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

Natasha Henschke a,b,* , Jason D. Everett a,b,c , Iain M. Suthers a,b , James A. Smith a,b , Brian P.V. Hunt d , Martina A. Doblin b,c , Matthew D. Taylor a

a Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia
b Sydney Institute of Marine Science, Building 22, Chowder Bay Road, Mosman NSW 2088, Australia
c Plant Functional Biology and Climate Change Cluster, Faculty of Science, University of Technology Sydney, PO Box 123 Broadway, Sydney, NSW 2007, Australia
d Department of Earth, Ocean and Atmospheric Sciences, University of British Columbia, 6339 Stores Rd, Vancouver, British Columbia, Canada V6T 1Z4

ARTICLE INFO

Article history:
Received 11 August 2014
Received in revised form 21 June 2015
Accepted 24 June 2015
Available online 25 June 2015

Keywords:
Zooplankton
Trophic niche
Stable isotopes
Tasman Sea
Water types

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). δ13C values ranged from −22.6 to −19.4‰ as a result of the copepod Euchaeta 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 trophozoon isotopic niche, however, were still highly variable as result of oceanographic variation within water types.

© 2015 Elsevier Ltd. All rights reserved.

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 δ15N 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 δ13C 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 δ13C–δ15N 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).
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 Thy-sanoessa 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 Aquatracker 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 at 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 ($-20^\circ$C) until later analysis.

Zooplankton collection was subsequently performed at each station. A Multiple Opening/Closing Net and Environmental
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 δ13C values (<1% for C:N ratios between 3.3 and 5; 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 Euro 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). δ13C and δ15N 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 δ13C and δ15N respectively.

2.3. Statistical analyses

A one-way analysis of variance (ANOVA) was used to test the null hypothesis of no significant difference in δ13C or δ15N 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. 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

δ13C values for POM differed significantly from any other water type. Mean δ13C (± SD) values for POM differed significantly across water types (F2,24 = 4.794, p = 0.02; Table 2, Fig. 4a). δ13C was lowest in the CCE (−23.4 ± 0.65) and significantly higher in the IS (−21.7 ± 1.71). δ13C in the WCE did not differ significantly from any other water type. Mean (± SD) δ15N values for POM followed a similar trend (Table 2, Fig. 4b). δ15N 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; F2,24 = 16.12, p < 0.001). The WCEp was significantly more depleted in both δ13C (−24.8 ± 0.6) and δ15N (1.7 ± 0.6) than the WCE (F11,4 = 23.96, p < 0.001; F11,4 = 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). δ13C values ranged from −24.1‰ to −18.0‰, and δ15N values ranged from 3.1‰ to 8.7‰ (Fig. 3). Mean δ13C (± SD) values for POM differed significantly across water types (F2,24 = 4.794, p = 0.02; Table 2, Fig. 4a). δ13C was lowest in the CCE (−23.4 ± 0.65) and significantly higher in the IS (−21.7 ± 1.71). δ13C in the WCE did not differ significantly from any other water type. Mean (± SD) δ15N values for POM followed a similar trend (Table 2, Fig. 4b). δ15N 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; F2,24 = 16.12, p < 0.001). The WCEp was significantly more depleted in both δ13C (−24.8 ± 0.6) and δ15N (1.7 ± 0.6) than the WCE (F11,4 = 23.96, p < 0.001; F11,4 = 85.44, p < 0.001).
Euphausia spinifera, whereas δ\(^{13}\)C ranged from \(-22.6\) to \(-19.4\)%o as a result of the copepod Eucirella curticuda and E. spinifera (Fig. 3). Mean (± SD) \(^{15}\)N trophic enrichment over POM for all zooplankton overall was \(1.6 ± 1.2\)%o, however, this varied across water types. Trophic enrichment over POM for zooplankton was lowest in the IS water type (0.5%o) compared to the CCE (2.7%o) and WCE (1.6%o).

Mean δ\(^{13}\)C and δ\(^{15}\)N values for Thalia democratica ranged from \(-22.6\)%o to \(-21.0\)%o and 6.5%o to 6.9%o 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 \(-0.4\)%o to 2.0%o. 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

<table>
<thead>
<tr>
<th>Water type</th>
<th>Species</th>
<th>(n)</th>
<th>(\delta^{13})C</th>
<th>(\delta^{15})N</th>
<th>(\Delta)</th>
<th>C:N</th>
</tr>
</thead>
<tbody>
<tr>
<td>IS</td>
<td>POM</td>
<td>9</td>
<td>(-21.7 ± 1.7^{ab})</td>
<td>(7.1 ± 1.0^{p})</td>
<td>(-6.9 ± 1.0)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Thalia</td>
<td>9</td>
<td>(-21.9 ± 0.5)</td>
<td>(6.7 ± 1.0)</td>
<td>(-0.4 )</td>
<td>(4.8 ± 0.4)</td>
</tr>
<tr>
<td></td>
<td>Copepoda</td>
<td>10</td>
<td>(-20.5 ± 0.9)</td>
<td>(7.2 ± 1.6)</td>
<td>(0.2 )</td>
<td>(5.4 ± 1.4)</td>
</tr>
<tr>
<td></td>
<td>Euphausiacea</td>
<td>12</td>
<td>(-19.5 ± 0.4^{b})</td>
<td>(8.3 ± 0.4^{a})</td>
<td>(1.3 )</td>
<td>(3.7 ± 0.2)</td>
</tr>
<tr>
<td></td>
<td>Chaetognatha</td>
<td>7</td>
<td>(-20.0 ± 0.4^{a})</td>
<td>(8.2 ± 0.6^{a})</td>
<td>(1.1 )</td>
<td>(4.0 ± 0.4)</td>
</tr>
<tr>
<td>CCE</td>
<td>POM</td>
<td>10</td>
<td>(-23.4 ± 0.7^{a})</td>
<td>(4.5 ± 1.1^{p})</td>
<td>(-6.5 ± 0.4)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Thalia</td>
<td>2</td>
<td>(-22.3 ± 0.5)</td>
<td>(6.5 ± 0.9)</td>
<td>(2.0 )</td>
<td>(4.6 ± 0.4)</td>
</tr>
<tr>
<td></td>
<td>Copepoda</td>
<td>12</td>
<td>(-21.4 ± 1.4)</td>
<td>(6.4 ± 1.1)</td>
<td>(1.9 )</td>
<td>(5.6 ± 1.4)</td>
</tr>
<tr>
<td></td>
<td>Euphausiacea</td>
<td>18</td>
<td>(-20.3 ± 0.6^{b})</td>
<td>(7.6 ± 1.0^{a})</td>
<td>(3.1 )</td>
<td>(3.7 ± 0.2)</td>
</tr>
<tr>
<td></td>
<td>Chaetognatha</td>
<td>2</td>
<td>(-20.2 ± 0.0^{ab})</td>
<td>(8.6 ± 0.8^{a})</td>
<td>(4.1 )</td>
<td>(3.7 ± 0.0)</td>
</tr>
<tr>
<td>WCE</td>
<td>POM</td>
<td>8</td>
<td>(-22.8 ± 1.0^{ab})</td>
<td>(5.2 ± 0.9^{ab})</td>
<td>(-6.2 ± 0.5)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Thalia</td>
<td>4</td>
<td>(-21.6 ± 0.6)</td>
<td>(6.9 ± 0.8)</td>
<td>(1.7 )</td>
<td>(4.9 ± 0.5)</td>
</tr>
<tr>
<td></td>
<td>Copepoda</td>
<td>7</td>
<td>(-21.6 ± 0.7)</td>
<td>(6.7 ± 1.4)</td>
<td>(1.6 )</td>
<td>(10.1 ± 2.9)</td>
</tr>
<tr>
<td></td>
<td>Euphausiacea</td>
<td>8</td>
<td>(-20.3 ± 0.7^{a})</td>
<td>(7.0 ± 0.8^{b})</td>
<td>(1.8 )</td>
<td>(3.7 ± 0.2)</td>
</tr>
<tr>
<td></td>
<td>Chaetognatha</td>
<td>7</td>
<td>(-21.3 ± 0.9^{a})</td>
<td>(6.6 ± 1.9^{a})</td>
<td>(1.5 )</td>
<td>(3.8 ± 0.2)</td>
</tr>
<tr>
<td>WCEp</td>
<td>POM</td>
<td>8</td>
<td>(-24.8 ± 0.6^{b})</td>
<td>(1.7 ± 0.6^{c})</td>
<td>(-7.5 ± 1.1)</td>
<td></td>
</tr>
</tbody>
</table>

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.

Fig. 3. Bi-plot of mean \((± SE)\) \(\delta^{13}\)C (%o) vs. \(\delta^{15}\)N (%o) 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).
other zooplankton overall and δ¹³C and δ¹⁵N values did not significantly differ across water types (Table 2, Fig. 4). Mean (± SD) δ¹³C values ranged from –22.6‰ for the carnivore E. curticauda to –19.8 ± 0.72‰ for Subeucalanus crassus, an omnivore (Table 3; Fig. 3). Sapphirina augusta was the most δ¹⁵N depleted (3.9 ± 0.6‰) compared to the more δ¹⁵N 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).


Mean (± SD) δ¹³C and δ¹⁵N 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 (F₂,₃₅ = 7.791, p = 0.002; F₂,₃₅ = 8.029, p = 0.001; Table 2, Fig. 4). All euphausiids identified were omnivorous (Table 3; Fig. 3). δ¹³C and δ¹⁵N 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 δ¹³C in the WCE compared to the IS (F₂,₁₃ = 5.191, p = 0.022), however, δ¹⁵N 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, δ¹⁵N 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).

3.4. Trophic niche widths across species

The copepod E. elongatus had a significantly larger trophic niche width (mean SEₐ = 5.27; 95% Bayesian credible interval (BCI) = 2.00–9.86) than T. democratica (mean SEₐ = 1.81; 95% BCI = 1.03–2.79) and the euphausiid T. gregaria (mean SEₐ = 2.06; 95% BCI = 1.23–3.06; F₂,₄₂ = 53.66, p < 0.001; Fig. 6). Mean (± SD) δ¹³C 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; F₂,₃₆ = 23.36, p < 0.001).

Table 3

<table>
<thead>
<tr>
<th>Species</th>
<th>Feeding group</th>
<th>n</th>
<th>δ¹³C</th>
<th>δ¹⁵N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Copepod</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sapphirina augusta*</td>
<td>Parasite</td>
<td>2</td>
<td>–21.5 ± 0.3</td>
<td>3.9 ± 0.6</td>
</tr>
<tr>
<td>Nannocalanus minor</td>
<td>Omnivore</td>
<td>2</td>
<td>–22.2</td>
<td>5.9</td>
</tr>
<tr>
<td>Euchirella rostrata</td>
<td>Omnivore</td>
<td>2</td>
<td>–21.6</td>
<td>4.5</td>
</tr>
<tr>
<td>Calanus australis*</td>
<td>Omnivore</td>
<td>2</td>
<td>–21.6 ± 3.3</td>
<td>7.0 ± 1.3</td>
</tr>
<tr>
<td>Eucalanus elongatus*</td>
<td>Omnivore</td>
<td>6</td>
<td>–21.1 ± 1.2</td>
<td>6.5 ± 1.3</td>
</tr>
<tr>
<td>Eucalanus hyalinus*</td>
<td>Omnivore</td>
<td>5</td>
<td>–21.2 ± 0.7</td>
<td>6.8 ± 1.0</td>
</tr>
<tr>
<td>Neocalanus tonus</td>
<td>Omnivore</td>
<td>1</td>
<td>–22.2</td>
<td>7.4</td>
</tr>
<tr>
<td>Subeucalanus crassus*</td>
<td>Omnivore</td>
<td>5</td>
<td>–19.9 ± 0.7</td>
<td>7.6 ± 1.1</td>
</tr>
<tr>
<td>Undeuchaeta major</td>
<td>Omnivore</td>
<td>2</td>
<td>–22.0 ± 0.7</td>
<td>7.7 ± 0.3</td>
</tr>
<tr>
<td>Euchirella biturnida</td>
<td>Carnivore</td>
<td>8</td>
<td>–21.5</td>
<td>7.4</td>
</tr>
<tr>
<td>Euchirella curticauda</td>
<td>Carnivore</td>
<td>8</td>
<td>–22.6</td>
<td>6.8</td>
</tr>
<tr>
<td>Paraeuchaeta exigua</td>
<td>Omnivore</td>
<td>9</td>
<td>–20.6</td>
<td>8.3</td>
</tr>
<tr>
<td>Euphausiacea</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Euphausia gibba</td>
<td>Omnivore</td>
<td>10</td>
<td>–19.9 ± 1.1</td>
<td>7.3 ± 1.6</td>
</tr>
<tr>
<td>Euphausia recrura*</td>
<td>Omnivore</td>
<td>10</td>
<td>–20.1 ± 0.8</td>
<td>7.8 ± 0.6</td>
</tr>
<tr>
<td>Euphausia similis*</td>
<td>Omnivore</td>
<td>10</td>
<td>–19.8 ± 0.6</td>
<td>7.9 ± 0.4</td>
</tr>
<tr>
<td>Euphausia spinifera</td>
<td>Omnivore</td>
<td>10</td>
<td>–19.4</td>
<td>10.3</td>
</tr>
<tr>
<td>Thysonosia gregaria*</td>
<td>Omnivore</td>
<td>18</td>
<td>–20.4 ± 0.7</td>
<td>7.5 ± 1.0</td>
</tr>
<tr>
<td>Thysonopoda acutifrons</td>
<td>Omnivore</td>
<td>2</td>
<td>–19.8 ± 0.3</td>
<td>7.6 ± 0.1</td>
</tr>
<tr>
<td>Thysonopoda pectinata</td>
<td>Omnivore</td>
<td>1</td>
<td>–19.6</td>
<td>8.5</td>
</tr>
</tbody>
</table>

Fig. 4. (a) δ¹³C and (b) δ¹⁵N isotope values (mean ± SE) of POM and zooplankton across water types in the Tasman Sea. δ¹³C and δ¹⁵N values were sorted in order of increasing trophic level (based on average δ¹⁵N). IS – inner shelf, CCE – cold core eddy, WCE – warm core eddy.

Fig. 5. δ¹⁵N enrichment (A) for zooplankton taxa over POM (dashed line) across water types. IS – inner shelf, CCE – cold core eddy, WCE – warm core eddy. δ¹⁵N enrichment for the copepod species Eucalanus elongatus and the euphausiid species Thysonosia gregaria are represented in their taxa groups for the CCE (+) and WCE (*).
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 was 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‰ δ13C; Goericke et al., 1994) and within the range previously found in the Tasman Sea (−21.5‰ δ13C, 2.3–8.4‰ δ15N; Davenport and Bax, 2002). Both δ13C and δ15N values for POM were significantly enriched in the IS compared to the CCE and WCE. Several factors can alter the δ13C and δ15N 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 (Raguenneau 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 13C and 15N 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 13C and 15N values in the POM compared to the previous sample.

4.2. Isotopic enrichment of Tasman Sea zooplankton

In this study, average enrichment in 15N 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 15N enrichment of 2.1‰ for invertebrates, significantly lower than vertebrates (2.9‰; Vanderklift and Ponsard, 2003). Therefore, a lower 15N 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 15N enrichment than ammonotelic vertebrates (Vanderklift and Ponsard, 2003). All taxa exhibited 13C 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 13C enrichment between 0.8‰ and 2.7‰ over POM for marine zooplankton (del Giorgio and France, 1996). The large 13C 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 δ15N values across all water types (Table 2). 15N enrichment relative to POM ranged from 0.8‰ to 2.0‰ across both the WCE and CCE. In the IS, however, T. democratica was 15N 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 Fromeman, 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: Eu- chirella bitumida, E. curticauda and Paraeuchaeta exigua. With the exception of Sapphirina augusta, relative δ13N values for both
copepod and euphausiid species were consistent with their previously established feeding groups (Table 3). Copepod δ13C values were more variable than euphausiids values across all water types, indicating that copepods had a more diverse diet (Post, 2002). S. augusta was 15N depleted compared to all other zooplankton species and POM. Sapphirina spp. sampled in the Leeuwin Current off Western Australia have also been observed with 15N 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 15N (mean 0.2‰; Altabet, 1988), was associated with low δ15N values for S. ovata lanceolata-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, δ15N 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 15N 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. democra
tica, 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 15N 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 niche competition. Niche differentiation can be clearly seen for T. gregaria, which was feeding on items more enriched in 13C. 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 (SEAb) 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 (F2,40 = 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.

Acknowledgements

This research was funded by ARC Discovery Grant DP120100728 held by IMS and MDT. The authors thank the captain and crew of the RV Southern Surveyor voyage 08/2010, as well as the assistance of our colleagues during the voyage. We also wish to thank the anonymous reviewers who have helped to improve this manuscript. This is contribution 158 from the Sydney Institute of Marine Science.

References

Research and Development Corporation Project 95/122.
Paffenhofer, G.A., Lewis, K.D., 1989. Feeding behaviour of nauplii of the genus Eu-