The zooplankton prey field for rock lobster phyllosoma larvae in relation to oceanographic features of the south-eastern Indian Ocean

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The western rock lobster, Panulirus cygnus, provides Australia’s most valuable wild caught fishery but, in recent years, there has been a dramatic decline in settlement of the post-larval phase into their natal coastal habitat. One hypothesis for this decline was that the oceanographic conditions no longer favour the survival, feeding and growth of the larval (phyllosoma) phase. To explore this, the oceanography and corresponding zooplankton prey field along five latitudinal transects in the south-eastern Indian Ocean were quantified during July 2010. Leeuwin Current Water (LCW) and Sub-Tropical Surface Water (STSW) were distinguished and a prominent front at $\approx 30^\circ$S characterized by strong eastward flow separated them. Although zooplankton abundance increased towards the north, the prey field was unevenly distributed with patches of higher prey concentration associated mainly with LCW. Chaetognaths were the most abundant prey item (means: 17.2 and 4.1 m$^{-3}$ in LCW and STSW, respectively) and were positively correlated with chlorophyll $a$ in both water masses. Panulirus cygnus phyllosoma had a highly patchy distribution but, despite lower prey concentrations, were more abundant in STSW than LCW, particularly south of the front. Our results suggest that LC meso-scale features with...
strong fronts may be implicated in phyllosoma aggregations and shoreward transport of late-stage larvae and that this warrants further investigation.

KEYWORDS: biological oceanography; *Panulirus cygnus*; water masses; Leeuwin Current; Western Australia; chaetognaths; chlorophyll a

INTRODUCTION

Spiny lobsters (Palinuridae) are economically important and widely distributed through tropical and temperate marine environments around the world. Their life-cycle is characterized by a long, planktonic larval phase (from a few months to almost two years) which is spent in the open ocean (Lipcius and Eggleston, 2000). During this period, the larvae (phyllosoma) feed on zooplankton prey, grow and develop through 7 to 13 phyllosoma stages until the final-stage phyllosoma metamorphoses into a non-feeding puerulus stage which settles into the benthic environment (Lipcius and Eggleston, 2000).

Planktonic decapod larvae feeding at relatively high trophic levels may be particularly vulnerable to starvation (Pearre, 2003), since their prey are normally sparse in much of the water column and show an uneven distribution with only occasional high density patches (Folt and Burns, 1999). Thus, the distribution and abundance of zooplankton prey would be expected to have a large impact on the growth and survival of phyllosoma in the open ocean. Food availability (i.e. the prey field) for phyllosoma can ultimately influence metamorphosis into the puerulus stage and subsequent settlement along the coast. Thus, feeding success in the patchy oceanic prey field could influence rates of recruitment to fisheries of adult lobsters.

Off the west coast of Australia, the western rock lobster (*Panulirus cygnus*) is distributed between latitudes 22°S and 34°S with the fishery concentrated between 28°S and 32°S (Caputi, 2009; Caputi, 2008). *Panulirus cygnus* eggs hatch from December to February and the phyllosoma larvae are transported offshore into the Indian Ocean (Phillips et al., 1979). During their planktonic phase (9–11 months), *P. cygnus* phyllosoma actively feed and are widely dispersed in the south-eastern Indian Ocean (Phillips et al., 1979; Griffin et al., 2001). The final stage phyllosoma metamorphose into pueruli that migrate across the continental shelf in order to settle in benthic habitats along the coast of Western Australia (WA); peak settlement occurs from 29 to 31°S between September and January (Phillips, 1986; Caputi, 2008). In recent years, there has been a dramatic decline in settlement of pueruli of *P. cygnus* along the coast and the long-established relationship between sea-level height in Fremantle and settlement has broken down (Feng et al., 2011). Sea level height measured in Fremantle is influenced by the El Niño/La Niña cycle and reflects the strength of the Leeuwin Current, which is the major boundary current along the west coast of Australia (Feng et al., 2008).

*Panulirus cygnus* phyllosoma have a patchy distribution pattern in the south-eastern Indian Ocean, with highest concentrations found between latitudes 27°S and 31°S and 400–1000 km off the coast of WA (Chittleborough and Thomas, 1969; Phillips et al., 1978, 1979). During this extended planktonic period, the phyllosoma are strongly influenced by their physical environment; the strength of the Leeuwin Current, sea surface temperature (SST) and westerly winds all being closely correlated with the inter-annual variations in puerulus settlement of western rock lobster off the WA coast (Caputi et al., 2001; Caputi, 2008). However, relatively little is known about how the biological environment including the zooplankton prey field influences the phyllosoma stages of *P. cygnus*. Previous investigations in the Indian Ocean report on low zooplankton biomass, particularly in the open ocean, which suggests a sparse prey field for *P. cygnus* phyllosoma (Tranter, 1962; Tranter and Kerr, 1969).

Various investigations have indicated that spiny lobster phyllosoma larvae have a preference for soft-bodied prey such as medusae, salps, ctenophores and chaetognaths (Mitchell, 1971; Kittaka, 1994; Macmillan et al., 1997; Johnston and Ritar, 2001; Cox and Johnston, 2003a,b). Furthermore, laboratory studies have shown that early-stage *P. cygnus* phyllosoma show an increased feeding response when offered soft-textured moist formulated diets (Johnston and Johnston, 2007). Our recent experimental work at sea, testing food preferences of wild-caught phyllosoma, indicated that chaetognaths were clearly a preferred prey item (Saunders et al., 2012). DNA evidence suggests that radiolarians may also be important prey items in this region (O’Rorke et al., 2012). In the wild, any such preferences would be dependent on the availability of such organisms to the phyllosoma in the prey field. This becomes critical for nutrition and survival of phyllosoma in an oligotrophic environment such as that of the south-eastern Indian Ocean. It is therefore important to
quantify which potential prey organisms are available in the natural pelagic environment of *P. cygnus* phyllosoma. By mapping the natural prey field against the backdrop of *in situ* oceanographic conditions, we can obtain an improved understanding of which prey items are available to be consumed and stored as internal energy reserves for later usage during the non-feeding puerulus stage (Lipcius and Eggleston, 2000).

The aims of the present study were to:

- Investigate the bio-physical parameters of the south-eastern Indian Ocean where the planktonic phyllosoma stages of *P. cygnus* occur.
- Investigate the spatial and vertical distribution of potential prey items for *P. cygnus* phyllosoma.
- Identify bio-physical drivers of the prey field in the south-eastern Indian Ocean.

**METHODS**

**Study region**

The study was undertaken from the R.V. Southern Surveyor (voyage 05/2010) in the austral winter (6–27 July 2010) to coincide with the period when phyllosoma larvae would be actively feeding and amassing energy reserves prior to metamorphosis into the non-feeding puerulus stage (Phillips *et al.*, 1979; Lemmens and Knott, 1994). The south-eastern Indian Ocean off the western coast of Australia was sampled from 28°8S to 32°8S and offshore to 111.5°E. The spatial and vertical distribution of zooplankton was investigated along a grid of five inshore/offshore transects located at 1° latitude intervals with 30 oceanographic stations located at 0.5° longitude intervals (Fig. 1A).

**Field sampling and analyses**

Depth-stratified plankton samples were taken with an opening and closing EZ net at the 30 stations on the grid (regardless of time of day the ship arrived on station). The EZ net was fitted with multiple nets of 335 μm mesh (mouth area 1.0 m²), a flow meter and an electronic interface to the vessel whereby the operation of the net in the water column could be controlled. The following depth strata were sampled: 200–150, 150–100, 100–50 and 50 m surface. The net was towed at a ship speed of ~2 knots and slowly retrieved from 200 m depth allowing about 15 min in each depth stratum.

The zooplankton samples from the EZ net were fixed in 5% buffered formaldehyde in seawater immediately after collection. In the laboratory, an estimate of overall zooplankton abundance for each station was obtained by allowing the sample to settle in a graduated measuring cylinder for 24 h and expressing the value as mL of settled zooplankton per m³ of water filtered (zooplankton settled volume) (Gibbons, 1999). With the aid of a dissecting microscope, phyllosoma and larval fishes were removed from the sample and then counts of potential prey items (including siphonophores, salps, heteropods, medusae, chaetognaths, krill and squid larvae) were made. Where samples contained very many prey items, they were split using a Folsom plankton splitter, and only a fraction of the sample was counted. All phyllosoma larvae were identified to species where possible and staged using relevant literature (e.g. Ritz and Thomas, 1973; Braine *et al.*, 1979; Inoue and Sekiguchi, 2006). Concentrations of potential prey items were standardized as number per m³ and those of phyllosoma as number per 1000 m³.

Prior to, and during, the grid sampling, additional surface water zooplankton samples were collected (Fig. 1B).
to obtain phyllosoma and prey items for concurrent on board feeding preference studies (Saunders et al., 2012). These samples were taken at night, typically from 21:00 to 03:00, when phyllosoma are most likely to be encountered during their diel migration (Rimmer and Phillips, 1979). The surface net had a mouth area of 1 m², 1000 µm mesh, a flowmeter and was towed at a ship speed of ~2 knots. The numbers of live phyllosoma removed from each sample for feeding experiments were counted and the remainder of the surface zooplankton samples preserved in 5% formaldehyde in seawater or 95% ethanol. In the laboratory, these samples were sorted for any additional phyllosoma and total counts were calculated by adding these numbers to those initially removed. Total counts were expressed as number of phyllosoma per 1000 m³ of water filtered.

Hydrographic parameters were collected at stations immediately before plankton samples were collected with the EZ net, using a Sea-bird SBE911 conductivity-temperature-depth (CTD) profiler, fitted with a SBE43 oxygen sensor and a 24-Niskin bottle rosette sampler. The CTD was equipped with a Chelsea Aquatracker fluorometer, SeaTech transmissometer, Biospherical Photosynthetically Active Radiation sensor and a Satlantic ISUS nitrate sensor. Water samples were typically collected at depths of 0, 20, 35, 70, 90, 150, 200 and 1000 m and analysed for dissolved inorganic nutrients (nitrate, phosphate, silicate and ammonium) in unfiltered water samples using a LACHAT instrument on board the ship. Detection limits were 0.03 µM for nitrate, ~0.02 µM for phosphate and ~0.05 µM for silicate and ammonium. For calibration of the in situ fluorometer, 1-L water samples from six sampling depths (~100 m) at each station were filtered through 25-mm Whatman GF/F filters. Pigments (chlorophyll a) were extracted immediately in 90% acetone following the acidification technique and read on a Turner designs 10 AU fluorometer according to the methods of Parsons et al. (Parsons et al., 1984). In situ fluoresence was calibrated by using linear regression for pooled extracted chlorophyll a data from all transects (r² = 0.59), with a lower limit of detection of 0.04 µg Chl a L⁻¹. The in situ Satlantic ISUS nitrate sensor was calibrated by using a linear regression for pooled nitrate measurements on board the ship from all transects versus in situ nitrate sensor measurements (r² = 0.95).

Continuous underway measurements of SST were acquired with a SBE 3T Seabird thermosalinograph sensor and the horizontal current velocity along the ship’s track was obtained using a vessel mounted RDI 75 kHz Ocean Surveyor Acoustic Doppler Current Profiler (ADCP). The ADCP was set to record from just below the ship (10 m) to a maximum water column depth of 300 m and data were averaged in 8 m depth bins.

Data analyses

Statistical analyses were performed in SPSS (version 17.0 for Mac OS X) and in R version 2.15.0 GUI 1.51. Water masses were defined based on the mean temperature-salinity (TS) profiles in the water column down to 200 m. Sampling stations were classified as being located within either Leeuwin Current water (LCW) mass or Subtropical surface water (STSW) (Pearce et al., 2006). The mixed layer depth (MLD) was determined at the depth at which the temperature was 0.4°C less than that observed at 10 m or salinity was 0.03 more than that measured at 10 m (Condie and Dunn, 2006).

A principal component analysis (PCA) using version 1.24 of ‘FactoMineR’ (Lé et al., 2008) in R was used to explore the entire data set, including both abiotic (derived from CTD casts) and biotic variables in the water column down to 200 m. This allowed us to reduce the number of variables in the data matrix into two principal components. PC scores were derived from the PC loadings and were used to generate scatter plots to visualize differences between the water masses and any clustering of stations.

Any spatial (using mean water column data from each station) and vertical (using depth strata (200–150, 150–100, 100–50 and 50 m-surface) data from each station) differences in abiotic and biotic variables between the water masses were investigated with a non-parametric Mann–Whitney U-test. Variation in prey densities from the whole survey was analysed using a Kruskal–Wallis test and the pairwise Mann–Whitney U-test was used to determine the significance of differences among prey items. Concentrations of P. cycgnus phyllosoma from the EZ net hauls were not included in any of the statistical analyses as they were captured in low numbers at only seven of the 30 EZ stations.

RESULTS

Physical oceanography and chl a concentrations

Remotely sensed altimetry (sourced from http://oceancurrent.imos.org.au) and SST data from the study period clearly indicated a large seaward meander in the Leeuwin Current in the north of the study area and a more typical, narrower Leeuwin Current along the edge of the continental shelf south of 30°S (Fig. 2A–C). Shipboard ADCP showed strong southward surface flow (130 cm s⁻¹) associated with the LC at the shelf-edge stations and an easterly surface current component was dominant ~30°–30.5°S where current velocities attained 113 cm s⁻¹ (Fig. 2D). Several meso-scale circulation features were also evident in the study area (Fig. 2A–C).
The TS profiles and chlorophyll a concentrations indicated that there was significant spatial variability in these three variables in the study area. Two main water masses were identified: (i) lower salinity (<35.6 psu), warmer (>20°C) LCW with relatively high chl a concentration on the northern transects (latitudes 28°S and 29°S) and along the shelf-edge stations (19, 30 and 41) further south in the study area, and (ii) cooler (18°–20°C), higher-salinity (>35.6 psu) STSW located offshore of the LC at most of the southern stations which were often associated with lower chl a concentrations (Fig. 3; Table I). The MLD across the study area varied from 33 to 227 m with...
station 8 on the shelf at 28°S having a completely mixed water column to the seafloor at 51 m. The average MLD from all the stations was 112 m with the STSW generally having a deeper MLD than the LCW.

Cross-sections of temperature, salinity and chl a (Fig. 4) showed some clear differences within the water column between transects. Warm, low salinity water with relatively high chl a concentration was associated with the northern most latitudes (28°S and 29°S). Although warm LCW dominated the surface waters along transect 28°S, both the satellite imagery and the cross-section (Figs 2 and 4) indicated the presence of a cyclonic cold core (CC) eddy at about 113°E. A large offshore meander of LCW was evident on transect 29°S, with isothermal low salinity water extending to >200 m depth (Fig. 4). Along the 30°S transect, cooler STSW was more dominant although part of the LC meander did cross the transect at around 113°E (Figs 2 and 4). The 31°S transect was mainly STSW except near the shelf-edge where the warm LCW prevailed (Fig. 4). Most of the 32°S transect was characterized by STSW with warm LCW at the shelf-edge and evidence of an anticyclonic warm core (WC) eddy at around 112°E (Figs 2 and 4) towards the end of the study period.

Chl a concentrations in the two water masses ranged from below the detection limit to 0.62 μg L⁻¹ and, over all stations, were significantly greater in the LCW than the STSW mass (Table I, the Mann–Whitney U-test, \( P < 0.05 \)). Relatively high chl a concentrations were associated with the extensive meander along transect 29°S (Figs 4 and 5F).

**Chemical oceanography**

There was a clear distinction in the chemical composition of the LCW and STSW, with significantly greater % light transmission, DO and phosphate concentrations in the STSW (Table I, the Mann–Whitney U-test, \( P < 0.01; P < 0.001; P < 0.05 \), respectively). Ammonia and silicate concentrations were significantly greater in the LCW compared with the STSW (Table I, the Mann–Whitney U-test, \( P < 0.01; P < 0.001 \), respectively). There were similarities between the water-column vertical profiles of nitrate and phosphate (\( \rho = 0.939, P < 0.001 \), both nutrients being depleted in the surface layer (0–50 m) and with peaks in concentration associated with the deeper waters (100–200 m) and transect 30°S (the Mann–Whitney U-test, \( P < 0.05 \)). Silicate concentrations ranged from 1.4 to 3.2 μmol L⁻¹, with highest concentrations in the northern part of the study region (transects 28°S and 29°S). Silicate and ammonium concentrations were significantly correlated (\( \rho = 0.312, P < 0.01 \)) and highest concentrations of ammonium (0.3 μmol L⁻¹) were found on transect 28°S.

**Zooplankton abundance and distribution**

The highest mean zooplankton (including copepods) settled volume (mL m⁻²) occurred on transect 28°S and

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**Table I:** Mean, minimum and maximum values of the abiotic and biotic variables measured in the Leeuwin Current Water and Sub-Tropical Surface Water in the upper 200 m in the south-eastern Indian Ocean in July 2010

<table>
<thead>
<tr>
<th>Variable</th>
<th>LCW (Mean (min–max))</th>
<th>STSW (Mean (min–max))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature (°C)</td>
<td>21.2 (19.8–22.9)**</td>
<td>18.1 (14.6–19.9)</td>
</tr>
<tr>
<td>SigmaT</td>
<td>35.4 (35.2–35.7)**</td>
<td>35.8 (35.5–35.9)**</td>
</tr>
<tr>
<td>% light transmission</td>
<td>71.0 (68.7–72.1)**</td>
<td>71.5 (70.6–72.4)**</td>
</tr>
<tr>
<td>DO (μmol L⁻¹)</td>
<td>221 (215–226)**</td>
<td>234 (226–239)**</td>
</tr>
<tr>
<td>Nitrate (μmol L⁻¹)</td>
<td>0.53 (0.10–1.31)*</td>
<td>0.92 (0.01–4.50)*</td>
</tr>
<tr>
<td>Phosphate (μmol L⁻¹)</td>
<td>0.11 (0.08–0.18)</td>
<td>0.16 (0.08–0.43)*</td>
</tr>
<tr>
<td>Silicate (μmol L⁻¹)</td>
<td>2.75 (2.39–3.29)**</td>
<td>1.98 (1.43–2.53)</td>
</tr>
<tr>
<td>Ammonium (μmol L⁻¹)</td>
<td>0.06 (0.01–0.26)**</td>
<td>0.04 (0.01–0.11)</td>
</tr>
<tr>
<td>Chl a (μg L⁻¹)</td>
<td>0.33 (BD – 0.49)*</td>
<td>0.25 (BD – 0.62)</td>
</tr>
<tr>
<td>Settled zooplankton volume (mL m⁻²)</td>
<td>0.47 (0.12–2.01)**</td>
<td>0.27 (0.05–1.70)</td>
</tr>
<tr>
<td>Chaetognaths (m⁻³)</td>
<td>17.2 (6.60–64.6)*</td>
<td>4.06 (0.14–19.8)</td>
</tr>
<tr>
<td>Krill (m⁻³)</td>
<td>6.81 (1.01–31.6)**</td>
<td>2.61 (0.09–15.2)</td>
</tr>
<tr>
<td>Larval fishes (m⁻³)</td>
<td>0.94 (0.12–3.26)**</td>
<td>0.23 (0.02–2.05)</td>
</tr>
<tr>
<td>Siphonophores (m⁻³)</td>
<td>3.91 (0.10–30.7)**</td>
<td>1.22 (0.09–3.92)</td>
</tr>
<tr>
<td>Salps (m⁻³)</td>
<td>5.34 (0.09–48.4)**</td>
<td>1.44 (0.09–11.2)</td>
</tr>
<tr>
<td>Larval squid (1000 m⁻³)</td>
<td>33.4 (3.30–138)**</td>
<td>6.80 (0.40–40.0)</td>
</tr>
<tr>
<td>Heteropods (1000 m⁻³)</td>
<td>9.71 (0.51–51.6)**</td>
<td>1.90 (0.20–20.3)</td>
</tr>
<tr>
<td>Medusae (1000 m⁻³)</td>
<td>15.4 (0–66.9)**</td>
<td>8.80 (0–110)</td>
</tr>
</tbody>
</table>

**Notes:** *P < 0.001, **P < 0.01, *P < 0.05, indicating significantly higher mean value. Mean values are calculated from all LCW and STSW stations over all depths from 0 to 200 m. BD, below detection, limit of 0.04 μg chl a L⁻¹.
reached a maximum of 2.0 mL m$^{-3}$ at the shelf station 9 (Fig. 5A). There was a significantly greater settled volume of zooplankton in the LCW, which was also associated with greater concentrations of individual prey items compared with the STSW (the Mann–Whitney U-test, $P < 0.01$) (Fig. 5B–E, Table I). The greatest zooplankton settled volume, in both LCW and STSW, was consistently associated with the 0–50 m depth stratum (the Mann–Whitney U-test, $P < 0.05$) (Fig. 6A, Table I).

Excluding copepods (which were not enumerated), chaetognaths were the most abundant potential prey item recorded in the study area and higher numbers were always found in the 0–100 m depth stratum (Fig. 6B); overall mean concentrations were 1.6–64.6 individuals m$^{-3}$ in the LCW and 0.1–19.8 individuals m$^{-3}$ in the STSW (Table I, Fig. 5B). Mean concentrations of 6.81 and 2.61 krill m$^{-3}$, 5.34 and 1.44 salps m$^{-3}$ and 3.91 and 1.22 siphonophores m$^{-3}$ were recorded in the LCW and STSW, respectively (Table I, Fig. 5C–E). Again, the highest concentrations of these potential prey items were associated with the 0–100 m depth stratum (Fig. 6C–E). The other zooplankton (fish larvae, squid larvae, medusae and heteropods) were recorded at much lower concentrations (Table I).

Both *Panulirus* and *Scyllarus* spp. phyllosoma larvae were collected during the voyage. However, only 7 out of the 30 EZ net hauls were successful in collecting *P. cygnus* phyllosoma, with larvae mainly found in the upper 100 m (Fig. 7). The coarser mesh, surface net, which was primarily used at night to catch animals for experiments, was more efficient in collecting *P. cygnus* phyllosoma (with net hauls at 35 out of 49 stations containing phyllosoma) (Fig. 7). The highest concentration of *P. cygnus* phyllosoma from the surface hauls (208 per 1000 m$^3$) was found at 30.7°S, 113.5°E, in a tow made at 02:16 on the 7th of July 2010 (WAST) [18:16 on the 6th of July (UTC)] in the eastward flow south of the front (Figs 2A and 7). Continuous underway measurements of SST and salinity were analysed in combination with *P. cygnus* phyllosoma concentrations and showed that this large aggregation
Fig. 5. (A) Mean zooplankton settled volume (mL m$^{-3}$), (B) mean concentrations of chaetognaths, (C) krill, (D) salps, (E) siphonophores per m$^3$ and (F) chl a (µg L$^{-1}$), in the upper 200 m (upper 100 m for chl a), across the south-eastern Indian Ocean study area.
was in STSW (water temperature 19.5°C and salinity 35.7 psu; Fig. 8).

Interactions between bio-physical parameters and zooplankton distribution in the south-eastern Indian Ocean

The first principal component (PC1) explained 44% of the variation in the abiotic and biotic data set, whereas the second component explained 14% of the variation (Fig. 9A). The main contributing variables (variables with loadings >0.5 and <−0.5) for PC1 included negative loadings for sigmaT, % light transmission, phosphate, nitrate and DO, and positive loadings for temperature, silicate and all biotic variables, including ammonium, chl a, zooplankton settled volume, fish larvae, chaetognaths, krill, salps, siphonophores and medusa (Fig. 9A).

The plot of the PC1 and PC2 scores for each station and depth stratum (Fig. 9B) separated out the two water masses (LCW and STSW), with all the LCW stations having positive PC1 loadings, except station 10, which was influenced by a cyclonic CC eddy. However, there was some evidence of mixing between the water masses as a few STSW designated stations had positive PC1 loadings (Fig. 9B). These stations included station 22 (0–50 m) on the 29°S transect which was influenced by the large LC meander; several stations along the 31°S transect, including 32 (0–50 m) and 33 (0–50 m) which were near the shelf edge in LC flow and both station 35 (0–50 and 50–100 m) and 36 (0–50 and 50–100 m) which were influenced by an anticyclonic WC eddy (Figs 2C and 4). A few stations along the 32°S transect also indicated mixing between the water masses, including 43 (0–50 m) where the surface layer appeared to still be in LC flow,

Fig. 6. Contrasting vertical distributions (50 m depth strata) along transect 29°S (grey dots) and 30°S (black dots) for (A) zooplankton settled volumes and (B) concentrations of chaetognaths, (C) krill, (D) salps, (E) siphonophores per m³ and (F) chl a (μg L⁻¹).
and stations 46 (0–50 and 50–100 m) and 47 (0–50 and 50–100 m) which were within an anticyclonic WC eddy (Figs 2C and 4).

The PC score plot showed clustering of shelf-edge LCW stations 8, 9 and 30 which had high zooplankton settled volumes, concentrations of chaetognaths, krill, salps, siphonophores, medusae and chl a (Fig. 9B). Two STSW stations (36 and 46) that were influenced by anticyclonic WC eddies had relatively high zooplankton settled volumes, concentrations of medusae, salps, siphonophores, krill chaetognaths and chl a (Figs 3 and 9B). Three STSW stations (22, 35, 47) were associated with relatively high water temperature and silicate and at two of these stations (35, 47) we also caught P. cygnus phyllosoma (Fig. 7). The highest water temperature was recorded at the most offshore LCW station (12) on latitude 28°S (Fig. 9C), while the lowest water temperature on this latitude was associated with a CC eddy at station 10 (Figs 4 and 9B).

DISCUSSION

Bio-physical parameters of the south-eastern Indian Ocean

The Leeuwin Current was a pervasive feature of the study area exhibiting a large meander in the north which returned eastward towards the coast before resuming its normal southward trajectory along the shelf edge. T-S
profiles confirmed two water masses; (i) LCW with warm, lower salinity tropical water and (ii) STSW with cooler and higher salinity water than the LCW. These two water masses were located on either side of a long-lived front (steep gradient in SST, chl \( a \) concentrations and zooplankton settled volume) situated around 30°S, which was persistent throughout the entire voyage. Furthermore, this front was characterized by a strong eastward surface current.

Previous studies have suggested that eastward surface currents, which commonly occur during the austral winter, provide an important mechanism for bringing late stage phyllosoma back to their natal waters along the WA coast (Griffin et al., 2001; Feng et al., 2011). In addition, the frequent occurrence of meanders and eddies in the waters off WA during the autumn-winter period also introduces randomness and patchiness into the distribution of \( P. cygnus \) phyllosoma (Griffin et al., 2001) and, thus, potentially their prey field as well.

Meso-scale eddies are common in the global ocean and the Leeuwin Current system has the highest surface kinetic energy of any mid-latitude eastern boundary current generating many meanders and eddies (Feng et al., 2005; Paterson et al., 2008). It has been estimated that up to 50% of the global new primary production may be due to eddy-induced nutrient fluxes (Falkowski et al., 1991). Recent investigations have shown that eddies are also hotspots of prokaryotic activities with warm core eddies being particularly active (Baltar et al., 2010). Eddies found off the coast of WA are thought to play an essential role in nutrient transport and productivity enhancement (Feng et al., 2007; Waite et al., 2007). Our study corroborates the importance of meso-scale features of the LC as the large meander along 29°S and eddies generated off the seaward edge of the south flowing LC were associated with elevated chl \( a \) and zooplankton concentrations.

**Bio-physical drivers of \( P. cygnus \) phyllosoma and their prey field in the south-eastern Indian Ocean**

During our voyage, we found that the distribution of \( P. cygnus \) phyllosoma was extremely patchy, which is consistent with earlier reports and results of rock lobster larval dispersal models (Phillips et al., 1978, 1979; Griffin et al., 2001). Overall, \( P. cygnus \) phyllosoma were more frequently encountered south of the prominent front at \( \sim 30° \)S and the highest concentration patch was sampled with the surface net at night between transects 30°S and 31°S. These stations were just south of the large LC meander and were located in a strong eastward surface current but had relatively low water temperatures (<20°C), zooplankton settled volume and chl \( a \) concentrations.

Immediately north or eastward of this front, the LC dominated water mass represented a significantly greater supply of prey for the phyllosoma. We suggest that the eddy field west of the LC provides particularly important oceanographic features for phyllosoma health as eddies can create hotspots of productivity thus structuring the available prey field for the phyllosoma. Based on our observations, the front between the LCW and STSW water is likely to be important in mediating eastward larval transport towards the shelf break. However, to cross the shelf, non-feeding pueruli must have built up substantial lipid stores. Thus, the health and concentration of prey in the STSW water mass and associated eddies are key factors for the accumulation of lipid reserves in \( P. cygnus \) larvae.

Zooplankton concentrations were generally similar to previously reported values for various taxa from the region (Tranter and Kerr, 1969, 1977; Muhling et al., 2007, 2008; Strzelecki et al., 2007; Gaughan et al., 2009; Holliday et al., 2012). In general, LCW was two to five times richer in zooplankton than STSW. Patches of higher zooplankton concentration, in both the LCW and the STSW, were often associated with higher chl \( a \) concentrations, making chlorophyll \( a \) a good tracer for prey-rich waters. In the LCW, greater zooplankton concentrations were associated with greater concentrations of both DO and ammonium, indicating that both photosynthesis and grazing were likely to have been locally high (Caron and Goldman, 1990). The shelf-edge stations in the LCW were particularly productive, having greater prey concentrations and more chl \( a \). This is consistent with the enhanced production noted in LCW during the autumn/winter bloom period and suggests that the LCW encourages productivity (Koslow et al., 2008; Thompson et al., 2011; Lourey et al., 2013).

The greatest abundances of \( P. cygnus \) phyllosoma were associated with the STSW mass. This was somewhat surprising as the optimal temperature for \( P. cygnus \) phyllosoma growth has been suggested to be 22–23°C, which is closer to that of LCW (Liddy et al., 2004). Why would \( P. cygnus \) phyllosoma occupy STSW if productivity is substantially lower than in LCW? Avoiding transport of phyllosoma away from the south-eastern Indian Ocean by the Leeuwin Current would be a likely explanation as could avoidance of predation by animals such as juvenile blue-fin tuna which migrate south along the West Australian shelf (Itoh et al., 2011). The latter possible explanation might invoke the ‘predator pit’ hypothesis (Bakun, 2006) where slower growth of larvae in less productive waters may be offset by much lower mortality from predation.

In both water masses, the preferred prey of phyllosoma, the chaetognaths (Saunders et al., 2012),
dominated the large (>200 µm) zooplankton prey field, with concentrations four times greater in the LC than STSW. Chaetognaths are highly abundant in all oceans and are strictly carnivorous (Feigenbaum and Maris, 1984), feeding primarily on copepods (Pearre, 1980). Previous studies off the Western Australian coast have indicated a dominance of siphonophores and chaetognaths among the carnivorous zooplankton, with higher species richness in winter compared with the summer, and chaetognaths more abundant than siphonophores (Gaughan and Fletcher, 1997; Gaughan et al., 2009).

Several studies have indicated that spiny lobster phyllosoma larvae have a preference for soft-bodied prey (Mitchell, 1971; Kittaka, 1994; Macmillan et al., 1997; Johnston and Ritar, 2001; Cox and Johnston, 2003a, b). However, recent studies of the DNA in the guts of some P. cygnus phyllosoma collected during this voyage revealed impoverished gut contents suggesting possible starvation (O’Rorke et al., 2012). Where prey was observed, the gut contents primarily contained taxa from transparent gelatinous zooplankton, including colonial radiolarians, chaetognaths, salps and siphonophores (O’Rorke et al., 2012), suggesting that the P. cygnus phyllosoma, despite their clear preference for chaetognaths, remain generalist and opportunistic feeders.

Opportunistic feeding behaviour would allow the P. cygnus phyllosoma to maximize the sparse and rapidly changing prey landscape in the oligotrophic waters off WA. In addition, by feeding on transparent prey such as chaetognaths, they would minimize the chance of being detected by potential predators while feeding. Krill, another relatively abundant prey item, contains the distinct red colour (astaxanthin) and consumption of this prey could make the transparent phyllosoma larvae more conspicuous and thus more vulnerable to predation (Pearre, 2003).

In conclusion, we have shown that the south-eastern Indian Ocean waters off the WA coast can basically be characterized into two water masses using a range of data including zooplankton, physical and chemical oceanographic observations. During July 2010, P. cygnus phyllosoma were most abundant near 30°S and between 113°E and 114°E. Mid-to-late stage P. cygnus phyllosoma appeared to rely on a patchy prey field, dominated by chaetognaths, which was closely linked to greater chl a concentrations. Our findings suggest that phyllosoma condition (and ultimately puerulus condition) is likely to be controlled by the availability and density of prey in the STSW which is largely disconnected from the direct biological influence of the LC. Nevertheless, the LC plays a direct physical role in forming long-lived fronts (potentially important in shoreward larval transport), and an indirect biophysical role by triggering/limiting eddy generation at the shelf break. As these offshore eddies influence productivity (Waite et al., 2007), closer examination of these meso-scale features relative to phyllosoma condition warrants investigation.

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