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Zooplankton trophic niches respond to different water types of the western Tasman Sea: A stable isotope analysis

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ABSTRACT

The trophic relationships of 21 species from an oceanic zooplankton community were studied using stable isotopes of carbon and nitrogen. Zooplankton and suspended particulate organic matter (POM) were sampled in three different water types in the western Tasman Sea: inner shelf (IS), a cold core eddy (CCE) and a warm core eddy (WCE). δ^{15}N values ranged from 3.9‰ for the parasitic copepod *Sapphirina augusta* to 10.2‰ for the euphausiid, *Euphausia spinifera*. δ^{13}C varied from −22.6 to −19.4‰ as a result of the copepod *Euchirella curticauda* and *E. spinifera*. The isotopic composition of POM varied significantly among water types; as did the trophic enrichment of zooplankton over POM, with the lowest enrichment in the recently upwelled IS water type (0.5‰) compared to the warm core eddy (1.6‰) and cold core eddy (2.7‰). The WCE was an oligotrophic environment and was associated with an increased trophic level for omnivorous zooplankton (copepods and euphausiids) to a similar level as carnivorous zooplankton (chaetognaths). Therefore carnivory in zooplankton can increase in response to lower abundance and reduced diversity in their phytoplankton and protozoan prey. Trophic niche width comparisons across three zooplankton species: the salp *Thalia democratica*, the copepod *Eucalanus elongatus* and the euphausiid *Thysanoessa gregaria*, indicated that both niche partitioning and competition can occur within the zooplankton community. We have shown that trophic relationships among the zooplankton are dynamic and respond to different water types. The changes to the zooplankton isotopic niche, however, were still highly variable as result of oceanographic variation within water types.

1. Introduction

Zooplankton are an essential component of marine food webs and changes in zooplankton assemblages can have cascading effects for the baitfish that feed on them (Johnson et al., 2011), through to top-predators (Frederiksen et al., 2006). Within the zooplankton food web are many diverse and interacting taxa (Thompson and Kesteven, 1942; Voronina, 1998) creating a challenge to understand their trophic relationships. Knowledge of the trophic niche of various zooplankton is necessary to evaluate their response to different oceanographic conditions, as zooplankton provide bottom-up regulation of marine food webs.

A species' trophic niche is the sum of all interactions that link it to other species within an ecosystem (Elton, 1927), representing both its habitat requirements and trophic position (Leibold, 1995). Stable isotope analysis is a common tool for characterizing the trophic niche, as it can identify trophic interactions (Peterson and Fry, 1987). The isotope ^{15}N can be used to estimate an organism's trophic position as stepwise enrichment between 1‰ and 5‰ (average 3.4‰) generally occurs between prey and predators (Minagawa and Wada, 1984; Post, 2002; Vander Zanden and Rasmussen, 1999). The isotope ^{13}C shows much lower trophic enrichment (average 0.4‰), and is used for identifying dietary sources (Post, 2002). Trophic niche width is often calculated using the variation in the isotopic signature of organisms (typically in δ^{13}C–δ^{15}N isotope space; Bearhop et al., 2004; Layman et al., 2007a). By comparing the trophic niche of an organism through time or during different oceanographic conditions, the changes in dietary behaviour can be identified (Layman et al., 2007b). A

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reduction in prey diversity, for example, can affect the consumer niche, which can manifest as either decreased trophic niche width (for grey snapper; Layman et al., 2007b) or increased carnivory (for copepods; Landry, 1981).

Suspended particulate organic matter (POM) is often used in stable isotope analysis as proxy for phytoplankton, and hence can be used as a baseline for marine food webs (Post, 2002). The $\delta^{13}C$ and $\delta^{15}N$ stable isotope signature of POM has been found to vary across water types in relation to different oceanographic conditions (Stowasser et al., 2012). Off southeast Australia, the western Tasman Sea has different water types including cyclonic cold core eddies (CCE), anti-cyclonic warm core (WCE) eddies (Nilsson and Cresswell, 1981) and nutrient-rich inner shelf (IS) waters (Henschke et al., 2011). CCEs may entrain IS water (Mullaney and Suthers, 2013), resulting in a 16% increase in chlorophyll *a* compared to surrounding waters (Everett et al., 2012). As well as enhanced primary production, coastal CCEs have been shown to promote zooplankton production (Kimura et al., 2000), and aid in the recruitment and survival of larval fish (Kasai et al., 2002). In comparison, WCEs have on average 28% less surface chlorophyll *a* compared to surrounding waters (Everett et al., 2012). As a result, the ecosystems that develop within a WCE are generally composed of smaller phytoplankton cells and lower zooplankton biomass (Waite et al., 2007b). Therefore, the different oceanographic conditions in IS, CCE and WCE water types should be reflected in the POM isotopic signature and subsequently the zooplankton isotopic signature.

The aim of this study was to quantify the zooplankton food web of the western Tasman Sea using stable isotope analysis. The trophic niche characteristics of zooplankton and their ^{15}N enrichment relative to POM were compared across three water types to determine the trophic outcomes of different oceanographic conditions. To investigate specific niche use, the trophic niches of three co-existing species were compared: the salp *Thalia democratica*, the copepod *Eucalanus elongatus* and the euphausiid *Thysanoessa gregaria*.

2. Methods

2.1. Field sampling

Zooplankton and phytoplankton samples were collected from a 2010 austral spring voyage (September–October) onboard the *RV Southern Surveyor* off south-eastern Australia in the Tasman Sea (Fig. 1). Sampling stations were chosen based on water type characteristics using daily Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery. The sampling area extended southward from Stockton Bight (32°43′S, 152°13′E) to Jervis Bay (35°03′S, 150°43′E). Three water types were sampled: inner shelf water (IS; $n=4$), a cold core eddy (CCE; $n=5$) and a warm core eddy (WCE). The WCE was sampled initially only for POM (WCEp; $n=4$) and then 10 days later was sampled for both POM and zooplankton (WCE; $n=4$) to compare changing POM communities.

At each sampling station, a Seabird SBE911-plus Conductivity-Temperature-Depth (CTD) probe equipped with a Chelsea Aqua-Tracker Mk3 fluorometer was used to profile salinity, temperature and fluorescence. Bulk POM samples for stable isotope analysis were collected from the surface and the chlorophyll *a* maximum. Between 2 and 6 L of seawater was filtered onto pre-combusted GF-F filter papers under low vacuum pressure (30–40 mm Hg). The POM samples were stored frozen (−20 °C) until later analysis.

Zooplankton collection was subsequently performed at each station. A Multiple Opening/Closing Net and Environmental

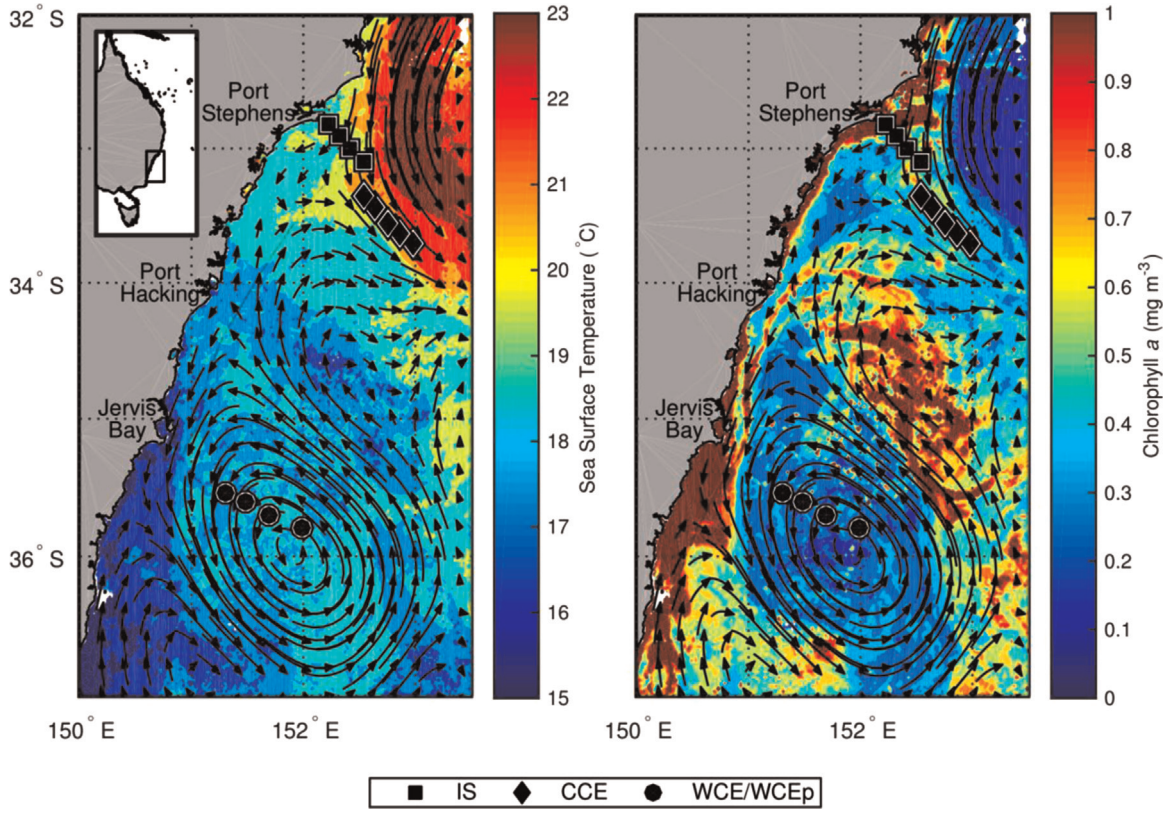

Fig. 1. Location plot with satellite-derived sea surface temperature (°C; left) and chlorophyll *a* (μg L^{-1}; right) overlaid which best represented conditions occurring during sampling (Table 1). Geostrophic currents are estimated through surface altimetry and are represented by arrows. Sampling locations in different water types are indicated with different shapes. IS – inner shelf, CCE – cold core eddy, WCE/WCEp – warm core eddy.

Table 1
Mean characteristics (± SD) over the top 50 m of the water column. The surface mixed layer depth is calculated from the minimum depth at which T < T (10 m) –0.4 °C or S > S (10 m)+0.03 following Condie and Dunn (2006). Values in parentheses correspond to ranges. n – number of stations; IS - inner shelf; CCE – cold core eddy; WCE – warm core eddy; WCEp – warm core eddy preliminary POM transect.

Water type	*n*	Temperature (°C)	Salinity	Nitrate + Nitrite (μmol m^{-3})	Chlorophyll*a* (μg L^{-1})	Mixed layer depth (m)
IS (27 Sept.)	4	18.07 ± 0.37 (17.54–18.37)	35.52 ± 0.03 (35.48–35.56)	2.25 ± 0.58 (1.64–2.86)	1.16 ± 0.19 (1.01–1.42)	13.40 ± 12.62 (2.98–29.79)
CCE (26 Sept.)	5	17.19 ± 0.51 (16.54–17.70)	35.56 ± 0.02 (35.53–35.59)	1.99 ± 0.40 (1.36–2.33)	1.46 ± 0.22 (1.18–1.71)	16.88 ± 8.22 (3.97–24.82)
WCE (3 Oct.)	4	17.51 ± 0.57 (16.76–17.99)	35.58 ± 0.02 (35.56–35.60)	1.68 ± 0.75 (0.75–2.58)	1.03 ± 0.33 (0.62–1.39)	137.17 ± 113.67 (20.85–274.80)
WCEp (23 Sept.)	4	18.03 ± 0.09 (17.91–18.11)	35.60 ± 0.00 (35.60–35.60)	2.45 ± 0.07 (2.35–2.53)	0.75 ± 0.34 (0.41–1.09)	282.97 ± 60.00 (215.31–350.13)

Sensing System (MOCNESS) was used for depth-stratified sampling of the entire zooplankton community. For this study, only samples collected from 0 to 100 m depth were used to correspond to POM sampling depths. Immediately after collection, the main representatives of the zooplankton community were identified to species and frozen (−20 °C). Once returned to the laboratory, these specimens were freeze-dried and homogenised, and loaded into tin capsules for stable isotope analysis. Multiple individuals were homogenised in each sample in order to meet the necessary weight requirements needed for stable isotope analyses.

2.2. Stable isotope analysis

In order to keep our data comparable with previous stable isotope research in the Tasman Sea (Davenport and Bax, 2002; Revill et al., 2009), we chose not to correct for lipid content. Both Davenport and Bax (2002) and Revill et al. (2009) deemed lipid removal to be unwarranted due to the low oil content (~1%) of most Australian fish and crustaceans (Nichols et al., 1998). With low lipid content, and relatively low C:N ratios across our zooplankton (mean ± SE: 4.8 ± 0.2) we are confident that normalisation would have had little influence on the δ^{13}C values (< 1‰ for C:N ratios between 3.3 and 5.1; McConnaughey and McRoy, 1979). Analysis of stable isotope samples were done at the Iso-Environmental Laboratory (http://www.isoenviron.co.za/), Rhodes University, South Africa, with a Europa Scientific 20-20 isotope ratio mass spectrometer (IRMS) linked to a preparation unit (ANCA SL). Casein and a mixture of beet sugar and ammonium sulphate were used as internal standards and were calibrated against the International Atomic Energy Agency (IAEA) standards CH-6 and N-1) and the IRMS certified reference material EMA-P2 (see Certificate BN/132357). δ^{13}C and δ^{15}N were determined in parts per thousand (‰) relative to external standards of Vienna Pee Dee Belemnite and atmospheric nitrogen. Repeated measurements of an internal standard indicated measurement precision of ± 0.09‰ and ± 0.19‰ for δ^{13}C and δ^{15}N respectively.

2.3. Statistical analyses

A one-way analysis of variance (ANOVA) was used to test the null hypothesis of no significant difference in δ^{13}C or δ^{15}N values among IS, CCE and WCE water types separately for each taxon. Tukey's HSD test was used for *a posteriori* pairwise comparisons between factor levels for all ANOVAs. Trophic niche widths were quantified using Bayesian ellipses (Jackson et al., 2011), using the R package SIAR (Parnell et al., 2010). This method generates standard ellipse areas (SEA_B; bivariate equivalents to standard deviations), and can be used to compare populations with variation in sample size as well as correct for small sample sizes (Jackson et al., 2011). There were no significant differences in δ^{13}C or δ^{15}N values for *E. elongatus* (CCE and WCE), *T. gregaria* (CCE and WCE) and *T. democratica* (IS, CCE and WCE) across water types for each species, so these were pooled for between species comparisons. To compare trophic niche widths among species, 15 random SEA_B values for each species were tested using a one-way ANOVA. Tukey's analysis was used for a posteriori pairwise comparisons between factor levels for all ANOVAs. All analyses were performed in R v. 3.0.3 (R Development Core Team 2012).

3. Results

3.1. Water type characterisation

During sampling, the East Australian Current (EAC) was approximately 22 °C and separated from the coast at 33°S (Fig. 1). A large WCE was evident off Jervis Bay (34°S; Fig. 1). When it was first sampled (WCEp), the WCE was deeply mixed (283 ± 60 m) and chlorophyll *a* concentrations were low (0.75 μg L^{-1}; Table 1). For the second sampling (WCE), the eddy began to encroach on the shelf and mix with inner shelf water, resulting in higher chlorophyll *a* concentrations (1.03 μg L^{-1}; Table 1) and a lower mixed layer with higher variability (137 ± 114 m; Table 1). A CCE was sampled at 32.5 °S and the adjacent inner shelf region at 32 °S. From observations of satellite imagery, upwelling occurred during sampling of the inner shelf water type (Fig. 1); however, this had not yet translated into the chlorophyll *a* signature (1.16 μg L^{-1}, Table 1). As well as satellite imagery, water types were further distinguished based on temperature-salinity profiles from the surface to 100 m depth (Fig. 2).

3.2. Particulate organic matter

δ^{13}C values for POM ranged from −24.1‰ to −18.0‰, and δ^{15}N values ranged from 3.1‰ to 8.7‰ (Fig. 3). Mean δ^{13}C (± SD) values for POM differed significantly across water types ($F_{2,24}$=4.794, p=0.02; Table 2, Fig. 4a). δ^{13}C was lowest in the CCE (−23.4 ± 0.65) and significantly higher in the IS (-21.7 ± 1.71). δ^{13}C in the WCE did not differ significantly from any other water type. Mean (± SD) δ^{15}N values for POM followed a similar trend (Table 2, Fig. 4b). δ^{15}N was significantly lower in the CCE (4.5 ± 1.1) and WCE (5.2 ± 0.9) than in the IS water type (7.1 ± 1.0; $F_{2,24}$=16.12, p < 0.001). The WCEp was significantly more depleted in both ^{13}C (−24.8 ± 0.6) and ^{15}N (1.7 ± 0.6) than the WCE ($F_{1,14}$=23.96, p < 0.001; $F_{1,14}$=85.44, p < 0.001).

3.3. Zooplankton isotope analysis

The zooplankton isotopic niche within this study encompassed a wide range of feeding types from herbivorous omnivores to obligate carnivores (Fig. 3). δ^{15}N values ranged from 3.9‰ for the parasitic copepod *Sapphirina augusta* to 10.2‰ for the euphausiid,

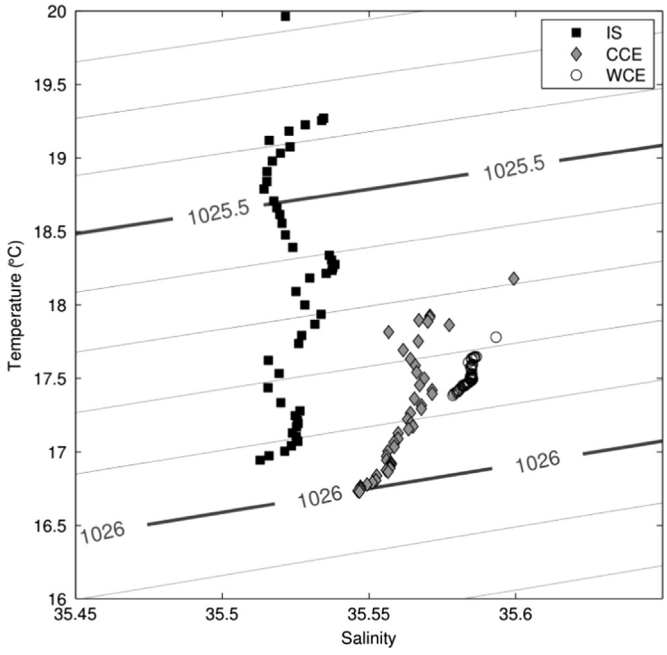

Fig. 2. Mean temperature-salinity signatures (0–100 m) for each water type: IS – inner shelf, CCE – cold core eddy and WCE – warm core eddy. Density contours are overlaid.

Euphausia spinifera, whereas δ^{13}C ranged from −22.6 to −19.4‰ as a result of the copepod *Euchirella curticauda* and *E. spinifera* (Fig. 3). Mean (±SD) ^{15}N trophic enrichment over POM for all zooplankton overall was 1.6±1.2‰, however, this varied across water types. Trophic enrichment over POM for zooplankton was lowest in the IS water type (0.5‰) compared to the CCE (2.7‰) and WCE (1.6‰).

Mean δ^{13}C and δ^{15}N values for *T. democratica* ranged from −22.6‰ to −21.0‰ and 6.5‰ to 6.9‰ respectively, and did not differ significantly across water types (Table 2, Fig. 4). Generally, *T. democratica* was the least enriched across all water types (Table 2; Fig. 5), with trophic enrichment varying from −0.4‰ to 2.0‰. In the IS, *T. democratica* samples were actually ^{15}N depleted compared to POM. There was no significant correlation between *T. democratica* and POM in ^{13}C (R=0.20, p=0.47) and ^{15}N (R=0.02, p=0.93).

Copepods had the largest δ^{13}C and δ^{15}N range compared to

Table 2
POM and zooplankton isotope values of δ^{13}C and δ^{15}N (mean±SD; ‰). n-sample size. Δ-^{15}N enrichment relative to POM. The result of Tukey's HSD test are indicated by letters (^{a,b,c}); isotopes within each taxa not sharing a letter are significantly different ($p<0.05$). Separate statistical tests were performed for δ^{13}C and δ^{15}N. δ^{13}C and δ^{15}N values for *Thalia democratica* and Copepoda did not significantly differ across water types.

Water type	Species	n	δ^{13}C	δ^{15}N	Δ	C:N
IS	POM	9	-21.7 ± 1.7^{b}	7.1 ± 1.0^{b}	–	6.9±1.0
	Thalia democratica	9	−21.9±0.5	6.7±1.0	−0.4	4.8±0.4
	Copepoda	10	−20.5±0.9	7.2±1.6	0.2	5.4±1.4
	Euphausiacea	12	-19.5 ± 0.4^{b}	8.3 ± 0.4^{a}	1.3	3.7±0.2
	Chaetognatha	7	-20.0 ± 0.4^{a}	8.2 ± 0.6^{a}	1.1	4.0±0.4
CCE	POM	10	-23.4 ± 0.7^{a}	4.5 ± 1.1^{a}	–	6.5±0.4
	Thalia democratica	2	−22.3±0.5	6.5±0.9	2.0	4.6±0.4
	Copepoda	12	−21.4±1.4	6.4±1.1	1.9	5.6±1.4
	Euphausiacea	18	-20.3 ± 0.6^{c}	7.6 ± 1.0^{a}	3.1	3.7±0.2
	Chaetognatha	2	-20.2 ± 0.0^{ab}	8.6 ± 0.8^{a}	4.1	3.7±0.0
WCE	POM	8	-22.8 ± 1.0^{ab}	5.2 ± 0.9^{ab}	–	6.2±0.5
	Thalia democratica	4	−21.6±0.6	6.9±0.8	1.7	4.9±0.5
	Copepoda	7	−21.6±0.7	6.7±1.4	1.6	10.1±2.9
	Euphausiacea	8	-20.3 ± 0.7^{c}	7.0 ± 0.8^{b}	1.8	3.7±0.2
	Chaetognatha	7	-21.1 ± 0.9^{b}	6.6 ± 1.9^{a}	1.5	3.8±0.2
WCEp	POM	8	-24.8 ± 0.6^{c}	1.7 ± 0.6^{c}	–	7.5±1.1

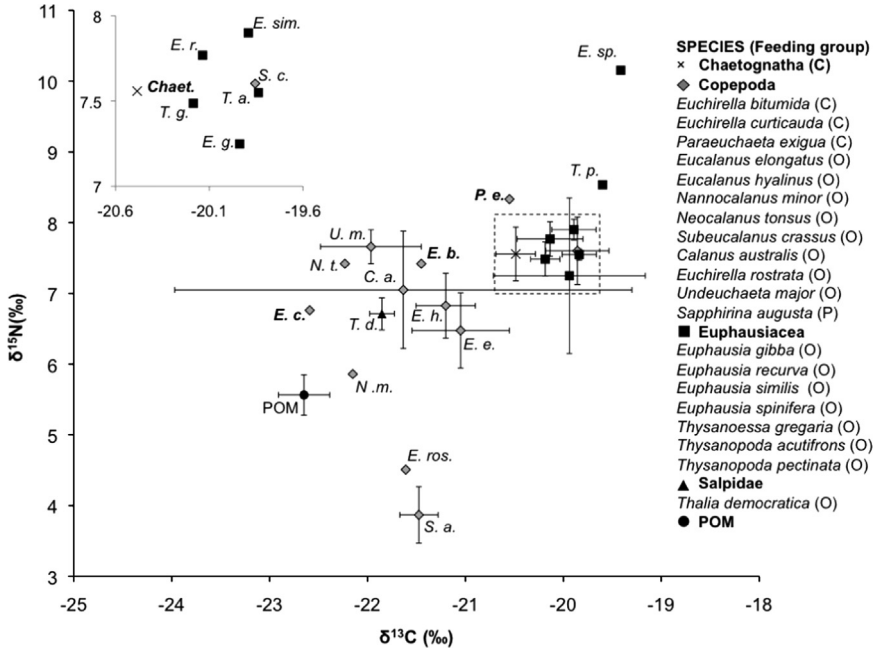

Fig. 3. Bi-plot of mean (±SE) δ^{13}C (‰) vs. δ^{15}N (‰) values of each zooplankton species pooled for each water type. Abbreviated species names are displayed adjacent to data points, with corresponding names and feeding groups presented next to the graph. Bold names represent carnivorous (C) species. *Sapphirina augusta* is a parasitic (P) copepod. All remaining copepod and euphausiid species and the salp *Thalia democratica* are omnivorous (O). POM is particulate organic matter. Feeding groups are based on references presented in Table 3. The inner groups have been enlarged (inset) for clarity (error bars not included).

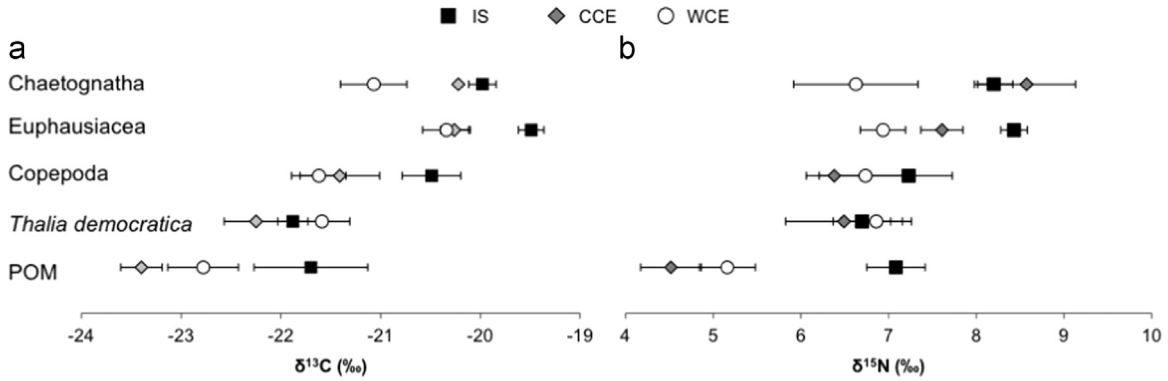

Fig. 4. (a) δ^{13}C and (b) δ^{15}N isotope values (mean ± SE) of POM and zooplankton across water types in the Tasman Sea. δ^{13}C and δ^{15}N values were sorted in order of increasing trophic level (based on average δ^{15}N). IS – inner shelf, CCE – cold core eddy, WCE – warm core eddy.

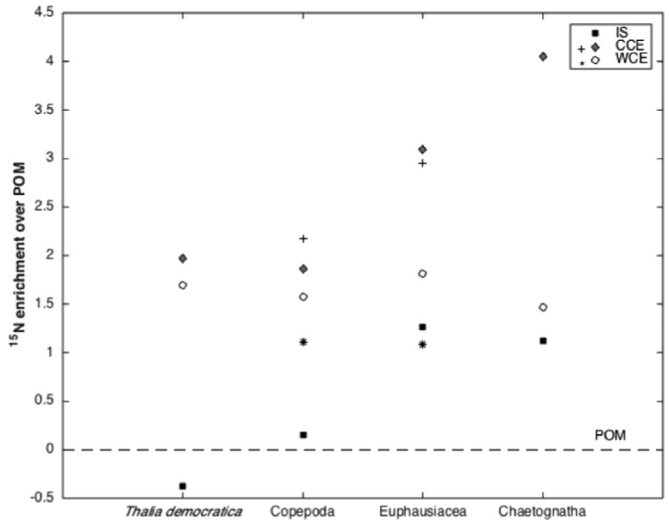

Fig. 5. ^{15}N enrichment (Δ) for zooplankton taxa over POM (dashed line) across water types. IS – inner shelf, CCE – cold core eddy, WCE – warm core eddy. ^{15}N enrichment for the copepod species *Eucalanus elongatus* and the euphausiid species *Thysanoessa gregaria* are represented in their taxa groups for the CCE (+) and WCE (*).

other zooplankton overall and δ^{13}C and δ^{15}N values did not significantly differ across water types (Table 2, Fig. 4). Mean (± SD) δ^{13}C values ranged from −22.6‰ for the carnivore *E. curticauda* to −19.86 ± 0.72‰ for *Subeucalanus crassus*, an omnivore (Table 3; Fig. 3). *Sapphirina augusta* was the most ^{15}N depleted (3.9 ± 0.6‰) compared to the more ^{15}N enriched carnivore *Paraeuchaeta exigua* (8.3‰; Table 3; Fig. 3). Trophic enrichment over POM for the copepods ranged from 0.2‰ in the IS to 1.9‰ in the CCE (Table 2, Fig. 5).

1. Wickstead (1962); 2. Kouwenberg (1994); 3. et al. 4. Timonin (1971); 5. Paffenhofer and Lewis (1989); 6. Zeldis et al. (2002); 7. Sano et al. (2013); 8. von Vaupel Klein (1998); 9. Park (1994); 10. Pillar et al. (1992).

Mean (± SD) δ^{13}C and δ^{15}N values for euphausiids differed significantly across the water types, with the most depleted values in the WCE and CCE and increasing in enrichment in the IS ($F_{2,35}$=7.791, p=0.002; $F_{2,35}$=8.029, p=0.001; Table 2, Fig. 4). All euphausiid species identified were omnivorous (Table 3; Fig. 3). δ^{13}C and δ^{15}N did not differ significantly across species and values ranged from −19.9‰ and 7.3‰ for *Euphausia gibba* to −20.7 and 10.2‰ for *E. spinifera*.

Chaetognaths also had significantly lower δ^{13}C in the WCE compared to the IS ($F_{2,13}$=5.191, p=0.022), however, δ^{15}N values did not significantly differ across water types (Table 2, Fig. 4). In the IS and CCE, euphausiids (3.1‰ CCE), including the euphausiid *T. gregaria* (3.0‰ CCE), and chaetognaths (4.1‰ CCE) occupied a higher trophic level than all copepods (1.9‰ CCE), the copepod *E. elongatus* (2.2‰ CCE) and *T. democratica* (2.0‰ CCE; Table 2, Fig. 5). However, trophic enrichment for both euphausiids (1.3‰ IS) and chaetognaths (1.1‰ IS) were lower than expected in the IS. In the WCE, ^{15}N trophic enrichment for copepods (1.6‰ for all copepods; 1.1‰ for *E. elongatus*) was similar to euphausiids (1.8‰ for all euphausiids; 1.1‰ for *T. gregaria*) and chaetognaths (1.5‰), suggesting that in the WCE they belong to a similar trophic level (Table 2; Fig. 5).

Table 3
Copepod and euphausiid isotope values of δ^{13}C and δ^{15}N (mean ± SD; ‰) separated by feeding group. *n*-sample size. References are indicated in brackets. All omnivorous copepods are predominantly herbivorous, with the exception of the predominantly carnivorous *Undeuchaeta major*. Some species were sampled across more than one water type (*), however, for each species δ^{13}C and δ^{15}N values did not significantly differ across water types.

Species	Feeding group	*n*	δ^{13}C	δ^{15}N
Copepoda				
*Sapphirina augusta**	Parasite (1)	2	−21.5 ± 0.3	3.9 ± 0.6
Nannocalanus minor	Omnivore (2)	1	−22.2	5.9
Euchirella rostrata	Omnivore (2)	1	−21.6	4.5
*Calanus australis**	Omnivore (3)	2	−21.6 ± 3.3	7.0 ± 1.3
*Eucalanus elongatus**	Omnivore (4)	6	−21.1 ± 1.2	6.5 ± 1.3
*Eucalanus hyalinus**	Omnivore (5)	5	−21.2 ± 0.7	6.8 ± 1.0
Neocalanus tonsus	Omnivore (6)	1	−22.2	7.4
*Subeucalanus crassus**	Omnivore (5)	5	−19.9 ± 0.7	7.6 ± 1.1
Undeuchaeta major	Omnivore (7)	2	−22.0 ± 0.7	7.7 ± 0.3
Euchirella bitumida	Carnivore (8)	1	−21.5	7.4
Euchirella curticauda	Carnivore (8)	1	−22.6	6.8
Paraeuchaeta exigua	Carnivore (9)	1	−20.6	8.3
Euphausiacea				
Euphausia gibba	Omnivore (10)	2	−19.9 ± 1.1	7.3 ± 1.6
*Euphausia recurva**	Omnivore (10)	5	−20.1 ± 0.8	7.8 ± 0.6
*Euphausia similis**	Omnivore (10)	8	−19.8 ± 0.6	7.9 ± 0.4
Euphausia spinifera	Omnivore (10)	1	−19.4	10.3
*Thysanoessa gregaria**	Omnivore (10)	18	−20.4 ± 0.7	7.5 ± 1.0
Thysanopoda acutifrons	Omnivore (10)	2	−19.8 ± 0.3	7.6 ± 0.1
Thysanopoda pectinata	Omnivore (10)	1	−19.6	8.5

3.4. Trophic niche widths across species

The copepod *E. elongatus* had a significantly larger trophic niche width (mean SEA_B=5.27; 95% Bayesian credible interval (BCI)=2.00–9.86) than *T. democratica* (mean SEA_B=1.81; 95% BCI=1.03–2.79) and the euphausiid *T. gregaria* (mean SEA_B=2.06; 95% BCI=1.23–3.06; $F_{2,42}$=53.66, p < 0.001; Fig. 6). Mean (± SD) δ^{13}C values for *T. gregaria* (−20.2 ± 0.6) were significantly different from both *T. democratica* (−21.9 ± 0.5) and *E. elongatus* (−21.1 ± 1.2; $F_{2,36}$=23.36, p < 0.001).

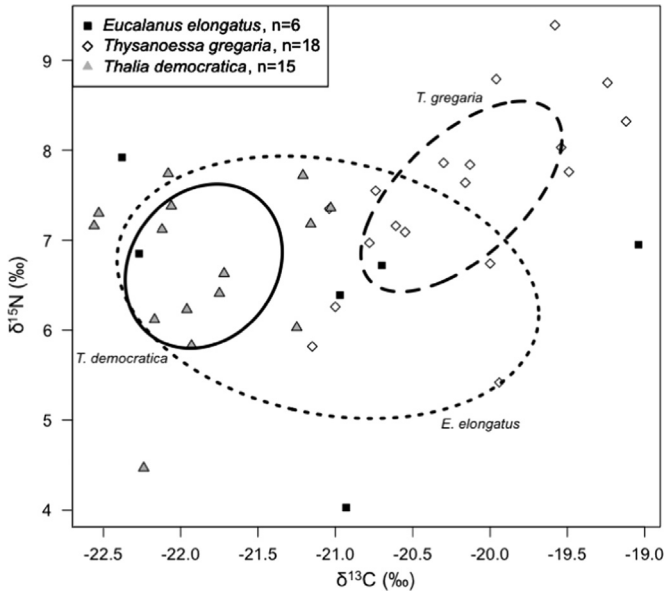

Fig. 6. δ^{13}C and δ^{15}N bi-plot for *Thysanoessa gregaria, Eucalanus elongatus* and *Thalia democratica.* Standard ellipse areas (SEA_B) are depicted with solid or dashed lines, with species labels displayed adjacent to ellipses. n – number of samples.

4. Discussion

This study quantified the POM and zooplankton food web across three water types of the western Tasman Sea using stable isotope analysis of 21 species. The variation between water types was evident in the isotopic values of POM, and was transferred to the zooplankton. Relative trophic level for the 21 species of zooplankton sampled were consistent with previously established feeding groups. However, there is also evidence that the diet of omnivorous zooplankton can vary in response to local conditions, with zooplankton becoming more carnivorous when chlorophyll *a* concentrations were low, such as in the WCE. A detailed niche width analysis of three co-existing zooplankton species provides evidence for food competition (between *E. elongatus* and *T. democratica*), but also for niche partitioning (between *T. gregaria* and the other two species). Water type is likely to have a large impact on the niche of the resident zooplankton, but careful sampling of numerous elements of the food web through time is needed to distinguish dietary changes from baseline isotopic changes driven by oceanographic events such as upwelling.

4.1. Particulate organic matter

The isotopic values for POM in this study were within the range for temperate marine phytoplankton (−18 to −28‰ δ^{13}C; Goericke et al., 1994) and within the range previously found in the Tasman Sea (−21.5‰ δ^{13}C, 2.3–8.4‰ δ^{15}N; Davenport and Bax, 2002). Both δ^{13}C and δ^{15}N values for POM were significantly enriched in the IS compared to the CCE and WCE. Several factors can alter the δ^{13}C and δ^{15}N values of POM including differences between phytoplankton species (Wong and Sackett, 1978), differences in species cell size (Rau et al., 1990) and differences in nutrient sources and concentrations which may result in different growth conditions for phytoplankton (Altabet and Francois, 1994). The IS water type was sampled off Stockton Bight (Fig. 1), an area known to be enriched in nutrients (Suthers et al., 2011) and chlorophyll *a* (Everett et al., 2014). Satellite images also indicated persistent upwelling occurring in the area prior to sampling. Correspondingly, we observed high abundances of the dinoflagellate *Noctiluca scintillans* in the IS water type (Henschke, unpublished data), which has been associated with upwelling events (Dela-Cruz et al., 2008). As diatoms tend to dominate in recently upwelled water (Ragueneau et al., 2000), this suggests that higher quantities of diatoms enriched the IS POM values compared to the CCE and WCE (Fryc and Wainright, 1991; Rau et al., 1990). Depleted ^{13}C and ^{15}N values in the WCEp coupled with low chlorophyll *a* concentrations (0.75 ± 0.34 μg L^{-1}), suggest that smaller phytoplankton species were abundant (Rau et al., 1990), and that the phytoplankton community within the WCEp was characteristic of an oligotrophic environment (Waite et al., 2007b). For the second sampling of the WCE, cooler water had been brought to the surface as a result of the eddy encroaching on the shelf promoting a phytoplankton bloom (chl-*a* 1.03 ± 0.33 μg L^{-1}). This mechanism most likely resulted in the more enriched ^{13}C and ^{15}N values in the POM compared to the previous sample.

4.2. Isotopic enrichment of Tasman Sea zooplankton

In this study, average enrichment in ^{15}N of zooplankton above POM across all water masses was 1.6‰. Previous studies in the Tasman Sea found trophic enrichment levels of ~1.5‰ for zooplankton (Davenport and Bax, 2002), and a meta-analysis has identified a mean ^{15}N enrichment of 2.1‰ for invertebrates, significantly lower than vertebrates (2.9‰; Vanderklift and Ponsard, 2003). Therefore, a lower ^{15}N trophic enrichment than the generally accepted 3.4‰ (Minagawa and Wada, 1984) may be a characteristic of zooplankton. This is likely due to differences in the synthesis and excretion of nitrogenous waste across taxa, as ammonotelic invertebrates were found to have significantly lower ^{15}N enrichment than ammonotelic vertebrates (Vanderklift and Ponsard, 2003). All taxa exhibited ^{13}C enrichment over POM ranging from 0.6‰ to 3.2‰ (mean 1.7‰), with the exception of *T. democratica* in the IS (−0.2‰). This level of trophic enrichment agrees with previously reported ranges of ^{13}C enrichment between 0.8‰ and 2.7‰ over POM for marine zooplankton (del Giorgio and France, 1996). The large ^{13}C enrichment over POM can be associated with variations in the time averaging of isotopes as they are integrated across trophic levels (O'Reilly et al., 2002). For example, as phytoplankton can have growth rates of 1.2 d^{-1} or higher (Hecky, 1991), their isotopic signature will represent the current environment, whereas slower growing zooplankton will have an isotopic signature which is an integration of food consumed prior to and during the sampling period (O'Reilly et al., 2002). Therefore caution must be taken when interpreting isotopic signatures across organisms with varying tissue turnover rates and life spans (O'Reilly et al., 2002).

T. democratica had the lowest δ^{15}N values across all water types (Table 2). ^{15}N enrichment relative to POM ranged from 0.8‰ to 2.0‰ across both the WCE and CCE. In the IS, however, *T. democratica* was ^{15}N depleted compared to POM (−0.4‰). Generally low nitrogen enrichment or depletion (around ±1‰) of salps relative to POM has been seen for *Salpa thompsoni* and *S. maxima* (Fanelli et al., 2011; Richoux and Froneman, 2009; Stowasser et al., 2012). If POM in the IS water types were isotopically enriched due to a recent upwelling event as observed in this study, these shifts may not have transferred to grazers at the time of sampling (O'Reilly et al., 2002; Rolff, 2000). This mechanism might explain why *T. democratica*, and other salps, can show low levels of trophic enrichment.

Copepods, euphausiids and chaetognaths are expected to occupy higher trophic levels than salps due to a higher level of carnivory. The majority of copepod species sampled were omnivorous (70%; Table 3), with only three carnivorous species sampled: *Euchirella bitumida, E. curticauda* and *Paraeuchaeta exigua.* With the exception of *Sapphirina augusta*, relative δ^{15}N values for both

copepod and euphausiid species were consistent with their previously established feeding groups (Table 3). Copepod $\delta^{13}C$ values were more variable than euphausiid values across all water types, indicating that copepods had a more diverse diet (Post, 2002). *S. augusta* was ^{15}N depleted compared to all other zooplankton species and POM. *Sapphirina* spp. sampled in the Leeuwin Current off Western Australia have also been observed with ^{15}N depleted compared to POM, which may be due to it feeding selectively on picoplankton (Waite et al., 2007a). More recently, suspended particulate nitrogen, such as marine snow, which is often depleted in ^{15}N (mean 0.2‰; Altabet, 1988), was associated with low $\delta^{15}N$ values for *S. ovatolanceolata-gemma* (Aberle et al., 2010). As there were high abundances of larvaceans during sampling (Henschke et al., 2014), *S. augusta* could be feeding on discarded larvacean houses, a major component of marine snow (Koski et al., 2007), or possibly on the faecal pellets of *T. democratica*. Unfortunately, the diet of species of *Sapphirina* remains uncertain (Wickstead, 1962).

In the CCE, $\delta^{15}N$ enrichment over POM for euphausiids (3.1‰) and chaetognaths (4.05‰) was consistent with their omnivorous and obligate carnivorous (Terazaki, 1998) feeding modes. Copepods in general were only enriched by 1.9‰, suggesting that they were more herbivorous compared to euphausiids. Considering their partial or complete carnivory, levels of ^{15}N enrichment over POM for copepods (0.2–1.5‰), euphausiids (1.3–2.0‰) and chaetognaths (1.1‰) were lower than expected in the IS water type (Table 2). As we outlined for the isotopic composition of *T. democratica*, the POM may have been enriched by a recent upwelling event, but with sampling of the IS water occurring before this enrichment had entered the copepods, euphausiids and chaetognaths.

Similar levels of ^{15}N enrichment among *T. democratica,* copepods, euphausiids and chaetognaths were observed in the WCE, indicating that the omnivorous species (*T. democratica,* the copepods and the euphausiids) were more carnivorous than in the CCE. POM isotopic variation and food biomass (chl-*a*) was low in the WCEp, suggesting that a prior limitation of phytoplankton forced the increased carnivory observed for the WCE zooplankton. This trend has been experimentally shown in the omnivorous copepod *Calanus pacificus,* which increased carnivory in response to a decrease in phytoplankton density (Landry,1981), and in euphausiids in low phytoplankton areas of the Southern Ocean (Richoux and Froneman, 2009).

4.3. Species-specific trophic niche width

Zooplankton may exhibit niche differentiation or partitioning to avoid competition and promote the coexistence of species in the same area, (Chase and Leibold, 2003). To explore this, we compared the trophic niche widths for three co-existing species: the omnivores *T. gregaria*, *E. elongatus* and *T. democratica*. Each species occurs in the top 100 m of the water column and does not show diel vertical migration outside this range (Barange, 1990; Gibbons, 1997; Longhurst, 1985), suggesting that they will be competing for phytoplankton and/or zooplankton in the same volume of water. As *T. democratica* can consume phytoplankton particles (<1 µm–1 mm) more efficiently than other zooplankton (Vargas and Madin, 2004), niche differentiation and an omnivorous feeding pattern is one way for both *E. elongatus* and *T. gregaria* to avoid competition. Niche differentiation can be clearly seen for *T. gregaria*, which was feeding on items more enriched in ^{13}C. Similar patterns have been seen in three *Neocalanus* species, where trophic niche partitioning promoted their coexistence in the same region (Doi et al., 2010). A significantly larger trophic niche width (SEA_B) for *E. elongatus* suggests it is feeding on greater diversity than both *T. gregaria* and *T. democratica* (Fig. 6). Although this could be a result of a much lower sample size for *E. elongatus* ($n=6$ compared to $n=15$ and $n=18$), as the ellipse based analysis used is sensitive to sample size (Jackson et al., 2011), random resampling for $n=6$ across all species still results in a significantly larger trophic niche for *E. elongatus* ($F_{2,42}=8.721$, $p<0.001$). Despite the larger niche width, the lack of niche differentiation between *E. elongatus* and the other two species suggests that *E. elongatus* may compete with both *T. gregaria* and *T. democratica* for food (e.g. Henschke et al., 2011). However, as niche overlap does not necessarily confirm that organisms are competing for the same food source, instead that they could be consuming food sources with similar isotopic signatures, an investigation of diet composition and foraging behaviour (such as spatial segregation) is needed to reveal the degree of competition that is occurring between these zooplankton species.

5. Concluding remarks

This study presents an analysis of the zooplankton trophic structure of Tasman Sea across three water-types and 21 different taxa. Water type was found to influence the zooplankton isotopic niche via the varying response of their phytoplankton prey and POM to oceanographic differences. However, oceanographic characteristics within a water type are not constant, and processes such as upwelling can create temporal mismatch between the isotopic signatures of POM and some zooplankton species. Some zooplankton species appear to adapt to changes in the marine environment. In less biologically productive water types, such as the WCE for example, zooplankton diets can shift from omnivory to carnivory. Similarly, some zooplankton species, such as *T. gregaria,* may be able to avoid competition through niche differentiation, whereas some form of competition may be unavoidable, such as seen between *T. democratica* and *E. elongatus.*

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