

Oceanographic influence on coastal zooplankton assemblages at three IMOS National Reference Stations in Western Australia

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Abstract. Knowledge about the coastal zooplankton of the south-eastern Indian Ocean is limited, with few studies having compared assemblages across the latitudinal range of the western seaboard of Australia. The dominant oceanographic feature in this region is the Leeuwin Current, which transports warm, lower-salinity, tropical waters southward along the shelf-edge. This study examined data collected by Australia's Integrated Marine Observing System at three coastal National Reference Stations located at 22°S 114°E, 32°S 115°E and 34°S 122°E. Spatial and temporal patterns in zooplankton abundance, composition and diversity were investigated, and differences in assemblage structure, particularly with respect to copepods, were related to oceanographic conditions. Clear dissimilarities among copepod assemblages were observed, becoming weaker in winter owing to enhanced connectivity of species driven by alongshore and cross-shelf transport in the Leeuwin Current. Both physical and biogeochemical factors were significant in structuring copepod assemblages, with seawater density, incorporating temperature and salinity, exerting the greatest influence. The results suggest that both broad-scale latitudinal gradients and mesoscale events contribute to variation in zooplankton assemblages in these waters. This study provides the first detailed comparison of zooplankton assemblages among the north-west, south-west and southern coastal waters of Western Australia, and enhances understanding of the processes influencing zooplankton distribution and structure.

Additional keywords: mesozooplankton, oceanography.

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Introduction

Zooplankton are generally short-lived, widely distributed and make very good indicators of changing ocean conditions (Hays *et al.* 2005; Richardson 2008). Changes in zooplankton distribution and population sizes can be driven by physical processes or biological interactions, with the rate of change being rapid enough to track seasonal and interannual variation in environmental conditions (Mackas *et al.* 2012). Within the zooplankton, copepods are the dominant and most diverse component and are, therefore, particularly useful to examine how changes in zooplankton assemblage structure reflect the underlying oceanography (Longhurst 1985; Dias *et al.* 2015).

Various zooplankton studies have demonstrated that plankton communities respond to the physical and chemical environment, as well as large- and small-scale ocean processes (e.g. Verheye and Richardson 1998; Mackas *et al.* 2001; Muhling and Beckley 2007; Richardson 2008). Specific zooplankton patterns of distribution and productivity have been related to ocean currents (Beaugrand *et al.* 2002a) and, particularly, boundary currents, such as the Benguela (Verheye *et al.* 2016), Humboldt (Ayón *et al.* 2008) and East Australian Currents (Johnson *et al.* 2011;

Kelly *et al.* 2016). Further studies have identified relationships between zooplankton and climate systems such as the El Niño Southern Oscillation (ENSO; Fromentin and Planque 1996; McKinnon *et al.* 2008), while recently, studies are increasingly providing evidence of climate change-mediated shifts in zooplankton geography and structure (Beaugrand *et al.* 2002b; Chiba *et al.* 2006; Steinberg *et al.* 2012; Brun *et al.* 2019).

Many of the valuable findings of zooplankton studies are a result of long-term ocean monitoring programs. Early significant interdisciplinary ocean surveys, such as the Discovery Investigations in the Southern Ocean (1950s; Hardy 1967) and the International Indian Ocean Expedition (1960s), were critical to establishing a baseline knowledge of zooplankton distribution patterns (Tranter and Kerr 1969; Tranter and Kerr 1977). The acknowledged importance and support for continued ocean monitoring is demonstrated by >30 countries holding multi-decadal zooplankton time-series (Mackas *et al.* 2012). On a global scale, continuous plankton recorder (CPR) surveys operate across all oceans and have been used to highlight variation in ocean conditions and differing biological responses to ocean change (Richardson and Schoeman 2004; Richardson *et al.* 2015).

Table 1. Characteristics of the three National Reference Stations located off the coast of Western Australia

Data adapted from Lynch *et al.* (2014). Data for bioregions are as per Commonwealth of Australia (2006). NRS, National Reference Station; WA, Western Australia; NW, north-west; SW, south-west; S, south

NRS	Location in WA	Latitude (°S)	Longitude (°E)	Distance offshore (nm)	Depth (m)	Operating period	Frequency of sampling	Bioregion
Ningaloo	NW	21°52.0	113°56.82	3.5	55	2010–2013	Seasonally, four per year	Tropical
Rottneest	SW	32°00.0	115°25.0	13.5	50	2009–ongoing	Monthly	Transition
Esperance	S	33°56.0	121°51.0	1.5	50	2009–2013	Seasonally, four per year	Warm-temperate

Numerous sustained zooplankton observation programs in the northern hemisphere, such as the California Cooperative Oceanic Fisheries Investigations (CalCOFI), the Hawaii Ocean Time-series and the Bermuda Atlantic Time-series Study, have been significant in detecting region-specific seasonal physical processes, ocean warming, changing biogeochemical dynamics, and in tracing ocean–climate perturbations (Mackas *et al.* 2006; Jiang *et al.* 2007; Valencia *et al.* 2016).

In comparison, significant long-term zooplankton time-series are rare for the southern hemisphere. In Australia, the Integrated Marine Observing System (IMOS) began systematic monitoring of the physical and biogeochemical properties of coastal waters via a network of National Reference Stations (NRS) in 2006, with the aim of understanding changes in Australian waters (Lynch *et al.* 2014; Lara-Lopez *et al.* 2016). The IMOS zooplankton sampling program commenced in 2008 and continues to operate on a continental scale. The recent establishment of a comprehensive zooplankton monitoring program means that little is still known about the distribution, abundance, diversity, and long-term trends in zooplankton in these waters.

In Australia, with a mainland coastline that spans >35 000 km, the geographical isolation of study locations and logistical constraints have created challenges for sustained ocean monitoring (Lynch *et al.* 2014; Eriksen *et al.* 2019). This is particularly true of the western coast, with its unique and complex oceanography. The dominant oceanographic feature off Western Australia is the poleward flowing Leeuwin Current (LC), which originates near the North West Shelf (21°S) and transports warm, lower salinity, oligotrophic, tropical water southward along the shelf break and around Cape Leeuwin at 35°S, before turning eastward to flow towards Tasmania, a distance of almost 5500 km (Cresswell and Golding 1980; Ridgway and Condie 2004; Cresswell and Domingues 2009). The temperature–salinity profile of the LC is modified along its southward trajectory. As it flows south, the LC undergoes a gradual decrease in temperature and an increase in salinity, and, consequently, surface waters flowing in the LC are of greater density in the south than in the north (Waite *et al.* 2007; Weller *et al.* 2011). Seasonal and inter-annual variation in LC intensity occurs; the LC flow is stronger in the austral autumn–winter (Godfrey and Ridgway 1985; Cresswell 1991) and during La Niña years (Huang and Feng 2015). Further complexity is added to the environment by the opposing, wind-driven, cooler, Ningaloo (22°S–24°S) and Capes Currents (32°S–35°S;

Gersbach *et al.* 1999; Woo *et al.* 2006), and by localised physical processes, such as coastal upwelling, eddies and meanders (Pearce 1991; Waite *et al.* 2007).

Although numerous studies have examined the physical and chemical properties of the LC system, few have elucidated its influence on zooplankton. Studies of zooplankton assemblages in Western Australian waters include those in the Kimberley region (Holliday *et al.* 2011; McKinnon *et al.* 2015), the North West Shelf (McKinnon *et al.* 2003a, 2008; Wilson *et al.* 2003), Shark Bay (Kimmerer *et al.* 1985), south-western eddy system (Muhling *et al.* 2008; Säwström *et al.* 2014) and southern shelf (Gaughan and Fletcher 1997). Contributing to our understanding of the region's zoogeography are studies that have examined the influence of the LC on the distribution and composition of macrozooplankton and larval fishes (Muhling and Beckley 2007; Muhling *et al.* 2008; Beckley *et al.* 2009; Gaughan *et al.* 2009; Holliday *et al.* 2012). More recently, studies of chaetognaths and euphausiids in the LC have shown relationships between assemblage structures and latitudinal changes in LC water properties (Buchanan and Beckley 2016; Sutton and Beckley 2016). However, the mechanisms of the LC that structure mesozooplankton assemblages in Western Australian coastal waters remain largely unresolved.

This study is the first to present a comprehensive account of spatial and temporal variation in zooplankton assemblages at three IMOS NRS located in coastal Western Australian waters, at Ningaloo (22°S), Rottneest (32°S) and Esperance (34°S), and to relate the variation to oceanographic conditions. The time period of focus for the study was the 2-year period during which all three NRS were simultaneously functional (2011–2012). The specific research questions addressed by the study were as follows: (1) what are the oceanographic conditions at the three NRS, (2) what are the zooplankton assemblages at the three NRS, (3) do the copepod assemblages at the three NRS differ and (4) which oceanographic factors explain the variability in copepod assemblage structure among the three NRS?

Materials and methods

Study locations

The Ningaloo (NIN), Rottneest (ROT) and Esperance (ESP) NRS are located in Western Australian coastal waters and are adjacent to the path of the Leeuwin Current. The characteristics of the three NRS are summarised in Table 1.

Data sources and sampling methods

Data used in this study were sourced from the IMOS Australian Ocean Data Network Portal (AODN; <https://portal.aodn.org.au/>, accessed 3 October 2016). Data were derived from a combination of *in situ* moored sensors and vessel-based sampling. Statistical analyses were performed using data from 2011–2012, the period during which the three Western Australian NRS were simultaneously operational. This time period provided seasonal samples from the three NRS, but resulted in uneven sample numbers because of differences in sampling frequency (Ningaloo and Esperance, $n = 8$; Rottnest, $n = 22$; Table 1). Seasons were considered by grouping data from December to February (summer), March to May (autumn), June to August (winter) and September to November (spring).

Physical and chemical data

National Reference Station mooring-based *in situ* water quality monitors (WQM) (WETLabs) deployed in shallow (18–25 m) and deep (48–55 m) water collected continuous measurements of temperature ($^{\circ}\text{C}$), salinity (psu) and oxygen ($\mu\text{mol kg}^{-1}$; Seabird Model SBE 39). Data were collected at 1-s intervals across 1 min of continual sampling every 15 min and logged internally. WQM data harvesting was concurrent with mooring servicing, which occurred three times per year at Esperance and Rottnest, and twice annually at Ningaloo (Lynch *et al.* 2014).

Vessel-based water column profile sampling at the NRS involved conducting vertical conductivity, temperature and depth (CTD) casts using a Seabird Model SBE 19+ instrument. Casts were taken within 1 h of zooplankton sampling. Temperature ($^{\circ}\text{C}$), salinity (psu), density (kg m^{-3}) and dissolved oxygen concentration ($\mu\text{mol kg}^{-1}$) were measured at 1-s intervals through the water column to near the seabed (~ 50 m), and the resulting data were binned to 1-m measurements (Davies and Sommerville 2017).

Water samples were collected in 5-L Niskin bottles at 10-m depth intervals from the surface to 50 m. Triplicate samples were collected into 10-mL tubes for nitrate, phosphate and silicate ($\mu\text{mol L}^{-1}$) analysis via flow injection analysis on a LachatTM system. A composite water column sample consisting of equal parts of water from each 10-m depth sample was prepared on board, and from this mixed water sample, 4 L was used for phytoplankton pigment analysis using an established high performance liquid chromatography procedure (Davies and Sommerville 2017), and the determined chlorophyll *a* concentration (mg m^{-3}) was recorded.

Monthly mean Fremantle sea level and Southern Oscillation Index (SOI) data obtained from the Bureau of Meteorology (http://www.bom.gov.au/ntc/IDO70000/IDO70000_62230_SLD.shtml, accessed 24 September 2016) were examined to evaluate variation in the velocity and intensity of the Leeuwin Current.

Zooplankton data

Vessel-based sampling of mesozooplankton (0.2–20 mm) at the NRS was conducted using a weighted 100 μm mesh drop net (Heron 1982). The drop net collected a water column sample from the surface to near the seabed (~ 50 m). The zooplankton sample was preserved in 10% formalin before transfer to a

CSIRO laboratory for composition analysis by members of the IMOS Plankton Ecology group. Composition analysis was performed using a Leica M165C microscope with $\times 120$ magnification and data were recorded as number of individuals per cubic metre of water. Identification of zooplankton was guided by an assembled taxonomic library that is verified by the World Register of Marine Species (WoRMS; www.marinespecies.org), and performed to the lowest taxonomic level possible. Generally, adult copepods were identified to species level and juveniles to genus level, and thus, data for this zooplankton group formed the core biological data source for the analyses.

Data analyses

Water column profiles for temperature–salinity (TS) and nutrients (nitrate, phosphate and silicate) were examined using the vessel-based sampling data. High temporal resolution temperature and salinity data measured by the WQMs were used for finer detail time-series analysis of these water properties.

Copepod assemblage structure was examined using the software package PRIMER v6 PERMANOVA+ (Clarke and Gorley 2006; Anderson *et al.* 2008). Abundances were square-root transformed to reduce the weight of contribution by dominant taxa and a Bray–Curtis resemblance matrix was constructed. Analyses were performed on a reduced dataset of copepods identified to at least genus level. Cluster analysis was applied to identify similarities in copepod assemblages in terms of abundance and composition among NRS. The results of the cluster analysis were verified using a fixed, three-factor permutational multivariate analysis of variance (PERMANOVA; Anderson 2001), which was used to test for significant differences in copepod assemblages among the *a priori* factors of NRS, year and season, and any interaction among these factors. The similarity percentage (SIMPER) procedure was used to identify the copepod taxa most responsible for assemblage dissimilarities.

Distance-based linear modelling (DistLM; Anderson 2001) was used to examine the relationship between water column properties (predictor variables) and copepod assemblages (response matrix) and determine the set of predictor variables that best explained variation in copepod assemblage structure. Prior to the analysis, examination of draftsman plots showed that temperature and salinity were covariates, and seawater density was included in the DistLM as a combination of these variables. Dissolved oxygen and silicate were subsequently removed from the analysis because of their strong positive and negative correlations ($r = 0.92$, $r = -0.82$) respectively, with seawater density. The remaining data were standardised (by square-root transformation) to reduce skewness and normalised. A stepwise regression selection procedure with the adjusted R^2 selection criterion was used in the DistLM. Results were presented in a distance-based redundancy (dbRDA) bi-plot (Legendre and Anderson 1999).

Results

Physical oceanography

TS profiles of the water columns showed each NRS site to have distinct water column properties. Increasing latitude corresponded to a decrease in temperature ($\sim 8^{\circ}\text{C}$), and an increase in salinity (~ 0.7 psu) and, hence, seawater density ($\sim 3 \text{ kg m}^{-3}$)

across the 12° latitudinal range (Fig. 1, Table 2). Water columns at the three NRS were well mixed, indicating the presence of a single water mass at each site. The TS profiles and WQM time-series data indicated the presence of warm (22–29°C), lower salinity (34.5–35.0 psu) surface waters at Ningaloo that were characteristic of Tropical Surface Water (TSW; >22°C, <35 psu, <1024 kg m⁻³; Woo and Pattiaratchi 2008; Fig. 2, Table 2). The TSW was modified as it was transported south by the LC, with waters at Rottnest being, on average, cooler (21.1°C), more saline (35.3 psu), and, hence, denser (1025 kg m⁻³). Further south at Esperance, cool (16–21°C), higher salinity (>35 psu), dense (>1025 kg m⁻³) waters indicated that the dominant water mass was Sub Tropical Surface Water (STSW; <21°C, >35.4 psu,

>1025 kg m⁻³; Pearce *et al.* 2006; Fig. 2, Table 2). Despite its southern location, waters at Esperance remained warm in autumn, maintaining a mean temperature of 20.2°C, as LC water penetrated around Cape Leeuwin and along the southern coast (Fig. 3).

All three NRS presented well defined seasonal patterns of water temperature and salinity, with maxima in summer–early autumn and minima in late winter–early spring (Fig. 3). Elevated water temperatures at the NRS in 2011 relative to 2012 reflected the strong La Niña event that affected the Western Australian coast in the austral summer of 2010–2011 (Feng *et al.* 2013). The La Niña event caused rapid warming of ocean temperatures that exceeded long-term monthly means and peaked in February–March along much of the

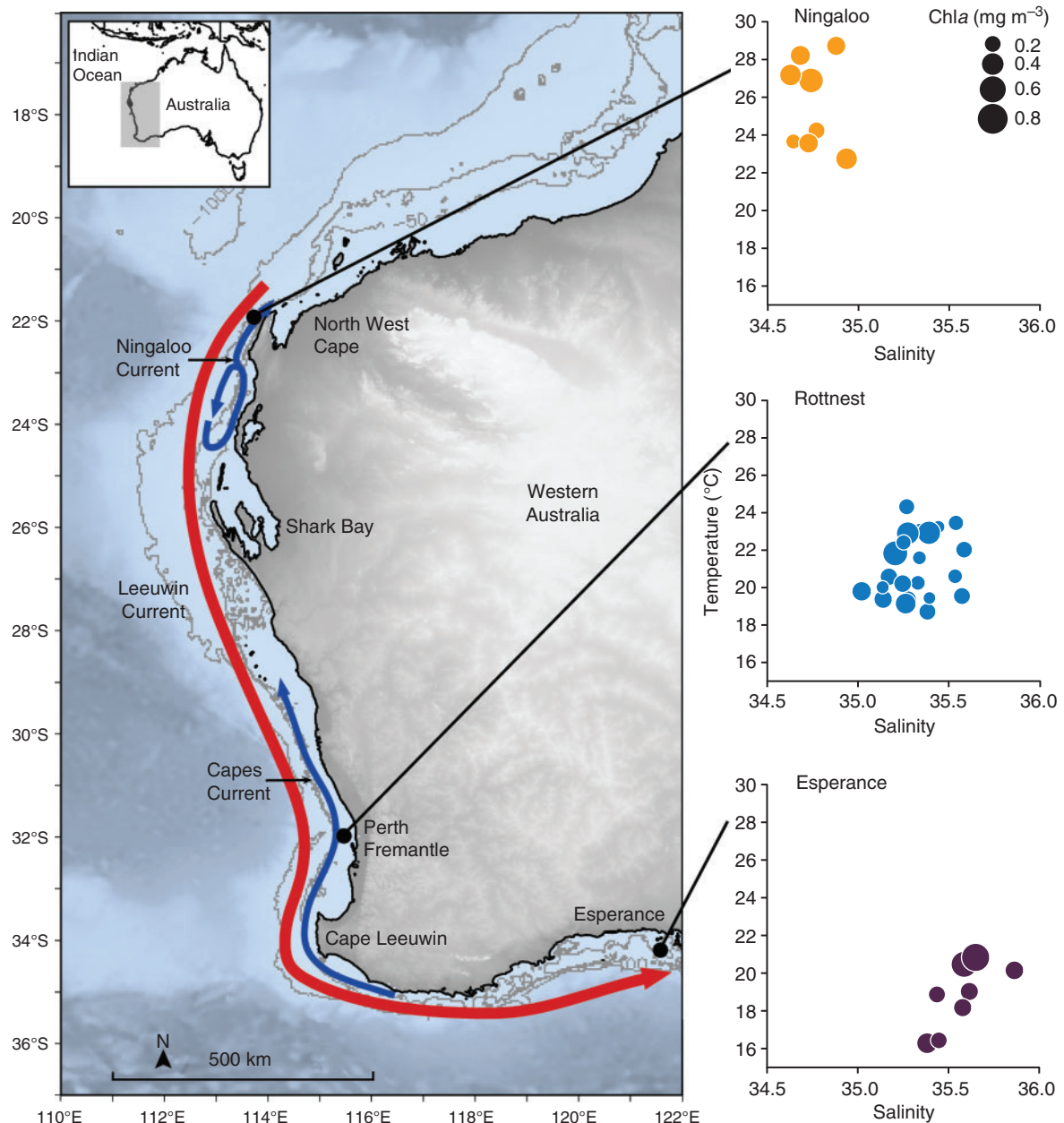


Fig. 1. Mean temperature, mean salinity and depth-integrated chlorophyll-*a* concentration at the three National Reference Stations, and their location on the Western Australian coast.

Table 2. Mean, minimum and maximum values of the environmental variables measured at the three National Reference Stations in 2011–2012

Parameter	Ningaloo		Rottnest		Esperance	
	Mean	(min–max)	Mean	(min–max)	Mean	(min–max)
Temperature (°C)	25.3	(22.2–29.2)	21.1	(18.3–24.6)	18.8	(16.2–20.9)
Salinity (psu)	34.8	(34.5–35.0)	35.3	(35.0–35.7)	35.6	(35.4–35.9)
Dissolved oxygen ($\mu\text{mol L}^{-1}$)	207	(193–217)	219	(198–232)	230	(221–241)
Density (kg m^{-3})	1023	(1022–1024)	1025	(1024–1026)	1026	(1025–1026)
Silicate ($\mu\text{mol L}^{-1}$)	3.38	(2.80–4.20)	1.96	(0.70–2.90)	0.03	(0.01–0.10)
Nitrate ($\mu\text{mol L}^{-1}$)	0.30	(0.01–2.00)	0.24	(0.01–1.60)	0.06	(0.01–0.13)
Phosphate ($\mu\text{mol L}^{-1}$)	0.10	(0.05–0.18)	0.08	(0.01–0.19)	0.07	(0.02–0.39)
Chlorophyll <i>a</i> (mg m^{-3})	0.34	(0.19–0.54)	0.26	(0.13–0.56)	0.38	(0.23–0.72)

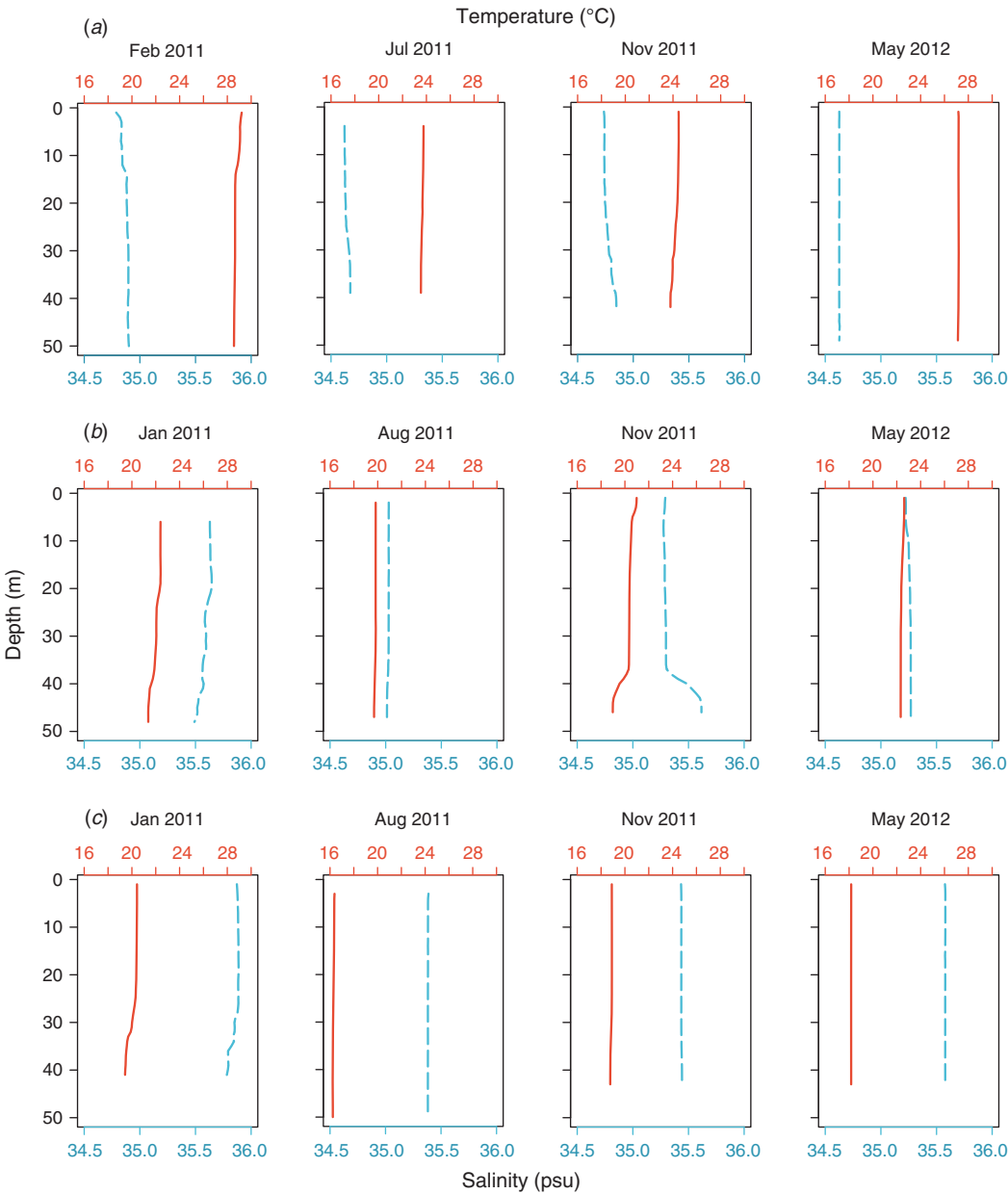


Fig. 2. Temperature (solid line) and salinity (dashed line) profiles (0–50 m) for water columns at (a) Ningaloo, (b) Rottnest and (c) Esperance National Reference Stations.

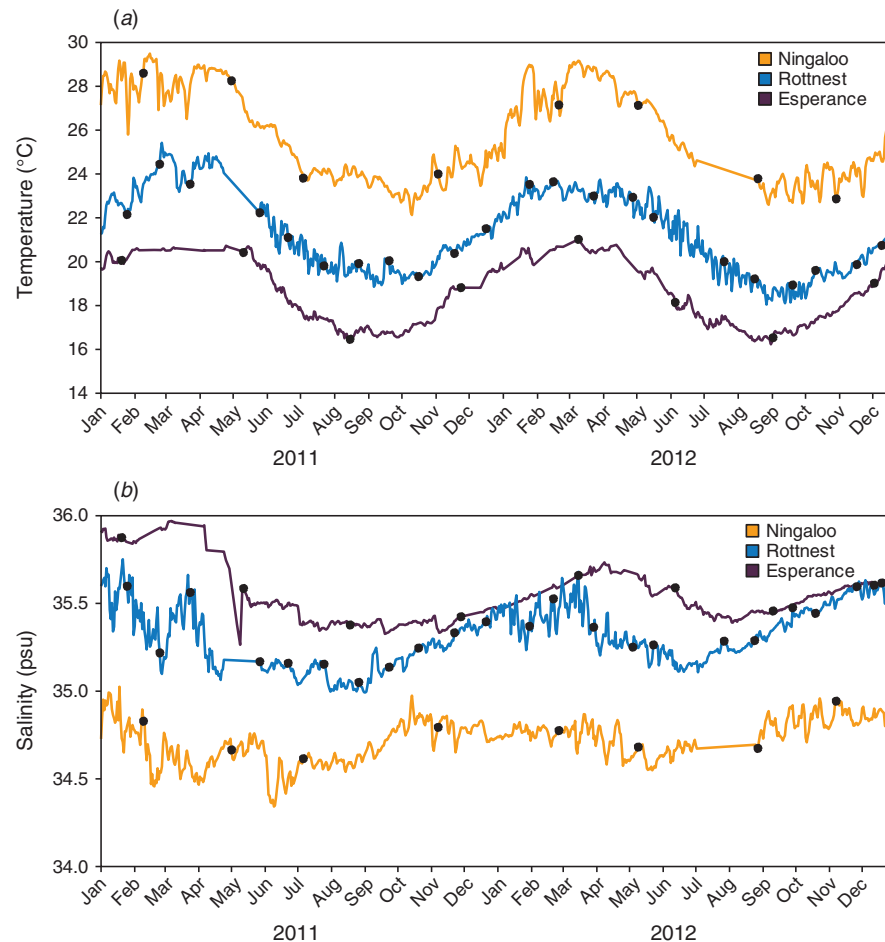


Fig. 3. Time-series of (a) mean daily temperature and (b) mean daily salinity collected by the shallow (18–25 m) mooring-based *in situ* water-quality monitors at the three National Reference Stations. Dates at which vessel-based zooplankton sampling occurred are indicated by black circles.

coastline (Pearce and Feng 2013). Accordingly, waters were, on average, $>1^{\circ}\text{C}$ warmer at Ningaloo in summer 2011, and $>0.7^{\circ}\text{C}$ warmer at Rottnest and Esperance in autumn 2011, than in 2012.

Chemical oceanography

Generally, NRS waters were nutrient poor, and became more depleted as the latitude increased. Overall, silicate had concentrations exceeding $4\ \mu\text{mol L}^{-1}$ at Ningaloo, but declined to a mean of $1.96\ \mu\text{mol L}^{-1}$ at Rottnest and $0.3\ \mu\text{mol L}^{-1}$ at Esperance (Table 2). Nitrate concentrations rarely exceeded $0.5\ \mu\text{mol L}^{-1}$ at the three NRS, the exception being Ningaloo waters in spring 2012, which recorded a concentration of $1.2\ \mu\text{mol L}^{-1}$. Phosphate concentrations were similar across the three NRS and ranged from 0.01 to $0.39\ \mu\text{mol L}^{-1}$.

Chlorophyll *a* concentrations were generally $<0.4\ \text{mg m}^{-3}$ and increased from north to south along the coast (Table 2). Higher chlorophyll *a* concentrations were associated with autumn–winter at Rottnest and Esperance, with an increase of $\sim 0.2\text{--}0.4\ \text{mg m}^{-3}$ from summer values (Fig. 4). Ningaloo did not present a consistent seasonal signal for chlorophyll *a*.

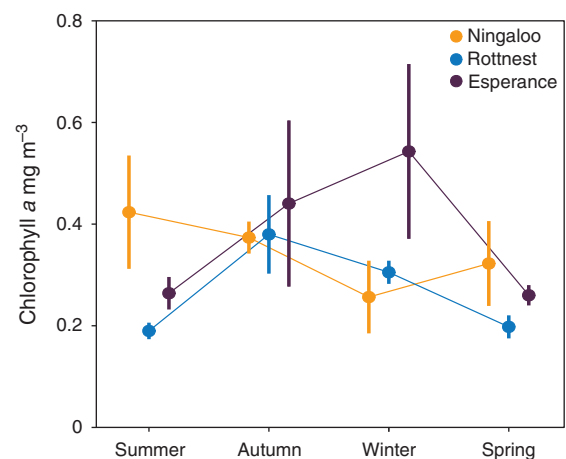


Fig. 4. Mean value of depth-integrated chlorophyll-*a* concentrations for each season during 2011–2012 at the three National Reference Stations. Error bars represent the standard error of the mean.

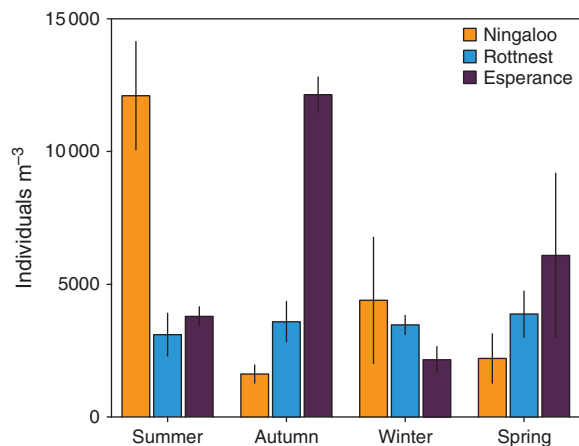


Fig. 5. Seasonal variation of mean zooplankton abundance for 2011–2012 at the three National Reference Stations. Number of samples: Ningaloo, $n = 8$; Rottnest, $n = 22$; and Esperance, $n = 8$. Error bars represent the standard error of the mean.

Zooplankton diversity, abundance and distribution

The total abundance of zooplankton organisms caught was highly variable across the NRS (893 individuals (ind) m^{-3} to 14 131 ind m^{-3}) and there was no discernible effect of latitude. Variability was mainly attributed to sporadically high densities of copepodites, which reached >5100 ind m^{-3} and contributed $>50\%$ of abundance in some samples. On average, Esperance recorded the highest abundance (mean \pm s.e., 6043 ± 1552 ind m^{-3} , $n = 8$), which was slightly higher than that for Ningaloo (5084 ± 1696 SE ind m^{-3} , $n = 8$), and Rottnest had the lowest abundance (3512 ± 355 ind m^{-3} , $n = 22$). A strong seasonal cycle in abundance was observed at Ningaloo and Esperance, with maxima in summer and autumn respectively, whereas this was not obvious at Rottnest (Fig. 5).

In total, 226 zooplankton taxa representing 12 phyla and 76 genera were identified at the three NRS (see Supplementary material Table S1 available at the journal's website). Copepods were the most numerous group in the zooplankton assemblages and comprised 66–77% of the abundance and 149 of the identified taxa. The relative proportions of other zooplankton groups to assemblages varied. From north to south, contributions of Appendicularia (family Oikopleuridae) and Chaetognatha (family Sagittidae) to the overall zooplankton assemblages declined, whereas the proportion of Mollusca increased. Assemblage compositions varied throughout the year, with seasonal blooms of larval Bivalvia and Gastropoda at all three NRS, in addition to blooms of Oikopleuridae (larvaceans) and Cladocera (mostly *Penilia avirostris*) at Ningaloo and Esperance respectively. The zooplankton also comprised lesser numbers of meroplanktonic Polychaeta, Bryozoa, Decapoda and Echinodermata.

Copepods comprised 116 identified species, of which 34 were distributed across all three NRS. On average, a greater number of copepod species was identified per sampling event at Ningaloo (27), than at Rottnest (23) and Esperance (22), indicating a decline in species richness with latitude. This was supported by examination of species accumulation curves

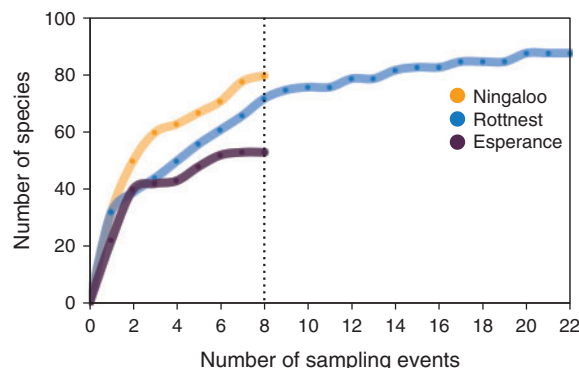


Fig. 6. Species accumulation curves based on presence/absence of copepod species at the National Reference Stations during the 2011–2012 sampling period.

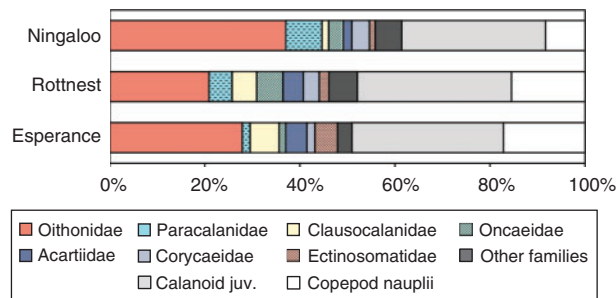


Fig. 7. The composition of copepod families at the three National Reference Stations. Also shown is the contribution of the highly abundant juvenile calanoid copepods and nauplii of copepods (not identified to family level).

constructed by combining data on copepod species occurrences obtained during the 2011–2012 sampling period. The species accumulation curves demonstrated a levelling off of species richness at Rottnest and Esperance, which contrasted with a continued upward trajectory of an increasing species richness at Ningaloo (Fig. 6). This indicated underestimation of copepod species richness at Ningaloo, which had not become saturated at the completion of the 2-year sampling period at this NRS. Species richness varied throughout the year, being greatest in autumn at Ningaloo and Esperance, and in winter at Rottnest (data not shown).

Copepod assemblages were dominated by Calanoida (48–63%), most of which were copepodites ($>70\%$), with Cyclopoida comprising 31–47%, and Harpacticoida 5–6%. Among the calanoid copepods, the family Paracalanidae was dominant at Ningaloo (16%), where high abundances, generally >60 ind m^{-3} , of species that typically dominate tropical copepod assemblages, such as *Paracalanus indicus* and *Parvocalanus crassirostris* (McKinnon *et al.* 2003b; McKinnon and Duggan 2014), were recorded (Fig. 7, Table 3). At Rottnest and Esperance, two calanoid families associated with cooler water, namely, Clausocalanidae (9–10%) and Acartiidae (7%; Frost and Fleminger 1968; Brylinski 1981), were important; the mean abundance of taxa of these families exceeded 100 ind m^{-3} . The majority of the cyclopoid copepods were of the family Oithonidae and formed a key component of assemblages (22–38%).

Table 3. Mean abundance of the dominant zooplankton taxa at the three National Reference Stations in 2011–2012

Taxa listed comprise those that had the 10 highest mean abundance values at each site. Data are number of individuals per cubic metre of water sampled

Group	Family	Taxon	Individuals m ⁻³		
			Ningaloo	Rottnest	Esperance
Copepoda					
Calanoida	Acartiidae	<i>Acartia tonsa</i>	—	37	66
	Acartiidae	<i>Acartia</i> spp.	—	60	112
	Clausocalanidae	<i>Clausocalanus furcatus</i>	—	110	92
	Clausocalanidae	<i>Clausocalanus</i> spp.	—	—	133
	Paracalanidae	<i>Bestiolina similis</i>	45	—	—
	Paracalanidae	<i>Paracalanus indicus</i>	63	67	—
Cyclopoida	Paracalanidae	<i>Parvocalanus crassirostris</i>	88	—	—
	Oithonidae	<i>Dioithona rigida</i>	47	51	107
	Oithonidae	<i>Oithona nana</i>	138	—	—
	Oithonidae	<i>O. similis</i>	—	—	40
	Oithonidae	<i>O. simplex</i>	62	—	—
	Oithonidae	<i>Oithona</i> spp.	1117	382	814
Harpacticoida	Oncaeidae	<i>Oncaea</i> spp.	97	106	—
	Ectinosomatidae	<i>Microsetella norvegica</i>	—	—	167
	Euterpinae	<i>Euterpina acutifrons</i>	130	50	—
Cladocera	Podonidae	<i>Pseudevadne tergestina</i>	—	62	—
	Sididae	<i>Penilia avirostris</i>	—	120	780
Chaetognatha	Sagittidae	<i>Zonosagitta pulchra</i>	49	—	—
Thaliacea	Doliolidae	<i>Doliolum</i> spp.	—	—	45

In particular, *Oithona* spp., *O. nana*, *Dioithona rigida* and *O. similis* were ubiquitous and numerous, and reached mean abundances of >1100 ind m⁻³.

Copepod assemblage structure

Cluster analysis of copepod assemblages showed distinct groupings that were closely related to NRS (Fig. 8). Esperance assemblages all were grouped together and, in the SIMPER analysis, were shown to be similar (61%; Table 4). Rottneest assemblages were relatively well clustered together and were found to have an average similarity of 54%. Ningaloo assemblages were less closely related (44%). The observed clustering pattern was supported by PERMANOVA, which showed that there were significant dissimilarities in copepod assemblage structures in relation to NRS ($F = 4.44$, $P = 0.001$) and that NRS explained 18% of the variability in assemblage structure. SIMPER analysis identified *Oithona* spp. as the copepod taxon that most strongly typified the copepod assemblage at each NRS (Table 4).

The degree of dissimilarity among copepod assemblages corresponded to their spatial distribution, being greatest between Ningaloo and Esperance (58%) and least between Rottneest and Esperance (49%; Table 4). Dissimilarities between the assemblages at Ningaloo and Esperance were mostly due to the greater dominance of the tropical species *Oithona nana* (McKinnon and Duggan 2014), and comparatively low abundances of *Clausocalanus* spp. and *C. furcatus* at Ningaloo, relative to Esperance. *Clausocalanus furcatus* also distinguished Ningaloo and Rottneest assemblages, being 10 times more abundant, on average, at Rottneest. The tropical affinity of

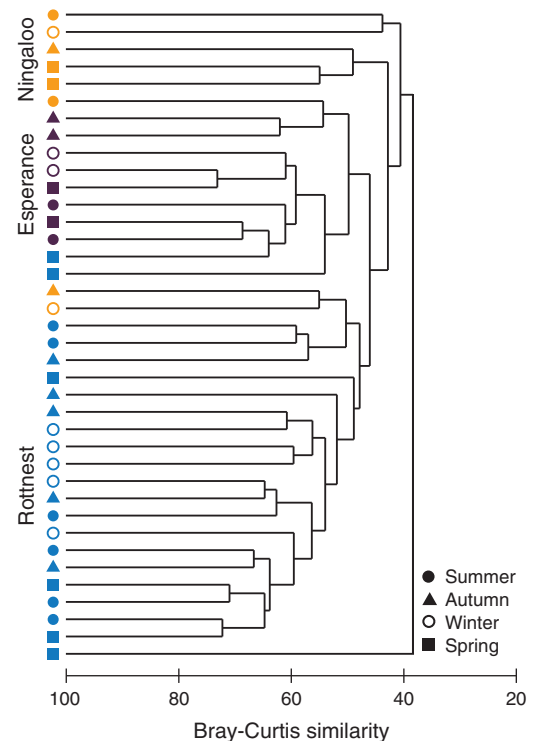


Fig. 8. Clustering dendrogram (group-average method), showing the similarity between copepod assemblages and across all seasons. Symbol colour denotes National Reference Station: Ningaloo (gold), Rottneest (blue), and Esperance (purple).

Table 4. Taxa contributing the most to characterising the copepod assemblages within (unshaded), and taxa distinguishing among (shaded) copepod assemblages at the three National Reference Stations, as identified by similarity percentage analyses (SIMPER)
Avg., average

	Ningaloo	Rottneest	Esperance
Ningaloo	Avg. similarity: 44%		
	<i>Oithona</i> spp. <i>O. nana</i> <i>Paracalanus indicus</i> <i>Oncaea</i> spp.		
Rottneest	Avg. dissimilarity: 53%		Avg. similarity: 54%
	<i>Clausocalanus furcatus</i> <i>Dioithona rigida</i> <i>Parvocalanus crassirostris</i> <i>Euterpina acutifrons</i>		<i>Oithona</i> spp. <i>Oncaea</i> spp. <i>Paracalanus indicus</i> <i>Oithona nana</i>
Esperance	Avg. dissimilarity: 58%		Avg. similarity: 61%
	<i>Clausocalanus furcatus</i> <i>Clausocalanus</i> spp. <i>Oithona nana</i> <i>Acartia</i> spp.		<i>Oithona</i> spp. <i>Clausocalanus</i> spp. <i>Acartia</i> spp. <i>A. tonsa</i>
	Avg. dissimilarity: 49%		
	<i>Clausocalanus</i> spp. <i>Oithona brevicornis</i> <i>Dioithona oculata</i> <i>Oncaea media</i>		

Euterpina acutifrons and *Paracalanus crassirostris* was apparent, with these two species being rarely recorded at the two southern NRS, but occurring at abundances of $>80 \text{ ind m}^{-3}$, on average, at Ningaloo, and being important discriminators for this site. Rottneest and Esperance were differentiated by an order of magnitude greater dominance of *Clausocalanus* spp. at Esperance, together with exclusivity of some particular taxa, namely, *Oncaea media* at Rottneest, and *Dioithona oculata* at Esperance (Table 4).

Dissimilarities among NRS assemblages varied temporally, being more pronounced in summer than in winter. A corresponding increase in the proportion of copepod taxa distributed across all three NRS occurred in winter (27%), relative to summer (20%). PERMANOVA indicated that there were significant differences in copepod assemblage structure among seasons ($F = 1.54$, $P = 0.04$), and an interaction between the two factors of NRS and season ($F = 1.67$, $P = 0.008$). The NRS–season interaction effect explained 15.8% of the variability in copepod assemblages, while season alone explained a further 7% of the variability.

Influence of oceanography on copepod assemblages

The distance-based linear model (DistLM) for copepod assemblages selected mean seawater density, depth-integrated chlorophyll *a*, and depth-integrated nitrate for inclusion in the best model explaining the variance in assemblage structures (adjusted $R^2 = 0.17$). The model explained 17% of the overall variation, with the two significant explanatory variables, namely, seawater density and chlorophyll *a*, accounting for 9.7% ($F = 3.5$, $P = 0.0001$) and 4.8% ($F = 1.7$, $P = 0.0346$) respectively. There was no significant correlation of nitrate concentration with copepod assemblage structure ($F = 1.5$, $P = 0.0817$). For the fitted model, the dbRDA bi-plot showed the first and second axes to significantly explain 87% of the variation in copepod assemblage structure (Fig. 9).

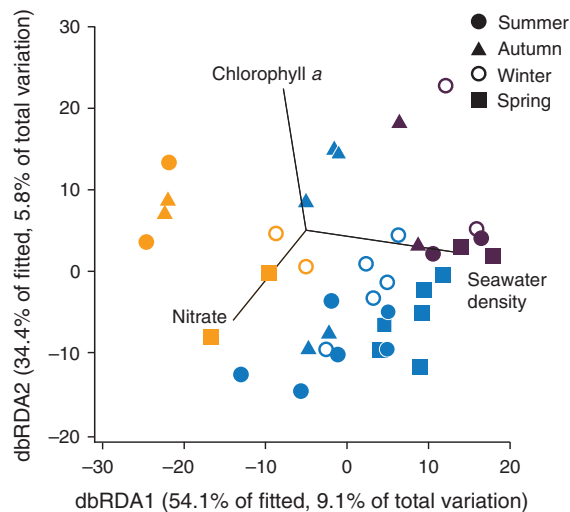


Fig. 9. Distance-based redundancy bi-plot of the structuring of copepod assemblages (coded by season) in relation to a set of environmental variables. Symbol colour denotes National Reference Station: Ningaloo (gold), Rottneest (blue), and Esperance (purple).

Discussion

The three NRS sites examined in this study had clearly distinct water mass properties and oceanographic characteristics across the 12° latitudinal range. Ningaloo was generally characterised by TSW, which was modified as it was transported south in the LC; at Rottneest, the modified TSW was cooler and more saline, owing to the inflow of more dense offshore water, air–sea heat flux and evaporation (Weller *et al.* 2011). Despite its location in the temperate zone, waters at Esperance remained warm ($>18^{\circ}\text{C}$) throughout much of the year, with a stronger STSW signature of cooler, more dense water evident in winter because

of wind-forcing and the subsequent heat loss that occurs along this coast (Middleton and Bye 2007). Waters were generally depleted of nutrients and, with typically low chlorophyll *a* concentrations ($<1 \text{ mg m}^{-3}$), were representative of the oligotrophic nature of Western Australian coastal waters, which is consequence of the downwelling-favourable LC suppressing nutrient enrichment (Hanson *et al.* 2005; Thompson *et al.* 2011). Chlorophyll *a* enriched waters in autumn–winter at Rottnest and Esperance were indicative of the annual shelf-wide phytoplankton bloom known to occur at that time (Koslow *et al.* 2008; Thompson *et al.* 2009; Lourey *et al.* 2013).

Temporal oceanographic change occurred at the sites as they were exposed to physical forcing and the strong La Niña event that occurred in early 2011. At Ningaloo, the sporadic presence of denser, nitrate-enriched water provided an indication of spring upwelling (Rossi *et al.* 2013). Similar conditions at Rottnest were likely to be an indication of localised upwelling that was driven by the Capes Current (Gersbach *et al.* 1999; Lourey *et al.* 2013). Associated with the La Niña event were exceptionally high positive SOI values and high sea levels at Fremantle (Bureau of Meteorology 2012), indicative of an intensified LC. Driven by the strong La Niña conditions, the surging LC frequently flooded the coastal shelf (Feng *et al.* 2013) and was sufficient to suppress the northward-flowing, summer coastal Ningaloo and Capes Currents. Sustained elevated water temperatures along the Western Australian coast associated with the La Niña (Pearce and Feng 2013; Benthuisen *et al.* 2014) were demonstrated at all three sites, but were particularly marked at Esperance, where unseasonably warm water ($>20^\circ\text{C}$) persisted throughout summer and autumn in 2011.

Zooplankton abundance at the NRS was highly variable and largely driven by fluctuations in numbers of copepodites and nauplii, with the substantial abundances of these small organisms captured in the zooplankton samples being a result of sampling using a 100- μm net. However, domination of the zooplankton by small copepods is typical of marine systems (Longhurst 1985). NRS copepod assemblages were clearly distinct, and the strength of dissimilarity corresponded to the degree of spatial separation and variation in oceanographic conditions among sites. The composition of the Ningaloo assemblage resembled that of previous studies of Western Australian tropical, coastal waters, particularly its dominance by the copepod families Paracalanidae and Oithonidae, that conferred an Indo-Pacific influence (Kimmerer *et al.* 1985; McKinnon *et al.* 2008; McKinnon *et al.* 2015). The location of the Rottnest NRS in a marine overlap zone (Commonwealth of Australia 2006) was demonstrated by its copepod assemblage, which resembled both the Ningaloo and Esperance assemblages. This included proportions of Corycaidae and Oncaeaidae copepods similar to those at Ningaloo, and proportions of Acartidae and Clausocalanidae copepods similar to those at Esperance. Greater dominance of taxa from the latter two families in the Esperance assemblage distinguished this site and reflected its warm-temperate bioregion.

Observations at the three NRS showed that there were no significant differences in overall compositions of copepod assemblages between years, despite a shift from La Niña to more stable conditions in 2012. However, substantially greater densities of some copepod species common in tropical waters

such as *Dioithona oculata*, *D. rigida* and *Microsetella norvegica* (McKinnon and Duggan 2014) in mid- and higher-latitude coastal waters in 2011 than in 2012, may reflect the increased water temperatures associated with La Niña.

A decline in copepod species richness with an increasing latitude along the Western Australian coast was found, similar to the pattern observed for marine crustaceans and fishes along both the western and eastern coasts of Australia (O'Hara and Poore 2000; Fox and Beckley 2005). Species accumulation curves suggested an incomplete inventory of the copepod species pool at Ningaloo. This is supported, for example, by a study of copepods of the inshore waters at the North West Cape by McKinnon *et al.* (2008), which used a 73- μm plankton net and found >120 species to occur, compared with the 80 species identified here. These findings are relevant for the sampling designs of future zooplankton studies in these waters, which could, through extended sampling, yield a more accurate measure of zooplankton species diversity at Ningaloo.

Plankton assemblages have been linked with the physical and biogeochemical properties of water masses (Hopcroft *et al.* 2010; Holliday *et al.* 2011; Beckley *et al.* 2019). Discrete water masses on the basis of the water column properties were identified at the NRS sites. Examination of the relationship between oceanography and copepod assemblages using distance-based linear modelling showed that seawater density, indicative of the underlying water mass, was the most significant environmental variable shaping copepod assemblage structure, although it explained only a small proportion of the underlying variation in the assemblage structure. Seawater density has similarly been found to be important in structuring plankton assemblages in other studies of LC plankton, including larval fishes (Muhling *et al.* 2008), euphausiids (Sutton and Beckley 2016) and chaetognaths (Buchanan and Beckley 2016).

The latitudinal modification in water mass from lower density TSW to denser STSW corresponded to a change in assemblage structure, from primarily tropical copepod taxa at Ningaloo, to a mix of tropical–subtropical–temperate taxa in the transition zone at Rottnest, to mainly temperate-associated taxa at Esperance. At Ningaloo, the dominant TSW provides conditions favourable for Indo-Pacific copepods, whereas, in contrast, at Esperance, lower tropical species richness and abundance suggest exceedance of species temperature tolerance limits. The varied assemblage at Rottnest is likely to be influenced by both LC intrusion (Weller *et al.* 2011) and an opposing inshore Capes Current from the south, resulting in an intersection of entrained pelagic species. A similar overlap of plankton of varied bioregional affinity occurs as a result of the convergence of waters in the East Australian Current–Tasman Sea transition zone on the eastern coast of Australia (Keane and Neira 2008).

Chlorophyll *a* concentrations at the sites also explained some of the variation in copepod assemblage structure, although its influence was less significant. This is not surprising because any response of copepod assemblages to chlorophyll *a* concentration would be indirect and subject to lag as the effect worked along the food chain (Legendre 1990). Greater abundances of predominantly herbivorous copepods in assemblages, such as *Clausocalanus* spp., *Temora* spp., *Temora turbinata* and *Paracalanus indicus* (Kouwenberg 1994), appeared to be associated with an increased chlorophyll *a* concentration. Previous studies

have found that opportunistic herbivorous copepods can achieve rapid growth and production rates in response to a higher chlorophyll *a* concentration (Peterson and Hutchings 1995; Rosa *et al.* 2016), and this may also be the case here.

Besides the underlying water masses, the LC may also influence the distribution of zooplankton along the Western Australian coast, particularly in autumn–winter when it is at maximum strength and along-shore transport and onshore intrusion of warm water increases, resulting in entrainment of species that are dispersed poleward or across the shelf (Hutchins and Pearce 1994; Gaughan *et al.* 2009; Holliday *et al.* 2012). This conveyance of plankton in the LC plays a role in enhancing the species richness, in particular, the tropical component, of assemblages in temperate Western Australian waters (Maxwell and Cresswell 1981; Gaughan and Fletcher 1997). This study found that, in winter, dissimilarities among the NRS assemblages weakened, the number of copepod species in common across sites increased, and species richness was enhanced, including a stronger presence of offshore species on the shelf and tropical species in the south. This suggests that the seasonal oceanography of the LC enhances connectivity among copepod assemblages across a broad latitudinal range, increasing diversity in temperate waters that are otherwise known for their high level of endemism (Fox and Beckley 2005). Reduced dissimilarities among plankton assemblages in south-eastern Australian waters have, similarly, been attributed to poleward transport of species in a strengthened East Australian Current (Keane and Neira 2008; Kelly *et al.* 2016).

Populations of copepods with tropical and subtropical affinities also occurred throughout the year at Rottnest and Esperance. It is unclear whether these copepods are representative of a broad trend of range extensions and shifts towards dominance by small-bodied and warm-water copepods in temperate waters, as is evident in Tasmania (Kelly *et al.* 2016), the Southern Benguela (Huggett *et al.* 2009), and the large ocean basins (Beaugrand *et al.* 2002b). Alternatively, the persistence of warm-water copepod species at higher latitudes on the Western Australian coast may be further confirmation of the influence of the LC, which injects warm, subtropical, lower salinity water to the coast. Sustained monitoring is required to investigate this pattern.

This study is the first to relate differences in oceanographic conditions to variation in zooplankton abundance, diversity and distribution among north-western, south-western and southern coastal waters of Western Australia. This study has highlighted the role of the LC in driving variability in zooplankton assemblages at both spatial and temporal scales. Although seawater density and chlorophyll *a* were identified as significant in explaining copepod assemblage structure, a large amount of variation remained unexplained. Thus, there remains large scope for future research of the zooplankton of this vastly understudied system, using the significant amount of environmental and biological data that IMOS will continue to provide.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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