



8 January 2021

Dear Prof Curchitser

Enclosed for your consideration is an original manuscript, titled: "Vertically resolved zooplankton biomass and size-structure across a continental shelf under the influence of a western boundary current". This manuscript has not been published nor is currently under consideration for publication elsewhere. All authors have agreed with its content and approved submission in its present form.

Our paper addresses a significant gap in the broad understanding of zooplankton communities. Using a towed optical plankton counter, this paper is the first to present high resolution depth resolved transects of the zooplankton community across a continental shelf. We find significant horizontal and vertical declines in biomass as well as an altered size structure of the zooplankton community, particularly in the regions where the East Australian Current was present. By undertaking a global synthesis, we then show that these horizontal patterns in the zooplankton community are consistent globally and we present a conceptual figure of how the zooplankton community changes across continental shelves.

This study has significance for the fields of oceanography, zooplankton ecology and fisheries. It is critical we understand how oceanographic processes influence the pelagic biological communities of continental shelves as they are one of the most exploited marine environments in the world. As a key observational study linking oceanography and pelagic ecology with global implications, we believe *Progress in Oceanography* is the ideal journal for this paper.

Building on previous work in *Progress in Oceanography*, Everett et al (2014) showed strong oceanographic driven patterns in chlorophyll *a* in the east Australian region. Our current paper builds upon this research to extend the influence of oceanography into the higher zooplankton trophic groups and we think it would be ideal to publish this work in the same journal.

Sincerely

Dr Hayden Schilling
Postdoctoral Research Associate, Sydney Institute of Marine Science & UNSW

Reference

Everett, J. D., Baird, M. E., Roughan, M., Suthers, I. M., and Doblin, M. A. 2014.
Relative impact of seasonal and oceanographic drivers on surface chlorophyll *a* along a Western Boundary Current. *Progress in Oceanography*, 120: 340–351.

**Vertically resolved zooplankton biomass and size-structure across a continental shelf
under the influence of a western boundary current**

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Main text ≈ 6500 words, 1 Table, 8 Figures

22 **Abstract**

23 Continental shelves are the interface between society and the oceans, supporting over 90%
24 of the world's fisheries through highly productive ecosystems. Boundary currents drive
25 oceanographic processes on many continental shelves, yet it is uncertain how boundary
26 currents affect the continental shelf zooplankton community. With an optical plankton
27 counter and CTD mounted on an undulating towed body, we present the first high-
28 resolution vertically resolved profiles of the zooplankton size structure across four transects
29 over a continental shelf. Zooplankton biomass is highest inshore, which declines with
30 increasing distance from shore and with increasing depth in the water column. The front
31 between the warm East Australian Current (EAC) and cooler continental shelf waters also
32 showed increased biomass of zooplankton. Landward of the front is the inner-shelf water,
33 created by EAC uplifting slope waters, resulting in zooplankton ecosystems with smaller
34 geometric mean sizes and steeper size spectrum slopes. South of the EAC separation from
35 the coast, the continental shelf zooplankton was more spatially homogenous but still
36 displayed the same horizontal and vertical patterns in zooplankton. These patterns are
37 consistent with zooplankton distributions on other continental shelves where the inner-
38 shelf has higher biomass of zooplankton with a steeper NBSS-slope compared to offshore.
39 Inner-shelf zooplankton communities support important temperate reef ecosystems and
40 coastal fisheries, through their consistently high biomass.

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43 Key words: Upwelling, Size spectrum, Optical Plankton Counter, Production, East Australian
44 Current, Great Southern Reef

45 Introduction

46 Continental shelves are the interface between society and the oceans. While
47 accounting for less than 7% of the earth's ocean surface area, continental shelf regions
48 support over 90% of the world's fisheries catch (Pauly *et al.*, 2002). These fisheries are
49 supported by high chlorophyll *a* biomass, often driven by the coastal processes including
50 upwelling, river plumes, boundary currents, and eddies. The high chlorophyll *a* levels often
51 observed on the continental shelf, particularly the inner shelf (Lucas *et al.*, 2011) are a key
52 driver of zooplankton communities which are a key resource for fisheries. In boundary
53 current systems such as the East Australian Current and the Benguela Current, zooplankton
54 can support over 50% of fish biomass on coastal reefs (Truong *et al.*, 2017; Maia *et al.*,
55 2018), making it a key link between primary production and higher trophic levels.

56 The transfer of energy between trophic levels is complex but as predation is largely
57 driven by size in the marine environment (Barnes *et al.*, 2010), the size frequency
58 distribution of a community can provide valuable insight. Within a community, the size of all
59 individuals, irrespective of species identity, can be described by the size-frequency which
60 typically yields a histogram that is strongly right-skewed with many small individuals, and a
61 few large individuals (Blanchard *et al.*, 2017; Heneghan *et al.*, 2019). On log-log axes, the
62 negative linear slope of the zooplankton size spectrum (Sprules and Barth, 2015; Edwards *et al.*, 2017), provides insight into energy transfer and community function (Kerr and Dickie, 2001; White *et al.*, 2007). The size spectrum implicitly reflects the outcome of all ecological processes including predation, the growth of individuals through different size classes, and the repopulation of smaller size classes through reproduction (Sprules and Barth, 2015; Andersen *et al.*, 2016; Blanchard *et al.*, 2017). The elevation of the spectrum reflects the environmental effects of nutrients and temperature and can result in differences between

water masses (Baird *et al.*, 2008). Steeper slopes in the size-spectrum represent inefficient energy transfer between trophic levels which can occur under both oligotrophic conditions as nutrients become scarce and eutrophic conditions as many bloom taxa are relatively large yet unpalatable which increases the chances of mass sinking of ungrazed blooms leading to reduced efficiency of energy transfer (Atkinson *et al.*, 2020).

Cross-shelf patterns in zooplankton size spectrum slopes have been examined on several continental shelves. In the southwest Atlantic, the zooplankton community on the continental shelf had higher biomass and a steeper zooplankton size spectrum slope compared to the offshore oceanic stations which were typically more stratified with higher biomass at depth (Marcolin *et al.*, 2013). This is similar to the northeast Atlantic where high zooplankton biomasses and steeper zooplankton size spectrum slopes were found in some but not all inshore regions (Sourisseau and Carlotti, 2006; Irigoien *et al.*, 2009; Vandromme *et al.*, 2014). Fewer studies have examined the vertical patterns of zooplankton on continental shelves and this remains a key knowledge gap. During late summer, in the northwest Atlantic, the vertical zooplankton distribution was strongly influenced by water mass with distinct zooplankton communities separated by a strong thermocline (Turner and Dagg, 1983). In a more homogenous water mass during winter on the Abrolhos Bank in the southwest Atlantic, copepod abundance peaked near the surface (20 – 40 m) and decreased with depth in the water column (Marcolin *et al.*, 2015). The causes of the observed patterns in zooplankton communities on continental shelves remain uncertain with oceanography, particularly boundary currents playing a key role.

Boundary currents are important drivers of productivity along continental shelves. Eastern boundary currents directly supply nutrient rich, cool waters from the poles towards the equator which then interact with wind driven upwelling to produce some of the most

productive fisheries in the world including those located in the Humboldt and California currents (Carr and Kearns, 2003). By contrast, western boundary currents (WBCs) are narrow currents which swiftly move warm oligotrophic water poleward. When WBCs interact with the adjacent continental shelf they induce upwelling of cold nutrient rich water on the inshore edge, generate eddies and form frontal regions (Everett *et al.*, 2012; Schaeffer *et al.*, 2013, 2014; Aguiar *et al.*, 2014). These processes facilitate a nutrient and productivity gradient from the oligotrophic WBC across the continental shelf into the coast. The interaction of the WBC and continental shelf water dominates the pathways by which nutrients and biological materials enter and leave the continental shelf system (Malan *et al.*, 2020).

Within both eastern and western boundary currents, cross-shelf flows are far smaller in magnitude than along-shelf flows but have a disproportional impact on shelf water properties such as plankton and fish distribution (Brink, 2016). Cross-shelf gradients in chlorophyll *a* (as a proxy for phytoplankton biomass) are commonly observed but are strongly influenced at the smaller-spatial scale by eddies and upwelling (Lucas *et al.*, 2011; Everett *et al.*, 2014). The cross-shelf gradient in chlorophyll *a* may be a key driver of increased zooplankton biomass which is often observed on continental shelves compared to offshore regions, particularly in the northeast (Sourisseau and Carlotti, 2006; Irigoien *et al.*, 2009; Vandromme *et al.*, 2014) and southwest Atlantic (Marcolin *et al.*, 2013; Pereira Brandini *et al.*, 2014).

The western boundary current of the South Pacific is the East Australian Current which generates eddies (Everett *et al.* 2012) and drives upwelling as it interacts with the continental shelf (Roughan and Middleton, 2002). These oceanographic processes influence nutrient availability and the biomass of chlorophyll *a* (Everett *et al.*, 2014), yet there are no

117 studies investigating the influence of the EAC driven production on higher trophic levels

118 including zooplankton. Here we investigate horizontal and vertical patterns in the

119 zooplankton community using four high-resolution vertically resolved, cross-shelf transects

120 of zooplankton on the eastern continental shelf of Australia to:

121 1) Identify latitudinal differences in zooplankton distribution across the continental

122 shelf in relation to the EAC, and

123 2) Examine the potential drivers of the observed patterns in zooplankton biomass

124 and size-structure, and

125 3) Relate our observations to previous research to propose a general concept of

126 zooplankton size-structure on continental shelves globally.

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128 **Materials and Methods**

129 *Study Region*

130 The East Australian Current (EAC) is the western boundary current of the South
131 Pacific gyre, forming between 10 and 20°S where the South Equatorial Current bifurcates off
132 the Great Barrier Reef and north-eastern Australia (Ridgway and Dunn, 2003). The
133 southward flowing component forms the EAC, flowing at 0.5 – 1.5 m s⁻¹ along the
134 continental shelf (Archer *et al.*, 2017) until the majority of the EAC separates from the coast
135 between approximately 30 – 32°S and flows eastward as the EAC eastern extension (Cetina-
136 Heredia *et al.*, 2014; Oke *et al.*, 2019). The remaining portion of the EAC continues to flow
137 south along the coast as part of the EAC southern extension generating a large eddy field
138 (Everett *et al.*, 2012). Along the continental shelf, particularly where the continental shelf
139 narrows, the EAC has significant impact on shelf circulation (Schaeffer and Roughan, 2015).
140 Current driven bottom friction leads to Ekman transport in the bottom boundary layer,
141 moving cooler denser water up the slope, resulting in uplift of isotherms and upwelling
142 (Schaeffer *et al.*, 2014). These intrusion events have been shown to bring nutrient rich water
143 into the euphotic zone, increasing nitrate (Rossi *et al.*, 2014) and chlorophyll *a* concentration
144 (Everett *et al.*, 2014), and controlling vertical phytoplankton abundance and composition
145 (Armbrecht *et al.*, 2014, 2015).

146 From 2nd – 13th September 2004, a research voyage on the on the RV Southern
147 Surveyor was undertaken from Sydney, Australia (33.82°S, 151.29°E) to Brisbane, Australia
148 (27.36°S, 153.17°E). During this period, the EAC was flowing southward along the coast until
149 approximately 31°S where it separated from the mainland and continued flowing to the

east. This separation resulted in the formation of a large warm-core eddy forming off the coast at approximately 33°S, 155°E (Figure 1).

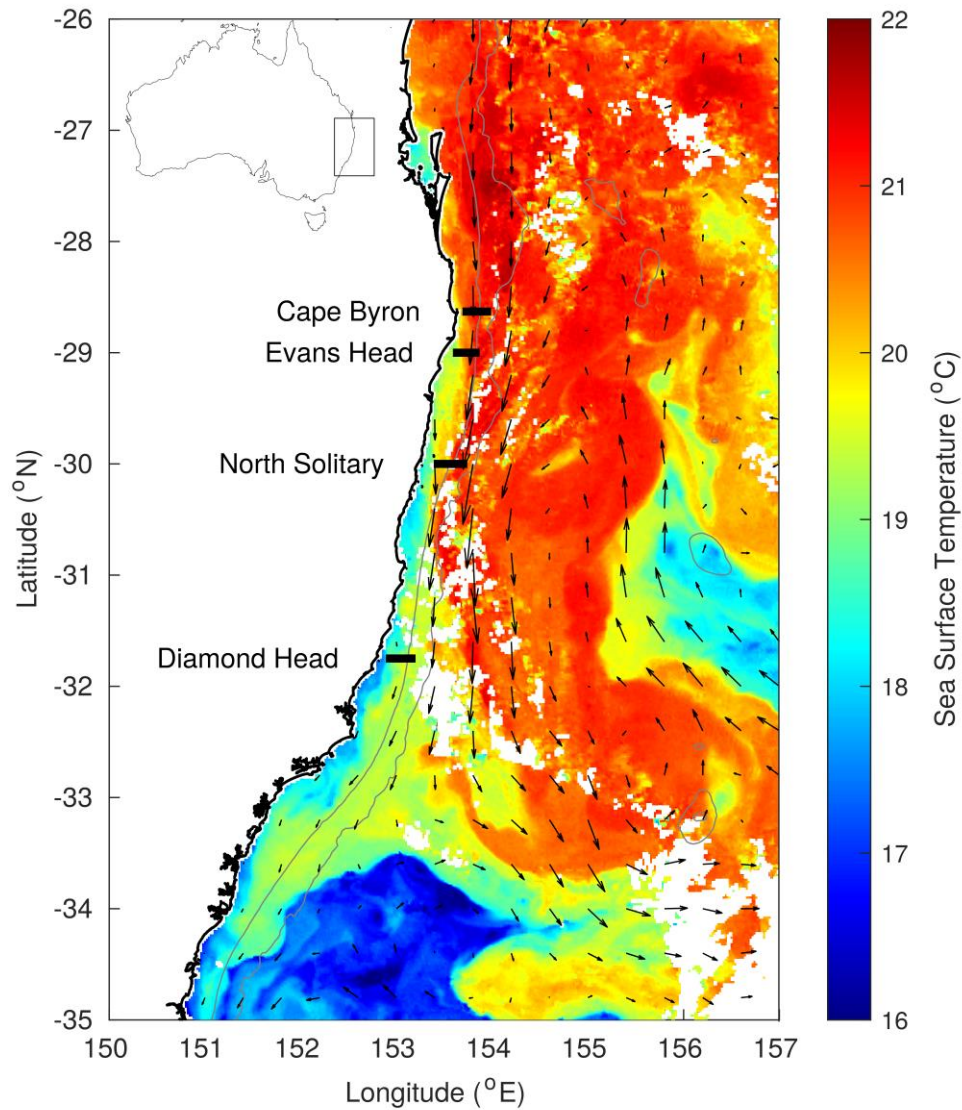


Figure 1 Locations of the four cross shelf sections which were sampled in September 2004.

The sea-surface temperature for 6th September 2004 is shown in colour with velocity arrows from satellite altimetry shown with black arrows. Grey isobaths represent 200 and 2000m depths.

158 *Sampling*

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3 159 Four transects were sampled roughly perpendicular to the coast over a seven-day period
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5 160 (6th – 12th September; Table 1, Figure 1) using a modified SeaSoar. The SeaSoar was towed
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8 161 from inshore to offshore and undulated between 10 and 120 m depth as used in previous
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10 162 studies (Baird *et al.*, 2008). Mounted on the SeaSoar was a dual CTD system (custom made
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13 163 interface combining a Seabird SBE3 temperature sensor, a Seabird SBE4 conductivity sensor
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16 164 and a Paroscientific 43K-027 pressure sensor) and an Optical Plankton Counter (OPC;
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18 165 Herman 1992) to continuously measure temperature, salinity and the size frequency
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21 166 distribution of particulate matter. An ADCP (Teledyne R. D. Instruments, USA, Model # VM-
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23 167 150) continuously monitored the current velocity profile beneath the vessel. Alongshore
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26 168 and cross-shelf velocity of currents was calculated by rotating the U and V vectors to
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29 169 account for the angle of the coastline at each location (Table 1).

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172 **Table 1** Summary of the four transects undertaken using the SeaSoar with attached optical
 173 plankton counter and CTD. Times are local, Australian Eastern Standard Time (GMT +10).

Transect	Coastline	Start	Start	End	End	Start Time	End Time
	Angle (°)	Longitude (° E)	Latitude (° S)	Longitude (° E)	Latitude (° S)		
Cape Byron	356	153.704	28.633	153.981	28.633	12/09/2004 08:11	12/09/2004 09:59
Evans Head	13	153.611	28.997	153.858	29.002	11/09/2004 10:55	11/09/2004 12:36
North	15	153.412	29.998	153.726	29.997	7/09/2004	8/09/2004
Solitary						21:41	00:05
Diamond	19	152.913	31.752	153.191	31.747	6/09/2004	6/09/2004
Head						20:00	21:53

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175 *Environmental Data*

176 To investigate environmental conditions leading up to and during the sampling of
 177 transects on the east Australian continental shelf, MODIS-Aqua Level 3 ocean-colour data
 178 (chlorophyll-a) were obtained from the Integrated Marine Observing System (IMOS) Data
 179 Portal (<http://imos.aodn.org.au/imos/>) at 1 km resolution. Chlorophyll-a was derived using
 180 the OC3 algorithm. Sea surface temperature was obtained from L3S AVHRR daily night
 181 product from the same portal, displayed as a map for the region (resolution of 0.02°).
 182 Surface geostrophic currents were derived from gridded sea level gradients from satellite
 183 altimetry, also taking into account sea level gauges to improve the estimate in coastal area
 184 (resolution of 0.2°). To quantify lead-up conditions to our sampling, MODIS chlorophyll-a

data were retrieved for 5×5 pixels (~25 km²) surrounding the western and eastern edges of each transect, for the month prior to the day of sampling.

To investigate the seasonal variation of EAC strength in the region of our transects, 10 years (2004 – 2013) of surface geostrophic currents from satellite altimetry were obtained from the IMOS Data Portal (<http://imos.aodn.org.au/imos/>) for each of our transects. Alongshore and cross-shelf velocity of currents was calculated by rotating the U and V vectors to account for the angle of the coastline at each location (Table 1). The monthly mean (and standard deviation) alongshore velocity was calculated for the 10-year period by averaging the daily velocities. We assumed that faster alongshore velocity would be due to increased influence of the EAC which is known to seasonally widen, extending its influence over the continental shelf (Archer *et al.*, 2017).

The potential influence of wind driven circulation was investigated from wind data from Coffs Harbour meteorological station from the Bureau of Meteorology (30.311°S, 153.118°E) located close to shore at 5 m height. The hourly wind stress was calculated following Wood *et al.* (2016). Bathymetric data was sourced from GEBCO (GEBCO Bathymetric Compilation Group, 2019).

Zooplankton Size Structure

The OPC was a Focal Technologies Corporation Model OPC-2T with a sampling aperture of 2 x 10 cm (Herman, 1992). The OPC records equivalent spherical diameters (ESD) of particles that pass through the instrument in 0.5 s intervals (e.g. Suthers *et al.*, 2006; Baird *et al.*, 2008). The particle sizes were recorded digitally using 4096 size bins, corresponding within the operating range of the instrument to bins with a width varying

between 5 and 15 μm . The particles used in the following analysis were restricted to those above 250 μm ESD to account for the lower detection limit of the OPC (Suthers *et al.*, 2006). As the region of our study had low chlorophyll-a concentration and turbidity during our study we are confident in assuming there was a low amount of sediment that would not change the results of our assumption that all particles recorded are part of the planktonic ecosystem (Espinasse *et al.*, 2018). As we are most interested in quantifying the overall size-structure trend by looking at general trends in particle size and abundance, hereafter for simplicity, we refer to the OPC counts as zooplankton, but acknowledge that a proportion of the particles will be marine snow, moribund carcasses or appendages, all of which are an important part of the planktonic food web (Alldredge and Silver, 1988; Tsukamoto and Miller, 2020).

The volume of flow through the sample region was based on distance measured over a 6 s interval. It has been previously shown that a 6 s interval provides optimal vertical and horizontal resolutions (≈ 6 m vertically) of the size distribution in the Tasman Sea region, near the current study area (Baird *et al.*, 2008). To quantify the zooplankton community, several metrics were calculated for each interval of our transects (Krupica *et al.*, 2012). These included total biomass (mg m^{-3}), geometric mean size (GSM; μm ESD) and zooplankton size spectrum slope which we calculated as the shape parameter c of the Pareto distribution of the particles (equivalent to the traditional NBSS slope). The OPC records the time and size of each particle detected, allowing the Pareto distribution to be calculated without further binning of the raw digital signal that is necessary for the NBSS. The correlation between the more common NBSS Slope and shape parameter c of the Pareto distribution was also tested to confirm the relationship. The Pareto distribution has

been previously used in this region to spatially resolve the size distribution of particles (Suthers *et al.*, 2006; Baird *et al.*, 2008).

The Pareto distribution has a probability density function (*pdf*) defined as:

$$pdf(s) = ck^c s^{-(c+1)}$$

where s is the size of the particle, and c and k are the distribution's shape and scale parameters, respectively (Vidondo *et al.*, 1997). ESD values (μm) were converted to biomass (mg m^{-3}) as per Wallis *et al.* (2016), assuming the volume of a sphere and the density of water ($\rho=10^9 \text{ mg m}^{-3}$) using:

$$Biomass (\text{mg m}^{-3}) = \frac{4}{3}\pi \left(\frac{ESD}{2}\right)^3 \rho$$

Zooplankton data from the OPC were interpolated to create 2D visualisations of the profiles across the continental shelf using the 'akima' R package to interpolate a regular grid of points via bivariate interpolation (Akima and Gebhardt, 2020), then applying contours within the 'ggplot' package (Wickham 2011).

A global context

To place our east Australian transects in a global context and identify general trends in zooplankton communities on continental shelves, we examined 18 previous studies which investigated spatial changes in zooplankton communities over continental shelf regions. Where possible from each study we extracted values for total zooplankton biomass, abundance and the zooplankton size spectrum slope from the most inshore and furthest offshore sites (Table S1). From each study we extracted a maximum of one inshore and one

252 offshore value, averaged across the study as well as corresponding bathymetry values,
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2 253 except for two studies from the Bay of Biscay (Irigoien *et al.*, 2009; Vandromme *et al.*, 2014),
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4 254 where the east and south regions had very different zooplankton communities so there
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7 255 were kept as distinct regions. If there were multiple years or seasons within a study, an
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10 256 average was taken. As many studies only provided binned values or plots, data were
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12 257 estimated from plots using a colour sampling tool and binned data were assigned values
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15 258 equal to the mid-point of the bin (Table S1). As the studies reported a range of units, to
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17 259 make studies comparable in terms of inshore to offshore trends we present the ratio of
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20 260 inshore to offshore values.
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261 Results

262 *Regional Oceanography*

263 The three northern most transects (north of 30°S) all crossed from cool inshore
264 waters into warm (>21 °C) EAC water but the southern transect (Diamond Head 31.75°S)
265 was located south of where the EAC begins to separate from the shelf (“the separation
266 zone”), causing cooler (<19.5 °C) waters (Figure 1). All transects showed low chlorophyll
267 levels (<1.4 mg m⁻³; Figure S1) which was representative of the previous month of low
268 chlorophyll-a at these locations (Figure S2). Most transects were negligibly influenced by the
269 effects of wind in the 3 days prior to the transects (Figure S3), with most of the wind coming
270 from a southerly direction. The exception was the North Solitary (30°S) transect which was
271 subject to some wind driven upwelling prior to our sampling (Figure S3).

273 *Cape Byron (28.6°S)*

274 The northernmost transect at Cape Byron (28.6°S) was dominated by the EAC which
275 had a strong alongshore flow (1.50 m s⁻¹) centred over the 200 m isobath (27.6 km
276 offshore). Most of the continental shelf was flooded by warm EAC water (Figure 2). The EAC
277 showed slight onshore movement which increased offshore and with depth, peaking
278 between 100 and 200 m depth (up to 0.26 m s⁻¹, Figure S4). The strong EAC flow resulted in
279 strong current-driven uplift of the isotherms inshore of the EAC with the 21 °C isotherm
280 rising to the surface from 70 m depth over 5 km and the 20 °C isotherm rising to the surface
281 from 100 m depth over 15 km.

282 A decline in zooplankton biomass was observed from both inshore to offshore and
283 from the surface to depth with the highest biomass (~750 mg m⁻³; Figures 3, S5, S6)

observed at the surface ~20 km from the coastline, just inshore of the 21 °C isotherm (Figure 3a). This 21 °C isotherm appears to be a strong delineator of both zooplankton biomass and the size distribution. The EAC waters, warmer than 21 °C and $> 1.2 \text{ m s}^{-1}$ southward velocity, were characterised by low zooplankton biomass with a GMS of $\approx 450 \text{ }\mu\text{m}$ ESD (Figure 4) with steep zooplankton size spectrum slopes between -1 and -1.3 (Figure 5). The cooler water immediately inshore of the 21 °C isotherm had high zooplankton biomass, shallower zooplankton size spectrum slope (-0.9; Figure 5) with larger particles (GMS 500 μm ESD; Figure 4)). Further inshore again (15 -17 km from the coastline), in water $< 20 \text{ }^{\circ}\text{C}$, biomass remained high (Figure 3), but the particles were smaller (GMS $\approx 430 \text{ }\mu\text{m}$ ESD; Figure 4), resulting in a steeper zooplankton size spectrum slope (≈ -1.25 ; Figure 5).

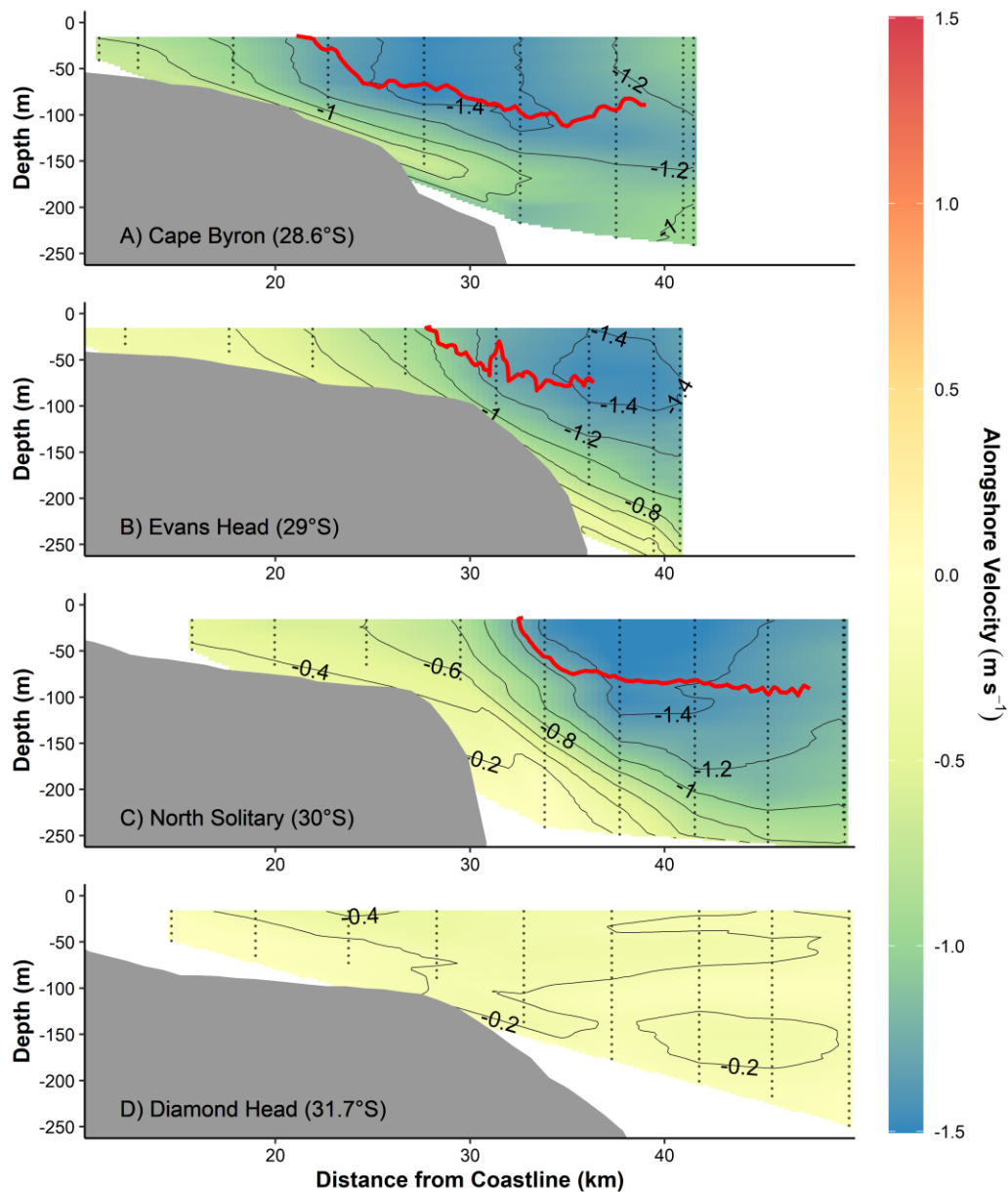


Figure 2 Alongshore velocity across the four cross shelf transects (Figure 1), from the vessel's Acoustic Doppler Current Profiler. Grey lines join areas of equal velocity. The red line shows the 21°C isotherm. Note the cooler water where there was no 21°C isotherm for Diamond Head.

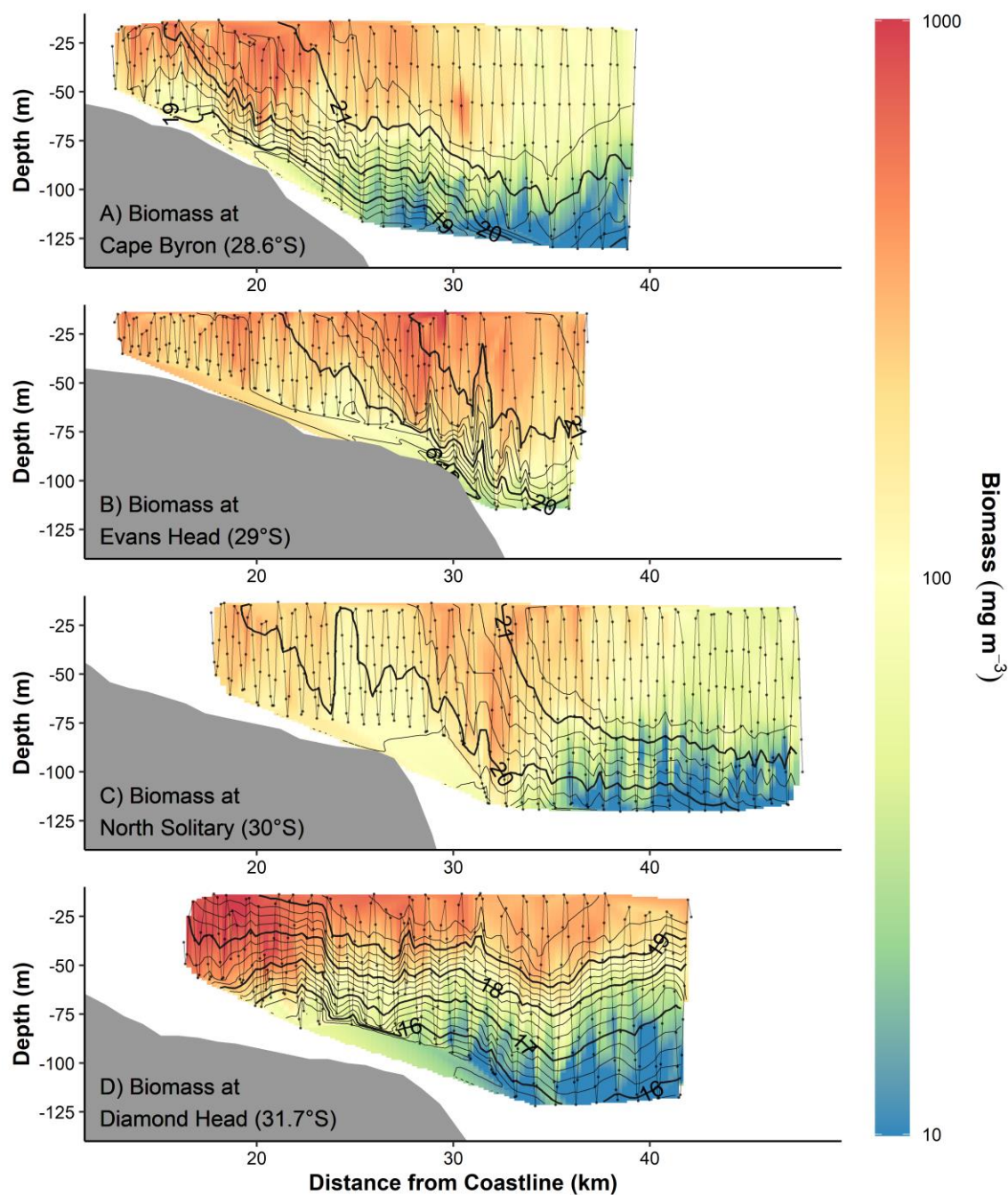


Figure 3 Zooplankton biomass (mg m^{-3}) distributions from the four cross shelf transects (Figure 1). Transects were conducted from inshore to offshore with an undulating towed body with the path shown by the grey line with midpoints of each sample shown as dots. Temperature ($^{\circ}\text{C}$) isotherms are shown in black. Note the log transformed colour scale.

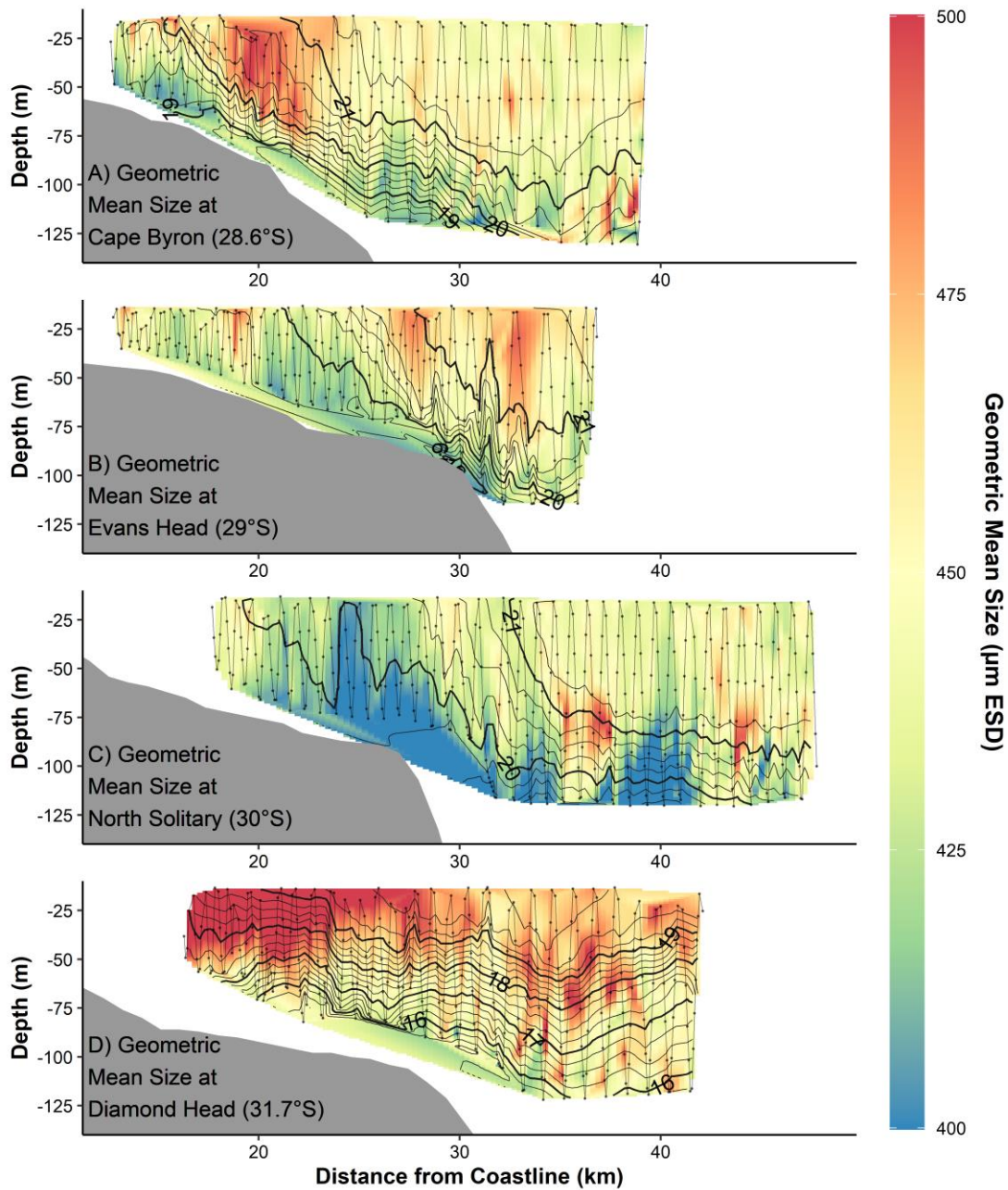


Figure 4 Geometric Mean Size (μm equivalent spherical diameter) of zooplankton from the four cross shelf transects (Figure 1). Transects were conducted from inshore to offshore with an undulating towed body with the path shown by the grey line with midpoints of each sample shown as dots. Temperature ($^{\circ}\text{C}$) isotherms are shown in black.

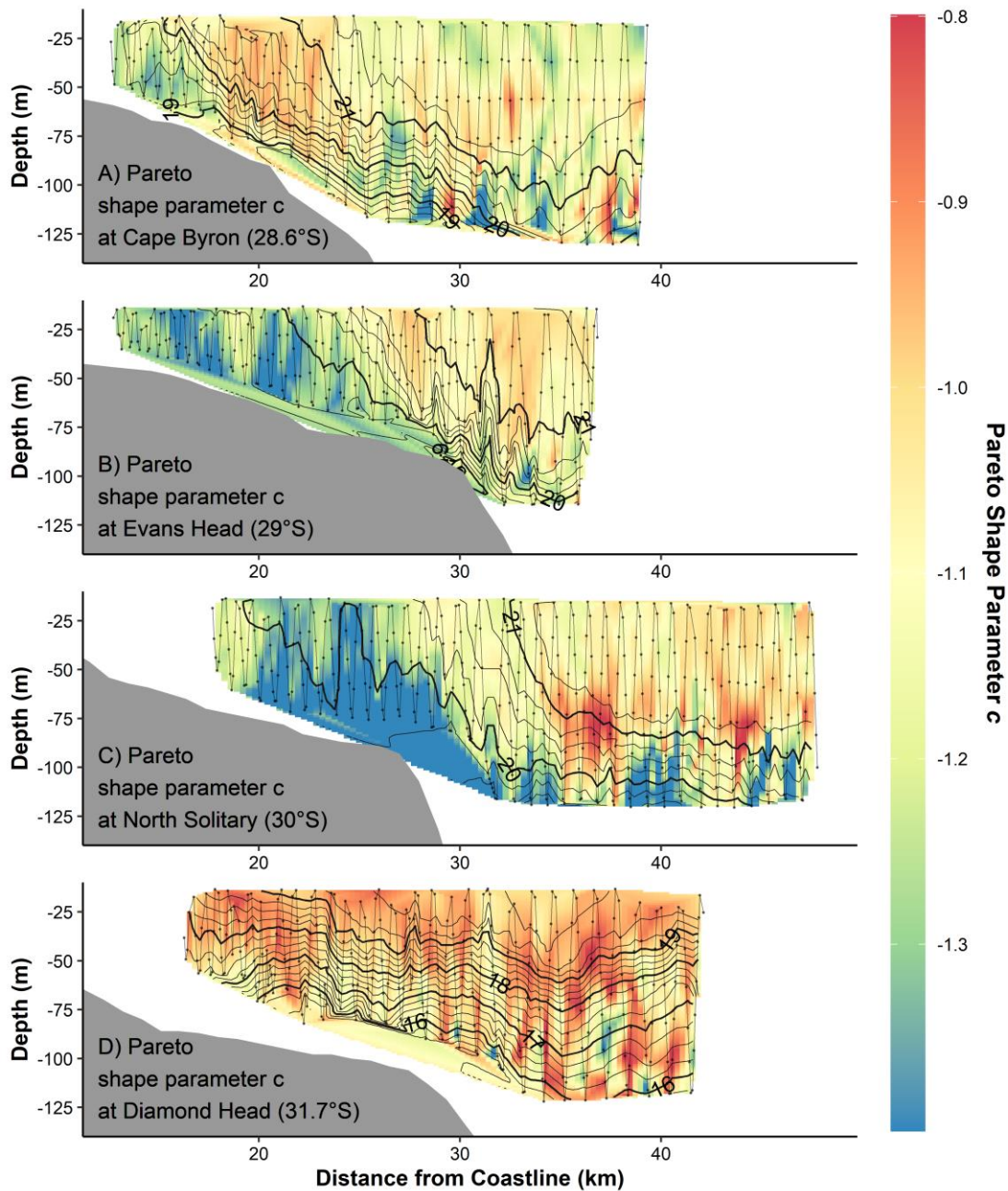


Figure 5 Interpolations of the shape parameter c from the Pareto distribution of zooplankton size from the four cross shelf transects (Figure 1). This is a robust estimate of the normalised biomass size spectrum slope (shown in Figure S7). Transects were conducted from inshore to offshore with an undulating towed body with the path shown by the grey line with midpoints of each sample shown as dots. Temperature ($^{\circ}$ C) isotherms are shown in black.

318 *Evans Head (29°S)*

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2 319 The transect slightly further south at Evans Head (29°S) did not go as far offshore as
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4 320 the other transects but was still largely influenced by the EAC which had a strong along-
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7 321 shore flow (1.47 m s^{-1}) centred 36.1 km from the coast, near the edge of the continental
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9 322 shelf (220 m seabed depth; Figure 2). The EAC showed offshore movement (0.27 m s^{-1})
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11 323 which increased with distance offshore (Figure S4). There was strong current driven uplift of
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13 324 the isotherms inshore of the EAC with the 21 °C isotherm rising to the surface from 70 m
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15 325 depth over 6 km and the 20 °C isotherm rising to the surface from 100 m depth over 15 km
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17 326 similar to the northern Cape Byron site (28.6° S).
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22 327 The zooplankton community was related to the water masses along the transect,
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25 328 especially in relation to water temperature. Around the front between the continental shelf
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27 329 water ($< 21 \text{ °C}$) and the warm ($> 21 \text{ °C}$) EAC water the zooplankton community showed a
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29 330 similar GMS of $\approx 450 \text{ }\mu\text{m}$ ESD to that observed at the northern Cape Byron transect but had a
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31 331 higher biomass and shallower pareto distribution shape parameter c (≈ -1 ; Figures 3, 4 & 5).
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33 332 In the cool inshore waters $< 20\text{°C}$, there remained high zooplankton biomass (Figure 3), but
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35 333 the community had shifted towards smaller particles which resulted in a steeper c (< -1.3 ;
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37 334 Figures 4 & 5).
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45 336 *North Solitary (30°S)*

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48 337 The transect at North Solitary (30°S) showed the strongest evidence of current
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51 338 driven uplift of any of the transects with the 21 °C isotherm rising to the surface from 70 m
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53 339 depth over 3 km and the 20 °C isotherm rising to the surface from 100 m depth over 10 km
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55 340 (Figure 3). The offshore portion of the transect continued to be dominated by the EAC which
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57 341 had a strong alongshore flow (1.59 m s^{-1}) centred 37.7 km offshore (310 m bathymetry;
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Figure 2). The EAC had slight onshore movement, in offshore waters 100-150m below the surface (0.15 m s^{-1} ; Figure S4).

Like the northern transects, the biomass of the zooplankton community generally decreased with distance offshore and with depth (Figures 3, S5 & S6). The EAC and further offshore, contained low zooplankton biomass with a shallow pareto distribution shape parameter c (-0.9) and GMS of $\sim 450 \mu\text{m}$ (Figures 3, 4 & 5). The 20°C isotherm appeared a strong boundary for zooplankton communities with zooplankton in water $< 20^\circ\text{C}$ having relatively low biomass and a much smaller GMS ($\sim 400\mu\text{m}$ ESD) resulting in a steeper c (< -1.3). This was particularly evident where the 20°C isotherm reach the surface $\sim 24 \text{ km}$ from the coastline, bringing with it a highly productive zooplankton community (Figures 4 & 5).

Diamond Head (31.75°S)

The most southern transect located at Diamond Head (31.75°S) was not influenced by the EAC which had separated from the coast to the north and was characterised by a more homogeneous water mass. Here, the alongshore velocities were low ($< 0.43 \text{ m s}^{-1}$, Figure 2) with low onshore movement of water (0.11 m s^{-1}) in the surface waters and offshore movement (0.27 m s^{-1}) in the deeper waters (Figure S4). There was minor uplift of the temperature isotherms with all isotherms rising approximately 20 – 40 m as they came onto the continental shelf. This uplift is likely caused by the separation of the EAC from the coast to the north, generating uplift through the creation of eddies near Diamond Head rather than current driven uplift observed at the northern EAC influenced sites (Roughan and Middleton, 2002; Schaeffer and Roughan, 2015).

The zooplankton community was not clearly related to water masses reflecting the more homogenous water mass here. Inshore, the zooplankton community was charactered

by larger individuals (GMS ~500 μm ESD; Figure 4) and had higher overall biomass which declined steadily with distance offshore and with depth (Figures 3, S5 & S6). The pareto distribution shape parameter c of the community was shallow over the whole transect (≈ 0.9 ; Figure 5).

Synthesis and Seasonal Context of the EAC

Satellite altimetry showed throughout the year alongshore velocity varies at our transects by approximately 0.25 m s^{-1} with the more northern sites having the fastest overall flow (Figure 6). The velocity at all sites slows in winter between April and August increasing in Spring (when our observations were taken) and Summer.

Both the EAC-influenced transects (three northern ones) and the transect in the separation zone (Diamond Head) showed that generally higher zooplankton biomasses were observed in continental shelf waters with declines offshore and with depth (Figures S5 & S6). Peaks in biomass were also observed at the front between the continental shelf waters and EAC waters (21°C isotherm; Figure 3). The transect at Evans Head did not show a noticeable decline in biomass with distance from the coast but this transect did not extend past the edge of the continental shelf where the declines were seen in the other 3 transects.

Three patterns in GMS were evident in our 4 transects. Cape Byron and Evans Head showed evidence of larger GMS around the front between the warm EAC and cooler inner shelf water (around the 21°C isotherm; Figure 4). North Solitary showed evidence of uplift with the small GMS community from deep uplifted to the surface. Diamond Head was very different with a more homogenous distribution of GMS although there was a trend of larger zooplankton inshore. The size structure of all sites was related to the GMS with steeper zooplankton size spectrum slopes in areas with smaller zooplankton (Figures 4 & 5). The

Pareto c shape parameter was highly correlated with the NBSS Slope but provided better fewer gaps (due to low numbers of particles) over the transects ($r = 0.934$, $t_{535} = 60.362$, $p < 0.001$, Figure S7).

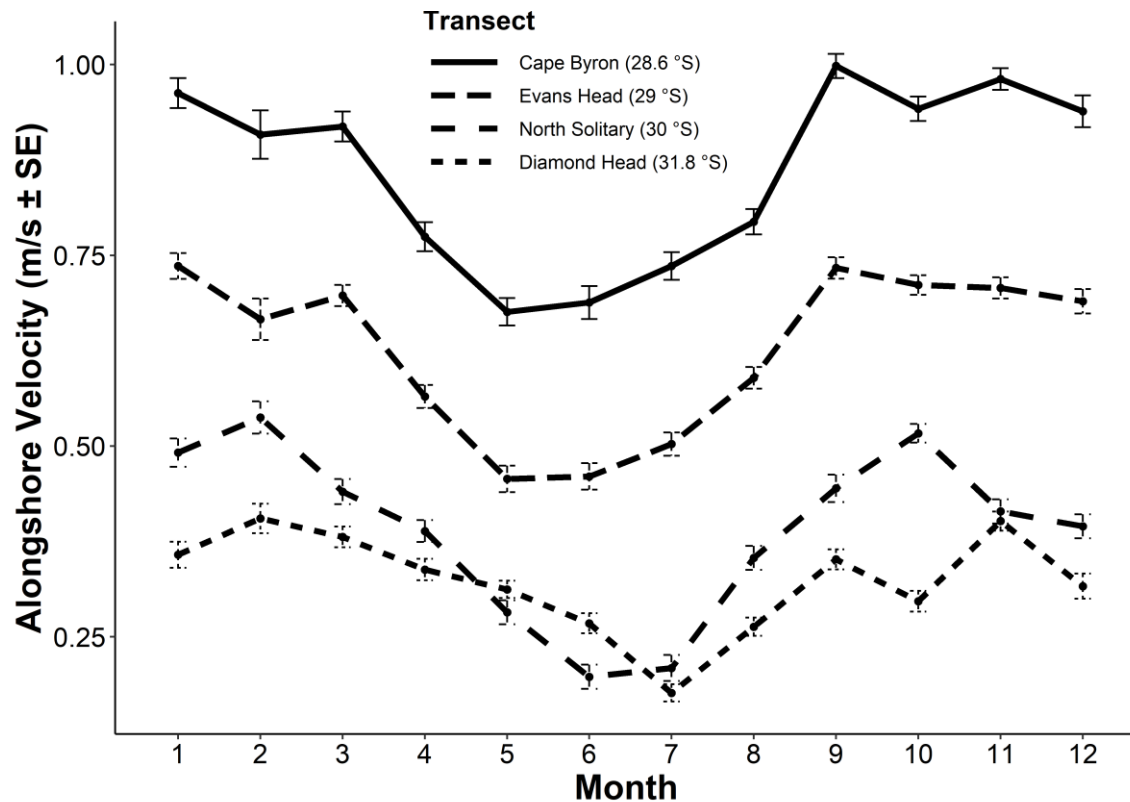


Figure 6 Seasonal changes in mean alongshore surface velocity at the Cape Byron (28.6°S), Evans Head (29°S), North Solitary Island (30°S) and Diamond Head (31.8°S) based upon 10 years of satellite altimetry data (2004 – 2013). Velocity data was downloaded for the eastern edge of each transect (Table 1) from the IMOS Data Portal (<http://imos.aodn.org.au/imos/>). The EAC separates from the coastline between approximately 28°S and 32°S (Cetina-Heredia *et al.*, 2014).

Global Synthesis

19 studies quantified the cross-shelf changes in zooplankton (including this study), revealing a broad consensus (Figure 7; Table S1), even though many studies were not influenced by a

western boundary current. Seven studies (including ours) reported abundance values for inshore and offshore and all found that abundance was higher in inshore regions compared to offshore regions. Six of these studies showed inshore areas abundance of 2.3 – 4.2 times higher than offshore values with one study from the eastern Bay of Biscay region finding a 22-fold difference (Sourisseau and Carlotti, 2006). For biomass, six of seven studies showed 1.5 – 4.1-fold greater biomass inshore compared with offshore (Figure 7; Table S1). The sixth study from the Western Mediterranean showed 20-fold higher biomass offshore compared to inshore values (Sabatès *et al.*, 1989).

In terms of size structure, 11 studies reported both inshore and offshore values with nine finding steeper zooplankton size spectrum slopes in inshore areas compared with offshore areas (Figure 7, Table S1). The southern Bay of Biscay and North Iberian Shelf studies were unusual in having a shallower inshore zooplankton size spectrum slope compared to the offshore areas (Nogueira *et al.*, 2004; Vandromme *et al.*, 2014).

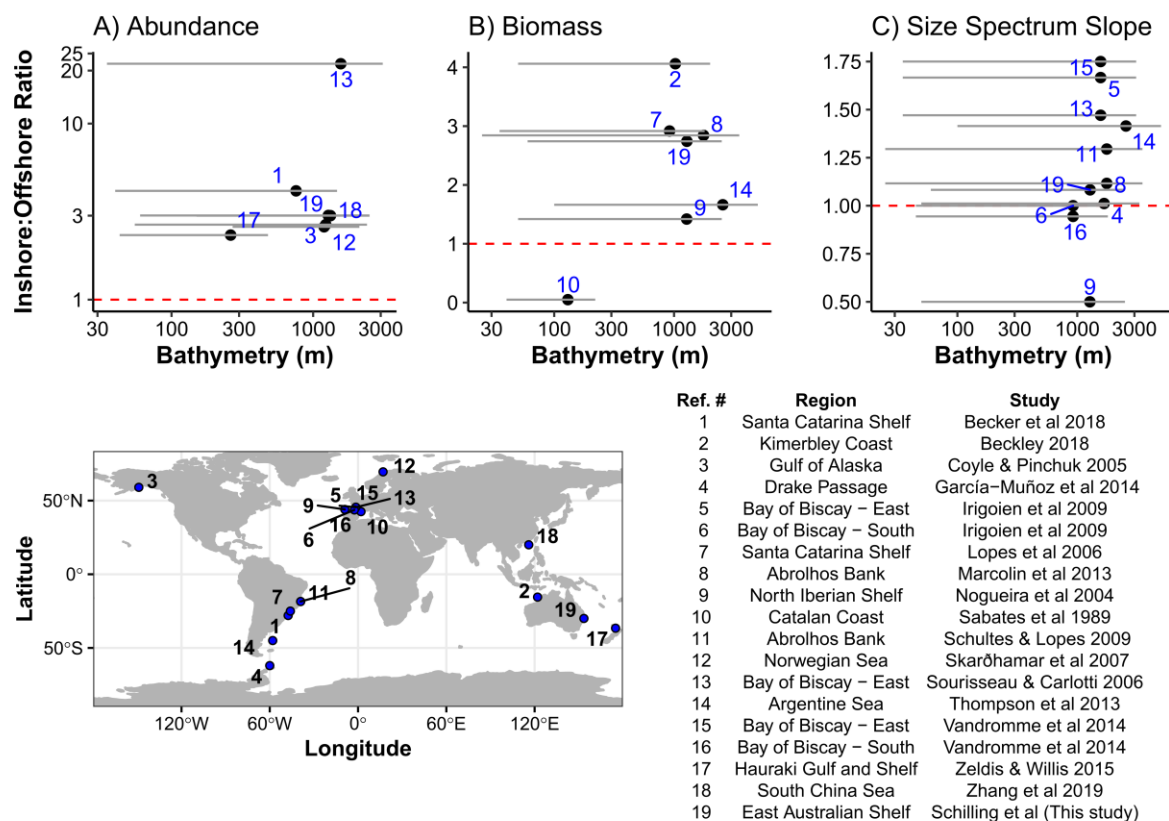


Figure 7 Summary of 18 previous studies investigating cross shelf patterns of zooplankton (#19 is the current study). The y-axis shows the ratio of the inshore to offshore reported values for zooplankton A) Abundance, B) Biomass, and C) the Size Spectrum Slopes. A ratio greater than 1 (red dashed line) means that the inshore region had a larger abundance/biomass or steeper size spectrum. Each numbered dot represents a study except for the studies in the Bay of Biscay which identified east and south as distinct region so they remain independent (Table S1; Irigoien *et al.*, 2009; Vandromme *et al.*, 2014). The x-axis represents the bathymetry range from each study with the dot on the mean value for that study. Note the differing y-axes and \log_{10} x-axis on a), and that not all studies are in western boundary current influenced locations.

430 Discussion

1
2 431 The size-spectrum of zooplankton provides important information about the transfer
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5 432 of energy from phytoplankton to fish, from which we can learn more about the fisheries
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7 433 supported by our continental shelves. We found consistent declines from inshore to
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10 434 offshore in zooplankton biomass and altered size-structure horizontally and vertically across
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12
13 435 the narrow continental shelf off eastern Australia. These trends in the zooplankton
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15 436 community are consistent with the patterns in zooplankton size-structure across other
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18 437 continental shelves (Figure 8) and are an outcome of cross-shelf flows and sporadic
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20 438 upwelling processes driven by ocean currents and coastal winds (Roughan and Middleton,
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23 439 2002; Everett *et al.*, 2014; Malan *et al.*, 2020).

24
25 440 Zooplankton biomass and mean size was generally constrained by the horizontal and
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28 441 vertical structure of the water column over the continental shelf. Peaks in zooplankton
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31 442 biomass coincided with the front between the continental shelf water and oligotrophic EAC,
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33 443 where the interaction of water masses often creates strong instabilities and vertical
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36 444 velocities producing a highly productive environment (Nakata *et al.*, 2000; Baird *et al.*,
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38 445 2008). Distinct from the warmer offshore EAC, the cooler shelf water revealed a
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41 446 zooplankton community with higher biomass, smaller geometric mean size and steeper size
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44 447 spectrum slope (Figure 8). These observations are consistent with higher chlorophyll *a* on
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46 448 the continental shelf (Everett *et al.*, 2014) and are likely driven by uplift of the cooler water
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49 449 due to the EAC interacting with the sloping topography (Schaeffer and Roughan, 2015). As
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51 450 zooplankton are the basis of many coastal food webs, this consistent supply of nutrients is
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54 451 an important factor in the distribution and abundance of planktivorous fish and the higher
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56 452 trophic level fisheries found on continental shelves (Pauly *et al.*, 2002; Truong *et al.*, 2017;
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59 453 Holland *et al.*, 2020).

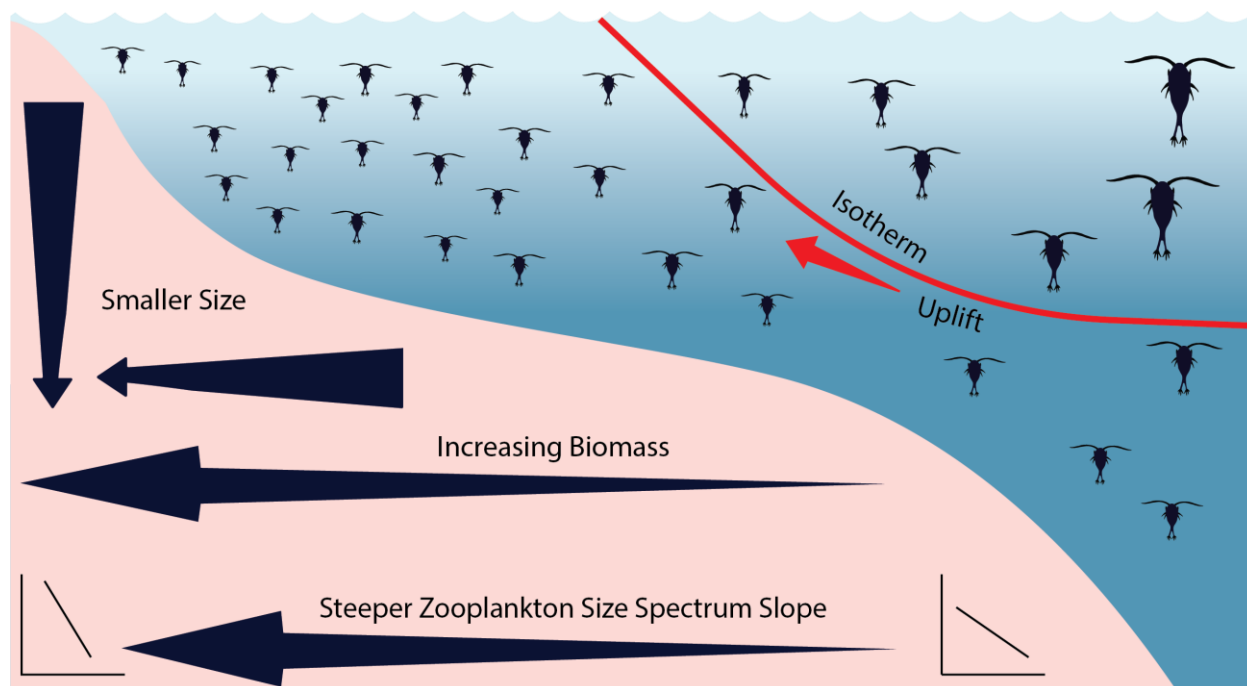


Figure 8 Conceptual diagram of the zooplankton community and how it changes over a continental shelf and with depth. Note all zooplankton are represented by copepods in this diagram.

Effects of the EAC on zooplankton

The separation of the EAC from the Australian coast, where it often bifurcates towards the east, forms a front between the northern oligotrophic waters, and the southern eutrophic Tasman Sea waters (Oke *et al.*, 2019). Offshore, this can separate distinct zooplankton communities (Baird *et al.*, 2008) and with impacts on abundance and diet of fish (Hobday and Hartmann, 2006; Revill *et al.*, 2009). On the continental shelf, the influence of the EAC separation on the distribution of zooplankton and fish is less well known. Our results suggest that along the three northern transects strongly influenced by the EAC, the continental shelf waters are influenced by uplift of deep nutrient-rich water (Roughan and Middleton, 2002), which drives the higher biomass of phytoplankton (Everett *et al.*, 2014) and zooplankton. Closer inshore, the effects of predation pressure from fish in the littoral

zone, particularly on temperate reefs, may remove larger plankton (Truong *et al.*, 2017; Holland *et al.*, 2020). Therefore a steeper zooplankton size spectrum slope could arise not only from increased production of smaller zooplankton (Guet *et al.*, 2016), but also by predation on larger zooplankton prey by planktivorous fish (Moore and Suthers, 2006).

In contrast to the northern transects, the southern transect (Diamond Head; 31.75°S) was south of the EAC separation zone and dominated by Tasman Sea water resulting in larger particles and a shallower zooplankton size spectrum slope. The same pattern of decreasing biomass offshore, and with depth in the water column occurred. In general, the Tasman Sea has an elevated nutrient concentration and higher zooplankton biomass compared to the oligotrophic EAC waters (Baird *et al.*, 2008). At our southern site there are two possibilities for this cross shelf gradient. Firstly, as there was minimal EAC influence at the southern site it is possible that the zooplankton are being retained on the continental shelf in this location due to weak flow in the lee of the EAC separation (Everett *et al.*, 2014; Schaeffer and Roughan, 2015). Secondly, this region has been shown to have high chlorophyll *a* production due to both wind driven and current driven upwelling with wind driven upwelling reliably generating increases in chlorophyll *a* (Everett *et al.*, 2014). This production may then flow through into the zooplankton community.

Previous research on the biophysical properties of oceanographic fronts in this region demonstrated an order of magnitude increase in the biomass of zooplankton in frontal regions (Baird *et al.*, 2008), similar to our observations of a increase in both zooplankton biomass and a steeper size spectrum slope at the front between the continental shelf water and warm EAC water. This increase in productivity around fronts may be a driver of previously observed relationships between fish abundance and frontal features (Fiedler and Bernard, 1987; Reese *et al.*, 2011).

Where there are interactions of currents (such as at fronts) or other upwelling promoting mechanisms, such as boundary currents, there is consistently higher zooplankton biomass and a steeper zooplankton size spectrum inshore compared to offshore (Figure 7, 8). Due to the increased production, there is typically high production of small zooplankton with increased abundance and biomass transferred to the larger size classes and higher trophic levels.

While this study provides the first high-resolution depth-resolved cross shelf transects, we did not sample in areas where the bathymetry was less than 50 m, meaning that the inshore water masses which may be more heavily influenced by terrestrial inputs, waves, wind-driven vertical mixing, and interactions with the coastline were not sampled.

Comparison to other studies

Our study showed a consistent decline in biomass horizontally (increasing distance from shore) and vertically (increasing depth in the water column) with the largest biomasses observed in the surface inner shelf waters. This was similar to almost all other comparable studies with the exception being the western Mediterranean which is not located in a boundary current system but included in our continental shelf comparison for completeness (Sabatès *et al.*, 1989). In the northeast Atlantic, the declining pattern of biomass across the shelf was attributed to coastal nutrient inputs and long residence times of water masses over the shelf break (Sourisseau and Carlotti, 2006; Irigoien *et al.*, 2009; Vandromme *et al.*, 2014). However, in the Brazilian Bight (southwest Atlantic), the increase in inshore zooplankton biomass was attributed to bottom intrusions of cooler nutrient rich South Atlantic Central Water (Pereira Brandini *et al.*, 2014). To the south, similar results were observed on the Abrolhos Bank where higher zooplankton biomass was observed on the

continental shelf due to the Brazilian Current interacting with the sea-floor, generating uplift and eddies which increased mixing over the continental shelf (Marcolin *et al.*, 2013).

In regions such as the southwest Pacific where our study was conducted, there are relatively small terrestrial influences compared to other sources of nutrients such as upwelling (Apte *et al.*, 1998; Dai and Trenberth, 2002; Pritchard *et al.*, 2003; Suthers *et al.*, 2011), and oceanographic drivers are important. Similar to the Brazilian Current and the Abrolhos bank, in the southwest Pacific the EAC interacts with the topography which in turn generates uplift of cooler water onto the continental shelf (Roughan and Middleton, 2002).

Steeper zooplankton size spectrum slopes in inshore regions is another feature of zooplankton communities which are consistently observed. In some regions the areas of steepest slopes have been linked to estuarine-derived nutrients (Moore and Suthers, 2006; Irigoien *et al.*, 2009), which are exploited by nearshore planktonic communities while steep slopes occurring further offshore are more temporally consistent and potentially due to local circulation patterns and retention (Vandromme *et al.*, 2014). Within the cross-shelf patterns of zooplankton, biomass and mean size also tend to decline with depth in the water column, possibly as a response to light availability (Aarflot *et al.*, 2019).

There are exceptions to the general trends in biomass, abundance and size spectrum slope. For example, Nogueira *et al.* (2004) showed a shallow inshore slope compared to offshore, which was attributed to nearby continental inputs increasing the proportion of large zooplankton possibly due to a eutrophic environment (Atkinson *et al.*, 2020). Some studies also show these onshore-offshore gradients are highly variable as observed in the East China Sea where onshore-offshore gradients in different years showed no consistency, but insufficient data was provided for these samples to be included in our analysis (García-Comas *et al.*, 2014).

While none of the previous studies have examined the vertical structure of continental shelf zooplankton communities in the same detail as horizontal structure, several studies have made similar conclusions to that observed in the current study. In the southeast Atlantic, a higher biomass of zooplankton was found above the pycnocline attributed to the increased chlorophyll-a in these waters (Marcolin *et al.*, 2013). In the northwest Atlantic, a similar strong association was found with a thermocline, with distinct zooplankton communities across the continental shelf separated by the 15° C thermocline (Turner and Dagg, 1983). Similar patterns in zooplankton size structure are observed around thermoclines in subtropical Australia (Suthers *et al.*, 2006).

Implications for the future

While the distributions and patterns observed in the current study align with global observations, they are only a snapshot and at other times of the year the patterns may vary. Our analysis of seasonal influence by the EAC showed that while there are seasonal variations in alongshore current velocity due to the EAC (Figure 6), the velocities observed in our study reflect a large portion of the year in terms of the velocities at our transect locations. Despite this, the EAC is strengthening and the increasing water temperatures in the southeast Australian region are already impacting the zooplankton communities as the region becomes increasingly tropicalised (Kelly *et al.*, 2016). At long term observing stations in the southeast Australian region, warming waters have resulted in a reduction in the spring phytoplankton bloom and > 60% decline phytoplankton growth during spring (Thompson *et al.*, 2009). These changes may have significant bottom-up effects on the overall distribution of zooplankton biomass, size structure and community composition on

continental shelves as zooplankton are impacted across the globe in similar ways

(Richardson, 2008).

Conclusions

Based upon the previous research into zooplankton distributions on continental shelves and the current study, we suggest a general process for the distribution of zooplankton on continental shelves influenced by boundary currents. This heuristic model includes expectations for future studies to examine, such as the decline in zooplankton biomass with distance offshore and with depth in the water column. This is potentially driven by western boundary currents which drive productivity on the shelf through uplift of nutrient rich waters. Future studies could answer these questions with more sustained monitoring of cross-shelf patterns throughout the year.

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588 Author Contributions

589 MEB & IMS conceived the study and collected the data. HTS, JDE, AS & PY analysed the data.

590 HTS wrote the first draft and all authors contributed to and approved the final manuscript.

591

592 Data Availability

593 All data used in this study are freely accessible. The data from the Southern Surveyor voyage

594 08/2004 is available from the CSIRO Data Trawler

595 (<https://www.marine.csiro.au/data/trawler/>). The long term environmental data is available

596 from the Australian Ocean Data Network (<https://portal.aodn.org.au/>). All code used for the

597 analysis in this paper is available in the GitHub repository

598 <https://github.com/HaydenSchilling/Inner-Shelf-Water>.

599

600 Competing Interests Statement

601 The authors declare no competing interests.

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