Progress in Oceanography

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

--Manuscript Draft--

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Abstract:	Continental shelves are the interface between society and the oceans, supporting over 90% of the world's fisheries through highly productive ecosystems. Boundary currents drive oceanographic processes on many continental shelves, yet it is uncertain how boundary currents influence the continental shelf zooplankton community. With an optical plankton counter and CTD mounted on an undulating towed body, we present the first high-resolution vertically resolved profiles of the particle (zooplankton) size structure across four transects over a continental shelf. Particulate (zooplankton) biomass was highest inshore, declining with increasing distance from shore and with increasing depth in the top 100m of the water column. In the region adjacent to the East Australian Current, uplift generated by either the EAC interacting with the continental slope or upwelling favourable winds, resulted in smaller geometric mean sizes and steeper size spectrum slopes. South of the EAC separation from the coast, the continental shelf water mass was more homogenous but still displayed the same horizontal and vertical patterns in particulate (zooplankton) biomass and mean size. These patterns are consistent with zooplankton distributions on other continental shelves where the inner-shelf has higher biomass of zooplankton with a steeper size spectrum slope compared to offshore. Inner-shelf zooplankton communities support important temperate reef ecosystems and coastal fisheries, through their consistently high biomass.
Suggested Reviewers:	Angus Atkinson, PhD Plymouth Marine Laboratory aat@pml.ac.uk Recently published on zooplankton size spectrum theory
	Catarina R Marcolin Universidade Federal do Sul da Bahia catmarcolin@gmail.com Published similar research in the southwest Atlantic
	Rubens Lopes University of Sao Paulo: Universidade de Sao Paulo rubens@usp.br Experienced zooplankton scientist
	Xiaoxia Sun Chinese Academy of Sciences

	xsun@qdio.ac.cn Recently published on biomass size spectra in the South China Sea.
Opposed Reviewers:	
Response to Reviewers:	See attached response document.

14 May 2021

Dear Prof Curchitser

Enclosed for your consideration is our revised manuscript, titled: “Vertically resolved particulate (zooplankton) biomass and size-structure across a continental shelf under the influence of a western boundary current”. This is a resubmission of PROOCE-D-21-00004. 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.

We received detailed comments from two reviewers which has led to substantial improvements in our manuscript. Among the 94 comments, the most helpful changes were:

- Suggestions to include more physical oceanographic data including cross-shelf transects of more variables. These have now been included as supplementary figures.
- Discussion of the likely zooplankton composition. We have sourced separate Continuous Plankton Recorder data from our study area to show the likely composition of the zooplankton, now shown in Figure 3.
- Clarifying the common driver of the globally consistent onshore-offshore patterns in zooplankton. We now explicitly discuss how this is facilitated by nutrient enrichment near the coast. This enrichment is from different sources but the resulting enrichment is the most likely driver of observed zooplankton patterns.
- Increased discussion of seasonality in the study region.

We look forward to your response,

Sincerely,

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Response to Reviewers **Schilling et al**

Thank you for the opportunity to respond to the reviews. This response letter is formatted to give each editor/reviewer comment (numbered) followed by a response to each comment in blue and quotes from the main text in *blue italics*. We received two comments from two reviewers with no additional comments from the editor.

Reviewer 1:

Comment #1: Zooplankton play important roles in marine ecosystem. The observation of biological oceanography is far behind the physical and chemical oceanography due to the limitation of the observing technique of biological variables. The authors presented the high resolution vertically resolved profiles of the zooplankton biomass and size structure across four transects over a continental shelf, and discussed the relationship between zooplankton and relevant physical processes, which provided important information on the zooplankton characteristics on the eastern continental shelf of Australia and insights of the zooplankton pattern over the continental shelf. However, the single cruise, the lack of the simultaneous chemical oceanographic observation, the lack of zooplankton taxa and statistical analysis make the mechanism more descriptive.

Response: We appreciate the reviewer highlighting the importance of our study in describing the zooplankton characteristics over the eastern continental shelf of Australia and acknowledge that our study is largely descriptive. This descriptive nature is due to the sampling design of 4 transects which may bias any statistical analyses due to autocorrelation. Rather than calculate spurious statistics we prefer to present the observed patterns. Remarkably, the cross-shelf patterns we observe seems to reflect other coasts around the world (Figure 8).

We have now incorporated more chemical oceanographic observations which we think provide more certainty in some of our findings and help to place the observations from our study in a broader seasonal context. The newly included chemical observations all provided in the supplementary material include cross shelf transects of Salinity, Nitrate, Silicate, Oxygen and Chlorophyll *a* all overlaid with temperature contours for comparison (Supplemental Figures 9, 10, 11, 12,13). Unfortunately, zooplankton composition was not analysed in the samples collected on this voyage for logistical reasons (primarily due to the initial focus on larval fish). We agree that taxonomic information would add further value (and now present some information on this in comment #6), but the biomass, abundance and size-distribution information we present nonetheless provides important information about energy transfer within the planktonic ecosystem.

Comment #2: 1) Zooplankton biomass is highest inshore, which declines with increasing distance from shore and with increasing depth in the water column. This is true for most continental shelves or transects from the coast to the open ocean according to the published work. One purpose is to relate the observations to previous research to propose a general concept of zooplankton size-structure on continental shelves globally. The continental shelf is different globally, if there is a globally general pattern, does that mean that the influence of the western boundary current is not the key process affecting the zooplankton community structure? Maybe different inherent mechanisms can be classified based on different locations, not necessarily one general concept globally.

Response: The common fundamental process that unites all studies is the nutrient enrichment that occurs in all near-coastal waters, due to many different upwelling processes (coastal winds, reverse Ekman, or topographic effects) and estuarine processes and run-off from land. Therefore, western boundary currents do have a major influence on coastal enrichment, but are not the only cause. This drives the ubiquitous "green-ribbon" (Lucas et al. 2011) in chlorophyll *a* observed along most coasts world-wide, and our study together with related work establishes a general pattern in zooplankton

size and abundance. We have now made a point in the discussion of how the general patterns in zooplankton are likely due to coastal nutrient enrichment which can be caused by both western boundary current among other causes. The discussion now states:
"These horizontal trends in the particulate (zooplankton) size-structure are consistent with the patterns in size-structure across other continental shelves and likely are an outcome of nutrient enrichment which tends to occur on continental shelves. This enrich can come from a variety of sources including cross-shelf flows and sporadic upwelling processes driven by ocean currents and coastal winds (Roughan and Middleton, 2002; Malan et al., 2020), estuarine process (Morris et al., 1995) or run-off from land (Correll et al., 1992)."

We have also added some discussion about how the cross-shelf gradients (produced as discussed above) are a key component of the observed zooplankton dynamics:
"Despite different regional dynamics, cross-shelf and vertical gradients in water-masses, here driven by the EAC and uplift, seem to be the dominant factor for the patterns observed at various locations worldwide."

Comment #3: 2) According to the previous research, the change of the vertical patterns of the zooplankton size related to the depth of the target area. For example, the zooplankton became larger with increasing depth (>100 m) in some areas. The depth of this research is about 100 meters or less, I think the authors should clarify that in the range of 0-100m, the size become smaller with the increasing depth.
Response: We have now clarified this point in the abstract, results and discussion. For example, the abstract now states:
"Particulate (zooplankton) biomass was highest inshore, declining with increasing distance from shore and with increasing depth in the top 100m of the water column."

Comment #4: 3) The survey was conducted in one week. Considering that one purpose of this work is to find a general concept, are there any evidences that can prove that the seasonal change is not dramatic in this area?
Response: There are substantial seasonal changes in the strength of the East Australian Current (faster in spring and summer, Fig. 2), and therefore in the frequency of upwelling (strongest in spring, Rossi *et al* 2014). We selected spring when many commercial fish spawn, but as shown in Fig. 8 these patterns seem to be ubiquitous regardless of season or location. It would be interesting in the future to compare these changes in other seasons in relation to seasonal cross-shelf distributions of chlorophyll. We expect the patterns in other seasons to be similar (i.e. in proportion to the cross-shelf chlorophyll gradient), and interestingly this effect is evident in our most southern transect off Diamond Head (i.e. less horizontal gradients). We have clarified the effect of seasonality in the Methods section. This section now reads:
"Along the continental shelf, particularly where the continental shelf narrows, the EAC has significant impact on shelf circulation (Schaeffer and Roughan, 2015). Current driven bottom friction leads to Ekman transport in the bottom boundary layer, moving cooler denser water up the slope, resulting in uplift of isotherms and upwelling (Schaeffer et al., 2014). These intrusion events have been shown to bring nutrient rich water into the euphotic zone, increasing nitrate (Rossi et al., 2014) and chlorophyll a concentration (Everett et al., 2014), and controlling vertical phytoplankton abundance and composition (Armbrecht et al., 2014, 2015). These EAC-driven upwelling or uplift events vary latitudinally rather than seasonally. Using a monthly climatology of altimetry over 12 years, Rossi et al. (2014) showed that the occurrence of these events is relatively consistent all year long north of the EAC separation ~32°S, and quite rare further south."

We have also identified the value of further sampling in terms of our seasonal understanding in the conclusions:
"Future studies could answer these questions with more sustained monitoring of cross-shelf patterns in zooplankton size structure throughout the year."

Comment #5: 4) The 21 °C isotherm is considered to be the dividing line for the change of zooplankton community characteristics. However, it seems not that clear for either biomass or particle size spectrum from the figures. Temperature, prey, depth, stability of the water mass, are all environmental factors that may affect zooplankton. It'll be ideal to conduct statistical analysis to discern the most critical factors that affect the size and biomass of zooplankton in the West Boundary Current area.
Response: Unfortunately, due the study design of 4 individual transects, the data are extremely autocorrelated with no true replicates and we were unable to run any statistical tests with confidence. As both reviewers have identified the 21C isotherm as not a very distinct boundary we have substantially removed our focus on this as a potential dividing line by deleting the discussion of this isotherm in the results and discussion.

Comment #6: 5) Due to the limitation of OPC, there is no taxa composition of zooplankton. In addition to fish mentioned in the article, predation among zooplankton is also an important factor that may cause the change of zooplankton size spectrum. That means the dominant zooplankton species or taxa are important for the size spectrum. Can you provide the background information of the zooplankton composition in this area?
Response: Information on zooplankton composition in this study area is limited and there are no zooplankton composition samples matching the spatial and temporal resolution of the study. To overcome this, we have now included the Continuous Plankton Recorder data from the spatial region of our study but from different times (2009 – 2018) to show the monthly averaged zooplankton composition. Assuming 2004 was of typical zooplankton composition this shows that in September almost 80% of zooplankton individuals are copepods and with only small proportions of other taxa. The composition is relatively stable in the adjacent months (August-October) and we are confident this represents the 2004 community sampled in our paper. We have added this detail to the methods and results. The methods section now states:
"As zooplankton was not sampled for taxonomic investigation in the current study, in order to understand the likely composition of zooplankton at this time we explored Continuous Plankton Recorder (CPR) Data (Richardson et al., 2006). We extracted all CPR zooplankton abundance data within 28 – 32° S and 152 -155° E from the Australian Ocean Data Network (https://portal.aodn.org.au/). Using the 'higher taxonomic groups classifications" we calculated the average composition (by abundance) of zooplankton for each month in the study region."

The results section now states:
"Based upon 455 CPR observations within our study region, ranging from 2009 – 2020, we found some variation in zooplankton composition between months although copepods were always the most abundant. Within months there was smaller variation and during our sampling period, samples are typically dominated by copepods (> 90%; Figure 3)."

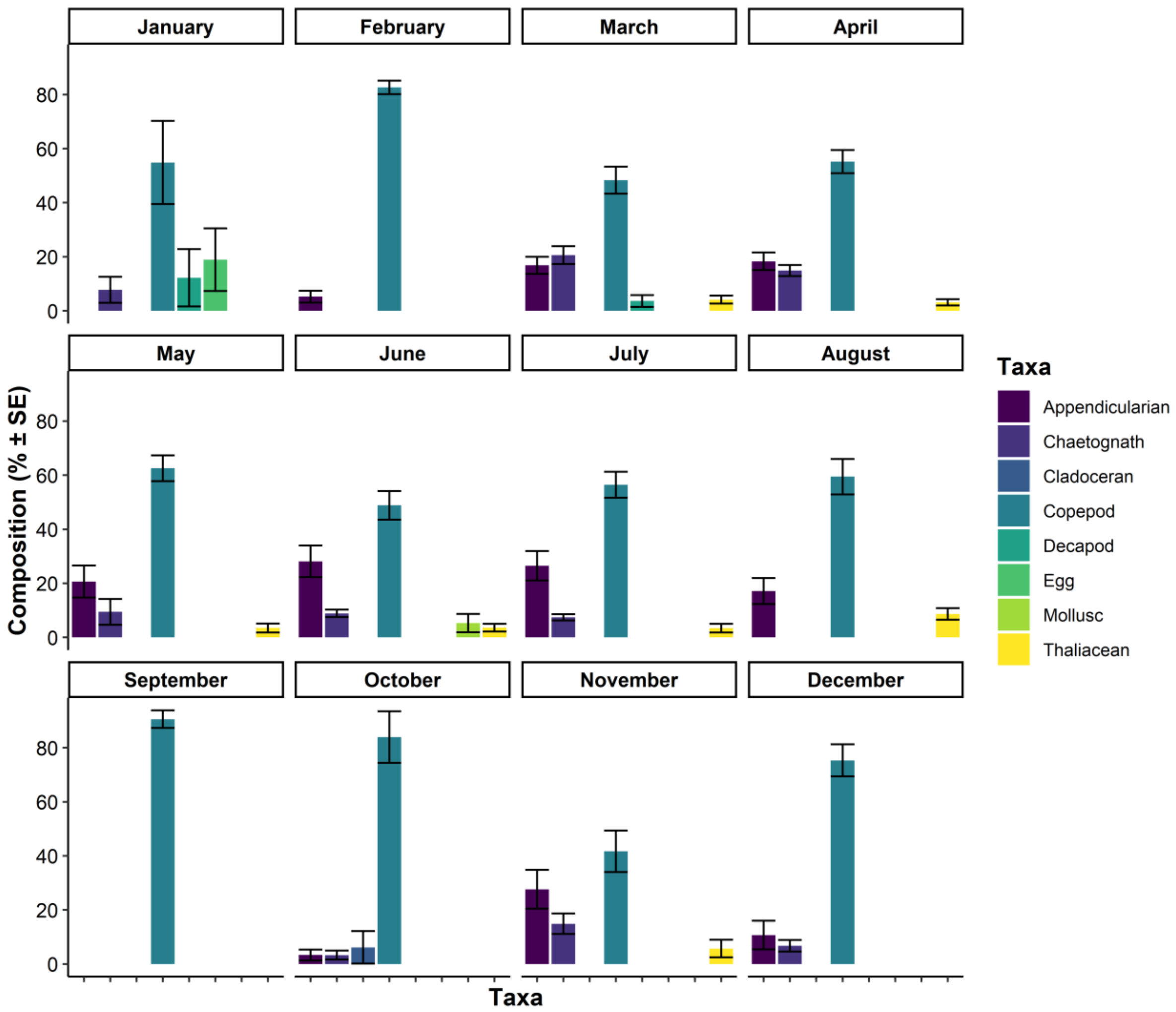


***Figure 3** Monthly zooplankton composition based upon continuous plankton recorder data (n = 455) in eastern Australia (28 – 32°S, 152- 155°E, 2009 - 2020). Error bars show ±1 standard error. Note Taxa are also arranged alphabetically along the x-axis and taxa <3 % in all months were omitted from the plots.*

Comment #7: 6) Please check the minor problems, such as, P2L33, resulting in "zooplankton ecosystems", usually we don't say zooplankton ecosystems.
Response: This phrase has been deleted. Several other minor issues have been resolved with full details provided in the following comments.

Comment #7: P7L146, "a research voyage on the on the RV Southern", delete "on the", etc. Please check other parts of the manuscript.
Response: The repeated "on the" has been deleted.

Comment #8: 7) P31L531-533, "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)." Light is the limiting factor of phytoplankton, don't understand why the light availability could affect zooplankton.
Response: This section has been deleted.

<u>Reviewer 2:</u>

Comment #9: This study presents an interesting dataset of spatial patterns of zooplankton in pelagic ecosystems associated with the East Australian Current. Study motivation and sampling design seem to be proper and interesting enough. However, overall data analyses and what has been done with results constitutes basic research. In general the study could be much improved and strengthened in itself.

Response: We acknowledge that our research may be considered "basic research" as this research has not yet been conducted in the East Australian Current region, and in general cross-shelf studies are rare in the literature, including none in the southwest Pacific. By including 18 international studies a general pattern emerges at the crucial interface of oceans and society. This is also the first paper to present depth resolved transects of zooplankton size-structure across a continental shelf anywhere in the world. We have improved the current study by now discussing the zooplankton composition based upon continuous plankton recorder data and also include a wider range of physical oceanography data in the supplementary as suggested. For further details on how the study has been improved see the following comments.

Comment #10: Below I point out a few general comments, while more specific are included in the pdf.

Response: Thank you for the comments, we have responded below to all the general and specific comments.

Comment #11: - The title says 'zooplankton' but in truth you are analyzing particulates (plankton and detritus), please focus particulates or change the title.

Response: The title has been changed to *"Vertically resolved particulate (zooplankton) biomass and size-structure across a continental shelf under the influence of a western boundary current"*

We know from previous research in this area has shown that the vast majority of particulates are zooplankton with only minor amounts of marine snow or detritus (Suthers et al 2004, Suthers unpublished data) which is an important part of the planktonic ecosystem. We are including zooplankton in brackets after particulates to help the readership both understand and find the paper if they are interested in zooplankton dynamics. With such low levels of detritus, we can assume the OPC is accurately quantifying zooplankton (Zhang et al 2000).

Suthers, I. M., Taggart, C. T., Kelley, D., Rissik, D., & Middleton, J. H. (2004). Entrainment and advection in an island's tidal wake, as revealed by light attenuance, zooplankton, and ichthyoplankton. *Limnology and oceanography*, *49*(1), 283-296.

Zhang, X., Roman, M., Sanford, Aa, Adolf, H., Lascara, C., Burgett, R. Can an optical plankton counter produce reasonable estimates of zooplankton abundance and biovolume in water with high detritus?, *Journal of Plankton Research*, Volume 22, Issue 1, January 2000, Pages 137–150, https://doi.org/10.1093/plankt/22.1.137

Comment #12: - The manuscript requires greater supporting data to justify the claims made.

Response: We respond below to the specific areas where the reviewers suggests additional data are needed. This includes the cross-shelf CTD data such as salinity, nitrate, silicate and oxygen. We have also added information on likely zooplankton composition. See comment #6 for more information.

Comment #13: - The manuscript requires restructuring to improve the flow.

Response: In line with the reviewer suggestions (detailed below) the manuscript has been restructured. For full details see later responses.

Reviewer 2 comments from annotated pdf

Comment #14: Line 45: Introduction: Summary

- Please restructure to improve flow (physics, nutrients, chl a and particulates/zooplankton)
- - Please include how top down processes could influence particulate size structure

Response: We thank you for these suggestions. We were concerned if we started off with a physics to ecology structure, the reader would not find zooplankton until the 3rd paragraph. Our paper is about zooplankton size-structure, in a physical-nutrient-chlorophyll context rather than about coastal oceanography. With respect, we feel this paper benefits more from the present structure which highlights the biological and ecological importance of firstly continental shelves followed by zooplankton. We have included some additional information in these first paragraphs, about how top-down processes could influence particulate size structure.

The new text is:
"Top-down pressure from larger predators can also increase the steepness of the size spectrum as increase the mortality rate of the zooplankton, thereby decreasing the efficiency of energy transfer along the spectrum (Moore and Suthers, 2006; Rossberg et al., 2019)."

Comment #15: Line 49: High chlorophyll a concentrations doesn't always translate to high primary productivity. High rates of primary productivity increase ecosystem productivity...

Response: This line has been rephrased to read
"These fisheries are supported by high primary productivity (Bakun and Weeks, 2008; Mackinson et al., 2009), often enhanced by coastal processes including upwelling, boundary currents and eddies (D'Croz and O'Dea, 2007; Patti et al., 2008)."

Comment #16: Line 50: References

Response: References have been added, see above comment (#15) for new text.

Comment #17: Line 52: Requires references

Response: Reference add, this line now reads:
"The high chlorophyll a levels often observed on the continental shelf, particularly the inner shelf (Lucas et al., 2011a, 2011b) are a key driver of zooplankton communities which are a key resource for fisheries (Mitra et al., 2014)."

Comment #18: Line 58: Insight into what?

Response: This sentence has been changed to:
"the size frequency distribution of a community can provide valuable insight into the trophic dynamics of a community (Blanchard et al., 2017)"

Comment #19: Line 64: delete "all"

Response: deleted.

Comment #20: Line 66: and predation

Response: Predation is mentioned at the beginning of this sentence. It reads:
"The size spectrum implicitly reflects the outcome of 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)"

Comment #21: Line 68: Here you identity environmental variables that are important to zooplankton size structure. Need to follow through and present this information in this study.
Response: As requested we now present information on environmental variables in the current study. We discuss the CTD sampled variables of Nitrate, salinity, oxygen, silicate in the results of each transect. The cross-shelf figures are also now available in the supplementary as Figures S9-S13. Temperature was already included in most of the plots as contour lines.

Comment #22: Line 69: Are there any other variables that have been found to explain variation in particle size-spectra?
Response: Size spectra are essentially a visualisation of the community response to any environmental factors, integrating many ecological processes as we discussed in the above sentences. We do not think it is worthwhile discussing individual instances of environmental variables being linked to size spectrum and would rather discuss the interpretation of the size spectra and how these may relate to environmental variables.

This section now reads:
"While there is variability in interpretations of size spectra depending on the size of particles in the spectrum due to sampling efficiency and natural 'dome shapes' in some communities (Marcolin et al., 2013; Rossberg et al., 2019), within the mesozooplankton size range (≈0.2 – 3mm), the elevation of the spectrum reflects the environmental effects which overall primary production and biomass of a community (Moore and Suthers, 2006; Zhou, 2006). Higher primary production and biomass tends to result in a higher elevation (or intercept) with such impacts demonstrated with nutrient input in both estuarine and pelagic ecosystems (Moore and Suthers, 2006; 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). Top-down pressure from larger predators can also increase the steepness of the size spectrum as increase the mortality rate of the zooplankton, thereby decreasing the efficiency of energy transfer along the spectrum (Moore and Suthers, 2006; Rossberg et al., 2019)."

Comment #23: Line 69: Should also consider how slope values are related to the size of range of particles studied (Marcolin et al 2013).
Response: This is a good point, we have made clearer we are referring to the mesozooplankton size range. This section now reads:
"While there is variability in interpretations of size spectra depending on the size of particles in the spectrum due to sampling efficiency and natural 'dome shapes' in some communities (Marcolin et al., 2013; Rossberg et al., 2019), within the mesozooplankton size range (≈0.2 – 3mm), the elevation of the spectrum reflects the environmental effects which overall primary production and biomass of a community (Moore and Suthers, 2006; Zhou, 2006)."

Comment #24: Line 80: Include biophysical processes that influenced observations.
Response: This information has now been included. This section now reads:
"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, most often in the lower salinity, higher chlorophyll a coastal water, indicating potential effects of freshwater discharge (Sourisseau and Carlotti, 2006; Irigoien et al., 2009; Vandromme et al., 2014)."

Comment #25: Line 82: Why is this important? Identify the need for cross-shelf vertically resolved observations of particulates.
Response: This line has been rephrased to highlight the need for cross-shelf vertically resolved observations. The line now reads:
"Fewer studies have examined the vertical patterns of zooplankton on continental shelves and this remains a key knowledge gap despite widespread recognition of variation in vertical distributions of zooplankton often attributed to diel vertical migration (Lampert, 1989), and the 3-dimensional influences of continental shelf oceanography (Schaeffer et al., 2013)."

Comment #26: Line 84: What is it about the thermocline influences the distribution of particles.
Response: This has been reworded, the thermocline was not attributed to any differences in the original paper and was merely used by the original authors to highlight difference water masses. The new line is: "During late summer, in the northwest Atlantic, the vertical zooplankton distribution was strongly influenced by water mass with distinct zooplankton communities in the observed warmer and colder water masses (Turner and Dagg, 1983)."

Comment #27: Line 87: Contents of this paragraph does not lead to this concluding sentence. There is a number of studies that document the effects that oceanography have on zooplankton/particulate communities.
Response: This sentence has been rewritten to better reflect the paragraph. It now reads:
"As observations of vertical patterns in zooplankton communities on continental shelves remain uncertain in many regions of the world, it is important to demonstrate how oceanographic features including boundary currents influence the zooplankton community in shallow coastal waters."

Comment #28: Line 90: The following two paragraphs should come earlier on as they are the primary mechanisms (bottom up drivers) of shelf ecosystem productivity. Add context of:
- physical properties (flooding/upwelling/downwelling/ekman/fronts/uplift/temp/sal/ect)
- nutrients
- aggregation

Response: This is very similar to comment #14 (also from reviewer 2). We were concerned if we started off with a physics to ecology structure, the reader would not find zooplankton until the 3rd paragraph. Our paper is about zooplankton size-structure, in a physical-nutrient-chlorophyll context rather than about coastal oceanography. With respect, we feel this paper benefits more from the present structure which highlights the biological and ecological importance of continental shelves followed by zooplankton.

Comment #29: Line 98: Need to present this supporting information.
Response: This is now supported by references to Schaeffer et al (2013), Everett et al (2014) and Kobari et al (2018). The line now reads:
"These processes often facilitate a nutrient and productivity gradient from oligotrophic WBCs across the continental shelves into the coast (Schaeffer et al., 2013; Everett et al., 2014; Kobari et al., 2018)."

Comment #30: Line 103: rephrase paragraph - along shelf flows are the primary mechanisms responsible for cross shelf flow dynamics.
Response: This section has been rephrased. It now reads:
"Within both eastern and western boundary currents, cross-shelf flows are often driven by along shore flows and mesoscale oceanographic features (Malan et al., 2020). Cross shelf flows are usually in smaller in magnitude than along-shelf flows but have a disproportional impact on shelf water properties such as plankton and fish distribution (Brink, 2016)."

Comment #31: Line 128 (Methods): Restructure to describe:

- context of the voyage in relation to seasonal variation in oceanography
- Characterise the seasonal variation in EAC dynamics in area of interest (SSH, SST, velocity, chl a) (Is there any data from IMOS moorings that be used w sat data to do this ?)
- Observed vertically resolved cross shelf plots of temperature, salinity, nutrients, chl a/fluorescence, particulates/zooplankton
- Actual zooplankton samples for community composition information would help verify cross shelf plots (are the RMT samples available)?

Response: We have restructured the methods section as suggested. We now first address the voyage context in terms of seasonal oceanographic variation. The typical oceanographic features in this region including the EAC are now described before we the use of satellite SST and altimetry data to investigate the seasonality in both oceanography and zooplankton composition at our sampling locations. This section now includes increased discussion of the seasonal dynamics of the EAC and chlorophyll production.

Following the discussion of seasonality, we introduce the sampling procedures including the cross shelf transects with both the SeaSoar and CTD. Then we detail the use of the OPC to generate zooplankton size structure data. Finally, we provide the methods for the global comparison.

The requested vertically resolved plots of temperature, salinity, nutrients, chlorophyll *a* and zooplankton are now all provided.

Actual zooplankton samples for community composition information are not available for this cruise as they have not been sorted for taxonomic composition, only fish larvae were sorted as part of Mullaney *et al.* (2014). Instead, we have provided the likely zooplankton composition from the continuous plankton recorder data within the study area, see comment #6 for more information.

Mullaney, T.J., Gillanders, B.M., Heagney, E.C. and Suthers, I.M. (2014), Entrainment and advection of larval sardine, *Sardinops sagax,* by the East Australian Current and retention in the western Tasman Front. Fish. Oceanogr., 23: 554-567. https://doi.org/10.1111/fog.12089

Comment #32: Line 153 (Figure 1): Need to add legend for velocity strength, also include SSH and Chl a plot here.

Response: A legend for velocity strength has been added to Figure 1. A plot of SSH and Chl has now been added to the supplementary as Figure S1.

The revised Figure 1 is:

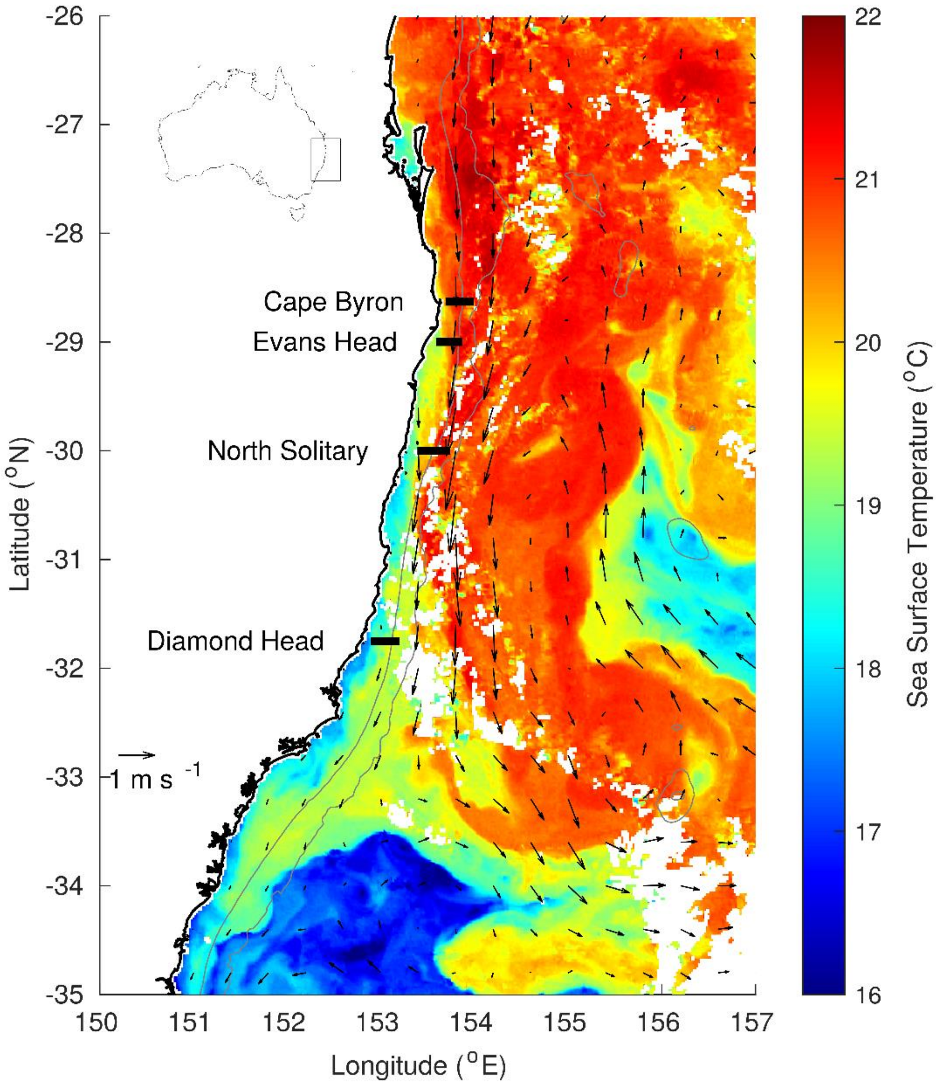


Figure 1 *Locations of the four cross shelf sections which were sampled in September 2004. The sea-surface temperature for 6th September 2004 is shown in colour with velocity arrows from satellite altimetry shown with black arrows. Grey isobaths represent 200 and 2000m depths.*

The new Figure S1 is:

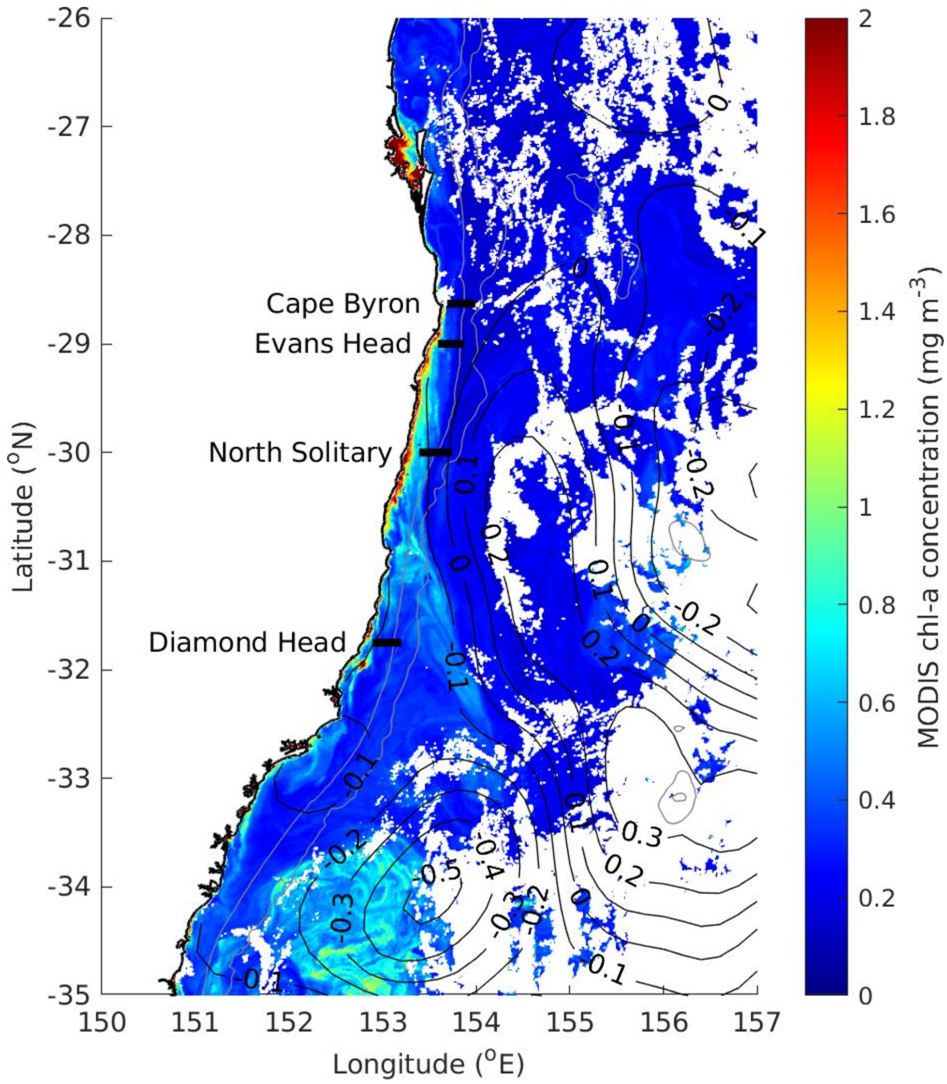


Figure S1 *MODIS Chlorophyll a (mg m^{-3}) in the region during our study showing low amounts of Chlorophyll at all the transect sites (black lines) during our study. Black contour lines connect areas of equal sea surface height anomaly.*

Comment #33: Line 172 (Table 1): Add a day night field and add diel timing of transects to discussion
Response: We have added day/night information to the caption of Table 1 (local time is already in table) and added some discussion of diel timing in the discussion. The new text reads:
"While this study provides the first high-resolution depth-resolved cross shelf transects, it is limited to the top 100m of the water column and there may be some influence of diel vertical migration of zooplankton on the vertical distribution. Despite this possibility we think the results are robust as two of the samples were conducted at night and two during the day with all four transect showing similar vertical gradients in particulate (zooplankton) properties."

Comment #34: Line 210: Seasonal variation and cross shelf plots of chlorophyll required in this study
Response: Cross shelf plots of chlorophyll *a* are now included in the supplementary material (Figure S11). These plots show overall low concentrations with minimal changes in chlorophyll across the transects. All transects showed between 1 and 1.5 mg m^{-3} with slight decreases with depth. Seasonal variation in surface chlorophyll *a* in this region was extensively investigated in Everett et al (2014) based upon satellite data and it shows that the chlorophyll *a* values observed in our study are typical of the region (within 1 SD of the geometric mean chlorophyll *a* values). Chlorophyll *a* does

typically have a spring bloom in but in the latitudinal region in the current study the mean chlorophyll in spring is typically lower than in winter and the spring is more of a moderate bloom (typically 27 -79 % increase on the annual average). The major spring bloom and seasonality patterns occurs to the south of our study (south of 32°S). Some of this information has now been highlighted better in our manuscript. The introduction now reads:
"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 creating consistent observations where the spring bloom is typically south of 34°S with the northern areas having more consistent chlorophyll a levels (Everett et al., 2014), yet there are no studies investigating the influence of the East Australian Current on higher trophic levels including zooplankton."

For the reviewer we are here providing Figure 4 from Everett et al, showing the long term time series of chlorophyl in this region. Showing that spring (September) 2004 is largely typical. We have added the following line to the methods section:
"The observed chlorophyll a levels in the area are also typical of those observed in September (Everett et al., 2014)."

J.D. Everett et al. / Progress in Oceanography 120 (2014) 340–351 345

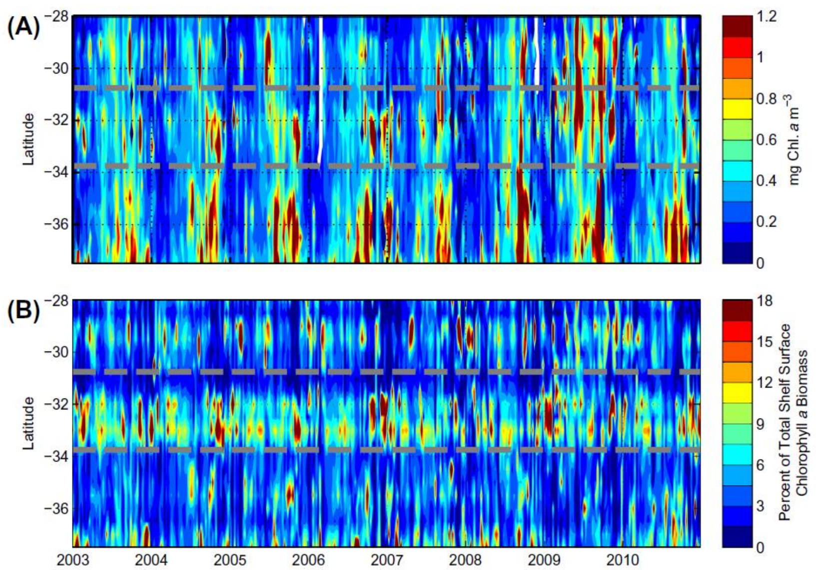


Fig. 4. (A) Mean Chl. *a* (8-day composite) for all latitudinal bands within the study domain (2003–2010) and (B) Percentage of total shelf Chl. *a*, for each latitudinal band (2003–2010). Total shelf Chl. *a* is the sum of all pixels on the shelf within each latitudinal band. The data is presented as a percentage of total shelf Chl. *a* for each time-step. The white sections represent missing data and the dashed grey line indicates the boundaries of the northern, central and southern zones as defined in the results.

The typical nature of 2004 is also shown in Figure 5a of Everett et al, again pasted below:

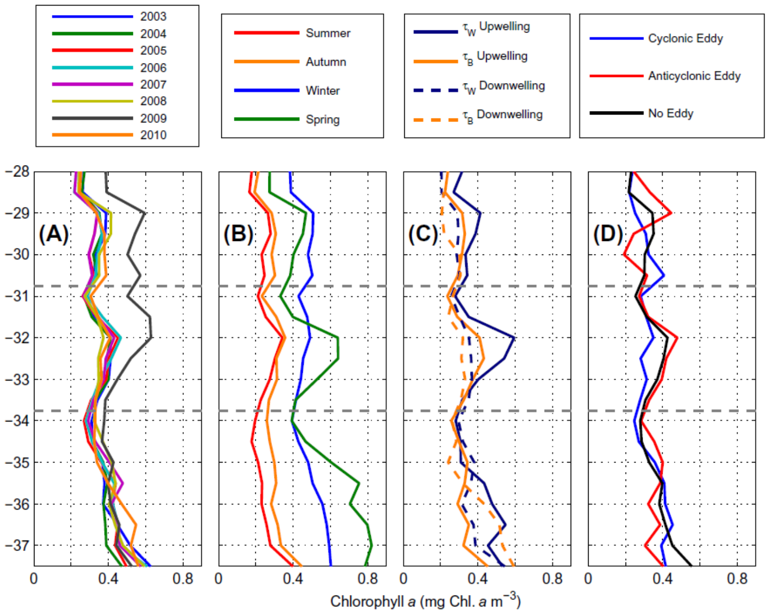


Fig. 5. Mean Chl. *a* for each latitudinal band presented as a temporal-average for (A) Year, (B) Season, (C) Upwelling and downwelling-favourable wind (τ_W) and bottom (τ_B) stress and (D) Eddy encroachment (Eddy edge <50 km to the continental shelf). The dashed grey line indicates the boundaries of the northern, central and southern zones as defined in the results. Due to the availability of output from BRAN, bottom-stress and wind-stress are calculated for 2003–2008. The Chl. *a* and eddy characteristics are calculated for the period 2003–2010, in order to use all the available data.

Comment #35: Line 215: I'd prefer OPC observations referred to as particulates and in-situ observations of zooplankton (RMT net samples) used to verify OPC observations. Is this possible?
Response: The zooplankton samples collected in this voyage have not been inspected for taxonomic composition (except larval fish) but some samples were independently analysed with a lab based OPC with the resulting biomass and size spectrum estimates comparable to that observed in our study with the towed OPC (Mullaney et al 2014). While being sorted for larval fish there was no noticeable sediment or inorganic detritus.

Previous plankton sampling in the region in which samples were inspected onboard the voyages has shown that inorganic particulate matter is extremely rare (<1%) and almost all collected "particles" consist of whole or fragmented zooplankton with it being likely that significant fragmentation of zooplankton is occurring in the net during the collection process. This fragmentation problem is not relevant for the towed OPC samples and can be seen as an advantage. While we are confident >95% of particles from the OPC are in act zooplankton and if not they would be part of the planktonic ecosystem comprising of marine snow which is an essential part of the carbon cycle (Turner, 2015).

Previous work in this region (including this OPC dataset) has shown that zooplankton biomass modelled off the OPC data correlates significantly with biomass derived from the CPR despite the methodology differences (White 2018). This lends additional support the argument that the majority of 'particles' measured are in fact zooplankton. As a compromise, we now refer to the 'particles' as particulates (zooplankton).

Mullaney, T.J., Gillanders, B.M., Heagney, E.C. and Suthers, I.M. (2014), Entrainment and advection of larval sardine, Sardinops sagax, by the East Australian Current and retention in the western Tasman Front. Fish. Oceanogr., 23: 554-567. https://doi.org/10.1111/fog.12089

Turner, J. T. (2015). Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. *Progress in Oceanography*, *130*, 205-248.

White (2018) The spatial distribution of zooplankton production in the western Tasman Sea: A size-spectra approach. Masters Thesis (UNSW Australia) http://handle.unsw.edu.au/1959.4/60494

Comment #36: Line 224: Biovolume is commonly used in the literature, useful for comparisons and to be consistent. Abundance would be a useful metric to include as well for ecological and global comparison purposes.

Response: We have now included plots of cross-shelf Abundance as supplementary material as it is highly correlated with biomass (and biovolume) and geometric mean size (as expected).

We have retained the original wording of biomass for the majority of our paper for 4 main reasons.

1. Biomass aligns with the recently published compilation of zooplankton data in Australia (including LOPC and OPC derived biomass). This database is detailed here: McEnnulty, F.R., Davies, C.H., Armstrong, A.O. *et al.* A database of zooplankton biomass in Australian marine waters. *Sci Data* **7,** 297 (2020). https://doi.org/10.1038/s41597-020-00625-9
2. Biomass is more readily understand and is more tangible to marine scientists in general, particularly those concerned with ecosystem modelling which often uses biomass as a key input parameter (eg. Ecopath models are built upon biomass)
3. Biomass is also commonly reported in the literature for OPC/LOPC, for example:
    a. Espinasse, B. et al. Conditions for assessing zooplankton abundance with LOPC in coastal waters. Progress in Oceanography 1–0 (2017) doi:10.1016/j.pocean.2017.10.012.
    b. Kwong, L., Suchy, K., Sastri, A., Dower, J. & Pakhomov, E. Comparison of mesozooplankton production estimates from Saanich Inlet (British Columbia, Canada) using the chitobiase and biomass size spectra approaches. Mar Ecol Prog Ser 655, 59–75 (2020).
    c. Krupica, K. L., Sprules, W. G. & Herman, A. W. The utility of body size indices derived from optical plankton counter data for the characterization of marine zooplankton assemblages. Continental Shelf Research 36, 29–40 (2012).
4. Due to the conversion of ESD to biomass assuming plankton have the density of water, our biomass value (mg m^{-3}) is directly convertible to biovolume (mm^3 m^{-3}) and we have added this information to the legend of the cross-shelf biomass plot and made specific reference to this in the methods section.

The new text now reads:

"Under our assumption that our particles have the density of water, 1mg is therefore equivalent to 1mm^3, resulting in our $Biomass\ (mg\ m^{-3})$ being equivalent to biovolume (mm^3 m^{-3}) and we have labelled our plot axes as such."

The revised Biomass/Biovolume plots is as follows:

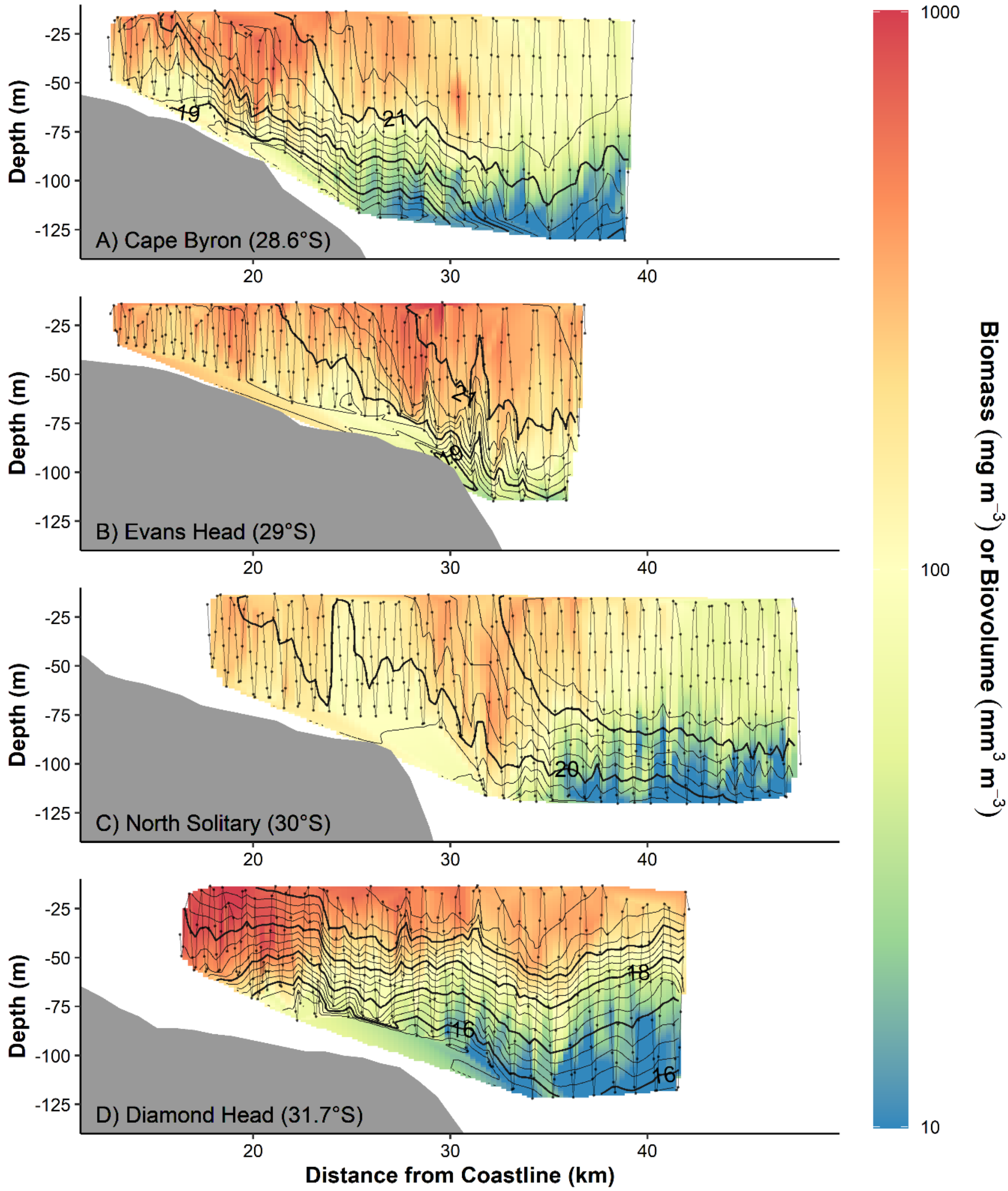


Figure 5 *Zooplankton biomass (mg m^{-3}) and biovolume (mm m^{-3}) distributions from the four cross shelf transects (Figure 1). Transects were conducted from inshore to offshore with an undulating towed body with the path shown by the grey line with midpoints of each sample shown as dots. Temperature (°C) isotherms are shown in black. Note biomass the log transformed colour scale.*

The new supplementary abundance plot is as follows:

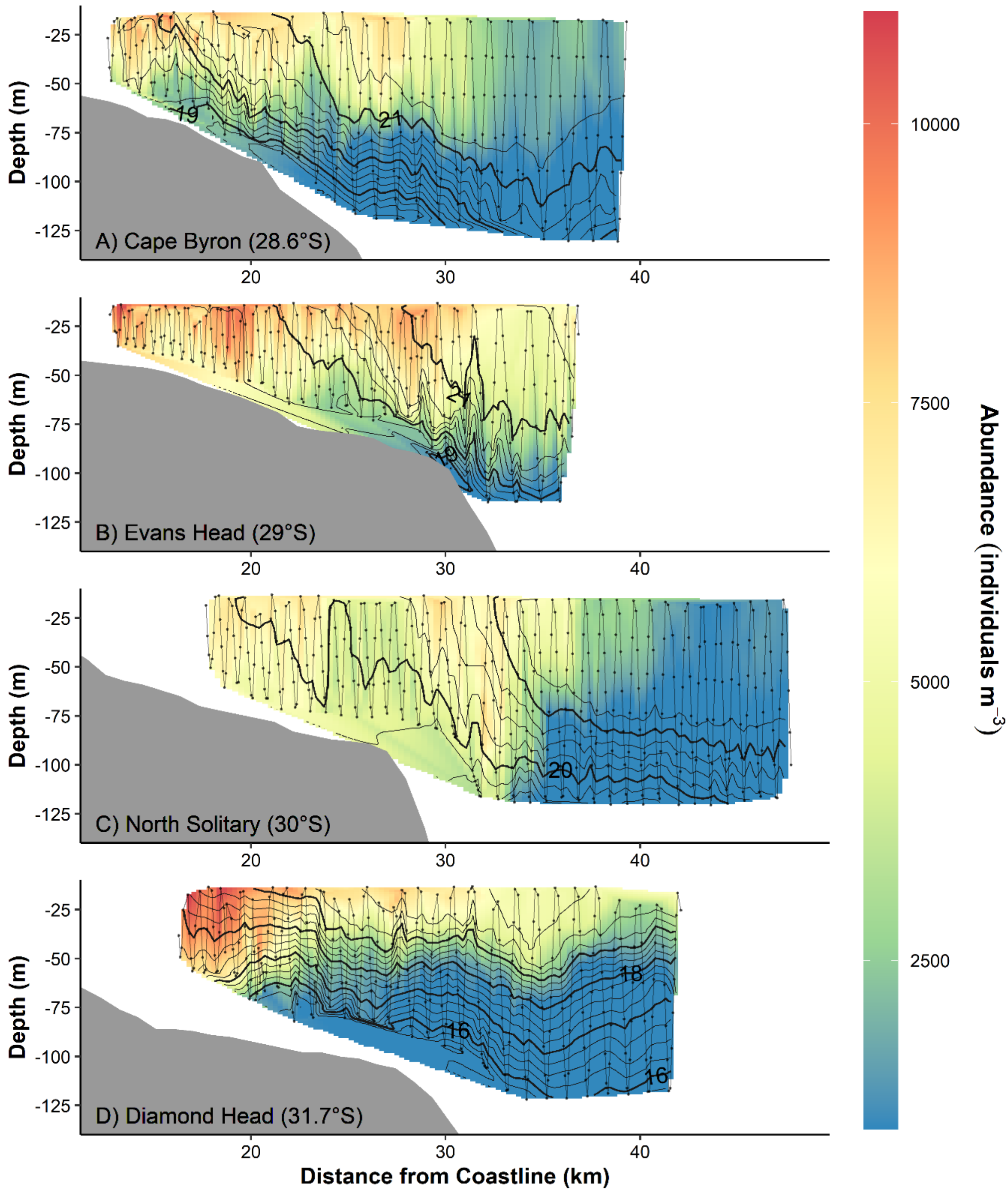


__Figure S7__ Cross-shelf interpolations of zooplankton abundance (individuals m^{-3}*). Measurements were taken as part of a CTD transect (data points shown as dots). Black lines connect areas of equal temperature (°C). Transects were conducted from inshore to offshore with an undulating towed body with the path shown by the grey line with midpoints of each sample shown as dots. Temperature (° C) isotherms are shown in black.*

Comment #37: Line 236: Common practice in literature is to refer to as biovolume.
Response: See comment #36.

Comment #38: Line 245: Many of these studies describe results in context of environmental and ecological covariates. Please include some way to characterise environmental and ecological context of studies.
Response: Similar to the point raised by reviewer 1 in comment #2, we agree that the studies which we have combined in our global analysis are from a variety of locations, incorporating different environmental and ecological contexts. With 19 different studies it is not feasible to address the environmental and ecological contexts in a meaningful way without substantially increasing the length of the paper. Instead, we have made clearer the links between all the studies by highlighting the fundamental process that links all the continental shelf studies.

The common fundamental process that unites all studies is the nutrient enrichment that occurs in all near-coastal waters, due to many different upwelling processes (coastal winds, reverse Ekman, or topographic effects) and estuarine processes and run-off from land. Therefore, western boundary currents do have a major influence on coastal enrichment, but are not the only cause. This drives the ubiquitous "green-ribbon" (Lucas et al. 2011) in chlorophyll *a* observed along most coasts world-wide, and our study together with related work establishes a general pattern in zooplankton size and abundance. We have now made a point in the discussion of how the general patterns in zooplankton are likely due to coastal nutrient enrichment which can be caused by many mechanisms. The discussion now states:
"These horizontal trends in the particulate (zooplankton) size-structure are consistent with the patterns in size-structure across other continental shelves and likely are an outcome of nutrient enrichment which tends to occur on continental shelves. This enrich can come from a variety of sources including cross-shelf flows and sporadic upwelling processes driven by ocean currents and coastal winds (Roughan and Middleton, 2002; Rossi et al., 2014; Malan et al., 2020), estuarine process (Morris et al., 1995) or run-off from land (Correll et al., 1992)."

We have also added some discussion about how the cross-shelf gradients (produced as discussed above) are a key component of the observed zooplankton dynamics:
"Despite different regional dynamics, cross-shelf and vertical gradients in water-masses, here driven by the EAC and uplift, seem to be the dominant factor for the patterns observed at various locations worldwide."

In the methods section we have also made clearer the reasoning behind using all these studies in this way. The new text reads:
"While each continental shelf is unique and the ecological and environmental context of each study will differ, nutrient enrichment is common along all continental shelves. This enrichment comes from a variety of sources including upwelling (Roughan and Middleton, 2002; Malan et al., 2020), run-off (Correll et al., 1992) and estuarine processes (Morris et al., 1995) but for the context of our global comparison we are only concerned with the resulting pattern of zooplankton across the continental shelves."

Comment #39: Line 261: As suggested in the methods sections please restructure to describe:
- Seasonal variation in EAC dynamics (distance from shore, velocity, SSH, SST, chl a)
- Observations of vertically resolved cross shelf plots of temperature, salinity, nutrients, chl a/fluorescence, particulates/zooplankton
- In-situ Zooplankton samples for community composition information would help verify cross shelf plots (RMT)?

Response: As suggested we have restructured the results section to first cover the seasonal variation in regional oceanography (and zooplankton composition) before addressing the specifically sampled cross-shelf transects. The results section ends with the global comparison section.

Comment #40: Line 266: rephrase/remove
Response: This line has been rephrased, it now reads:
"At the time of our sampling, the three northern most transects (north of 30°S) all crossed from cooler inshore waters into warm EAC water but the southern transect (Diamond Head 31.75°S) was located south of where the EAC begins to separate from the shelf ("the separation zone"; Figure 1)."

Comment #41: Line 276: Report EAC centered at xx km offshore above the xxx m depth contour. In the discussion cover how the center of EAC was located x distance from shore / above x depth contour. And how its proximity to coast the depth of water it flowed in influenced uplift?
Response: This section has been rephrased as suggested and now reads:
"The northernmost transect at Cape Byron (28.6°S) was dominated by the EAC which had a strong alongshore flow (1.50 m s^{-1}; Figure 4). The EAC was centred 27.6km offshore, above the 200 m isobath. Most of the continental shelf was flooded by warm EAC water (Figure 4). There was evidence of uplift with the 21° C isotherm rising to the surface from 70 m depth over 5 km and the 20° C isotherm rising to the surface from 100 m depth over 15 km. The EAC showed slight onshore movement which increased offshore and with depth, peaking between 100 and 200 m depth (up to 0.26 m s^{-1}, Figure S4)."

We have now added this discussion to the discussion. The new text reads:
"At Cape Byron and Evans Head, the EAC was in high proximity to the continental slope and the lack of upwelling-favourable wind stress (Figure S3) suggests that the observed isotherm uplift is likely to be current-driven, as shown in Schaeffer et al. (2014). This was contrasted by North Solitary where the EAC was further offshore and it was likely the uplift was at least partially caused by the upwelling favourable winds in the hours prior to sampling (Figure S3). As a contrast, Diamond Head which was located south of the EAC separation and therefore free from its influence was largely homogenous with little horizontal structure and limited uplift of isotherms."

Comment #42: Line 279: Include data from along and cross shelf flow to make this point.
Response: This section has been rephrased and the requested along and cross shelf data are referred to as part of the revised paragraph. See above comment for new text.

Comment #43: Line 285: Data does not support the strength of this statement.
Response: This statement has been deleted.

Comment #44: Line 291: This paragraph would benefit from consideration of cross shelf patterns in temperature, salinity, nutrients, chl a/ fluorescence
Response: This consideration in temp, salinity, chl a and fluorescence has now been added. This section now reads:
"No depth resolved cross shelf chlorophyll a or nutrient data was available for the Cape Byron transect but there was a gradient in both salinity and temperature across the shelf. Warmer saltier water was found in offshore water, with the salinity both showing similar uplift onto the shelf as described above for the temperature isotherms (Figure S9)."

Comment #45: Line 295 (Figure 2): Describe the direction of flow +- represents in the caption.
Response: This information has been added to the caption. The caption now reads:
"Figure 2: *Alongshore (towards ~195°, minor variation in coastline angle between sites) velocity across the four cross shelf transects (Figure 1), from the vessel's Acoustic Doppler Current Profiler. Grey lines join areas of equal velocity."*

Comment #46: Line 319: Rephrase
Response: This has been rephrased and now reads:

"The transect at Evans Head (29°S) extended only 5km past the continental shelf edge but was still largely influenced by the EAC. The EAC was centred 36.1km from the offshore above the 220m contour. The EAC had a strong along-shore flow (1.47 m s-1; Figure 4)."

Comment #47: Line 322: Report EAC centered at xx km offshore above the xxx m depth contour. In the discussion cover how the center of EAC was located x distance from shore / above x depth contour at each station. And how its proximity to coast / depth of water it flowed over influenced uplift.
Response: This has been rephrased as suggested. It now reads: "The transect at Evans Head (29°S) extended only 5km past the continental shelf edge but was still largely influenced by the EAC. The EAC was centred 36.1km from the offshore above the 220m contour. The EAC had a strong along-shore flow (1.47 m s^{-1}; Figure 2). The EAC showed offshore movement (0.27 m s^{-1}) which increased with distance offshore (Figure S4). There was strong current driven uplift of the isotherms inshore of the EAC with the 21 °C isotherm rising to the surface from 70 m depth over 6 km and the 20 °C isotherm rising to the surface from 100 m depth over 15 km."

We have now added this discussion to the discussion. The new text reads:
"At Cape Byron and Evans Head, the EAC was in high proximity to the continental slope and the lack of upwelling-favourable wind stress (Figure S3) suggests that the observed isotherm uplift is likely to be current-driven, as shown in Schaeffer et al. (2014). This was contrasted by North Solitary where the EAC was further offshore and it was likely the uplift was at least partially caused by the upwelling favourable winds in the hours prior to sampling. As a contrast, Diamond Head which was located south of the EAC separation and therefore free from its influence was largely homogenous with little horizontal structure and limited uplift of isotherms."

Comment #48: Line 323: Include data on along and cross shelf flow to support this point.
Response: This information is now included in this paragraph. It reads:" The transect at Evans Head (29°S) extended only 5km past the continental shelf edge but was still largely influenced by the EAC. The EAC was centred 36.1km from the offshore above the 220m contour. The EAC had a strong along-shore flow (1.47 m s^{-1}; Figure 2). The EAC showed offshore movement (0.27 m s^{-1}) which increased with distance offshore (Figure S4). There was strong current driven uplift of the isotherms inshore of the EAC with the 21 °C isotherm rising to the surface from 70 m depth over 6 km and the 20 °C isotherm rising to the surface from 100 m depth over 15 km."

Comment #49: Line 324: This paragraph would benefit from the inclusion of cross shelf patterns in temperature, salinity, nutrients, chl a/ fluorescence
Response: This has now been added. The paragraph reads:
"The zooplankton size structure varied along the transect. The EAC was warmer and saltier compared to the inner shelf water (Figure S9). There was also a slight gradient in Nitrate and chlorophyll with higher levels of both in the inshore waters (3 mmol m^{-3} and 1.35 mg m^{-3} respectively; Figures S10 & S11). Around the front between the continental shelf water (< 21 °C) and the warm (> 21 °C) EAC water the zooplankton community showed a similar GMS of ≈450 µm ESD to that observed at the northern Cape Byron transect but had a higher biomass and shallower pareto distribution shape parameter c (≈-1; Figures 3, 4 & 5)."

Comment #50: Line 327: Size structure of particulates, community refers to species or functional groups. Data does not support this statement
Response: This has been rephrased. It now reads:
"The zooplankton size structure varied along the transect."

Comment #51: Line 331: Results are not as clear-cut as reported

Response: This section has been rephrased. It now reads: "The zooplankton size structure varied along the transect. The EAC was warmer and saltier compared to the inner shelf water (Figure S9). There was also a slight gradient in Nitrate and chlorophyll with higher levels of both in the inshore waters (3 mmol m^{-3} and 1.35 mg m^{-3} respectively; Figures S10 & S11). In the warmer offshore water the zooplankton biomass and geometric mean size was similar that offshore at Cape Byron while in the cool inshore waters, there was again high zooplankton biomass (Figure 5), but the community had shifted towards smaller particles which resulted in a steeper c (< -1.3; Figures 4 & 5). There was also low abundance in the deeper samples (Figure S7)."

Comment #52: Line 334: Abundance data would be useful
Response: Abundance data has been added. See above response for example.

Comment #53: Line 337: Include numbers of along and cross shelf flow to make this point.
Response: This information has been added. This section now reads:
"The EAC was centred of the EAC was 37.7 km offshore (alongshore flow 1.59 m s^{-1}), located above the 310 m bathymetry contour (Figure 4). This uplift could potentially have been driven by the upwelling favourable winds in the hours leading up to sampling (Fig S3). The offshore waters of the EAC showed slight onshore movement, at depths of 100-150m (0.15 m s^{-1}; Figure S4)."

Comment #54: Line 340: Report EAC centered at xx km offshore above the xxx m depth contour. In the discussion cover how the center of EAC was located x distance from shore / above x depth contour. And how its proximity to coast the depth of water it flowed in influenced uplift?
Response: This has been rephrased as suggested. It now reads: "The EAC was centred of the EAC was 37.7 km offshore (alongshore flow 1.59 m s^{-1}), located above the 310 m bathymetry contour (Figures 4)".

We have now added this discussion to the discussion. The new text reads:
"At Cape Byron and Evans Head, the EAC was in high proximity to the continental slope and the lack of upwelling-favourable wind stress (Figure S3) suggests that the observed isotherm uplift is likely to be current-driven, as shown in Schaeffer et al. (2014). This was contrasted by North Solitary where the EAC was further offshore and it was likely the uplift was at least partially caused by the upwelling favourable winds in the hours prior to sampling. As a contrast, Diamond Head which was located south of the EAC separation and therefore free from its influence was largely homogenous with little horizontal structure and limited uplift of isotherms."

Comment #55: Line 342: Rephrase
Response: This has been rephrased. It now reads: "The offshore waters of the EAC showed slight onshore movement, at depths of 100-150m (0.15 m s^{-1}; Figure S4)."

Comment #56: Line 343: This paragraph would benefit from the inclusion of cross shelf patterns in temperature, salinity, nutrients, chl a/ fluorescence
Response: This has now been included. The paragraph now reads:
"Biomass and abundance generally decreased with distance offshore and with depth (Figures 5, S5 & S6 & S7). The warmer water, located offshore, contained low biomass with a shallow pareto distribution shape parameter c (-0.9) and GMS of ~450 µm (Figures 5, 6 & 7). Zooplankton in cooler water < 20 °C had a much smaller GMS (~400µm ESD) resulting in a steeper c (< -1.3). This was particularly evident where the 20°C isotherm reach the surface ~24 km from the coastline, bringing with it a highly productive zooplankton community (Figures 6 & 7). This peak also aligned with a minor peak in chlorophyll a (1.45 mg m^{-3}; Figure S11). North Solitary showed evidence of uplift with the small GMS community from deep uplifted to the surface. The uplift could have resulted from the close-by EAC and the short upwelling-favourable wind a few hours before sampling. The deep cold

water (< 16°C) had higher levels of Nitrate and Silicate (Figure S10 & S12), but this does not appear to have been lifted to the surface waters with the surface waters low in nutrients across the transect."

Comment #57: Line 344: Rephrase
Response: This line has been rephrased. See comment #56 (above) for full paragraph.

Comment #58: Line 344: particle biomass
Response: This line has been rephrased. See comment #56 for full paragraph.

Comment #59: Line 345: Data does not support this.
Response: Figures S5 and S6 clearly support this pattern, particularly on the log scale and are pasted here for reference:

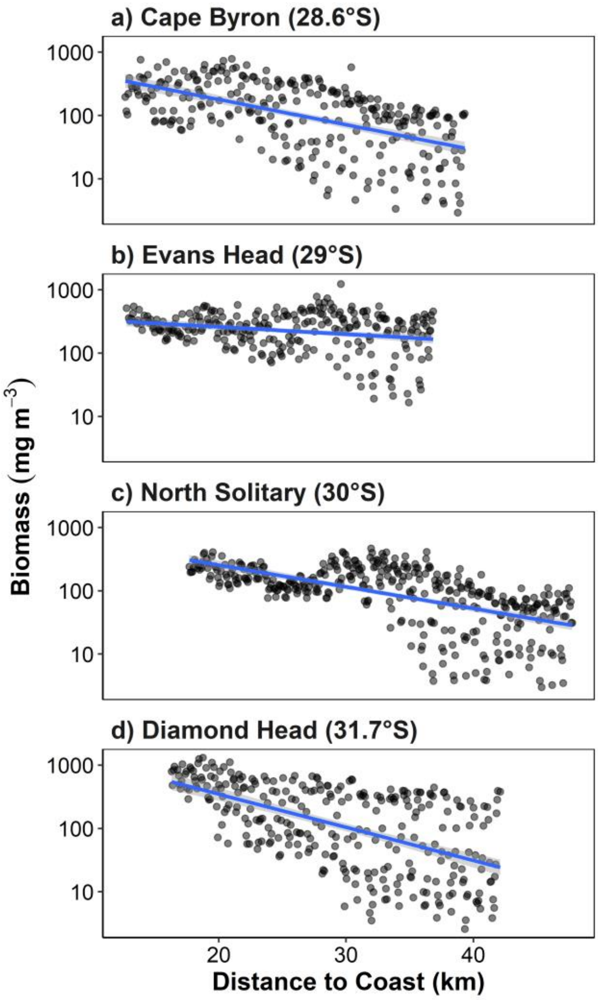


Figure S5 Biomass by distance from the coast for the four transects. Note the $\log_{10}$ transformed y-axis. Each dot represents a 6 s integration from the OPC mounted on the undulating towed body. Blue lines represent the linear trend line with the 95% confidence intervals shown in grey.

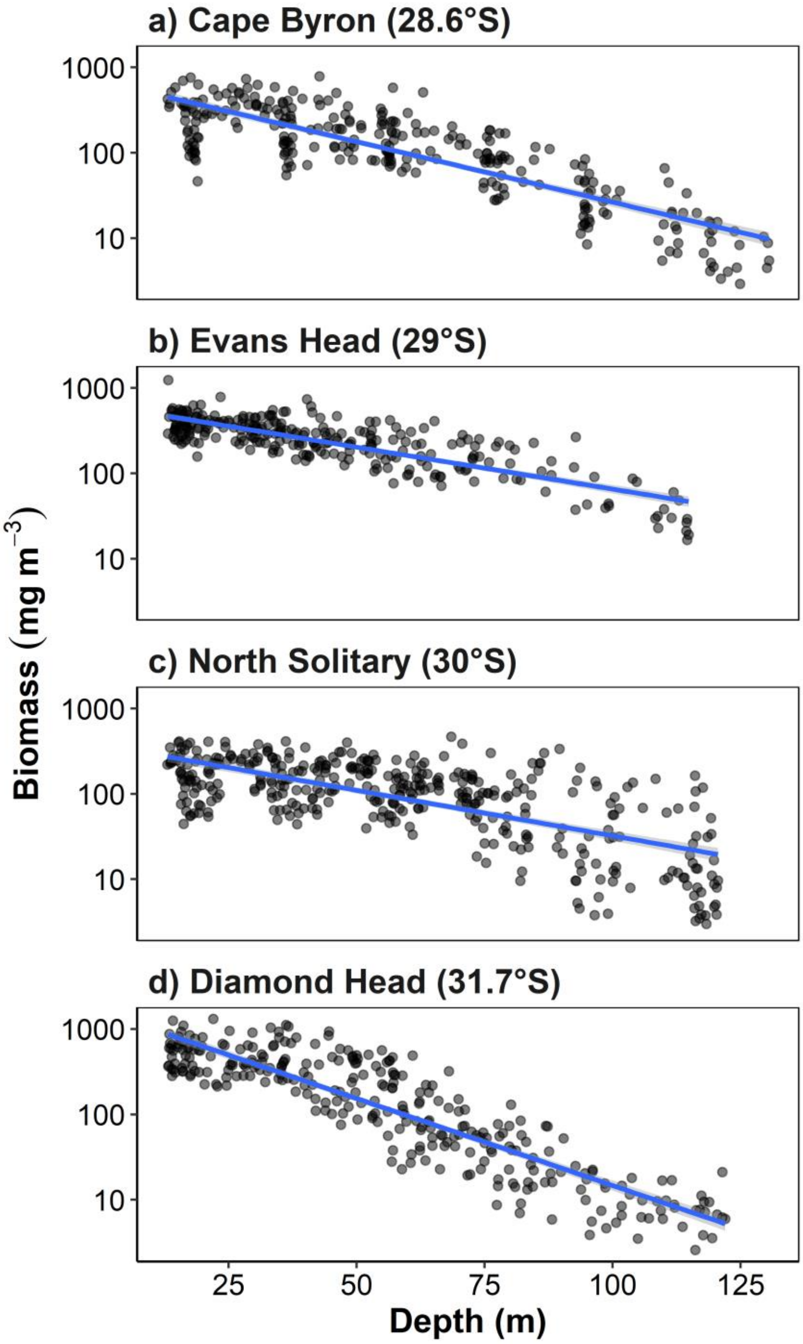


Figure S6 Biomass by sample depth for the four transects. Note the $\log_{10}$ transformed y-axis. Each dot represents a 6 s integration from the OPC mounted on the undulating towed body. Blue lines represent the linear trend line with the 95% confidence intervals shown in grey.

Comment #60: Line 345: Rephrase

Response: This line has been rephrased. See comment #56 for full paragraph.

Comment #61: Line 348: Data does not support this statement.
Response: This line has been deleted.

Comment #62: Line 357: This paragraph would benefit from the inclusion of cross shelf patterns in temperature, salinity, nutrients, chl a/ fluorescence
Response: This information has been added. The paragraph now reads:
"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 m s-1, Figure 4) 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). The lack of horizontal variation was reflected in the Nitrate, Silicate, temperature and salinity with almost all variation being observed with depth (Figures S9, S10, S12). Chlorophyll and Oxygen showed small peaks (1.2 mg m^{-3} and 240 mmol m^{-3} respectively; Figures S11 & S13) at the surface near the beginning of the transect. 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)."

Comment #63: Line 364: Broad summary "This transect had the highest observed biomass of particles..."
Response: This has been added to the beginning of the paragraph as suggested. It now reads:
"This transect has the highest observed biomass of particles (1000 mg m^{-3}), particularly inshore (Figure 5)."

Comment #64: Line 365: delete "zooplankton community"
Response: This has been rephrased. It now reads:
"The zooplankton size structure was not clearly related to water masses reflecting the more homogenous water mass here"

Comment #65: Line 371: Synthesis of EAC position relative to distance from shore and depth, along and cross shelf flow and how it determines uplift at transect is required
Response: We have added a comment about the relative influence of the EAC on cross-shelf flow at the different sites. This section now opens with:
'The influence of the EAC varied between the three transects. The three northern transects were influenced strongly by the EAC, particularly the offshore sections while the Diamond Head transect was not influenced by the EAC. At the two northern sites the EAC was located close to the continental shelf and likely drove current driven upwelling. In contrast at the North Solitary site, the EAC was located further offshore, and the weaker observed uplift was potentially caused by wind driven upwelling (Fig S3)."

Comment #66: Line 371: See comment about restructure
Response: The results section was restructured as suggested and now starts with a discussion of seasonality, followed by the transect observations then a synthesis of the observations.

Comment #67: Line 374: Rephrase
Response: This has been rephrased. It now reads:
"The alongshore velocity at all sites was reduced between April and August before increasing in Spring (when our observations were taken) and Summer. This seasonality is consistent with previous findings from higher-resolution HF radar observations around 30°S (Archer et al., 2019)."

Comment #68: Line 376: Rephrase
Response: This has been rephrased. It now reads:
"The Cape Byron, North Solitary and Diamond Head transects had higher zooplankton biomasses observed in continental shelf waters with declines offshore and with depth in the top 100m of the water column (Figures S5 & S6). 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."

Comment #69: Line 379: Data does not support this.
Response: This statement has been deleted.

Comment #70: Line 385: I suspect that an alternative mechanism might have generated localised uplift, 24km from the coast at Nth Solitary, as pattern is not observed in alongshore and cross shelf velocity profiles.
Response: North Solitary showed evidence of uplift with the small GMS community from deep uplifted to the surface. The uplift could have resulted from the close-by EAC and the short upwelling-favourable wind a few hours before sampling. We have added this to the manuscript where the lines read:
"North Solitary showed evidence of uplift with the small GMS community from deep uplifted to the surface. The uplift could have resulted from the close-by EAC and the short upwelling-favourable wind a few hours before sampling."

Comment #71: Line 434: Particulate
Response: This has been changed to *"We found consistent declines from inshore to offshore in particulate (zooplankton) biomass"*

Comment #72: Line 434: biovolume
Response: See response to comment #36 regarding biovolume and biomass.

Comment #73: Line 434: ? altered
Response: This has been rephrased. It now reads:
"We found consistent declines from inshore to offshore in particulate (zooplankton) biomass and variation in size-structure both horizontally and vertically across the narrow continental shelf off eastern Australia."

Comment #74: Line 437: Need to present and describe results in context of along and cross shelf flow.
Response: This sentence is part of the summary paragraph to open the discussion. We have now expanded on this in the following paragraph. This paragraph now begins with:
"The cross-shelf observations of chlorophyll a and nutrients showed little patterns across our transects the majority of variation in water properties being observable through temperature and salinity. The warm salty EAC dominated the upper 100m of the offshore portions of the three northern transects with cooler inner shelf water. At Cape Byron and Evans Head, the EAC was in high proximity to the continental slope and the lack of upwelling-favourable wind stress (Figure S3) suggests that the observed isotherm uplift is likely to be current-driven, as shown in Schaeffer et al. (2014). This was contrasted by North Solitary where the EAC was further offshore and it was likely the uplift was at least partially caused by the upwelling favourable winds in the hours prior to sampling. As a contrast, Diamond Head which was located south of the EAC separation and therefore

free from its influence was largely homogenous with little horizontal structure and limited uplift of isotherms."

Comment #75: Line 440: Particulate biovolume
Response: This has been changed to: *"Particulate (zooplankton) biomass"*.

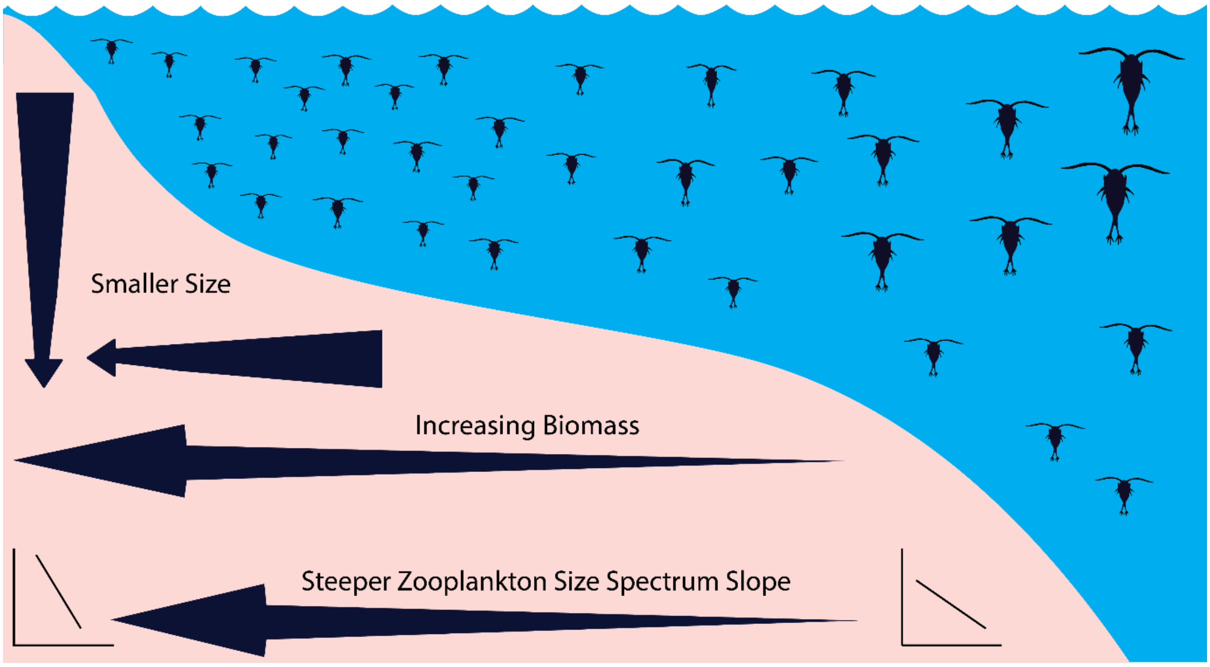
Comment #76: Line 441: Rephrase
Response: This has been rephrased to:
"Particulate (zooplankton) biomass and mean size was generally reflective of the horizonal and vertical structure of the water. Distinct from the warmer offshore EAC, the cooler shelf water revealed a zooplankton community with higher biomass, smaller geometric mean size and steeper size spectrum slope (Figures 5, 6 & 7)."

Comment #77: Line 447: Need to present data to support this statement
Response: This data is presented in Figures 5, 6 & 7. This is now referred to in text as:
"Distinct from the warmer offshore EAC, the cooler shelf water revealed a zooplankton community with higher biomass, smaller geometric mean size and steeper size spectrum slope (Figures 5, 6 & 7)."

Comment #78: Line 448: add data to support this statement.
Response: The data to support this statement are reflected by the citations now provided. This is now referred to in text as:
"These observations are consistent with higher chlorophyll a on the continental shelf (Everett et al., 2014) and are likely driven by uplift of the cooler water due to the EAC interacting with the sloping topography (Schaeffer et al., 2014; Schaeffer and Roughan, 2015)."

Comment #79: Line 451: Go on and discuss how planktivorous fish are associated with shelf habitats / shelf break / boundary currents and how they can influence the size structure of zooplankton communities.
Response: We have expanded on this idea and added following sentence:
"Therefore, a steeper zooplankton size spectrum slope could arise not only from increased production of smaller zooplankton (Guiet et al., 2016), but also by predation on larger zooplankton prey by planktivorous fish (Moore and Suthers, 2006). In the region of our study, planktivorous fish such as mackerel and scad consume zooplankton in the 0.5-1 mm particle diameters (Schilling, unpublished data) and are often found aggregating at the shelf edge (Holland et al., 2021). Such predators could steepen the slope of the zooplankton biomass size spectrum as they target larger prey."

Comment #80: Line 455 (Figure 8): Does the data your presenting support this? might need more detail as it looks like light is the primary background.
Response: Yes, our data does support this, the horizontal gradient is widely supported and the vertical response holds with what few observations are available including this study. To reduce confusions with light driving patterns, the background colour has been changed to a constant blue. The new figure is shown below:



Comment #81: Line 467: Looks like along shelf flow has a greater influence ? cross shelf flow not strongly supportive of this statement. Cross shelf plots of temperature, salinity, nutrients and fluorescence will help here.
Response: Cross shelf plots of Temperature, salinity, nutrient and chlorophyll *a* are now available in the supplementary (Figures S9, S10, S11, S12). Minor uplift of nutrient rich water is visible in Figure S10. This section of text now reads:
"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 to a small extent influenced by uplift of deep nutrient-rich water mostly driven by the close proximity of the EAC to the continental shelf (Roughan and Middleton, 2002), which drives the higher biomass of phytoplankton (Everett et al., 2014) and therefore 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, 2021)."

Comment #82: Line 470: See comment above. How could these fish communities possibly contribute to observations of biomass and size of particles across the shelf?
Response: As noted above (comment #79); and note that the subsequent sentences address this question. *"Therefore, a steeper zooplankton size spectrum slope could arise not only from increased production of smaller zooplankton (Guiet et al., 2016), but also by predation on larger zooplankton prey by planktivorous fish (Moore and Suthers, 2006). In the region of our study, planktivorous fish such as mackerel and scad consume zooplankton in the 0.5-1 mm particle diameters (Schilling, unpublished data) and are often found aggregating at the shelf edge (Holland et al., 2021). Such predators could steepen the slope of the zooplankton biomass size spectrum as they target larger prey."*

Comment #83:
Line 478: Inclusion of recommended data would strengthen this statement.
Response: We have now included the recommended data as supplementary material and we refer to it in text here. The text now reads:
"In general, the Tasman Sea has an elevated nutrient concentration and higher zooplankton biomass compared to the oligotrophic EAC waters (Baird *et al.*, 2008), this was observed in our surveys to a

limited extent with the EAC showing very small nutrient concentrations compared to the deeper and inner shelf waters (Figure S10 & S12)."

Comment #84: Line 489: Provide details, looks like Baird et al 08 was focused on Tasman sea waters not shelf waters?
Response: This paragraph has been deleted as previous comments suggested we reduce the focus on frontal regions.

Comment #85: Line 495: Why ? What mechanisms drive this ? and relevance to this study?
Response: This paragraph has been deleted as previous comments suggested we reduce the focus on frontal regions.

Comment #86: Line 505: Compare and contrast results of this and other studies in context of large, mesoscale oceanography and the vertical structure of the water column.
Response: This section has been greatly expanded it now reads:
"Our study showed a consistent decline in biomass with increasing distance from shore and with increasing depth (to 100m depth) with the largest biomasses observed in the surface inner shelf waters, likely due to coastal nutrient enrichment (from a variety of mechanisms). 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). Despite different regional dynamics, cross-shelf and vertical gradients in water-masses, here driven by the EAC and uplift, seem to be the dominant factor for the patterns observed at various locations worldwide. 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). Further south of the Brazilian Bight, similar results were observed on the Abrolhos Bank where higher zooplankton biomass was observed on the continental shelf due to the Brazil Current interacting with the sea-floor, generating uplift and eddies which increased mixing over the continental shelf (Marcolin et al., 2013).

In the southwest Pacific, there are relatively small terrestrial influences compared to other sources of nutrients such as upwelling are important (Apte et al., 1998; Dai and Trenberth, 2002; Pritchard et al., 2003; Suthers et al., 2011). 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.

There are exceptions to the general trends that we identified 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). This temporal instability in some regions may suggest that repeated surveys under different oceanographic conditions may be necessary to fully understand the drivers of zooplankton on continental shelfs. The current study had no temporal replication and while it was shown that the conditions which were sampled are regularly occurring features, additional studies would be useful to confirm the occurrence of the patterns in particulate (zooplankton) biomass and size structure.
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)."

Comment #87: Line 506: Rephrase
Response: This has been rephrased. It now says:
"Our study showed a consistent decline in biomass with increasing distance from shore and with increasing depth (to 100m depth) with the largest biomasses observed in the surface inner shelf waters."

Comment #88: Line 507: Does the data support this statement.
Response: Yes, see Figures S5 and S6. These are also provided in the document above, see comment #59.

Comment #89: Line 516: ? (to the south)
Response: This has been rephrased. It now says:
"Further south of the Brazilian Bight, similar results were observed on the Abrolhos Bank…"

Comment #90: Line 520: Rephrase
Response: This has been rephrased. It now reads:
"In the southwest Pacific, there are relatively small terrestrial influences compared to other sources of nutrients such as upwelling are important (Apte et al., 1998; Dai and Trenberth, 2002; Pritchard et al., 2003; Suthers et al., 2011)."

Comment #91: Line 522: provide context of upwelling
Response: In this case, the context of the upwelling is irrelevant. We are simply stating that upwelling is a nutrient input in this region.

Comment #92: Line 534: Rephrase and caveats and add relevant others here as well.
Response: We have highlighted the major caveat of this study and rephrased this paragraph. It now reads:
"There are exceptions to the general trends that we identified 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). This temporal instability in some regions may suggest that repeated surveys under different oceanographic

conditions may be necessary to fully understand the drivers of zooplankton on continental shelfs. The current study had no temporal replication and while it was shown that the conditions which were sampled are regularly occurring features, additional studies would be useful to confirm the occurrence of the patterns in particulate (zooplankton) biomass and size structure."

Comment #93: Line 558: References

Response: References have been added. The line now reads:

"Despite this, the EAC is strengthening (Suthers et al., 2011; Wu et al., 2012), and the increasing water temperatures in the southeast Australian region (Malan et al., 2021), are already impacting the zooplankton communities as the region becomes increasingly tropicalised (Kelly et al., 2016)."

Comment #94: Line 566: Please include other examples and implications for ecosystem structure and function, there are some good examples from this area as well.

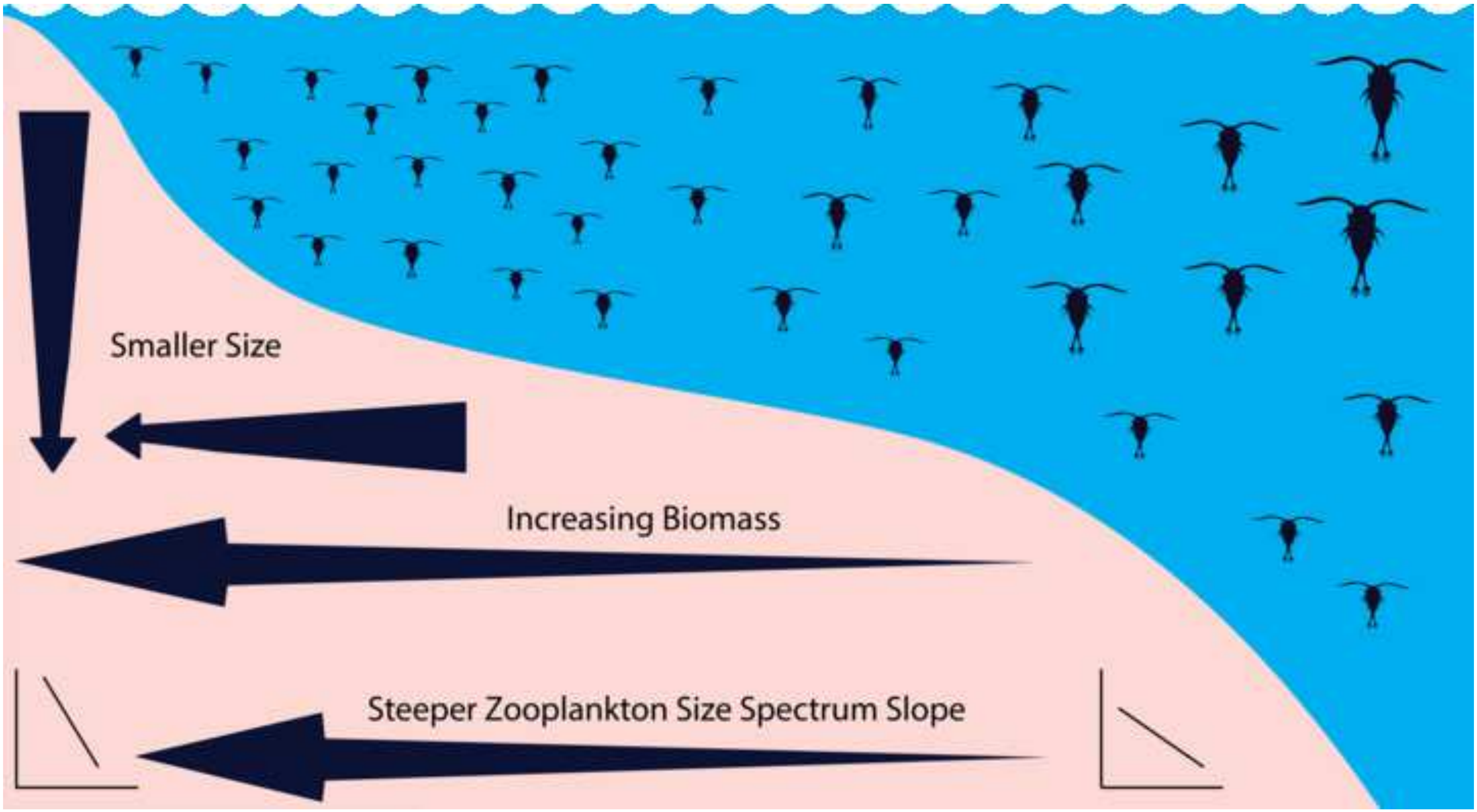
Response: We have expanded this section and it now reads:

"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). With the impacts of warming oceans already being observed at coastal observing stations and phytoplankton communities increasingly dominated by warm-water tolerant chain forming diatoms (Ajani et al., 2020), impacts from projected reductions in both phytoplankton and zooplankton biomass are likely to be amplified up the food chain with potentially large impacts on fisheries as food web become increasingly reliant on pelagic energy sources rather than benthic (Petrik et al., 2020)."

Highlights

- Depth resolved cross shelf transects of particulates were done off east Australia
- biomass was highest inshore, declining with increasing distance from shore
- Biomass declined with increasing depth in the top 100m of the water column
- Global comparisons of onshore-offshore zooplankton revealed consistent trends

Graphical Abstract



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

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Main text ≈ 8000 words, 1 Table, 9 Figures

Abstract

Continental shelves are the interface between society and the oceans, supporting over 90% of the world's fisheries through highly productive ecosystems. Boundary currents drive oceanographic processes on many continental shelves, yet it is uncertain how boundary currents influence the continental shelf zooplankton community. With an optical plankton counter and CTD mounted on an undulating towed body, we present the first high-resolution vertically resolved profiles of the particle (zooplankton) size structure across four transects over a continental shelf. Particulate (zooplankton) biomass was highest inshore, declining with increasing distance from shore and with increasing depth in the top 100m of the water column. In the region adjacent to the East Australian Current, uplift generated by either the EAC interacting with the continental slope or upwelling favourable winds, resulted in smaller geometric mean sizes and steeper size spectrum slopes. South of the EAC separation from the coast, the continental shelf water mass was more homogenous but still displayed the same horizontal and vertical patterns in particulate (zooplankton) biomass and mean size. These patterns are consistent with zooplankton distributions on other continental shelves where the inner-shelf has higher biomass of zooplankton with a steeper size spectrum slope compared to offshore. Inner-shelf zooplankton communities support important temperate reef ecosystems and coastal fisheries, through their consistently high biomass.

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

1. Introduction

Continental shelves are the interface between society and the oceans. While accounting for less than 7% of the earth's ocean surface area, continental shelf regions support over 90% of the world's fisheries catch (Pauly *et al.*, 2002). These fisheries are based upon high primary productivity (Bakun and Weeks, 2008; Mackinson *et al.*, 2009), facilitated by coastal winds, typography and processes including upwelling, boundary currents and eddies (D'Croz and O'Dea, 2007; Patti *et al.*, 2008). The high chlorophyll *a* levels often observed on the continental shelf, particularly the inner shelf (Lucas *et al.*, 2011a, 2011b), may be a key driver of zooplankton communities which are a key resource for fisheries (Mitra *et al.*, 2014). In boundary current systems such as the East Australian Current and the Benguela Current, zooplankton can support over 50% of fish biomass on coastal reefs (Truong *et al.*, 2017; Maia *et al.*, 2018; Holland *et al.*, 2020), making it a key link between primary production and higher trophic levels.

The transfer of energy between trophic levels is complex but as predation is largely driven by size in the marine environment (Barnes *et al.*, 2010), the size frequency distribution of a community can provide valuable insight into the trophic dynamics of a community (Blanchard *et al.*, 2017). Within a community, the size of all individuals, irrespective of species identity, can be described by the size-frequency which typically yields a histogram that is strongly right-skewed with many small individuals, and a few large individuals (Blanchard *et al.*, 2017; Heneghan *et al.*, 2019). On log-log axes, the 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 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). While there is variability in interpretations of size spectra depending on the size of particles in the spectrum due to sampling efficiency and natural 'dome shapes' in some communities (Marcolin *et al.*, 2013; Rossberg *et al.*, 2019), within the mesozooplankton size range (≈0.2 – 3mm), the elevation of the spectrum reflects the environmental effects which overall primary production and biomass of a community (Moore and Suthers, 2006; Zhou, 2006). Higher primary production and biomass tends to result in a higher elevation (or intercept) with such impacts demonstrated with nutrient input in both estuarine and pelagic ecosystems (Moore and Suthers, 2006; 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). Top-down pressure from larger predators can also increase the steepness of the size spectrum as increase the mortality rate of the zooplankton, thereby decreasing the efficiency of energy transfer along the spectrum (Moore and Suthers, 2006; Rossberg *et al.*, 2019).

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, most often in the lower salinity, higher chlorophyll *a* coastal water, indicating potential effects of freshwater discharge (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 despite widespread recognition of variation in vertical distributions of zooplankton often attributed to diel vertical migration (Lampert, 1989), and the 3-dimensional influences of continental shelf oceanography (Schaeffer *et al.*, 2013). During late summer, in the northwest Atlantic, the vertical zooplankton distribution was strongly influenced by water mass with distinct zooplankton communities in the observed warmer and colder water masses (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). As observations of vertical patterns in zooplankton communities on continental shelves remain uncertain in many regions of the world, it is important to demonstrate how oceanographic features including boundary currents influence the zooplankton community in shallow coastal waters.

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 often facilitate a nutrient and productivity gradient from oligotrophic WBCs across the continental shelves into the coast (Schaeffer *et al.*, 2013; Everett *et al.*, 2014; Kobari *et al.*, 2018). 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 often driven by along shore flows and mesoscale oceanographic features (Malan *et al.*, 2020). Cross shelf flows are usually in 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 smaller-spatial scales by eddies and upwelling (Lucas *et al.*, 2011a; 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* creating consistent observations where the spring bloom is typically south of 34°S with the northern areas having more consistent chlorophyll *a* levels (Everett *et al.*, 2014), yet there are no studies investigating the influence of the East Australian Current on higher trophic levels including zooplankton. Here we investigate horizontal and vertical patterns in particulate (zooplankton) size structure using four high-resolution vertically resolved, cross-shelf transects of particulates on the eastern continental shelf of Australia to:

1) Identify latitudinal differences in zooplankton distribution across the continental shelf in relation to the EAC, and
2) Examine the potential drivers of the observed patterns in particulate (zooplankton) biomass and size-structure, and
3) Relate our observations to previous research to propose a general concept of zooplankton size-structure on continental shelves globally.

2. Materials and Methods

2.1 Voyage Context and Seasonal Variation in Oceanography

The East Australian Current (EAC) is the western boundary current of the South Pacific gyre, forming between 10 and 20°S where the South Equatorial Current bifurcates off the Great Barrier Reef and north-eastern Australia (Ridgway and Dunn, 2003). The southward flowing component forms the EAC, a consistent southward jet, flowing at 0.8 – 1.5 m s^{-1} along the continental shelf with a maximum core velocity and a slight widening in summer (Archer *et al.*, 2017). The majority of the EAC separates from the coast between approximately 30 – 32°S and flows eastward as the EAC eastern extension (Cetina-Heredia *et al.*, 2014; Oke *et al.*, 2019). The remaining portion of the EAC continues to flow south along the coast as part of the EAC southern extension generating a large eddy field (Everett *et al.*, 2012). Along the continental shelf, particularly where the continental shelf narrows, the EAC has significant impact on shelf circulation (Schaeffer and Roughan, 2015). Current driven bottom friction leads to Ekman transport in the bottom boundary layer, moving cooler denser water up the slope, resulting in uplift of isotherms and upwelling (Schaeffer *et al.*, 2014). These intrusion events have been shown to bring nutrient rich water into the euphotic zone, increasing nitrate (Rossi *et al.*, 2014) and chlorophyll *a* concentration (Everett *et al.*, 2014), and controlling vertical phytoplankton abundance and composition (Armbrecht *et al.*, 2014, 2015). These EAC-driven upwelling or uplift events vary latitudinally rather than seasonally. Using a monthly climatology of altimetry over 12 years, Rossi *et al.* (2014) showed that the occurrence of these events is relatively consistent all year long north of the EAC separation ~32°S, and quite rare further south.

From 2nd – 13th September 2004, a research voyage on the RV Southern Surveyor was undertaken from Sydney, Australia (33.82°S, 151.29°E) to Brisbane, Australia (27.36°S, 153.17°E). During this period, the EAC was flowing southward along the coast until 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 (Figures 1 & S1), which is a common circulation in the area, irrespective of the month (Oke et al., 2019). The observed chlorophyll *a* levels in the area are also typical of those observed in September (Everett *et al.*, 2014).

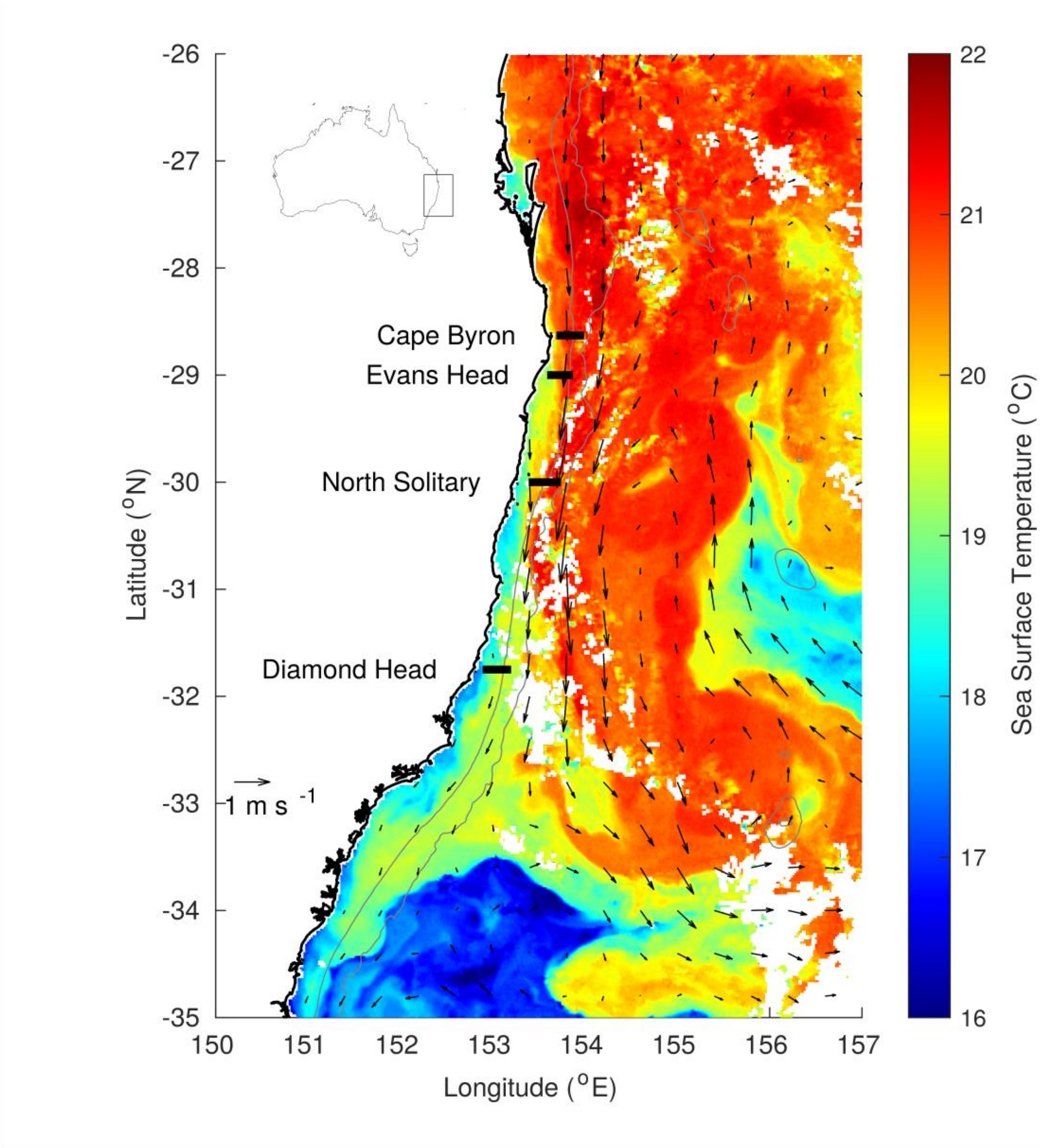


Figure 1 Locations of the four cross shelf sections which were sampled in September 2004. The sea-surface temperature for 6th September 2004 is shown in colour with velocity arrows from satellite altimetry shown with black arrows. Grey isobaths represent 200 and 2000m depths.

To investigate environmental conditions leading up to and during the sampling of transects on the east Australian continental shelf, MODIS-Aqua Level 3 ocean-colour data (chlorophyll *a*) were obtained from the Integrated Marine Observing System (IMOS) Data Portal (http://imos.aodn.org.au/imos/) at 1 km resolution. Chlorophyll *a* was derived using the OC3 algorithm. Sea surface temperature was obtained from L3S AVHRR daily night product from the same portal, displayed as a map for the region (resolution of 0.02^o). Surface geostrophic currents were derived from gridded sea level gradients from satellite altimetry, also taking into account sea level gauges to improve the estimate in coastal area (resolution of 0.2^o). To quantify lead-up conditions to our sampling, MODIS chlorophyll *a* data were retrieved for 5×5 pixels (~25 km^2) 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). Seasonal variation in surface Chlorophyll in this region was extensively investigated in Everett et al (2014) based upon satellite data showed that the chlorophyll values observed in our study are typical of the region (within 1 SD of the geometric mean Chlorophyll values).

Table 1 Summary of the four transects undertaken using the SeaSoar with attached optical plankton counter and CTD. Times are local, Australian Eastern Standard Time (GMT +10). Cape Byron and Evans Head were conducted in daylight while North Solitary and Diamond Head were conducted at night.

Transect	**Coastline Angle (°)**	**Start Longitude (° E)**	**Start Latitude (° S)**	**End Longitude (° E)**	**End Latitude (° S)**	**Start Time**	**End Time**
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 Solitary	15	153.412	29.998	153.726	29.997	7/09/2004 21:41	8/09/2004 00:05
Diamond Head	19	152.913	31.752	153.191	31.747	6/09/2004 20:00	6/09/2004 21:53

The potential influence of wind driven circulation was investigated using 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).

As zooplankton was not sampled for taxonomic investigation in the current study, in order to understand the likely composition of zooplankton at this time we explored Continuous Plankton Recorder (CPR) Data (Richardson *et al.*, 2006). We extracted all CPR zooplankton abundance data within 28 – 32° S and 152 -155° E from the Australian Ocean

Data Network (https://portal.aodn.org.au/). Using the 'higher taxonomic groups classifications" we calculated the average composition (by abundance) of zooplankton for each month in the study region.

2.2 Sampling

Four transects were sampled roughly perpendicular to the coast over a seven-day period (6th – 12th September; Table 1, Figure 1) using a modified SeaSoar. The SeaSoar was towed from inshore to offshore and undulated between 10 and 120 m depth as used in previous studies (Baird *et al.*, 2008). Mounted on the SeaSoar was a dual CTD system (custom made interface combining a Seabird SBE3 temperature sensor, a Seabird SBE4 conductivity sensor and a Paroscientific 43K-027 pressure sensor) and an Optical Plankton Counter (OPC; Herman 1992) to continuously measure temperature, salinity and the size frequency distribution of particulate matter. An ADCP (Teledyne R. D. Instruments, USA, Model # VM-150) continuously monitored the current velocity profile beneath the vessel. 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). Immediately following each SeaSoar deployments a transect of CTD deployments was conducted over the same course (in the opposite direction) to characterise nutrients, oxygen, and fluorescence along each transect. Fluorescence, temperature, salinity and oxygen were electronically measured, and nutrients (NO_3, PO_4 and Si) and bottle oxygen taken at the surface and depths of 25, 50, 75, 100, 150 and 200m (unless shallower). Nutrient analysis followed techniques described in Cowley (1999) and has an approximate accuracy of 0.02 µM. Chlorophyll *a* was calculated as per Baird et al. (2008) following the method of Jeffery & Humphery (1975). Calibration of the CTD fluorometer showed Chlorophyll *a* = 0.0157(Fluorescence) + 0.4421 (r^2 = 0.53).

2.3 Particulate 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, we therefore consider 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 ($\rho=10^9$ mg m^{-3}) using:

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

Under our assumption that our particles have the density of water, 1mg is therefore equivalent to 1mm^3, resulting in our $Biomass\ (mg\ m^{-3})$ being equivalent to the often reported biovolume (mm^3 m^{-3}) and we have labelled our plot axes as such. Particulate 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) within R v4.0.2 (R Core Team, 2020).

2.4 A global context

To place our east Australian transects in a global context and identify general trends in zooplankton size structure on continental shelves, we examined 18 previous studies which investigated spatial changes in zooplankton communities over continental shelf regions. While each continental shelf is unique and the ecological and environmental context of each study will differ, nutrient enrichment is common along all continental shelves. This enrichment comes from a variety of sources including upwelling (Roughan and Middleton, 2002; Malan *et al.*, 2020), run-off (Correll *et al.*, 1992) and estuarine processes (Morris *et al.*, 1995) but for the context of our global comparison we are only concerned with the resulting pattern of zooplankton across the continental shelves. Where possible from each study we extracted values for total zooplankton biomass (or biovolume), 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 offshore value, averaged across the study as well as corresponding bathymetry values, except for two studies from the Bay of Biscay (Irigoien *et al.*, 2009; Vandromme *et al.*, 2014), where the east and south regions had very different zooplankton communities so there were kept as distinct regions. If there were multiple years or seasons within a study, an average was taken. As many studies only provided binned values or plots, data were estimated from plots using a colour sampling tool and binned data were assigned values equal to the mid-point of the bin (Table S1). As the studies reported a range of units, to make studies comparable in terms of inshore to offshore trends we present the ratio of inshore to offshore values.

3. Results

3.1 Regional Oceanography and Seasonality

At the time of our sampling, the three northern most transects (north of 30°S) all crossed from cooler inshore waters into warm EAC water but the southern transect (Diamond Head 31.75°S) was located south of where the EAC begins to separate from the shelf ("the separation zone"; Figure 1). All transects showed low chlorophyll levels (<1.4 mg m^{-3}; Figure S1) which was representative of the previous month of low chlorophyll *a* at these locations (Figure S2). Most transects were negligibly influenced by the effects of wind in the 3 days prior to the transects (Figure S3), with most of the wind coming from a southerly direction. The exception was the North Solitary (30°S) transect which was subject to some wind driven upwelling prior to our sampling (Figure S3).

In terms of seasonality, 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 2). The alongshore velocity at all sites was reduced between April and August before increasing in Spring (when our observations were taken) and Summer. This seasonality is consistent with previous findings from higher-resolution HF radar observations around 30°S (Archer et al., 2019). Despite the seasonality in EAC speed, the main factor is latitude, with mean monthly velocities greater than 0.45 m s^{-1} all year round North of 30°S, compared to the Diamond Head site, where they never reach that magnitude (Figure 2). Therefore, we expect the observed cross-shelf gradients in water-masses (temperature, salinity) induced by the EAC in the northern sites to be consistent all year round.

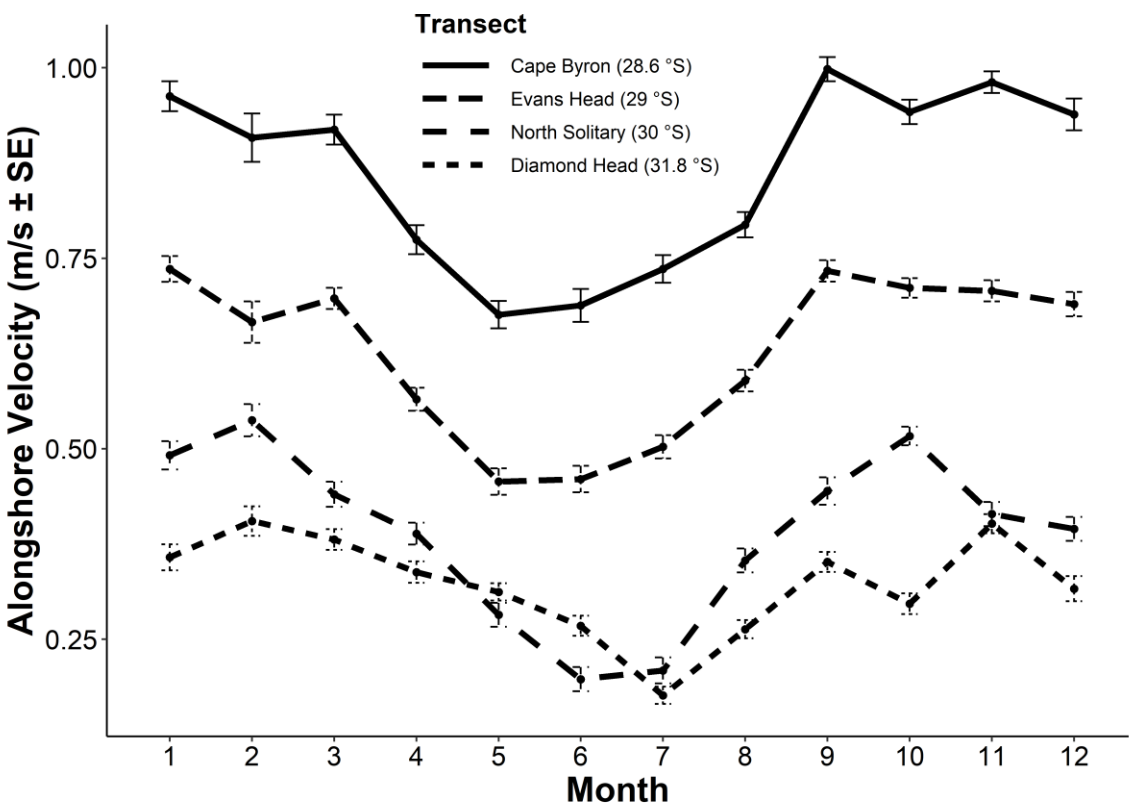


Figure 2 Seasonal changes in mean alongshore surface velocity (towards ~195°, minor variation in coastline angle between sites) at the Cape Byron (28.6°S), Evans Head (29°S), North Solitary Island (30°S) and Diamond Head (31.8°S) based upon 10 years of satellite altimetry data (2004 – 2013). Velocity 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). The alongshore flow is in a southerly direction.

Based upon 455 CPR observations within our study region, ranging from 2009 – 2020, we found some variation in zooplankton composition between months although copepods were always the most abundant. Within months there was smaller variation and during our sampling period, samples are typically dominated by copepods (> 90%; Figure 3).

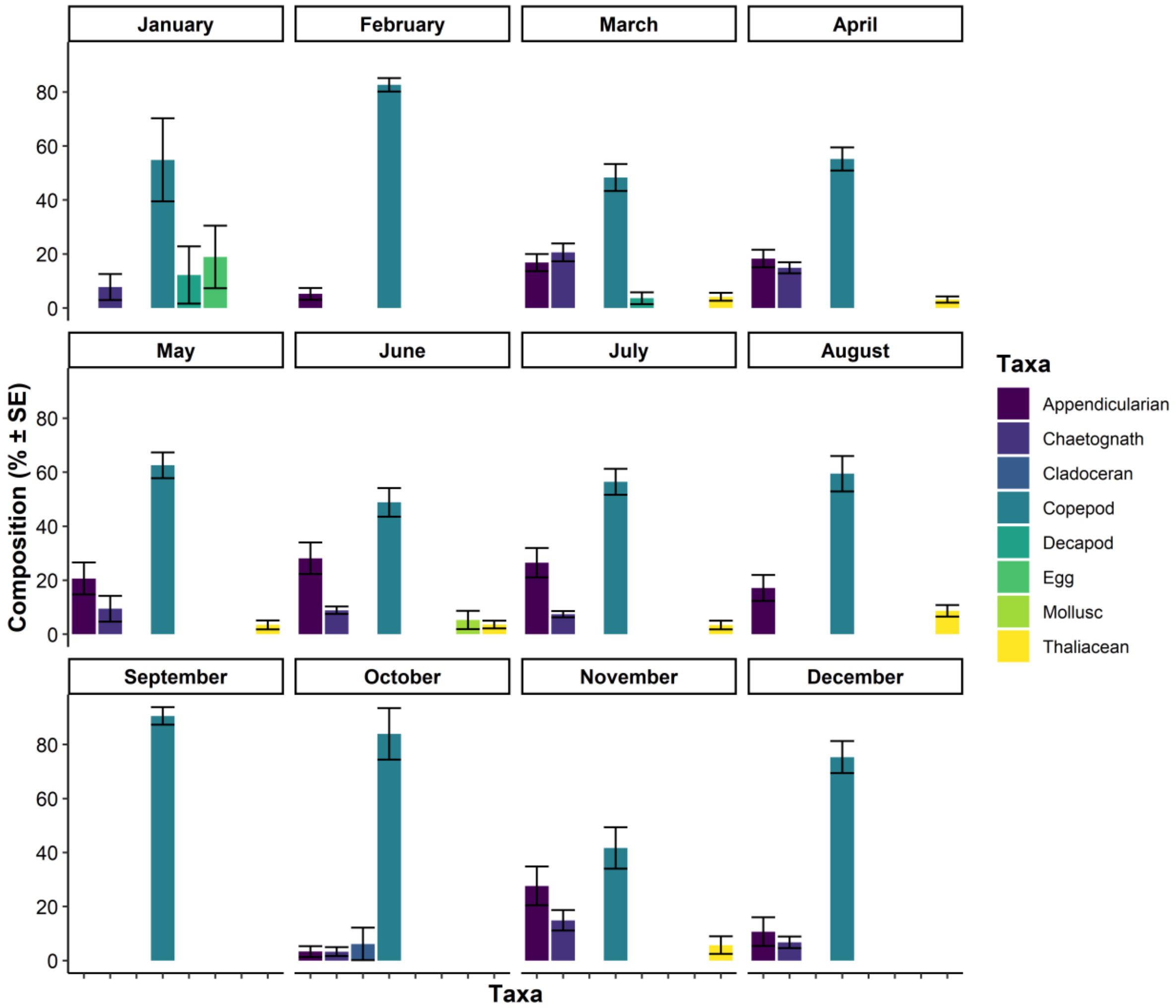


Figure 3 Monthly zooplankton composition based upon continuous plankton recorder data (n = 455) in eastern Australia (28 – 32°S, 152- 155°E, 2009 - 2020). Error bars show ±1 standard error. Note Taxa are also arranged alphabetically along the x-axis and taxa <3 % in all months were omitted from the plots.

3.2 Cape Byron (28.6°S)

The northernmost transect at Cape Byron (28.6°S) was dominated by the EAC which had a strong alongshore flow (1.50 m s^{-1}; Figure 4). The EAC was centred 27.6km offshore, above the 200 m isobath. Most of the continental shelf was flooded by warm EAC water (Figure 5). There was evidence of uplift with the 21 °C isotherm rising to the surface from 70 m depth over 5 km and the 20 °C isotherm rising to the surface from 100 m depth over 15 km. The EAC showed slight onshore movement which increased offshore and with depth, peaking between 100 and 200 m depth (up to 0.26 m s^{-1}, Figure S4). Due to the proximity of the strong EAC from the continental slope and the lack of upwelling-favourable wind stress (Figure S3), the isotherm uplift is likely to be current-driven, as shown in Schaeffer *et al*. (2014).

A decline in particulate (zooplankton) biomass and abundance was observed from both inshore to offshore and from the surface to depth with the highest biomass (~750 mg m^{-3}; Figures 5, S5, S6, S7) observed at the surface ~20 km from the coastline, just inshore of the 21 °C isotherm (Figure 5a). The warmer offshore EAC waters were characterised by lower zooplankton biomass with a GMS of ≈450 µm ESD (Figure 6) with steep size spectrum slopes between -1 and -1.3 (Figure 5). The cooler water immediately inshore of the 21 °C isotherm had high particulate (zooplankton) biomass and a shallower size spectrum slope (-0.9; Figure 5) with larger particles (GMS 500 µm ESD; Figure 6). Further inshore again (15 -17 km from the coastline), in water < 20 °C, biomass remained high (Figure 5), but the particles were smaller (GMS ≈430 µm ESD; Figure 6), resulting in a steeper size spectrum slope (≈-1.25; Figure 7). No depth resolved cross shelf chlorophyll *a* or nutrient data was available for the Cape Byron transect but there was a gradient in both salinity and temperature across the shelf. Warmer saltier water was found in offshore water, with the salinity both showing similar uplift onto the shelf as described above for the temperature isotherms (Figure S9).

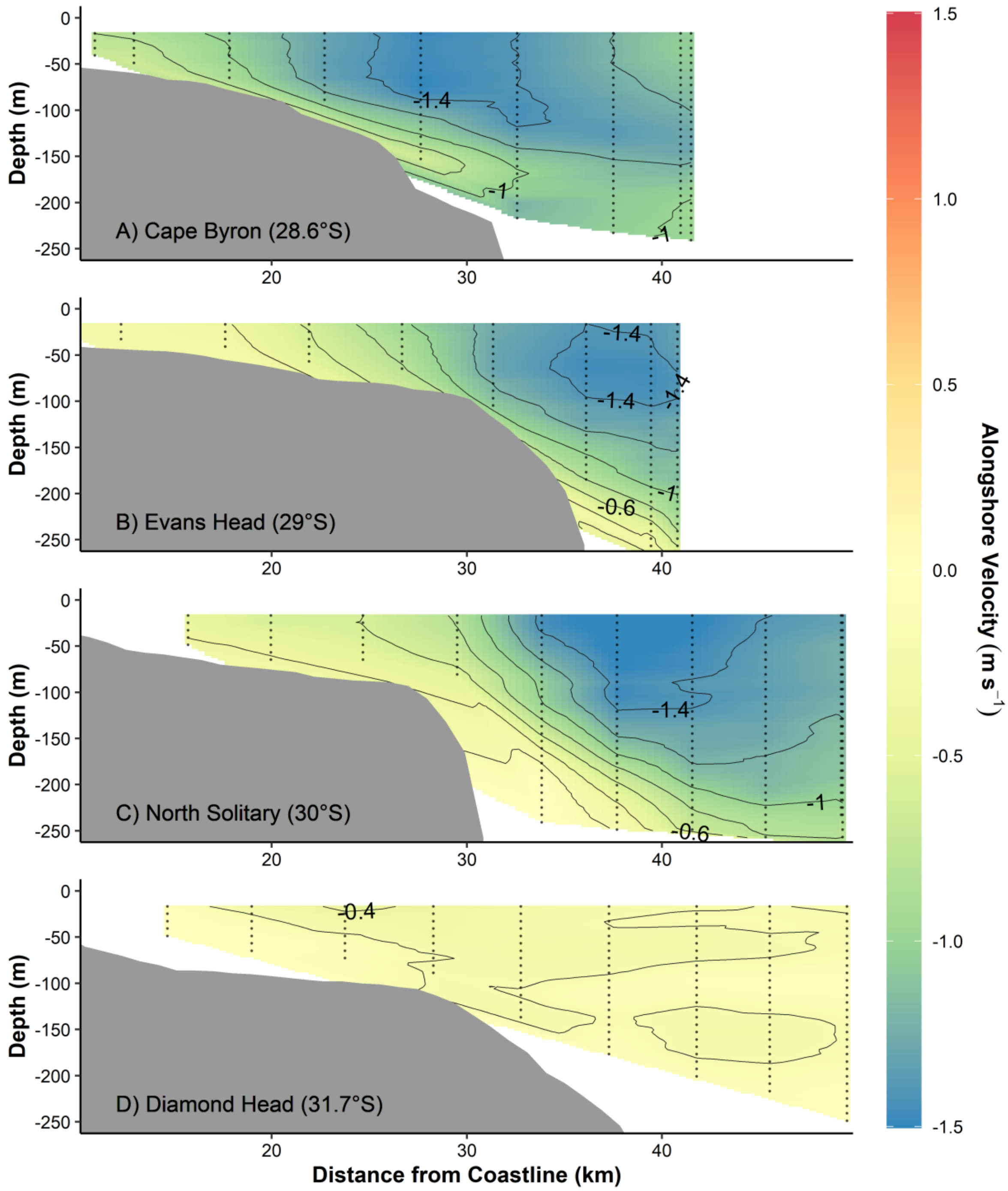


Figure 4 Alongshore (towards ~195°, minor variation in coastline angle between sites) velocity across the four cross shelf transects (Figure 1), from the vessel's Acoustic Doppler Current Profiler. Grey lines join areas of equal velocity.

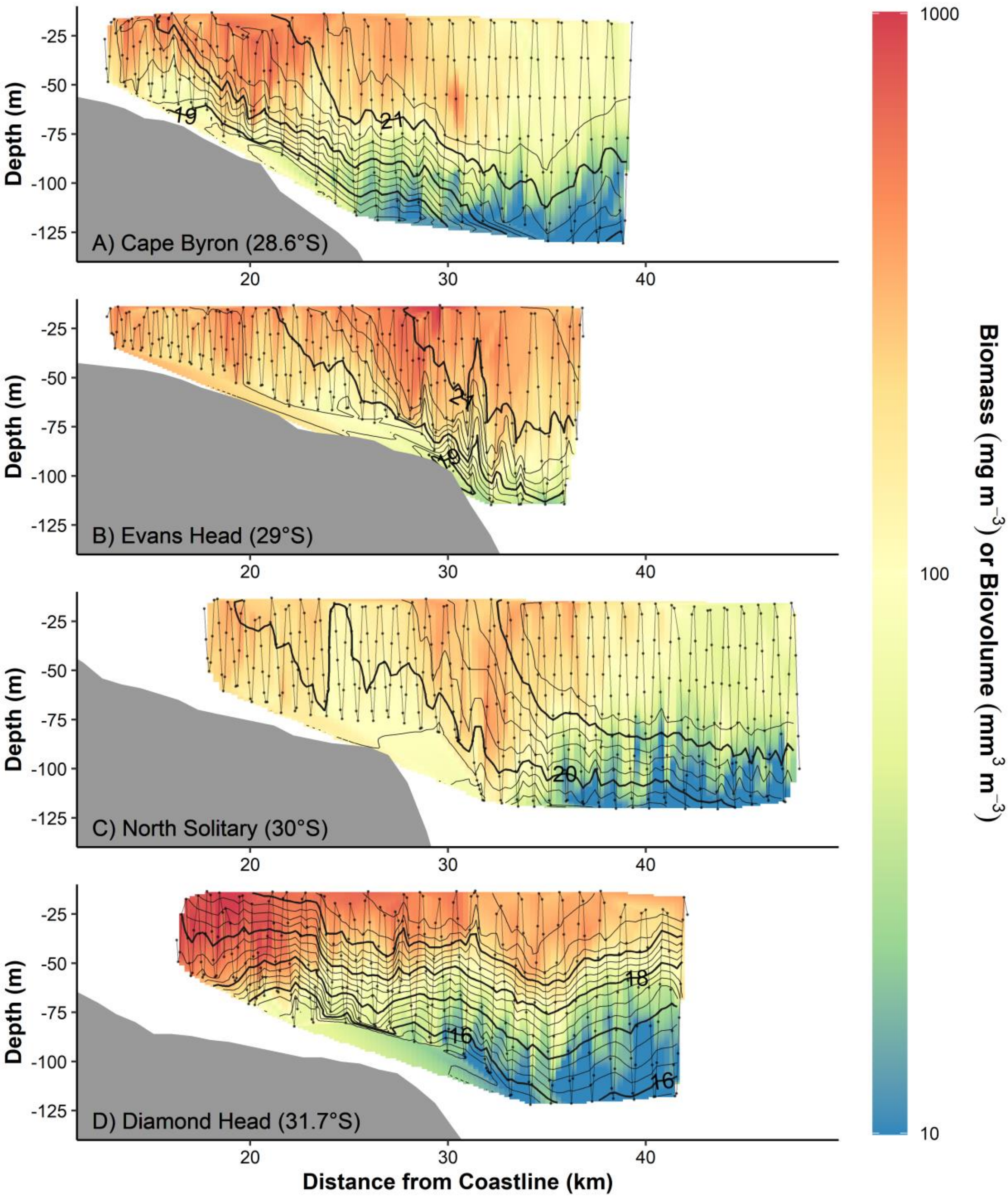


Figure 5 Particulate (zooplankton) biomass (mg m^{-3}) and biovolume (mm m^{-3}) distributions from the four cross shelf transects (Figure 1). Transects were conducted from inshore to offshore with an undulating towed body with the path shown by the grey line with midpoints of each sample shown as dots. Temperature (°C) isotherms are shown in black. Note biomass the $\log_{10}$ transformed colour scale.

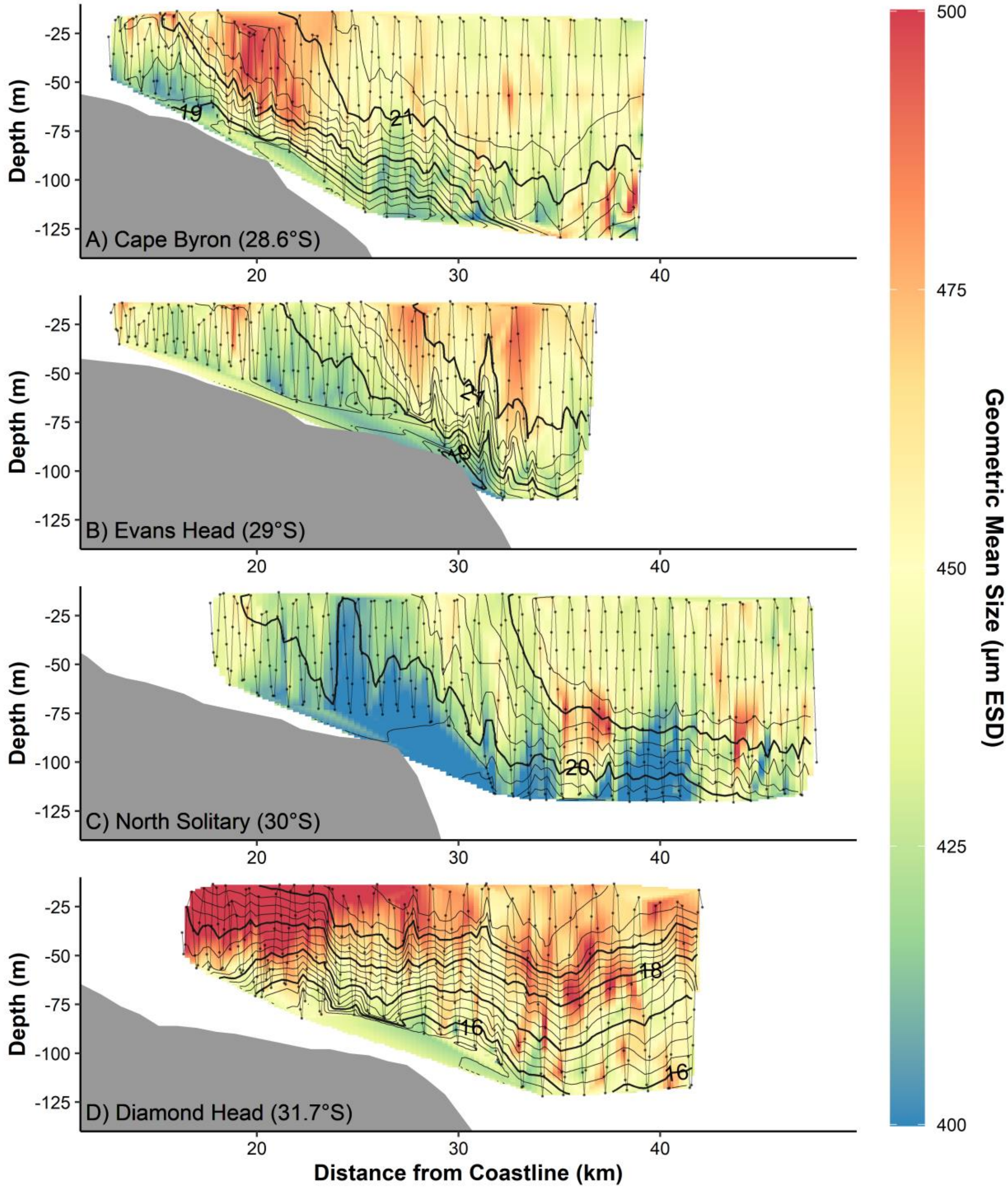


Figure 6 Geometric Mean Size (µm equivalent spherical diameter) of particulates (zooplankton) from the four cross shelf transects (Figure 1). Transects were conducted from inshore to offshore with an undulating towed body with the path shown by the grey line with midpoints of each sample shown as dots. Temperature (° C) isotherms are shown in black.

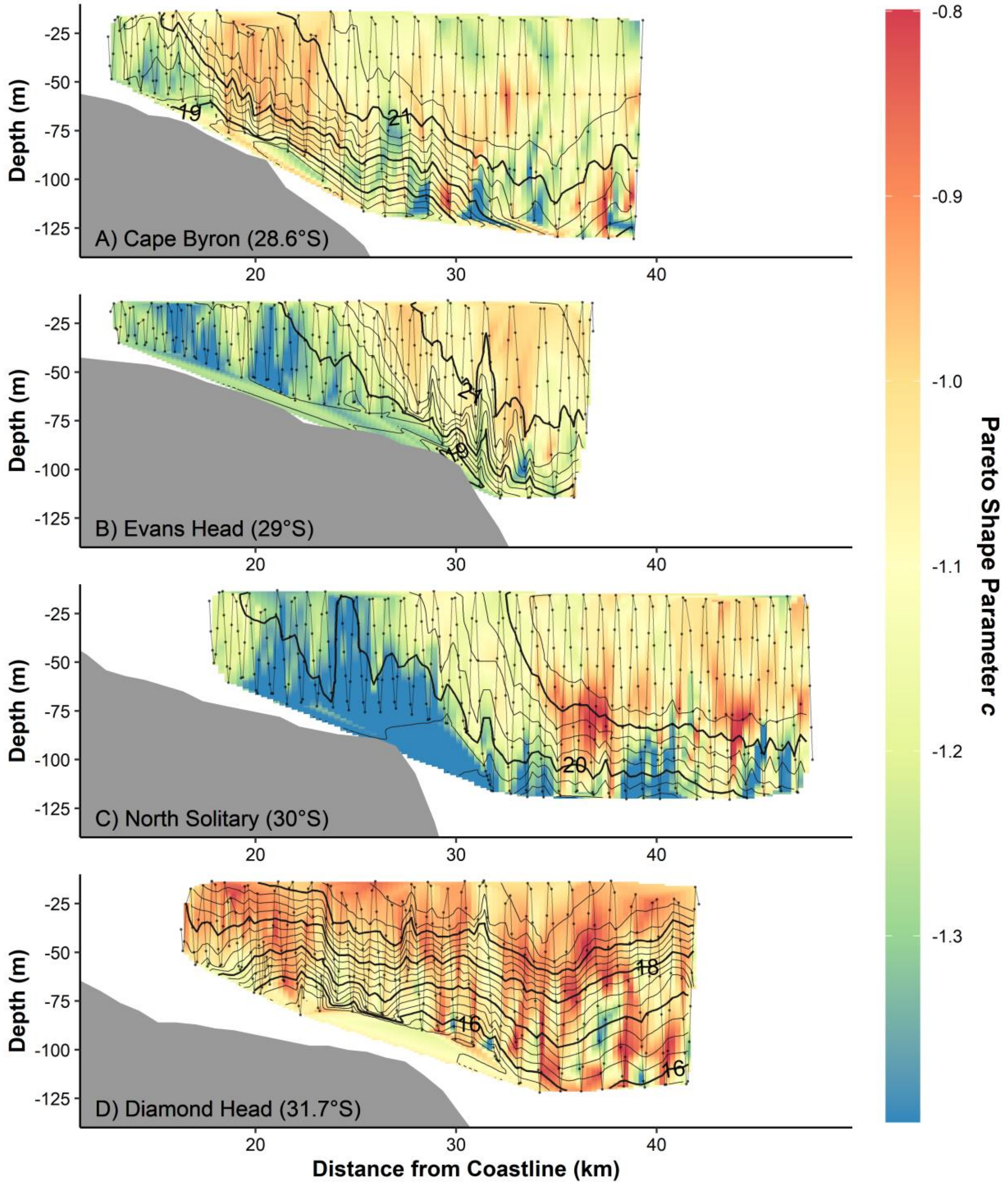


Figure 7 Interpolations of the shape parameter *c* from the Pareto distribution of particulate (zooplankton) size from the four cross shelf transects (Figure 1). This is a robust estimate of the normalised biomass size spectrum slope (shown in Figure S8). Transects were conducted from inshore to offshore with an undulating towed body with the path shown by the grey

line with midpoints of each sample shown as dots. Temperature (° C) isotherms are shown in black.

3.3 Evans Head (29°S)

The transect at Evans Head (29°S) extended only 5km past the continental shelf edge but was still largely influenced by the EAC. The EAC was centred 36.1km from the offshore above the 220m contour. The EAC had a strong along-shore flow (1.47 m s^{-1}; Figure 4). The EAC showed offshore movement (0.27 m s^{-1}) which increased with distance offshore (Figure S4). There was strong uplift of the isotherms inshore of the EAC with the 21 °C isotherm rising to the surface from 70 m depth over 6 km and the 20 °C isotherm rising to the surface from 100 m depth over 15 km. Due to the proximity of the strong EAC from the continental slope and the lack of upwelling-favourable wind stress (Figure S3), the isotherm uplift is likely to be current-driven, as shown in Schaeffer et al. (2014).

The particulate (zooplankton) size structure varied along the transect. The EAC was warmer and saltier compared to the inner shelf water (Figure S9). There was also a slight gradient in nitrate and chlorophyll *a* with higher levels of both in the inshore waters (3 mmol m^{-3} and 1.35 mg m^{-3} respectively; Figures S10 & S11). In the warmer offshore water the zooplankton biomass and geometric mean size was similar that offshore at Cape Byron while in the cool inshore waters, there was again high particulate (zooplankton) biomass (Figure 5), but the community had shifted towards smaller particles which resulted in a steeper *c* (< -1.3; Figures 5 & 6). There was also low abundance in the deeper samples (Figure S7).

3.4 North Solitary (30°S)

The transect at North Solitary (30°S) showed the strongest evidence of uplift of any of the transects with the 21 °C isotherm rising to the surface from 70 m depth over 3 km and the 20 °C isotherm rising to the surface from 100 m depth over 10 km (Figure 5). The EAC was centred of the EAC was 37.7 km offshore (alongshore flow 1.59 m s^{-1}), located above the 310 m bathymetry contour (Figure 4). This uplift could potentially have been driven by the upwelling favourable winds in the hours leading up to sampling (Fig S3). The offshore waters of the EAC showed slight onshore movement, at depths of 100-150m (0.15 m s^{-1}; Figure S4).

Biomass and abundance generally decreased with distance offshore and with depth (Figures 5, S5 & S6, S7). The warmer water, located offshore, contained low biomass with a shallow pareto distribution shape parameter *c* (-0.9) and GMS of ~450 µm (Figures 5, 6 & 7). Zooplankton in cooler water < 20 °C had a much smaller GMS (~400µm ESD) resulting in a steeper *c* (< -1.3). This was particularly evident where the 20°C isotherm reach the surface ~24 km from the coastline, bringing with it a potentially highly productive zooplankton community (Figures 6 & 7). This peak also aligned with a minor peak in chlorophyll *a* (1.45 mg m^{-3}; Figure S11). North Solitary showed evidence of uplift with the small GMS community from deep uplifted to the surface. The uplift could have resulted from the close-by EAC and the short upwelling-favourable wind a few hours before sampling. The deep cold water (< 16°C) had higher levels of nitrate and silicate (Figures S10 & S12), but this does not appear to have been lifted to the surface waters with the surface waters low in nutrients across the transect.

3.5 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 m s^{-1}, Figure 4) 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). The lack of horizontal variation was reflected in the nitrate, silicate, temperature and salinity with almost all variation being observed with depth (Figures S9, S10, S12). Chlorophyll *a* and oxygen showed small peaks (1.2 mg m^{-3} and 240 mmol m^{-3} respectively; Figures S11 & S13) at the surface near the beginning of the transect. 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).

This transect has the highest observed biomass of particles (>1000 mg m^{-3}), particularly inshore (Figure 5). The size structure was not clearly related to water masses reflecting the more homogenous water mass here. Inshore, the particulate (zooplankton) community was charactered by larger individuals (GMS ~500 µm ESD; Figure 6) and had higher overall biomass which declined steadily with distance offshore and with depth (Figures 5, S5 & S6). The pareto distribution shape parameter *c* of the community was shallow over the whole transect (≈-0.9; Figure 7).

3.6 Synthesis of Transect Patterns

The influence of the EAC varied between the three transects. The three northern transects were influenced strongly by the EAC, particularly the offshore sections while the Diamond Head transect was not influenced by the EAC. At the two northern sites the EAC was located close to the continental shelf and likely drove current driven upwelling. In contrast at the North Solitary site, the EAC was located further offshore, and the weaker observed uplift was potentially caused by wind driven upwelling (Fig S3).

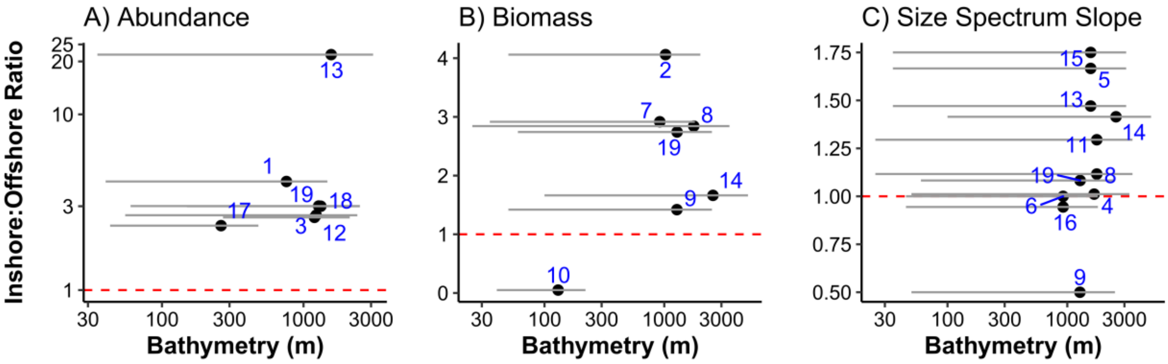
The Cape Byron, North Solitary and Diamond Head transects had higher particulate (zooplankton) biomasses observed in continental shelf waters with declines offshore and with depth in the top 100m of the water column (Figures S5 & S6). The transect at Evans Head did not show a noticeable decline in biomass 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.

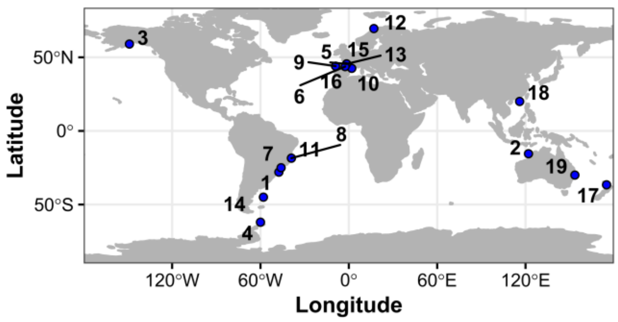
Three patterns in GMS were evident in our 4 transects. Cape Byron and to a lesser extent, Evans Head showed evidence of larger GMS around the front between the warm EAC and cooler inner shelf water (around the 21 °C isotherm; Figure 6). North Solitary showed evidence of uplift with the small GMS community from deep uplifted to the surface. The uplift could have resulted from the close-by EAC and the short upwelling-favourable wind a few hours before sampling. Diamond Head was very different with a more homogenous distribution of GMS although there was a trend of larger particulates (zooplankton) inshore. The size structure of all sites was related to the GMS with steeper size spectrum slopes in areas with smaller zooplankton (Figures 6 & 7). 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 S8).

3.7 Global Synthesis

19 studies quantified the cross-shelf changes in zooplankton (including this study), revealing a broad consensus (Figure 8; 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 8; 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 8, 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).





Ref. #	Region	Study
1	Santa Catarina Shelf	Becker et al 2018
2	Kimberley Coast	Beckley 2018
3	Gulf of Alaska	Coyle & Pinchuk 2005
4	Drake Passage	García−Muñoz et al 2014
5	Bay of Biscay − East	Irigoien et al 2009
6	Bay of Biscay − South	Irigoien et al 2009
7	Santa Catarina Shelf	Lopes et al 2006
8	Abrolhos Bank	Marcolin et al 2013
9	North Iberian Shelf	Nogueira et al 2004
10	Catalan Coast	Sabates et al 1989
11	Abrolhos Bank	Schultes & Lopes 2009
12	Norwegian Sea	Skarðhamar et al 2007
13	Bay of Biscay − East	Sourisseau & Carlotti 2006
14	Argentine Sea	Thompson et al 2013
15	Bay of Biscay − East	Vandromme et al 2014
16	Bay of Biscay − South	Vandromme et al 2014
17	Hauraki Gulf and Shelf	Zeldis & Willis 2015
18	South China Sea	Zhang et al 2019
19	East Australian Shelf	Schilling et al (This study)

Figure 8 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.

4. Discussion

The size-spectrum of zooplankton provides important information about the transfer of energy from phytoplankton to fish, from which we can understand how fisheries are supported on continental shelves. We found consistent declines from inshore to offshore in particulate (zooplankton) biomass and variation in size-structure both horizontally and vertically across the narrow continental shelf off eastern Australia (Figure 9). These horizontal trends in the particulate (zooplankton) size-structure are consistent with the patterns in size-structure across other continental shelves and likely are an outcome of nutrient enrichment which tends to occur on continental shelves. This enrich can come from a variety of sources including cross-shelf flows and sporadic upwelling processes driven by ocean currents and coastal winds (Roughan and Middleton, 2002; Rossi *et al.*, 2014; Malan *et al.*, 2020), estuarine process (Morris *et al.*, 1995) or run-off from land (Correll *et al.*, 1992).

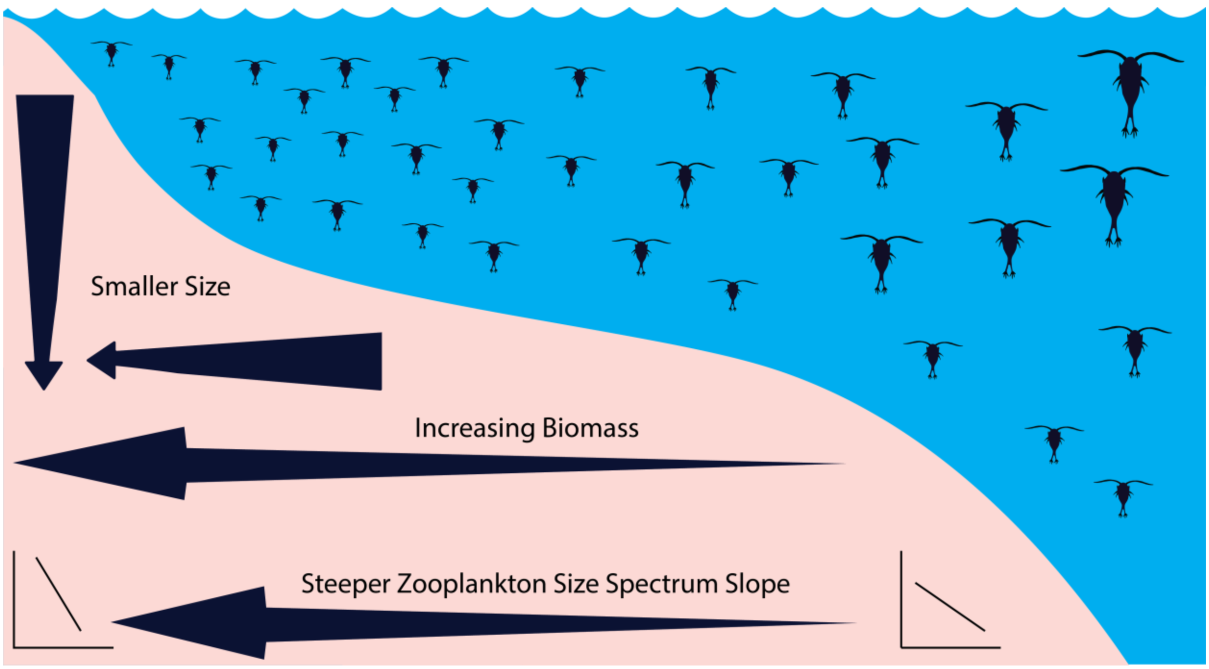


Figure 9 Conceptual diagram of the zooplankton community and how it changes over the

east Australian continental shelf and with depth. Note all zooplankton are represented by copepods in this diagram.

The cross-shelf observations of chlorophyll *a* and nutrients showed little patterns across our transects the majority of variation in water properties being observable through temperature and salinity. The warm salty EAC dominated the upper 100m of the offshore portions of the three northern transects with cooler inner shelf water. At Cape Byron and Evans Head, the EAC was in high proximity to the continental slope and the lack of upwelling-favourable wind stress (Figure S3) suggests that the observed isotherm uplift is likely to be current-driven, as shown in Schaeffer et al. (2014). This was contrasted by North Solitary where the EAC was further offshore and it was likely the uplift was at least partially caused by the upwelling favourable winds in the hours prior to sampling (Figure S3). As a contrast, Diamond Head which was located south of the EAC separation and therefore free from its influence was largely homogenous with little horizontal structure and limited uplift of isotherms. Particulate (zooplankton) biomass and mean size was generally reflective of the horizonal and vertical structure of the water. The cooler shelf water revealed a particulates (zooplankton) with higher biomass, smaller geometric mean size and steeper size spectrum slope (Figures 5, 6, 7), distinct from the warmer offshore EAC. These observations are consistent with sustained higher chlorophyll *a* on the continental shelf (Everett *et al.*, 2014) and are likely driven by uplift of the cooler water due to the EAC interacting with the sloping topography (Schaeffer *et al.*, 2014; Schaeffer and Roughan, 2015). As zooplankton are the basis of many coastal food webs, this consistent supply of nutrients is an important factor in the distribution and abundance of planktivorous fish and the higher trophic level fisheries found on continental shelves (Pauly *et al.*, 2002; 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 (Guiet *et al.*, 2016), but also by predation on larger zooplankton prey by planktivorous fish (Moore and Suthers, 2006). In the region of our study, planktivorous fish such as mackerel and scad consume zooplankton in the 0.5-1 mm particle diameters (Schilling, unpublished data) and are often found aggregating on the inside of the shelf edge (Holland *et al.*, 2021). Such predators could steepen the slope of the zooplankton biomass size spectrum as they target larger prey.

4.1 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 to a small extent influenced by uplift of deep nutrient-rich water mostly driven by the close proximity of the EAC to the continental shelf (Roughan and Middleton, 2002), which drives the higher biomass of phytoplankton (Everett *et al.*, 2014) and therefore 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, 2021). Therefore a steeper zooplankton size spectrum slope could arise not only from increased production of smaller zooplankton (Guiet *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 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 particulate (zooplankton) biomass compared to the oligotrophic EAC waters (Baird *et al.*, 2008), this was observed in our surveys to a limited extent with the EAC showing very small nutrient concentrations compared to the deeper and inner shelf waters (Figures S10 & S12). 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.

While this study provides the first high-resolution depth-resolved cross shelf transects, it is limited to the top 100m of the water column and there may be some influence of diel vertical migration of zooplankton on the vertical distribution. Despite this possibility we think the results are robust as two of the samples were conducted at night and two during the day with all four transect showing similar vertical gradients in particulate (zooplankton) properties. Furthermore, we did not sample in areas where the bathymetry was less than 50 m, where the inshore water masses are more influenced by terrestrial inputs, waves, wind-driven vertical mixing.

4.2 Comparison to other studies

Our study showed a consistent decline in biomass with increasing distance from shore and with increasing depth (to 100m depth) with the largest biomasses observed in the surface inner shelf waters, likely due to coastal nutrient enrichment (from a variety of mechanisms). 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). Despite different regional dynamics, cross-shelf and vertical gradients in water-masses, here driven by the EAC and uplift, seem to be the dominant factor for the patterns observed at various locations worldwide. 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). Further south of the Brazilian Bight, similar results were observed on the Abrolhos Bank where higher zooplankton biomass was observed on the continental shelf due to the Brazil Current interacting with the sea-floor, generating uplift and eddies which increased mixing over the continental shelf (Marcolin *et al.*, 2013).

In the southwest Pacific, there are relatively small terrestrial influences compared to other sources of nutrients such as upwelling are important (Apte *et al.*, 1998; Dai and

Trenberth, 2002; Pritchard *et al.*, 2003; Suthers *et al.*, 2011). Similar to the Brazil 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.

There are exceptions to the general trends that we identified 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). This temporal instability in some regions may suggest that repeated surveys under different oceanographic conditions may be necessary to fully understand the drivers of zooplankton on continental shelves. The current study had no temporal replication and while it was shown that the conditions which were sampled are regularly occurring features, additional studies would be useful to confirm the occurrence of the patterns in particulate (zooplankton) biomass and size structure.

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).

4.3 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 4), 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 (Suthers *et al.*, 2011; Wu *et al.*, 2012), and the increasing water temperatures in the southeast Australian region (Malan *et al.*, 2021), 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). With the impacts of warming oceans already being observed at coastal observing stations and phytoplankton communities increasingly dominated by warm-water tolerant chain forming diatoms (Ajani *et al.*, 2020), impacts from projected reductions in both phytoplankton and zooplankton biomass are likely to be amplified up the food chain with potentially large impacts on fisheries as food web become increasingly reliant on pelagic energy sources rather than benthic (Petrik *et al.*, 2020).

4.4 Conclusions

Based upon the general cross shelf patterns and the depth resolved data from the present study we suggest a general process for the distribution of zooplankton on continental shelves influenced by boundary currents (Figure 9). 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 cross-shelf differences in nutrient input which in our area was driven by the East Australia Current which drives productivity on the shelf through uplift of nutrient rich waters. Future studies could answer these questions with more sustained monitoring of cross-shelf patterns in zooplankton size structure throughout the year.

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Author Contributions

MEB & IMS conceived the study and collected the data. HTS, JDE, AS & PY analysed the data. HTS wrote the first draft and all authors contributed to and approved the final manuscript.

Data Availability

All data used in this study are freely accessible. The data from the Southern Surveyor voyage 08/2004 is available from the CSIRO Data Trawler (https://www.marine.csiro.au/data/trawler/). The long term environmental data is available from the Australian Ocean Data Network (https://portal.aodn.org.au/). All code used for the analysis in this paper is available in the GitHub repository https://github.com/HaydenSchilling/Inner-Shelf-Water.

Competing Interests Statement

The authors declare no competing interests.

References

Aguiar, A. L., Cirano, M., Pereira, J., and Marta-Almeida, M. 2014. Upwelling processes along a western boundary current in the Abrolhos–Campos region of Brazil. Continental Shelf Research, 85: 42–59.

Ajani, P. A., Davies, C. H., Eriksen, R. S., and Richardson, A. J. 2020. Global Warming Impacts Micro-Phytoplankton at a Long-Term Pacific Ocean Coastal Station. Frontiers in Marine Science, 7. Frontiers. https://www.frontiersin.org/articles/10.3389/fmars.2020.576011/full?utm_source=F-AAE&utm_medium=EMLF&utm_campaign=MRK_1467818_45_Marine_20201027_arts_A (Accessed 4 May 2021).

Akima, H., and Gebhardt, A. 2020. akima: Interpolation of Irregularly and Regularly Spaced Data. R package version 0.6-2.1. https://CRAN.R-project.org/package=akima.

Alldredge, A. L., and Silver, M. W. 1988. Characteristics, dynamics and significance of marine snow. Progress in Oceanography, 20: 41–82.

Andersen, K. H., Berge, T., Gonçalves, R. J., Hartvig, M., Heuschele, J., Hylander, S., Jacobsen, N. S., *et al.* 2016. Characteristic Sizes of Life in the Oceans, from Bacteria to Whales. Annual Review of Marine Science, 8: 217–241.

Apte, S. C., Batley, G. E., Szymczak, R., Rendell, P. S., Lee, R., and Waite, T. D. 1998. Baseline trace metal concentrations in New South Wales coastal waters. Marine and Freshwater Research, 49: 203–214.

Archer, M. R., Roughan, M., Keating, S. R., and Schaeffer, A. 2017. On the Variability of the East Australian Current: Jet Structure, Meandering, and Influence on Shelf Circulation. Journal of Geophysical Research: Oceans, 122: 8464–8481.

Armbrecht, L. H., Roughan, M., Rossi, V., Schaeffer, A., Davies, P. L., Waite, A. M., and Armand, L. K. 2014. Phytoplankton composition under contrasting oceanographic conditions: Upwelling and downwelling (Eastern Australia). Continental Shelf Research, 75: 54–67.

Armbrecht, L. H., Thompson, P. A., Wright, S. W., Schaeffer, A., Roughan, M., Henderiks, J., and Armand, L. K. 2015. Comparison of the cross-shelf phytoplankton distribution of two oceanographically distinct regions off Australia. Journal of Marine Systems, 148: 26–38.

Atkinson, A., Lilley, M. K. S., Hirst, A. G., McEvoy, A. J., Tarran, G. A., Widdicombe, C., Fileman, E. S., *et al.* 2020. Increasing nutrient stress reduces the efficiency of energy transfer through planktonic size spectra. Limnology and Oceanography, n/a. https://aslopubs.onlinelibrary.wiley.com/doi/abs/10.1002/lno.11613 (Accessed 26 October 2020).

Baird, M. E., Timko, P. G., Middleton, J. H., Mullaney, T. J., Cox, D. R., and Suthers, I. M. 2008. Biological properties across the Tasman Front off southeast Australia. Deep-Sea Research Part I-Oceanographic Research Papers, 55: 1438–1455.

Bakun, A., and Weeks, S. J. 2008. The marine ecosystem off Peru: What are the secrets of its fishery productivity and what might its future hold? Progress in Oceanography, 79: 290–299.

Barnes, C., Maxwell, D., Reuman, D. C., and Jennings, S. 2010. Global patterns in predator–prey size relationships reveal size dependency of trophic transfer efficiency. Ecology, 91: 222–232.

Blanchard, J. L., Heneghan, R. F., Everett, J. D., Trebilco, R., and Richardson, A. J. 2017. From Bacteria to Whales: Using Functional Size Spectra to Model Marine Ecosystems. Trends in Ecology & Evolution, 32: 174–186.

Brink, K. H. 2016. Cross-Shelf Exchange. Annual Review of Marine Science, 8: 59–78.

Carr, M.-E., and Kearns, E. J. 2003. Production regimes in four Eastern Boundary Current systems. Deep Sea Research Part II: Topical Studies in Oceanography, 50: 3199–3221.

Cetina-Heredia, P., Roughan, M., van Sebille, E., and Coleman, M. A. 2014. Long-term trends in the East Australian Current separation latitude and eddy driven transport. Journal of Geophysical Research: Oceans, 119: 4351–4366.

Correll, D. L., Jordan, T. E., and Weller, D. E. 1992. Nutrient flux in a landscape: Effects of coastal land use and terrestrial community mosaic on nutrient transport to coastal waters. Estuaries, 15: 431–442.

Cowley, R. 1999. Hydrochemistry operations manual. CSIRO Marine Laboratories, 236. CSIRO Div. of Marine Research, Hobart, Tasmania. https://doi.org/10.4225/08/585d676eb38c9.

Dai, A., and Trenberth, K. E. 2002. Estimates of Freshwater Discharge from Continents: Latitudinal and Seasonal Variations. Journal of Hydrometeorology, 3: 660–687.

D’Croz, L., and O’Dea, A. 2007. Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll. Estuarine, Coastal and Shelf Science, 73: 325–340.

Edwards, A. M., Robinson, J. P. W., Plank, M. J., Baum, J. K., and Blanchard, J. L. 2017. Testing and recommending methods for fitting size spectra to data. Methods in Ecology and Evolution, 8: 57–67.

Espinasse, B., Basedow, S., Schultes, S., Zhou, M., Berline, L., and Carlotti, F. 2018. Conditions for assessing zooplankton abundance with LOPC in coastal waters. Progress in Oceanography, 163: 260–270.

Everett, J. D., Baird, M. E., Oke, P. R., and Suthers, I. M. 2012. An avenue of eddies: Quantifying the biophysical properties of mesoscale eddies in the Tasman Sea. Geophysical Research Letters, 39: 5.

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.

García-Comas, C., Chang, C.-Y., Ye, L., Sastri, A. R., Lee, Y.-C., Gong, G.-C., and Hsieh, C. 2014. Mesozooplankton size structure in response to environmental conditions in the East China Sea: How much does size spectra theory fit empirical data of a dynamic coastal area? Progress in Oceanography, 121: 141–157.

GEBCO Bathymetric Compilation Group. 2019. The GEBCO_2019 Grid - a continuous terrain model of the global oceans and land.

Guiet, J., Poggiale, J.-C., and Maury, O. 2016. Modelling the community size-spectrum: recent developments and new directions. Ecological Modelling, 337: 4–14.

Heneghan, R. F., Hatton, I. A., and Galbraith, E. D. 2019. Climate change impacts on marine ecosystems through the lens of the size spectrum. Emerging Topics in Life Sciences, 3: 233–243.

Herman, A. W. 1992. Design and calibration of a new optical plankton counter capable of sizing small zooplankton. Deep Sea Research Part A. Oceanographic Research Papers, 39: 395–415.

Hobday, A. J., and Hartmann, K. 2006. Near real-time spatial management based on habitat predictions for a longline bycatch species. Fisheries Management and Ecology, 13: 365–380.

Holland, M. M., Smith, J. A., Everett, J. D., Vergés, A., and Suthers, I. M. 2020. Latitudinal patterns in trophic structure of temperate reef-associated fishes and predicted consequences of climate change. Fish and Fisheries, n/a. https://onlinelibrary.wiley.com/doi/abs/10.1111/faf.12488.

Holland, M. M., Everett, J. D., Cox, M. J., Doblin, M. A., and Suthers, I. M. 2021. Pelagic forage fish distribution in a dynamic shelf ecosystem – Thermal demands and zooplankton prey distribution. Estuarine, Coastal and Shelf Science, 249: 107074.

Irigoien, X., Fernandes, J. A., Grosjean, P., Denis, K., Albaina, A., and Santos, M. 2009. Spring zooplankton distribution in the Bay of Biscay from 1998 to 2006 in relation with anchovy recruitment. Journal of Plankton Research, 31: 1–17.

Jeffrey, S. W., and Humphrey, G. F. 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. Biochemie und Physiologie der Pflanzen, 167: 191–194.

Kelly, P., Clementson, L., Davies, C., Corney, S., and Swadling, K. 2016. Zooplankton responses to increasing sea surface temperatures in the southeastern Australia global marine hotspot. Estuarine, Coastal and Shelf Science, 180: 242–257.

Kerr, S. R., and Dickie, L. M. 2001. The biomass spectrum: a predator-prey theory of aquatic production. Columbia University Press.

Kobari, T., Makihara, W., Kawafuchi, T., Sato, K., and Kume, G. 2018. Geographic variability in taxonomic composition, standing stock, and productivity of the mesozooplankton community around the Kuroshio Current in the East China Sea. Fisheries Oceanography, 27: 336–350.

Krupica, K. L., Sprules, W. G., and Herman, A. W. 2012. The utility of body size indices derived from optical plankton counter data for the characterization of marine zooplankton assemblages. Continental Shelf Research, 36: 29–40.

Lampert, W. 1989. The Adaptive Significance of Diel Vertical Migration of Zooplankton. Functional Ecology, 3: 21–27. [British Ecological Society, Wiley].

Lucas, A. J., Dupont, C. L., Tai, V., Largier, J. L., Palenik, B., and Franks, P. J. S. 2011a. The green ribbon: Multiscale physical control of phytoplankton productivity and community structure over a narrow continental shelf. Limnology and Oceanography, 56: 611–626.

Lucas, A. J., Franks, P. J. S., and Dupont, C. L. 2011b. Horizontal internal-tide fluxes support elevated phytoplankton productivity over the inner continental shelf. Limnology and Oceanography: Fluids and Environments, 1: 56–74.

Mackinson, S., Daskalov, G., Heymans, J. J., Neira, S., Arancibia, H., Zetina-Rejón, M., Jiang, H., *et al.* 2009. Which forcing factors fit? Using ecosystem models to investigate the relative influence of fishing and changes in primary productivity on the dynamics of marine ecosystems. Ecological Modelling, 220: 2972–2987.

Maia, H. A., Morais, R. A., Quimbayo, J. P., Dias, M. S., Sampaio, C. L. S., Horta, P. A., Ferreira, C. E. L., *et al.* 2018. Spatial patterns and drivers of fish and benthic reef communities at São Tomé Island, Tropical Eastern Atlantic. Marine Ecology, 39: e12520.

Malan, N., Archer, M., Roughan, M., Cetina-Heredia, P., Hemming, M., Rocha, C., Schaeffer, A., *et al.* 2020. Eddy-Driven Cross-Shelf Transport in the East Australian Current Separation Zone. Journal of Geophysical Research: Oceans, 125: e2019JC015613.

Malan, N., Roughan, M., and Kerry, C. 2021. The Rate of Coastal Temperature Rise Adjacent to a Warming Western Boundary Current is Nonuniform with Latitude. Geophysical Research Letters, 48: e2020GL090751.

Marcolin, C. da R., Schultes, S., Jackson, G. A., and Lopes, R. M. 2013. Plankton and seston size spectra estimated by the LOPC and ZooScan in the Abrolhos Bank ecosystem (SE Atlantic). Continental Shelf Research, 70: 74–87.

Marcolin, C. da R., Lopes, R. M., and Jackson, G. A. 2015. Estimating zooplankton vertical distribution from combined LOPC and ZooScan observations on the Brazilian Coast. Marine Biology, 162: 2171–2186.

Mitra, A., Castellani, C., Gentleman, W. C., Jónasdóttir, S. H., Flynn, K. J., Bode, A., Halsband, C., *et al.* 2014. Bridging the gap between marine biogeochemical and fisheries sciences; configuring the zooplankton link. Progress in Oceanography, 129: 176–199.

Moore, S. K., and Suthers, I. M. 2006. Evaluation and correction of subresolved particles by the optical plankton counter in three Australian estuaries with pristine to highly modified catchments. Journal of Geophysical Research: Oceans, 111.

Morris, A. W., Allen, J. I., Howland, R. J. M., and Wood, R. G. 1995. The Estuary Plume Zone: Source or Sink for Land-derived Nutrient Discharges? Estuarine, Coastal and Shelf Science, 40: 387–402.

Nogueira, E., González-Nuevo, G., Bode, A., Varela, M., Morán, X. A. G., and Valdés, L. 2004. Comparison of biomass and size spectra derived from optical plankton counter data and net samples: application to the assessment of mesoplankton distribution along the Northwest and North Iberian Shelf. ICES Journal of Marine Science, 61: 508–517. Oxford Academic.

Oke, P. R., Roughan, M., Cetina-Heredia, P., Pilo, G. S., Ridgway, K. R., Rykova, T., Archer, M. R., *et al.* 2019. Revisiting the circulation of the East Australian Current: Its path, separation, and eddy field. Progress in Oceanography, 176: 102139.

Patti, B., Guisande, C., Vergara, A. R., Riveiro, I., Maneiro, I., Barreiro, A., Bonanno, A., *et al.* 2008. Factors responsible for the differences in satellite-based chlorophyll a concentration between the major global upwelling areas. Estuarine, Coastal and Shelf Science, 76: 775–786.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., Watson, R., *et al.* 2002. Towards sustainability in world fisheries. Nature, 418: 689–695. Nature Publishing Group.

Pereira Brandini, F., Nogueira, M., Simião, M., Carlos Ugaz Codina, J., and Almeida Noernberg, M. 2014. Deep chlorophyll maximum and plankton community response to oceanic bottom intrusions on the continental shelf in the South Brazilian Bight. Continental Shelf Research, 89: 61–75.

Petrik, C. M., Stock, C. A., Andersen, K. H., van Denderen, P. D., and Watson, J. R. 2020. Large Pelagic Fish Are Most Sensitive to Climate Change Despite Pelagification of Ocean Food Webs. Frontiers in Marine Science, 7. Frontiers. https://www.frontiersin.org/articles/10.3389/fmars.2020.588482/full (Accessed 4 May 2021).

Pritchard, T. R., Lee, R. S., Ajani, P. A., Rendell, P. S., Black, K., and Koop, K. 2003. Phytoplankton Responses to Nutrient Sources in Coastal Waters off Southeastern Australia. Aquatic Ecosystem Health & Management, 6: 105–117. Taylor & Francis.

R Core Team. 2020. R: A Language and Environment for Statistical Computing v4.0.2. R Foundation for Statistical Computing, Vienna, Austria.

Revill, A. T., Young, J. W., and Lansdell, M. 2009. Stable isotopic evidence for trophic groupings and bio-regionalization of predators and their prey in oceanic waters off eastern Australia. Marine Biology, 156: 1241–1253.

Richardson, A. J., Walne, A. W., John, A. W. G., Jonas, T. D., Lindley, J. A., Sims, D. W., Stevens, D., *et al.* 2006. Using continuous plankton recorder data. Progress in Oceanography, 68: 27–74.

Richardson, A. J. 2008. In hot water: zooplankton and climate change. ICES Journal of Marine Science, 65: 279–295.

Ridgway, K. R., and Dunn, J. R. 2003. Mesoscale structure of the mean East Australian Current System and its relationship with topography. Progress in Oceanography, 56: 189–222.

Rossberg, A. G., Gaedke, U., and Kratina, P. 2019. Dome patterns in pelagic size spectra reveal strong trophic cascades. Nature Communications, 10: 4396. Nature Publishing Group.

Rossi, V., Schaeffer, A., Wood, J., Galibert, G., Morris, B., Sudre, J., Roughan, M., *et al.* 2014. Seasonality of sporadic physical processes driving temperature and nutrient high-frequency variability in the coastal ocean off southeast Australia. Journal of Geophysical Research: Oceans, 119: 445–460.

Roughan, M., and Middleton, J. H. 2002. A comparison of observed upwelling mechanisms off the east coast of Australia. Continental Shelf Research, 22: 2551–2572.

Sabatès, A., Gili, J. M., and Pagès, F. 1989. Relationship between zooplankton distribution, geographic characteristics and hydrographic patterns off the Catalan coast (Western Mediterranean). Marine Biology, 103: 153–159.

Schaeffer, A., Roughan, M., and Morris, B. D. 2013. Cross-shelf dynamics in a western boundary current regime: Implications for upwelling. Journal of Physical Oceanography, 44: 2812–2813.

Schaeffer, A., Roughan, M., and Wood, J. E. 2014. Observed bottom boundary layer transport and uplift on the continental shelf adjacent to a western boundary current. Journal of Geophysical Research-Oceans, 119: 4922–4939.

Schaeffer, A., and Roughan, M. 2015. Influence of a western boundary current on shelf dynamics and upwelling from repeat glider deployments. Geophysical Research Letters, 42: 121–128.

Sourisseau, M., and Carlotti, F. 2006. Spatial distribution of zooplankton size spectra on the French continental shelf of the Bay of Biscay during spring 2000 and 2001. Journal of Geophysical Research: Oceans, 111.

Sprules, W. G., and Barth, L. E. 2015. Surfing the biomass size spectrum: some remarks on history, theory, and application. Canadian Journal of Fisheries and Aquatic Sciences, 73: 477–495. NRC Research Press.

Suthers, I. M., Taggart, C. T., Rissik, D., and Baird, M. E. 2006. Day and night ichthyoplankton assemblages and zooplankton biomass size spectrum in a deep ocean island wake. Marine Ecology Progress Series, 322: 225–238.

Suthers, I. M., Everett, J. D., Roughan, M., Young, J. W., Oke, P. R., Condie, S. A., Hartog, J. R., *et al.* 2011. The strengthening East Australian Current, its eddies and biological effects - an introduction and overview. Deep-Sea Research Part II-Topical Studies in Oceanography, 58: 538–546.

Thompson, P. A., Baird, M. E., Ingleton, T., and Doblin, M. A. 2009. Long-term changes in temperate Australian coastal waters: implications for phytoplankton. Marine Ecology Progress Series, 394: 1–19.

Truong, L., Suthers, I. M., Cruz, D. O., and Smith, J. A. 2017. Plankton supports the majority of fish biomass on temperate rocky reefs. Marine Biology, 164: 12.

Tsukamoto, K., and Miller, M. J. 2020. The mysterious feeding ecology of leptocephali: a unique strategy of consuming marine snow materials. Fisheries Science. https://doi.org/10.1007/s12562-020-01477-3 (Accessed 14 December 2020).

Turner, J. T., and Dagg, M. J. 1983. Vertical Distributions of Continental Shelf Zooplankton in Stratified and Isothermal Waters. Biological Oceanography, 3: 1–40.

Vandromme, P., Nogueira, E., Huret, M., Lopez-Urrutia, Á., González, G. G.-N., Sourisseau, M., and Petitgas, P. 2014. Springtime zooplankton size structure over the continental shelf of the Bay of Biscay. Ocean Science, 10: 821–835.

Vidondo, B., Prairie, Y. T., Blanco, J. M., and Duarte, C. M. 1997. Some aspects of the analysis of size spectra in aquatic ecology. Limnology and Oceanography, 42: 184–192.

Wallis, J. R., Swadling, K. M., Everett, J. D., Suthers, I. M., Jones, H. J., Buchanan, P. J., Crawford, C. M., *et al.* 2016. Zooplankton abundance and biomass size spectra in the East Antarctic sea-ice zone during the winter–spring transition. Deep Sea Research Part II: Topical Studies in Oceanography, 131: 170–181.

White, E. P., Ernest, S. K. M., Kerkhoff, A. J., and Enquist, B. J. 2007. Relationships between body size and abundance in ecology. Trends in Ecology & Evolution, 22: 323–330.

Wickham, H. 2011. ggplot2. WIREs Computational Statistics, 3: 180–185.

Wood, J. E., Schaeffer, A., Roughan, M., and Tate, P. M. 2016. Seasonal variability in the continental shelf waters off southeastern Australia: Fact or fiction? Continental Shelf Research, 112: 92–103.

Wu, L., Cai, W., Zhang, L., Nakamura, H., Timmermann, A., Joyce, T., McPhaden, M. J., *et al.* 2012. Enhanced warming over the global subtropical western boundary currents. Nature Climate Change, 2: 161–166. Nature Publishing Group.

Zhou, M. 2006. What determines the slope of a plankton biomass spectrum? Journal of Plankton Research, 28: 437–448. Oxford Academic.

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Conflict of Interest Statement

The authors declare no conflicts of interest.

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