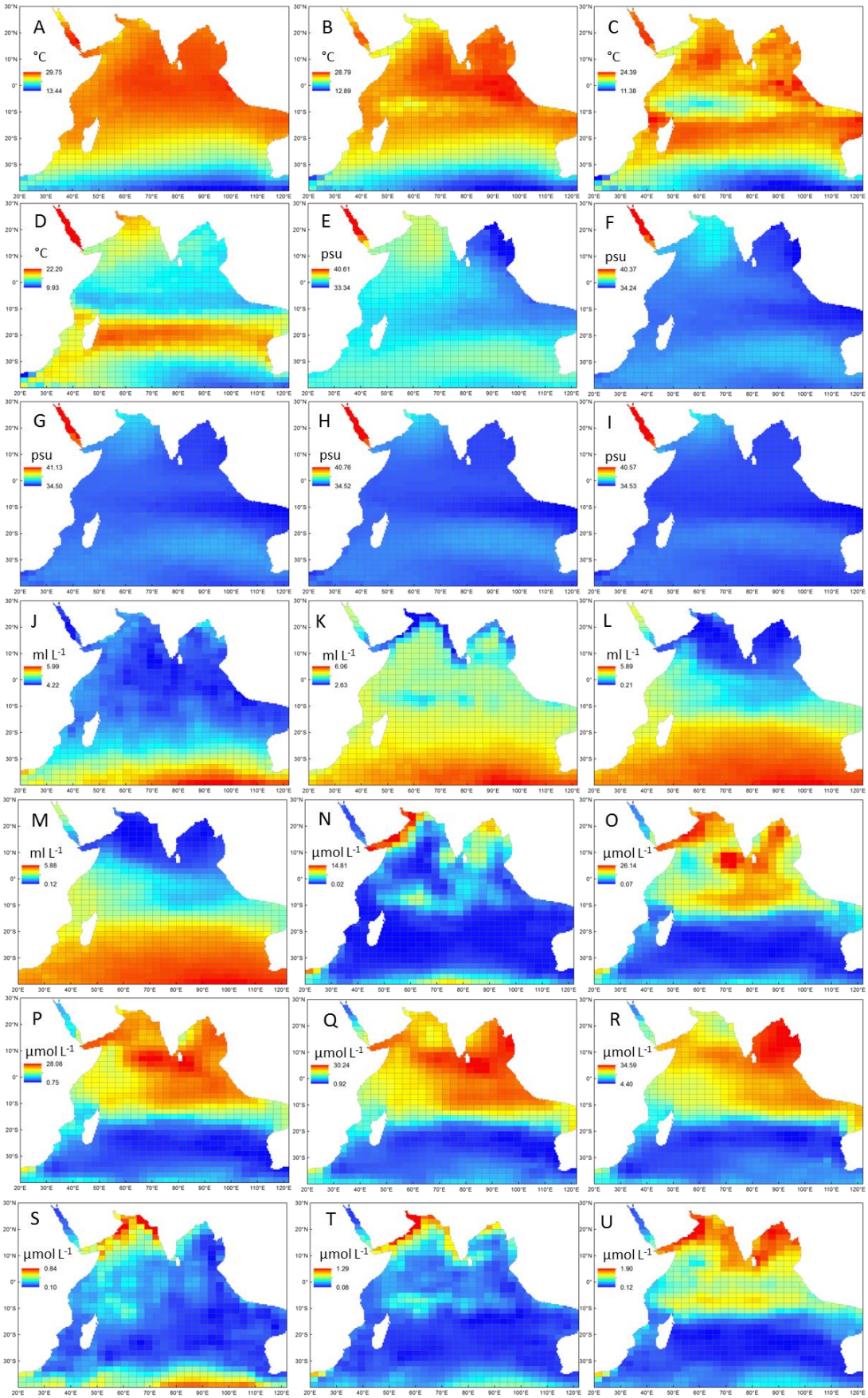
	LCW-Night $\bar{X}$ ± SE	**LCW-Day** $\bar{X}$ ± SE	**STSW-Night** $\bar{X}$ ± SE	**STSW-Day** $\bar{X}$ ± SE
Euphausia diomedeae	5.2 ± 2.7	0	0.4 ± 0.3	0.1 ± 0.1
Euphausia hemigibba	56.4 ± 17	0	52.6 ± 11.1	0
Euphausia mutica	182.2 ± 100.1	0	32.1 ± 14.1	0.2 ± 0.2
Euphausia recurva	155.4 ± 44.2	0.7 ± 0.4	266.2 ± 73.2	8.9 ± 4.1
Euphausia sanzoi	19.3 ± 9.2	0	0.8 ± 0.4	0
Euphausia similis	0	0	3.3 ± 3.1	0
Euphausia similis* var*. armata	0	0	2.1 ± 1.1	0
Euphausia tenera	94.6 ± 46.4	0	10.6 ± 3.5	0
Euphausia* spp*.	344.7 ± 122.8	0.6 ± 0.6	98.3 ± 35.5	0.1 ± 0.1
Nematobrachion flexipes	0	0	0.2 ± 0.1	0
Nematoscelis atlantica	6.4 ± 3.9	0	22.3 ± 6.1	1.0 ± 0.8
Nematoscelis microps	38.8 ± 13.4	3.7 ± 2.3	31.1 ± 8.7	5.0 ± 2.6
Nematoscelis* sp*.	23.3 ± 10.4	14.5 ± 7.96	34.8 ± 10.2	40.3 ± 11.4
Pseudeuphausia latifrons	146.8 ± 68.3	1.7 ± 1.2	50.6 ± 35.3	1.9 ± 1.2
Stylocheiron abbreviatum	59.5 ± 16.1	31.7 ± 13.2	27.6 ± 4.3	35.8 ± 17.7
Stylocheiron affine	9.1 ± 1.9	13.2 ± 9.6	1.0 ± 0.5	1.3 ± 0.5
Stylocheiron carinatum	528.0 ± 121.1	169.5 ± 133.5	83.6 ± 27.2	109.5 ± 49.1
Stylocheiron elongatum	0.1 ± 0.1	0	0	0
Stylocheiron longicorne	0	0	3.5 ± 1.5	1.5 ± 0.8
Stylocheiron microphthalma	6.4 ± 1.9	4.0 ± 2.6	2.1 ± 1.2	0.8 ± 0.5
Stylocheiron suhmi	66.4 ± 12.3	48.1 ± 34.6	5.2 ± 1.7	10.0 ± 5.1
Stylocheiron* spp*.	65.6 ± 27.5	21.4 ± 17.2	18.6 ± 5.3	6.2 ± 2.6
Thysanoessa gregaria	0	1.6 ± 1.6	10.0 ± 3.9	2.1 ± 1.7
Thysanoessa* sp*.	0	0	29.5 ± 10.6	0.8 ± 0.6
Thysanopoda aequalis	0	0	2.2 ± 1.3	0
Thysanopoda astylata	1.3 ± 0.9	0	2.8 ± 1.3	0
Thysanopoda monacantha	1.2 ± 1.0	0	0	0
Thysanopoda orientalis	0	0	0.4 ± 0.4	0
Thysanopoda* spp*.	22.8 ± 9.2	3.4 ± 2.5	31.8 ± 10.3	16.7 ± 8.9
Thysanopoda tricuspidata*				

**T. tricuspidata* was a qualitative record and was not included in analyses.

spp. denotes a collection of unidentified species belonging to an identified genus.

sp. denotes an unidentified species belonging to an identified genus.

Appendix 2


A
°C
29.75
13.44
B
°C
28.79
12.89
C
°C
24.39
11.38
D
°C
22.20
9.93
E
psu
40.61
33.34
F
psu
40.37
34.24
G
psu
41.13
34.50
H
psu
40.76
34.52
I
psu
40.57
34.53
J
ml L-1
5.99
4.22
K
ml L-1
6.06
2.63
L
ml L-1
5.89
0.21
M
ml L-1
5.88
0.12
N
µmol L-1
14.81
0.02
O
µmol L-1
26.14
0.07
P
µmol L-1
28.08
0.75
Q
µmol L-1
30.24
0.92
R
µmol L-1
34.59
4.40
S
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0.84
0.10
T
µmol L-1
1.29
0.08
U
µmol L-1
1.90
0.12

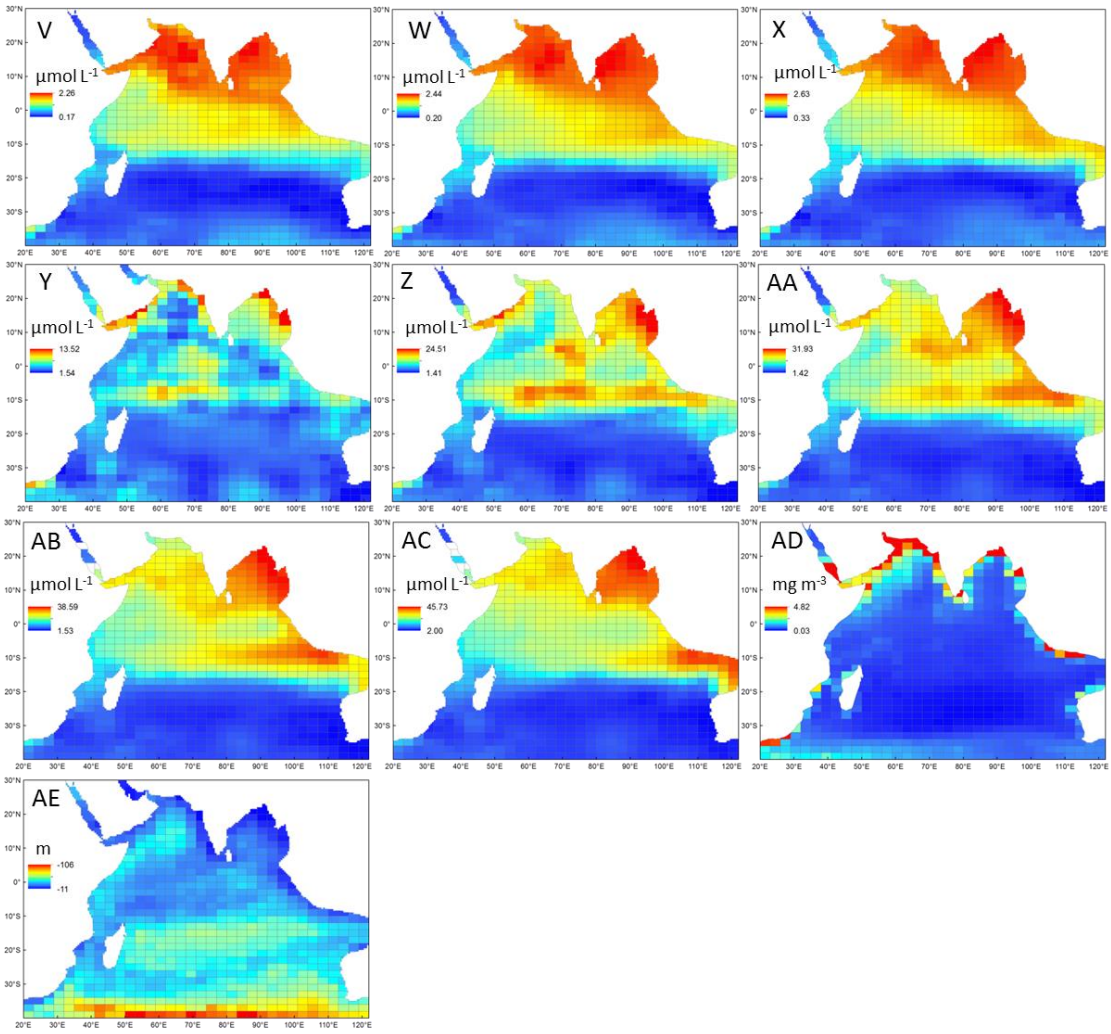

Figure 1: Derived environmental variables, used in a classification and regression tree (CART) analysis for species richness, average taxonomic distinctness and variation in taxonomic distinctness, extracted to each sampling cell for the Indian Ocean. A) sea surface temperature, B) temperature at 50 m depth, C) temperature at 100 m depth, D) temperature at 200 m depth, E) salinity at 50 m depth, F) salinity at 100 m depth, G) salinity at 150 m depth, H) salinity at 200 m depth, I) salinity at 300 m depth, J) surface oxygen, K) oxygen at 50 m depth, L) oxygen at 150 m depth, M) oxygen at 200 m depth, N) nitrate at 50 m depth, O) nitrate at 100 m depth, P) nitrate at 150 m depth, Q) nitrate at 200 m depth, R) nitrate at 300 m depth, S) surface phosphate, T) phosphate at 50 m depth, U) phosphate at 100 m depth, V) phosphate at 150 m depth, W) phosphate at 200 m depth, X) phosphate at 300 m depth, Y) silicate at 50 m depth, Z) silicate at 100 m depth, AA) silicate at 150 m depth, AB) silicate at 200 m depth, AC) silicate at 300 m depth, AD) Autumn chlorophyll, AE) mixed layer depth.

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