



## Mesoscale distribution of larval *Euphausia similis* in various water masses of the East Australian Current

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### ARTICLE INFO

#### Article history:

Received 21 August 2009

Received in revised form

3 June 2010

Accepted 7 June 2010

Available online 20 June 2010

#### Keywords:

*Euphausia similis*

Larvae

Krill predation

Cold core eddy

Top-down control

Diel-vertical migration

East Australian Current

### ABSTRACT

Larval *Euphausia similis* were collected off temperate eastern Australia in spring 2004 and 2006 to evaluate the relationships between larval populations, mesoscale oceanographic variability, and the wider planktonic community. Larval *E. similis* were present in greater numbers in the East Australian Current (EAC) relative to productive coastal waters. Larval *E. similis* density was homogenous across the EAC–Tasman Sea frontal region, but larvae were smaller in the Tasman Sea. Larval *E. similis* density was not enhanced within a cold core eddy relative to the surrounding EAC. We observed a negative correlation between larval *E. similis* density and larval fish density, and a weak positive correlation with fluorescence. Evaluation of a significant fish density  $\times$  fluorescence interaction term showed that the effect of fish density was reduced at high fluorescence values. Analysis of normalized biomass size spectrum (NBSS) provided evidence for potential competitive exclusion of copepods by krill. Data presented in this study suggest a predatory influence on surface *E. similis* populations by mesopelagic larval fish. The degree of predation appears to be dependent on food availability, potentially mediated by changes in the physiological condition of krill.

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### 1. Introduction

Euphausiids represent a key trophic component of oceanographic ecosystems, with biomass second only to copepods in some systems (Pakhomov, 2004). Euphausiids provide a direct link between photosynthetic food webs and large, long lived biogenic stores at higher trophic levels (e.g. whales, Pakhomov, 2004; de Guevara et al., 2008). The importance of euphausiids in coastal and oceanographic ecosystems is also evident in the relationships between temporal and spatial variability in euphausiid production and catches of commercial fish. These relationships can be positive, where euphausiids act as an important food source for adult fish (Young and Davis, 1992; Gomez, 1995); or negative, where euphausiids act as a predator of fish eggs and larvae (Bailey et al., 1993).

*Euphausia similis* is a widely distributed oceanic euphausiid common to the southern ocean, the western Pacific between 25°S and 55°S, and the Kuroshio Current (RAMS, 2009). *E. similis* is a major component of zooplankton communities off Australia (Sheard, 1965; Williams et al., 2001), and a dominant species of

the zooplankton community in the Subtropical Convergence Zone (Pakhomov et al., 1994). In Sagami Bay, Japan, *E. similis* comprises over half the total euphausiid biomass (Hirota et al., 1990), and species biomass increases in spring and summer to an average daily production of 1.33 mg C m<sup>-2</sup> (Hirota et al., 1990). In Australia, *E. similis* is one of the most abundant euphausiid species in the northern Tasman Sea (Griffiths, 1979). The species is identified as an important (> 50%) component in the diets of fish such as myctophids (Williams et al., 2001), skipjack tuna *Katsuwonus pelamis* (Ankenbrandt, 1985), hairtail *Trichiurus lepturus* (Martins et al., 2005), and rough scad *Trachurus lathami* (Katsuragawa and Ekau, 2003). Existing information suggest that *E. similis* originate in subtropical latitudes and are transported to higher latitudes by ocean currents (Bartel, 1976; Hirota et al., 1984), however there are no detailed studies on this species within western boundary currents in the south Pacific basin.

The broad objective of this study was to investigate *E. similis* off the east coast of mainland Australia, with special reference to the East Australian Current (EAC, the western boundary current of the Southern Pacific Gyre) and associated mesoscale variability. Spatial patterns in euphausiid distribution have rarely been interpreted in the context of mesoscale hydrographic features such as eddies (Bernard et al., 2007). Only limited distributional information exists for *E. similis* in the southern Pacific Ocean, and population differences have not been compared amongst the oceanographic features of the EAC. Climate change scenarios

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consistently indicate acceleration of the EAC (which warms at  $>2\text{ }^{\circ}\text{C century}^{-1}$ , Ridgway, 2007), further warming and greater mesoscale variability (eddies) in the Tasman Sea. These changes have consequences for primary productivity of coastal waters, carbon fluxes through benthic and pelagic trophic food webs, and the economies of coastal communities.

This study aimed to: (1) compare density and size of larval *E. similis* between EAC and coastal water, across the Tasman Front, and across a cold core eddy and (2) evaluate the biological processes contributing to larval *E. similis* density. Zooplankton may be monitored in real time with automated devices such as an optical plankton counter—a device which counts and sizes planktonic particles (Herman and Harvey, 2006). The slope and intercept of the resulting biomass size distributions (or “biomass size spectrum”) indicate the relative production, and provide evidence for top-down versus bottom-up processes in the zooplankton community (Suthers et al., 2006; Baird et al., 2008). The normalized biomass size spectrum (NBSS, Platt and Denman, 1977) regression, however, may be influenced by larval krill. We aimed to investigate this trend by simultaneously using a fine mesh net for smaller zooplankton and a larger pelagic trawl to sample larval krill, giving rise to aim (3) Examine the relationship between larval *E. similis* and total zooplankton biomass, as determined from the biomass size spectrum (Zhou, 2006) measured with an optical plankton counter (OPC).

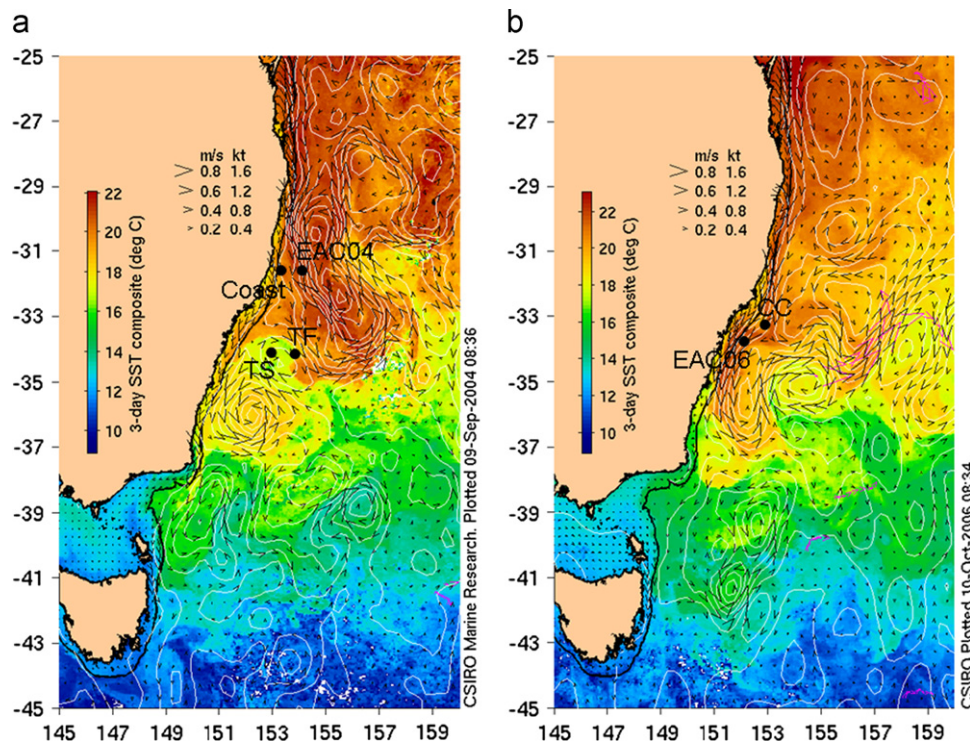
## 2. Methods

### 2.1. Study area and sampling design

The Eastern Australian Current (EAC) is a strong poleward flowing current that extends from the Coral Sea into Tasmanian waters (Mata et al., 2006). The EAC sporadically stimulates

upwelling and phytoplankton blooms through entrainment of nutrient rich coastal water or upwelling of cool bottom water (Oke and Middleton, 2001; Mata et al., 2006). The Current generally transports phytoplankton, zooplankton and fish larvae southward, with the age of planktonic communities increasing with latitude (Keane and Neira, 2008). The EAC dominates the oceanography of eastern Australia, and generates several distinct water bodies, including (1) a coastal water mass entrained on the continental shelf; (2) the Tasman Front region at  $\sim 34^{\circ}\text{S}$ , where the EAC interfaces with the northward flowing Tasman Current (Hamilton, 2006); and (3) cyclonic (cold-core) and anti-cyclonic eddies (Ridgway and Dunn, 2003).

Sampling was undertaken during research voyages onboard the RV *Southern Surveyor* during the austral spring in 2004 (2–12 September 2004) and 2006 (20 September–10 October 2006). In 2004, the EAC separated from the NSW coast at approximately  $31^{\circ}\text{S}$  and meandered southeast between  $32^{\circ}\text{S}$  and  $34^{\circ}\text{S}$  (Fig. 1a). At  $34^{\circ}\text{S}$  the EAC headed east towards New Zealand, forming the Tasman Front between the EAC (to the north) and the Tasman Sea (to the south). In 2006, the EAC separated from the NSW coast at approximately  $31^{\circ}\text{S}$  and flowed due south, diverging at  $33.5^{\circ}\text{S}$  to flow towards New Zealand (outer EAC), or towards the coast. The coastal component flowed parallel to the coast between  $33.5^{\circ}\text{S}$  and  $35^{\circ}\text{S}$  (inner EAC), with a cold core eddy forming between the EAC and the coast at approximately  $33.2^{\circ}\text{S}$  and  $152.6^{\circ}\text{E}$  (Fig. 1b). Sampling was undertaken in several regions (Table 1). In 2004 the Tasman Front (TF), the Tasman Sea (TS, south of the Tasman Front), the EAC (EAC04, north of the Tasman Front), and the coastal region north of the EAC04 (Coast) were sampled. In 2006, a small, cold core eddy system (CC) was sampled opportunistically, and compared with adjacent water in the EAC (EAC06). Currents and water masses at each tow location were identified by the vessel's underway thermosalinograph, fluorometer and acoustic Doppler current profiler (ADCP), and with daily updates of MODIS



**Fig. 1.** Oceanographic properties at the time of sampling in 2004 (a) and 2006 (b), showing the general circulation and mesoscale variability of the EAC. Data are averaged over a 6–9 d period. Images show sampling sites (Table 1) including coastal water (Coast), EAC in 2004 (EAC04), Tasman Front (TF), Tasman Sea (TS), EAC in 2006 (EAC06) and the cold core eddy (CC). The figure indicates sea surface temperature (SST, surface color), geostrophic velocity (black arrows) and sea level (white contours) (Image obtained from <http://www.marine.csiro.au/remotesensing/oceancurrents/SE>).

**Table 1**  
Sampling site locations and details, showing surface measurements of oceanographic parameters obtained from underway thermosalinograph and fluorometer. The dominant fish species captured, and fish density (# 1000 m<sup>-3</sup>) and richness are also presented.

Location	Site	Location	Date	No. of tows	Temperature (°C) (mean ± SE)	Salinity (mean ± SE)	Fluorescence (mean ± SE)	Dominant tax <sup>a</sup>	Density (D) and species richness (R) (mean ± SE) <sup>a</sup>
Tasman Sea	TS	33.8°S 152.9°E	4 September 2004	8	16.94 ± 0.12	35.615 ± 0.003	0.048 ± 0.004	Myctophidae	D=97.0 ± 4.0 R=10.0 ± 0.8
Tasman Frontal Region	TF	33.6°S 152.9°E	4–5 September 2004	8	19.55 ± 0.04	35.594 ± 0.003	0.018 ± 0.002	Myctophidae Bothidae	D=729.8 ± 18.5 R=25.0 ± 0.9
East Australian Current	EAC04	29.6°S 153.7°E	8–10 September 2004	6	21.19 ± 0.07	35.612 ± 0.009	0.025 ± 0.005	Myctophidae Carangidae	D=555.3 ± 33.3 R=27.2 ± 2.7
Coastal	Coast	29.5°S 153.5°E	10–12 September 2004	9	19.60 ± 0.08	35.593 ± 0.003	0.047 ± 0.007	Clupeidae Carangidae	D=695.3 ± 10.5 R=30.9 ± 1.4
East Australian Current	EAC06	33.5°S 151.9°E	10 October 2006	5	20.08 ± 0.03	35.670 ± 0.006	0.119 ± 0.003	Myctophidae	D=232.3 ± 1.8 R=15.0 ± 0.4
Cold Core Eddy	CC	33.2°S 152.6°E	10–11 October 2006	6	19.00 ± 0.08	35.562 ± 0.002	0.120 ± 0.003	Myctophidae	D=129.8 ± 4.5 R=22.2 ± 1.4

<sup>a</sup> (From Mullaney et al., 2007).

sea surface temperature (SST) and chlorophyll images (<http://modis.gsfc.nasa.gov/>).

In 2004, krill were sampled with oblique, midwater tows conducted at each station at 1–3 m s<sup>-1</sup> for 13–15 min, using a square rectangular midwater trawl (RMT; 1 m<sup>2</sup> net, 1 mm mesh, 2-point bridle, 40 kg depressor). A profiling CTD was used at each site to determine the depth of the mixed layer, prior to deployment of the RMT. The net was towed from the bottom of the mixed layer (usually 50–60 m) to the surface to sample *E. similis* larvae, which are dominant in the top 50 m of the water column (Hirota et al., 1984). Similar tows were conducted in 2006 using a larger RMT (1.5 × 0.75 m<sup>2</sup> mouth opening, 1.125 m<sup>2</sup>, 300 kg lower bar, 1 mm mesh), however a corresponding CTD was not undertaken at each of these sites. All tows took place at night to nullify daytime stratification of the planktonic community and to reduce net avoidance (Gray, 1998; Gray and Kingsford, 2003). A 20 cm diameter, 100 μm mesh plankton net was mounted inside the RMT for all tows, to collect samples for later analysis of size spectra using the optical plankton counter. In addition, a Sonardyne transponder (to monitor real-time depth), General Oceanics flow meter (to calculate water volume), and Vemco TDR data logger (to record temperature and depth) were mounted inside the RMT. RMT and plankton net samples were preserved in a 5% formaldehyde and seawater solution buffered with NaCO<sub>3</sub>.

## 2.2. Sample analysis

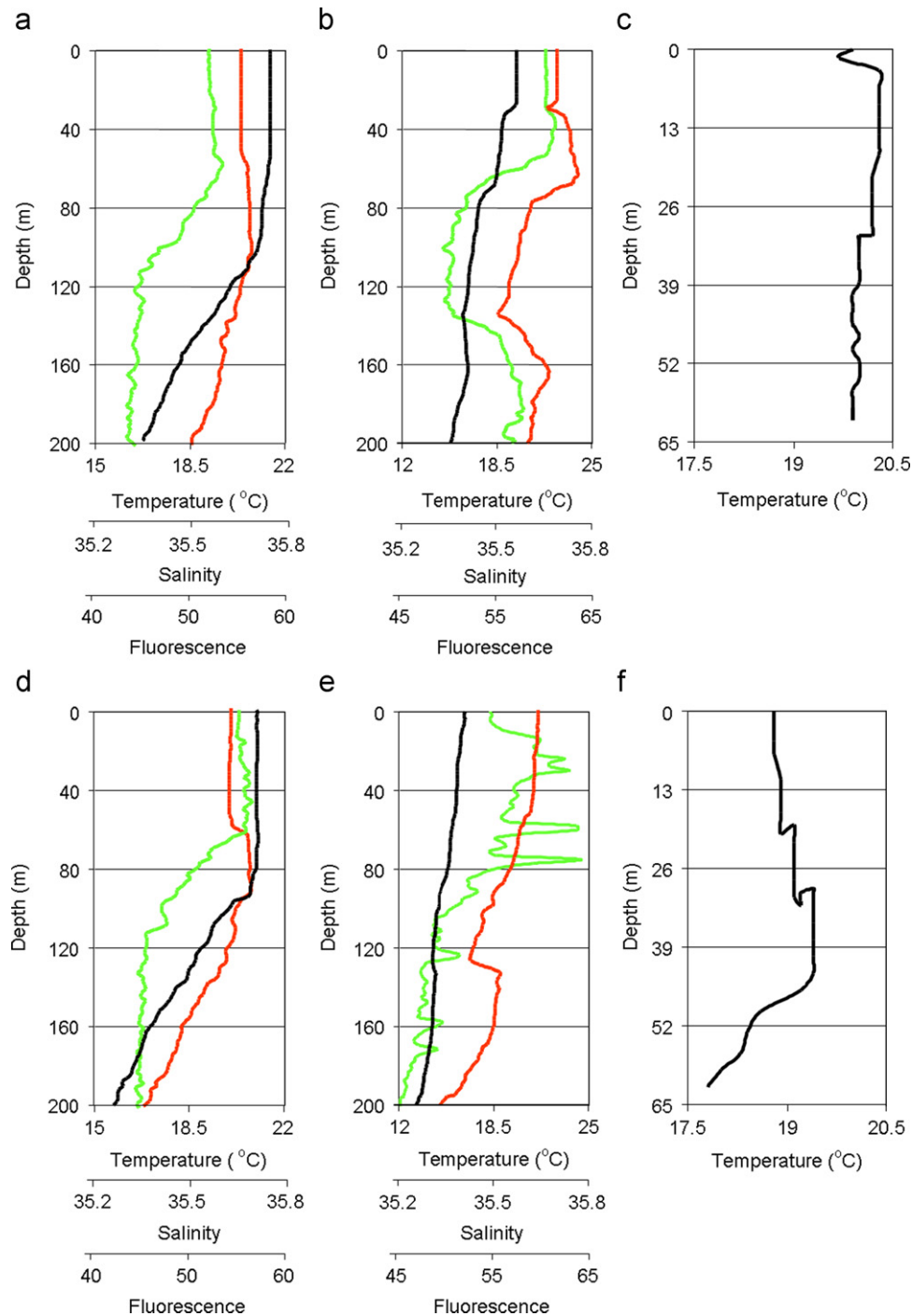
All euphausiids and fish were removed in the laboratory under low power using a dissecting microscope (Olympus SZH-ILLD) and stored in 95% ethanol. Furcilia stage *E. similis* larvae and any later stages (Hirota et al., 1984) were identified and sorted from euphausiid samples, and measured *en masse* using the method of Taylor (2008). Also, fish were identified to species using Neira et al. (1998), and counted. Euphausiids were spread evenly across a glass Petri dish containing a calibration bead, and photographed with a Kodak 5 megapixel digital camera. The size (lateral surface area) of each euphausiid was measured automatically using the count/size function in Image Pro Plus v 5 (Media Cybernetics, Silver Spring, Maryland, USA), and then manually checked for errors. The dry weight was calculated for each euphausiid using biomass–area relationships, developed as follows. Seventy-five *E. similis* were randomly sampled across different times, locations and sizes, and were photographed individually as described above. Images were measured for total length, and lateral surface area using Image Pro Plus v 5. Each euphausiid was air dried for 2 min to allow the ethanol to evaporate and wet weight was recorded. Samples were then lyophilized for 72 h, and reweighed (± 1 μg) using a Sartorius microbalance. Lateral surface area was then regressed against total length and individual biomass. Samples collected using the 100 μm mesh plankton net were analyzed using a Focal Technologies Model OPC-1L Optical Plankton Counter (a detailed description of OPC function, measurement and particle sizing calculations can be found in Zhang et al. (2000) and Moore and Suthers (2006)). Briefly, samples were filtered through 100 μm sieve to remove formalin, and measured by passing the entire sample through the OPC at a flow rate of 10 L min<sup>-1</sup>.

## 2.3. Statistical analysis

*E. similis* data were expressed in terms of density (*E. similis* 1000 m<sup>-3</sup>) and total length (TL, mm), by standardising measurements for the volume of water sampled in each tow and multiplying by 1000. Similarly, fish density was calculated for each taxa in the sample, and summed to estimate total fish

density in each tow. OPC data were processed as described in Suthers et al. (2006), using nominal bin sizes with Equivalent Spherical Diameters (ESD, Rissik and Suthers, 2000) of 531, 645, 761, 880, 1001, 1123, 1247, 1373, 1501, 1630, 1760, 1891, 2024, 2158, 2292, 2248, 2565, 2703, 2842, 2981, 3122  $\mu\text{m}$ . The normalized biomass ( $\beta$ ) of each individual size class is the total biomass ( $b$ ) of the size class divided by the width ( $w$ ) of the size class (Platt and Denman, 1977), and the slope is determined by  $NBS_{slope} = \partial \log_{10} \beta / \partial \log_{10} w$ , where  $\beta = bw$  for each size class. In other words, a normalized biomass has been adjusted by the

width of the selected size intervals (e.g. linear or logarithmic) so that the slope and intercept are independent of the size intervals. Separation of oceanographic features identified during sampling were tested using an analysis of similarities (ANOSIM; PRIMER, Plymouth, UK) on a Euclidian distance matrix of standardized oceanographic measurements, and inspected using a non-metric multidimensional scaling ordination (MDS; PRIMER, Plymouth, UK). For 2004 and 2006 samples, larval *E. similis* density and size were compared between water masses using single factor ANOVA. The relationship between larval and juvenile *E. similis* density in



**Fig. 2.** Vertical profiles showing oceanographic properties of water masses (Fig. 1) sampled during 2004 (CTD) and 2006 (Vemco TDR data logger), including EAC water sampled in 2004 (EAC04, a), coastal water (Coast, d), Tasman Front (TF, b), Tasman Sea (TS, e), EAC in 2006 (EAC06, c) and the cold core eddy (CC, f). Temperature (black line), salinity (red line) and fluorescence (green line) are shown to 200 m for water masses sampled in 2004, and temperature only is shown to 63 m for water masses sampled in 2006. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

both 2004 and 2006 was evaluated using a linear regression of density data for tows in which both larvae and juveniles were captured. The potential biological processes affecting larval *E. similis* density in 2004 were evaluated using multiple linear regression. The model tested the effects of standardized values of fish density, fluorescence, temperature, and a fish density  $\times$  fluorescence interaction term on larval *E. similis* density, with the best model selected using Akaike's Information Criteria (Bozdogan, 1987). The relationship between larval *E. similis* biovolume and the NBSS in 2004 was evaluated by fitting a linear regression for each site using the mean normalized biovolume for each size class. For each site, the residuals for each size class were determined for all size classes greater than an ESD of 1630  $\mu\text{m}$  (which corresponds to the smallest furcilia larvae detected in the samples), and evaluated in terms of the larval *E. similis* normalized biovolume for each size class-site combination using a linear regression model. All ANOVA and regression analyses were undertaken in R (Ihaka and Gentleman, 1996).

### 3. Results

#### 3.1. Mesoscale oceanography and larval *E. similis*

Vertical CTD profiles indicated that EAC water sampled in 2004 (EAC04, Fig. 2a) was characterised by a mixed layer of  $\sim 55$  m depth, and a major thermocline was present at 100 m depth. Temperatures were warmer at EAC04 than in adjacent coastal water (Coast, Fig. 2d), which was characterised by a similar mixed-layer depth to EAC04, but had greater fluorescence and slightly lower salinity. At the time of sampling, water at both EAC04 and Coast sites was moving southward at  $\sim 0.8$  and  $0.3$   $\text{m s}^{-1}$ , respectively. The water masses across the Tasman Front and Tasman Sea were well defined in 2004. The Tasman Front water mass was moving southeast at  $\sim 0.5$   $\text{m s}^{-1}$  whilst the adjacent Tasman Sea water mass formed a cyclonic eddy, with a velocity of  $\sim 0.3$   $\text{m s}^{-1}$  in the region where samples were collected. The Tasman Front had a mixed layer of 60 m (TF, Fig. 2b), however the mixed layer in the Tasman Sea was poorly defined and estimated to be  $\sim 50$  m deep (TS, Fig. 2e). The Tasman Front was warmer and had higher salinity than the Tasman Sea across the 200 m profile. The Tasman Sea also showed greater fluorescence, but there was much greater variability in fluorescence within the top 80 m. The East Australian Current was much weaker and cooler in 2006 than 2004, but vertical temperature profiles did indicate differences between water masses sampled in 2006. The temperature within the EAC (EAC06, Fig. 2c) was warmer than in an adjacent cold core eddy (CC, Fig. 2f), and water was moving at 0.6 and  $0.3$   $\text{m s}^{-1}$ , respectively. The temperature profile for the cold core eddy showed much greater variability with depth, with cooler temperatures in the top 30 m, and a rapid decline in temperature at depths  $> 40$  m (Fig. 2f).

ANOSIM on temperature, salinity and fluorescence data collected using the underway thermosalinograph and fluorometer confirmed the differences between water masses described above. TF and TS ( $R=0.971$ ,  $P=0.001$ ), EAC04 and Coast ( $R=0.308$ ,  $P=0.009$ ), and EAC06 and CC ( $R=0.53$ ,  $P=0.002$ ) were significantly different, and the major differences between these water masses were evident in non-metric MDS ordination on oceanographic data, with tows grouped by site (Fig. 3a and b).

Overall  $\sim 41,000$  *E. similis* were captured from the 2004 and 2006 cruises. In 2004, there was a significantly greater square-root transformed density of larval *E. similis* present within the EAC site relative to adjacent coastal water ( $F_{1,14}=6.268$ ,  $P=0.026$ ; Fig. 4), however there was no significant difference in larval density across the Tasman frontal region ( $F_{1,15}=0.206$ ,  $P=0.657$ ; Fig. 4). In 2006, there were no significant differences in larval ( $F_{1,10}=0.553$ ,

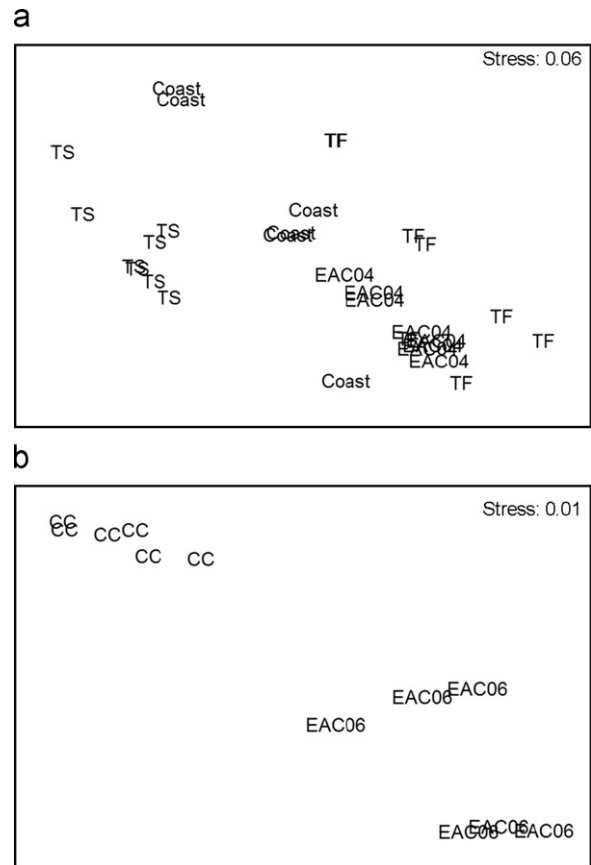


Fig. 3. Non-metric multidimensional scaling of standardized temperature, salinity and fluorescence measurements (Table 1) showing separation of RMT tows grouped as oceanographic features, for samples taken in 2004 (a) and 2006 (b).

$P=0.476$ ) density between the cold-core eddy or adjacent EAC waters (Fig. 4). Size distributions were relatively stable between oceanographic water bodies (Fig. 4), with the exception of a larger total length of larval *E. similis* within Tasman Front waters relative to the Tasman Sea ( $F_{1,15}=39.383$ ,  $P\ll 0.001$ ). There were no differences in larval *E. similis* total length between coastal and EAC water in 2004 ( $F_{1,14}=1.066$ ,  $P=0.321$ ), or between the cold-core eddy and EAC water in 2006 ( $F_{1,10}=2.637$ ,  $P=0.139$ ). Juvenile *E. similis* were present at densities  $\sim 100$  times lower than larval *E. similis*, and there was no significant relationship between the density of larval and juvenile *E. similis* (Fig. 5,  $b=-0.001$ ,  $t=0.152$ ,  $P=0.881$ ). There were negligible numbers of adult *E. similis* captured in the study.

#### 3.2. Biological processes controlling larval *E. similis* density

Fish density ranged between 97 and 730 fish per 1000  $\text{m}^3$ . Fish populations were dominated by members of Family Myctophidae ( $> 50\%$  of larval fish community), with the exception of coastal water which was dominated by Clupeidae (Table 1). Fish communities were diverse, with richness ranging from 10 to 31 (Table 1). Regression diagnostics indicated the absence of collinearity for standardized larval fish density (Tolerance=0.590), fluorescence (Tolerance=0.703), temperature (Tolerance=0.758) and the larval fish density  $\times$  fluorescence interaction (Tolerance=0.689). Inclusion of the larval fish density  $\times$  fluorescence interaction term improved  $R^2$  by 0.17 over a model of main effects only. Stepwise multiple regression produced a significant model (Adjusted  $R^2=0.505$ ,  $F_{3,38}=14.950$ ,  $P\ll 0.001$ ) between larval *E. similis* density and larval fish density (Fig. 6,  $b=-0.271$ ,  $t=-3.977$ ,  $P\ll 0.001$ ),

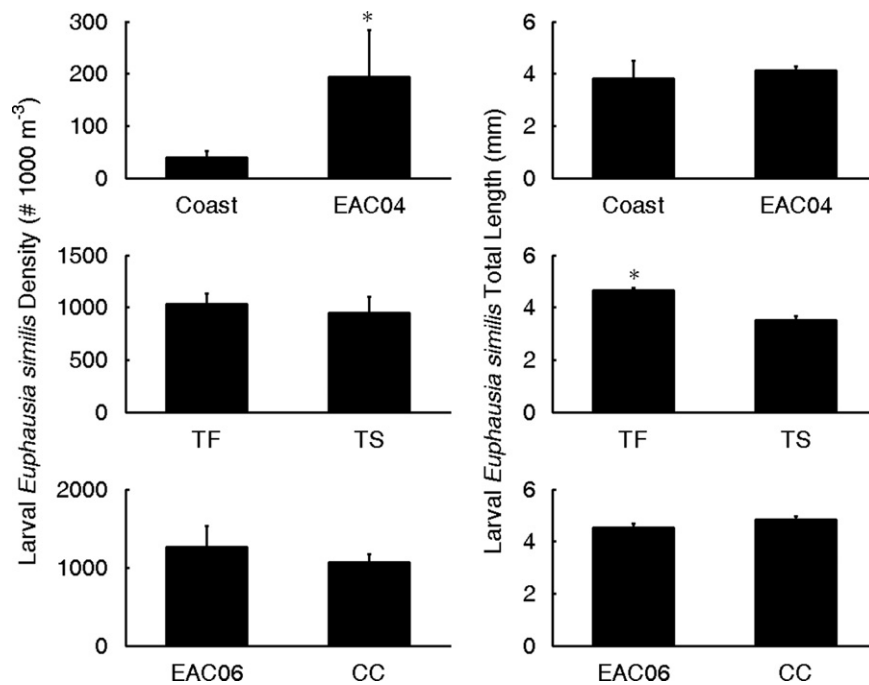


Fig. 4. Mean  $\pm$  SE density and total length of larval *Euphausia similis* at sites sampled in 2004 and 2006. Sites labels correspond to those listed in Table 1 (\*denotes significant difference at  $P < 0.05$ ).

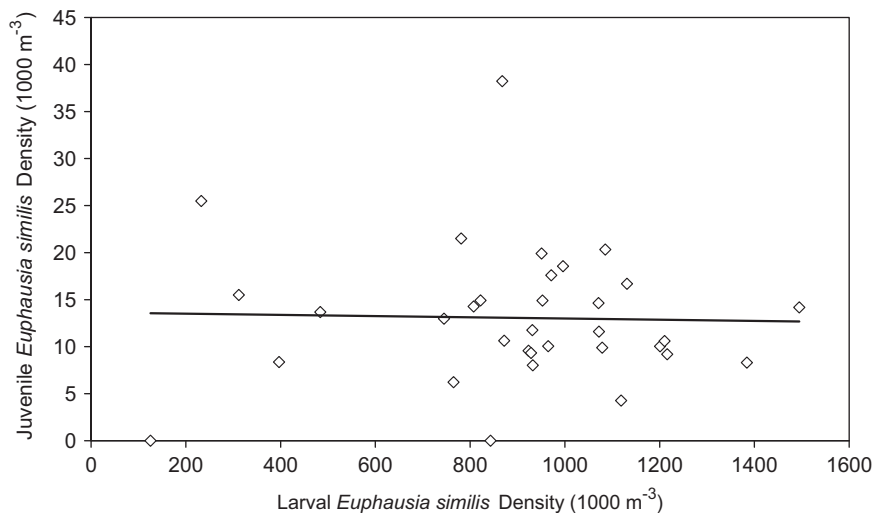


Fig. 5. Paired larval and juvenile *Euphausia similis* densities for tows undertaken in 2004 and 2006 in which both larvae and juveniles were captured, showing no relationship between larval and juvenile densities.

fluorescence ( $b=0.117$ ,  $t=1.870$ ,  $P=0.069$ ), and fish density  $\times$  fluorescence ( $b=-0.237$ ,  $t=-3.753$ ,  $P \ll 0.001$ ). The significant interaction term was evaluated through analysis of simple slopes (Quinn and Keough, 2002), which indicated that the effect of fish density was more pronounced for low fluorescence values ( $b=-0.580$ ,  $t=-4.384$ ,  $P \ll 0.001$ ), whereas the effect of fish density was weak and not significantly different from 0 for high fluorescence values ( $b=0.037$ ,  $t=0.532$ ,  $P=0.611$ ).

### 3.3. Larval *E. similis* and the normalized biomass size spectrum (NBSS)

The overall average NBSS for 2004 had a slope of  $-0.99$  (Fig. 7a,  $R^2=0.960$ ). Fig. 7b shows the relationship between the normalized biovolume of larval *E. similis*, and the residuals from

each site's normalized zooplankton biomass measurements from the fitted NBSS model. The relationship indicates that larval *E. similis* biovolume had a significant influence on the residual ( $b=-0.203$ ;  $t=-5.037$ ,  $P < 0.001$ ), which means that greater krill biomass is present when there is a lower total biomass of similar sized zooplankton than expected from a linear NBSS model ( $R^2=0.218$ ,  $F_{1,92}=25.373$ ,  $P < 0.001$ ).

## 4. Discussion

### 4.1. Mesoscale oceanography and larval *E. similis*

*E. similis* dominated the euphausiids in all tows, with other species (*Nyctiphanes australis*, *Nematobrachion* sp.) limited to the occasional presence of only a few individuals. Sampling occurred

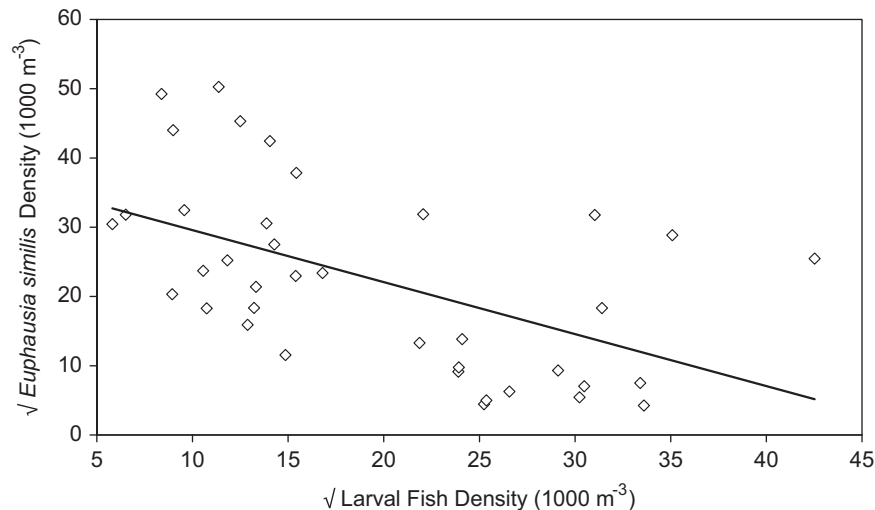


Fig. 6. Negative relationship between fish density and larval *Euphausia similis* density in samples collected in the EAC in 2004.

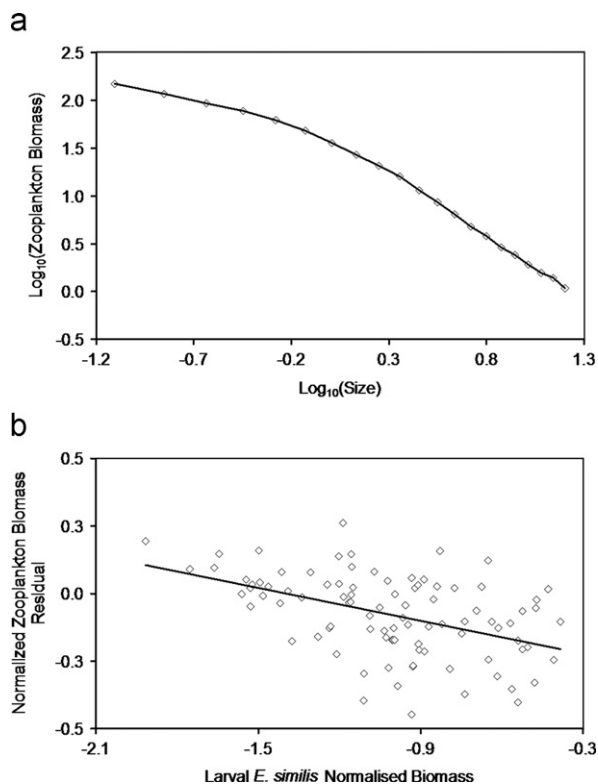


Fig. 7. Overall normalized biomass size spectrum (NBSS; a) for 2004 samples, and the relationship between the 2004  $\log_{10}$  normalized larval *Euphausia similis* biomass, and the site-specific residuals from the normalized biomass size spectrum (NBSS) linear model, for corresponding size classes (b).

in spring in both 2004 and 2006, which coincides with seasonal peaks in *E. similis* biomass (Hirota et al., 1990), and the density of *E. similis* larvae detected in this study was similar to that detected previously in the northern hemisphere (Hirota et al., 1984). Larval *E. similis* formed a relatively uniform distribution across the oceanographic features examined, with the exception of the Coast—EAC comparison in 2004 where EAC waters contained a larval density approximately four-fold higher than adjacent coastal water. The low density of *E. similis* larvae in coastal waters may be explained by two factors. Firstly, mesoscale oceanographic variability may restrict transport of *E. similis* larvae

to this location, as the species is spawned in lower latitudes and transported southward in the EAC (Bartel, 1976; Hirota et al., 1984). Northward flowing coastal currents are frequently present south of the EAC separation point (Roughan and Middleton, 2004), which means organisms being transported southward in the EAC are unlikely to be represented at the coastal site sampled here. Secondly, *E. similis* is an oceanic euphausiid undergoing substantial diel-vertical migration up to 350 m depth (Hirota et al., 1990). Thus, the shallow bathymetry in coastal water may restrict *E. similis* distribution to off-shelf waters which allow diel-vertical migration (DVM). Larval *E. similis* are known to undergo strong DVM in the Kuroshio Current (Hirota et al., 1984), however there was no DVM detected for *E. similis* in the South Banda Sea (van Couwelaar, 1994). The South Banda Sea *E. similis* population had a mean depth of  $\sim 350$  m, which is below the maximum depth determined by Hirota et al. (1984). Further investigation of larval, juvenile and adult *E. similis* across a wider range of depths is required to further characterise diel-vertical migration of the species in general, and also specifically within water masses of the East Australian Current.

Euphausiid density and biomass is typically enhanced within cold-core eddies relative to surrounding water, through a combination of entrainment and production (e.g. Lavaniegos, 1995; Bernard et al., 2007), however our data failed to reflect this. MODIS images show the cold core eddy sampled in 2006 had only formed 5 days prior to sampling which may partially explain the lower density of *E. similis*, as other *Euphausia* spp. have not shown a density or biomass response in cold core eddies until  $> 30$  days after formation (e.g. Endo and Wiebe, 2007). Furthermore, high densities of fish within the cold core eddy may have had a negative impact on krill density, as predicted by our regression model.

The homogenous larval *E. similis* densities between the Tasman Front and Tasman Sea were surprising. The Tasman Front is characterised by substantial biological changes over a small spatial area, such as a four-fold increase in Chl-*a* (Baird et al., 2008). Larval *E. similis* were also larger in the Tasman Front which may be a temperature effect, or simply due to the sampling of different populations in the Tasman Sea and Tasman Front, which may be slightly different ages. In the Kuroshio frontal region, euphausiids dominate ( $> 50\%$ ) zooplankton in terms of both summer biomass and number, with up to  $\sim 70$   $\text{mg m}^{-3}$  wet weight in the frontal region relative to  $0.8$   $\text{mg m}^{-3}$  wet weight in the adjacent Kuroshio Current (Nishikawa et al., 1995).

Given these existing relationships and the steep biological gradients across the Tasman Sea and Tasman Front, changes in the density of *E. similis* in response to these gradients were expected, but a potential explanation of the observed result may be found in the biological processes that affect larval *E. similis* biomass, as discussed below.

#### 4.2. Biological processes controlling larval *E. similis* density

Multiple regression analysis indicated the density of larval krill is influenced primarily by larval fish density. *E. similis* larvae feed primarily on phytoplankton (Field et al., 2006), whereas the dominant members of the larval fish community captured (e.g. Myctophidae) are primarily zooplanktivorous (Williams et al., 2001) so competitive exclusion of larval *E. similis* by fish is unlikely. There are, however, many examples of predator–prey interrelationships between zooplanktivorous fishes and krill eggs and larvae (e.g. Hureau, 1994; Dalpadado and Skjoldal, 1996; Williams et al., 2001; Ushakov and Prozorkevich, 2002). Given these established links and the patterns observed here it is possible that larval *E. similis* density is influenced by predation by young fish, particularly as *E. similis* is a major prey of myctophid fishes, such as *Diaphus danae*, *Hygophum hanseni* and *Lampanyctus australis* (Williams et al., 2001). These are characteristically deep-water species (700–1500 m), but are known to migrate to surface waters to feed. This relationship not only provides evidence for coupling between mesopelagic and epipelagic food webs in the EAC, but also demonstrates the potential for mesopelagic fishes to regulate prey populations in surface waters.

The interactive effect of fish density and fluorescence is interesting in that it may reflect the role of changes in the physiological condition of larval krill. Unlike adult krill, larvae cannot endure long periods without feeding and rapidly decrease in condition without food (Quetin and Ross, 1991). The observed interaction may indicate increasing susceptibility to predation as a result of decreased condition (resulting from decreased food), as is often hypothesized for fish (e.g. Lochmann et al., 1995; Suthers, 1998). Conversely, the diminishing importance of fish density in driving *E. similis* density at high fluorescence values may reflect the effect of improved condition on predator avoidance. We are unable to verify if this is the case from our data, however simultaneous analysis of organism condition in future studies (e.g. RNA:DNA ratios, Caldarone et al., 2003) would address these hypotheses.

#### 4.3. Larval *E. similis* and the normalized biomass size spectrum

The normalized biomass size spectrum (NBSS) characterizes the interaction between size-dependent physiological rates, growth, mortality and trophic dynamics. The dome and trough-like features within the spectrum are the result of biological processes such as growth and predation (Zhou, 2006). Our study observed departures from a linear spectrum, and the magnitude of this deviation is negatively related to the biovolume of krill larvae within the corresponding size class. In other words, lower than expected biomass at larger zooplankton sizes (sampled by the 20 cm diameter net) was correlated with the larval krill biomass sampled by the RMT. The sampling regime used in our study could conceivably contribute to the observed relationship, but previous studies suggest that the approach used is not likely to have under-sampled larger organisms (> 900 µm ESD) in the size range analyzed relative to the OPC (Ruberg et al., 2000; Herman and Harvey, 2006). A possible explanation for the observed relationship between deviations from the expected zooplankton biovolume and krill biovolume, may lie in

competitive interactions between species occupying the same trophic niche (Fragopoulou and Lykakis, 1990; Gasser et al., 1998). Zooplankton size spectra in surface waters off eastern Australia are dominated by copepods (Rissik et al., 1997; Rissik and Suthers, 2000), and copepods have been shown to share trophic niches with larval *Euphausia* sp. in other systems (Graneli et al., 1993). Copepods often rely on high phytoplankton biomass whereas krill can rapidly remove these resources (Graneli et al., 1993; Atkinson et al., 1999), and these interactions may contribute to the relationship observed in this study. This is an important finding as it demonstrates a link between larval euphausiids and the normalized biomass size spectrum, where this interaction has previously been assumed to be negligible (e.g. Pollard et al., 2002).

## 5. Conclusions

This is the first oceanographic study of larval *E. similis* in Australian waters, and there are few comparative studies. Despite only sampling near-surface waters over two consecutive springs, we found several factors that are important in determining the distribution and biomass of larval *E. similis*. Within the constraints of the physical and topographical factors that limit the population distribution, the density of *E. similis* appears to be influenced by larval Myctophidae, which implies potential top-down pressure on larval *E. similis* populations by mesopelagic fishes. There is also evidence for competitive exclusion of copepods by krill, which has previously been observed in the Southern Ocean (Atkinson et al., 1999). The relationships presented here support the bifurcation of controlling mechanisms on euphausiid populations (Atkinson et al., 2008), as a dynamic combination of bottom-up and top-down processes. Future research should target oceanographic features of the EAC with vertically stratified sampling to 500 m, to capture all stages of *E. similis* and the wider euphausiid community.

## Acknowledgments

The authors wish to thank the captain and crew of the Southern Surveyor (especially L. Pender, M. Underwood, D. Mills) as well as A. Ferguson, E. Venstra, M. Baird, J. Everett, N. Johnstone, G. Nippard, P. Burns and T. Miskiewicz for assistance during the sampling or sample processing and discussion. Research was funded by ARC Discovery Project DP0209193. This manuscript is Sydney Institute of Marine Science contribution number 0021.

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