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

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Scientific Significance Statement Topic

Our paper addresses a significant gap in the broad understanding of zooplankton communities. Using a towed optical plankton counter, this paper is the first to present high resolution depth resolved transects of the zooplankton community across a continental shelf. We find significant horizontal and vertical declines in biomass as well as an altered size structure of the zooplankton community, particularly in the regions where the East Australian Current was present. By undertaking a global synthesis, we then show that these horizontal patterns in the zooplankton community are consistent globally and we present a conceptual figure of how the zooplankton community changes across continental shelves. This study has significance for the fields of oceanography, zooplankton ecology and fisheries. It is critical we understand how oceanographic processes influence the pelagic biological communities of continental shelves as they are one of the most exploited marine environments in the world.

Scientific Significance Statement Outlet

As a key observational study linking oceanography and pelagic ecology with global implications, we believe L&O is the ideal journal for this paper.

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

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Statement of Significance

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Abstract

Western boundary currents influence continental shelf ecosystems through bottom water intrusions and coastal upwelling which stimulate production in the plankton community. Using an optical plankton counter and CTD mounted on an undulating towed body we present the first high-resolution vertically resolved profiles of the zooplankton community across a continental shelf at different latitudes. Zooplankton biomass is highest inshore with biomass declining with both increasing distance from shore and depth in the water column. The front between the warm East Australian Current (EAC) and cooler continental shelf waters also showed increased biomass of zooplankton. The EAC influenced the continental shelf waters by creating current driven uplift of slope waters, resulting in zooplankton communities with smaller geometric mean sizes and steeper slopes as estimated from the normalised biomass size spectrum, characteristics of a more productive community. South of the EAC separation from the coast, the continental shelf zooplankton community was more spatially homogenous but still displayed the same broad horizontal and vertical patterns in zooplankton. The patterns observed in this study align with other research on zooplankton distributions on continental shelves and we suggest that inner continental shelf regions are more productive and support high biomasses of zooplankton compared to offshore. Uplift stimulated productive zooplankton communities may be a driver of productive fisheries which are often found on continental shelves.

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Introduction

Western boundary currents (WBCs) transport warm water from the tropics towards the poles along continental boundaries. WBCs generally inhibit cross-shelf transport due to their strong along-shore flows (Roughan et al. 2011). At a smaller scale, WBCs interact with the continental shelves to generate eddies, fronts and upwelling that can increase transport across the shelf (Suthers et al. 2011). By increasing upwelling of cold water on the continental shelf (Schaeffer et al. 2013), WBCs contribute to the production of plankton and fish through the supply of nutrients normally found in cooler deeper water (Pereira Brandini et al. 2014).

The distribution of zooplankton on the shelf is the result of biophysical processes of transport and retention, prey availability and predator abundance as well as behaviour of the zooplankton (Huntley et al. 2000). Higher zooplankton biomass is often observed on the continental shelf compared to offshore regions and has been observed in the southeast Atlantic (Marcolin et al. 2013), northeast Atlantic (Sourisseau and Carlotti 2006; Irigoien et al. 2009; Vandromme et al. 2014) and southwest Atlantic (Pereira Brandini et al. 2014). While the increase in zooplankton biomass in nearshore environments is thought to be enhanced by increased nutrients from terrestrial discharge, some regions such as the southwest Pacific around Australia are known to have relatively small terrestrial influences when compared to other sources of nutrients such as upwelling (Apte et al. 1998; Dai and Trenberth 2002; Pritchard et al. 2003; Suthers et al. 2011).

The implications of shelf-based production of zooplankton are evident in the predominant biomass distribution of planktivorous fishes, found along vast stretches of continental shelves (Holland et al. 2020). As prey for zooplanktivorous fish, zooplankton transfer energy to higher trophic levels (Marquis et al. 2011; Champion et al. 2015) with zooplankton supporting up to 53 % of fish biomass on temperate coastal reefs (Truong et al. 2017). Predator-prey interactions involving zooplankton are usually driven by body size (Barnes et al. 2010), and by focusing on the size distribution of the zooplankton community, complex species-specific dynamics can be simplified (Blanchard et al. 2017).

One of the metrics commonly calculated based upon the size structure of the zooplankton community is the zooplankton size spectra slope (Sprules and Barth 2015; Edwards et al. 2017). This slope is a metric for quantifying the frequency distribution of individual body sizes within a community and can provide insight into community function (White et al. 2007). Usually calculated on a logarithmic body scale, the slope is negative and often linear. There are numerous ways of calculating the zooplankton size spectra slope for a community (Edwards et al. 2017). Two common methods are the Normalized Biomass Size Spectrum (NBSS; Kerr and Dickie 2001) and the shape parameter *c* of a Pareto distribution fit to the data (Vidondo et al. 1997; Suthers et al. 2006; Krupica et al. 2012). Regardless of the slope calculation method used, a steeper slope with a larger fraction of small particles infers higher production and/or higher predation while a shallow slope often represents lower predation and less ‘top-down’ pressure (Heath 1995; Kerr and Dickie 2001; Zhou et al. 2010).

In the southeast Atlantic, the zooplankton community on the continental shelf had higher biomass and a steeper zooplankton size spectra slope (indicating a more productive environment) compared to the offshore oceanic stations which were typically more vertically stratified (Marcolin et al. 2013). This is similar to the northeast Atlantic where high zooplankton biomasses and steeper zooplankton size spectra slopes were found in some but not all inshore regions (Sourisseau and Carlotti 2006; Irigoien et al. 2009; Vandromme et al.

2014). Compared with cross-shelf investigations, few studies have examined the vertical patterns of zooplankton on continental shelves. On the shelf off New York, during late summer the vertical zooplankton distribution was strongly influenced by water mass with distinct zooplankton communities separated by a strong thermocline (Turner and Dagg, 1983). This is contrasted with a winter study on the Abrolhos Bank where, on the shelf, copepod abundance peaked near the surface (20 – 40 m) and decreased with depth in the water column (Marcolin et al. 2015). Recently it has been suggested that light availability and predation by fish may be significant drivers of vertical zooplankton distributions (Aarflot et al. 2019).

Despite the previous research on cross-shelf distributions of zooplankton, there remains little knowledge about how WBCs effect zooplankton communities on temperate continental shelves, particularly in terms of the vertical structure. This lack of knowledge is highlighted in temperate eastern Australia where there has been no research into cross-shelf patterns of zooplankton. We aim to fill this knowledge gap by describing horizontal and vertical patterns in the zooplankton community by using a case study of four vertically resolved, cross-shelf transects of zooplankton on the eastern continental shelf of Australia to:

1) Identify latitudinal differences in zooplankton distribution across a continental shelf in a WBC region, and
2) Identify potential drivers of the observed patterns in zooplankton biomass and, size-structure, and
3) Relate our observations to previous research to propose a general concept of zooplankton on continental shelves under the influence of a WBC.

Materials and Methods

Study Region

The East Australian Current (EAC), the western boundary current of the South Pacific gyre, forms between 10 and 20°S when the South Equatorial Current diverges against the Great Barrier Reef and north-eastern Australia. The southward flowing component, the EAC, flows at approximately 0.5 – 1.5 m s^{-1} along the continental shelf (Archer et al. 2017) until the majority of the EAC separates from the coast at approximately 30 – 32°S and continues to flow 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).

From 2nd – 13th September 2004, a research voyage on the 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 (Figure 1).

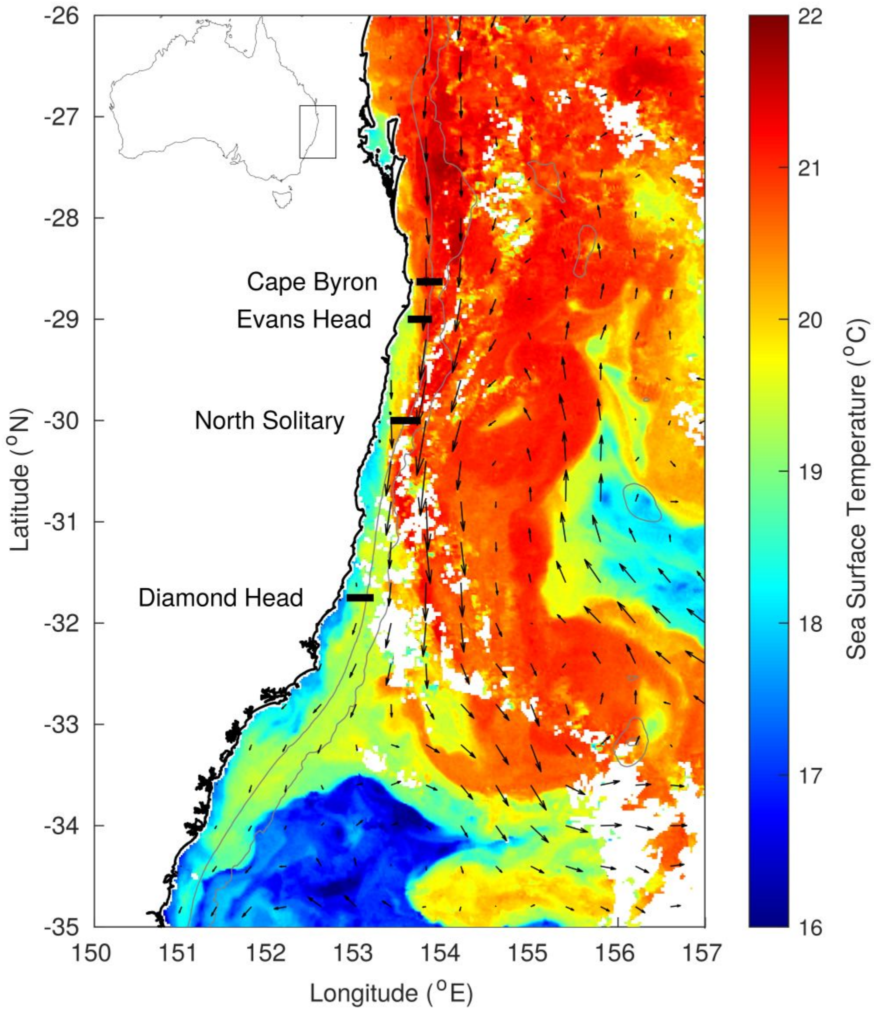

Figure 1 Locations of the four cross shelf sections which were sampled in September 2004. The sea-surface temperature for 6th September 2004 is shown in colour with velocity arrows from satellite altimetry shown with black arrows. Grey isobaths represent 200 and 2000m depths.

Sampling

Four constant latitude 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 (Tomczak et al. 2004; 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).

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

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

Environmental Data

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°). 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°). 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).

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

Zooplankton Data

The OPC was a Focal Technologies Corporation Model OPC-2T with a sampling aperture of 2 x 10 cm. 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 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 spectra slope which we calculated as the shape parameter *c* of the Pareto distribution of the particles (equivalent to the traditional NBSS slope). 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).

A global context

To place our east Australian transects in a global context and identify general trends in zooplankton communities on continental shelves, we examined previous studies which investigated spatial changes in zooplankton communities over continental shelf regions. We identified 14 additional studies which investigated changes in zooplankton communities over continental shelves and where possible from each study we extracted values for total zooplankton biomass, abundance and the zooplankton size spectra 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. Exceptions were 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 overall average was taken. As many studies only provided binned values or plots, data were estimated from plots 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.

Results

Regional Oceanography

The three northern most transects (north of 30°S) all crossed from cool inshore waters into warm (>21 °C) 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"), causing cooler (<19.5 °C) waters (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).

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}) centred over the 200 m isobath (27.6 km offshore). Most of the continental shelf was flooded by warm EAC water (Figure 2). The EAC showed slight onshore movement which increased offshore and with depth, peaking between 100 and 200m depth (up to 0.26 m s^{-1}, Figure S4). The strong EAC flow resulted in 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 5 km and the 20 °C isotherm rising to the surface from 100 m depth over 15 km.

A decline in zooplankton biomass was observed from both inshore to offshore and from the surface to depth with the highest biomass (~750 mg m^{-3}; Figures 3, S5, S6) observed at the surface ~20 km from the coastline, just inshore of the 21 °C isotherm (Figure 3a). This 21 °C isotherm appears to be a strong delineator of both zooplankton biomass and the size distribution. The EAC waters, warmer than 21 °C and > 1.2 m s^{-1} southward velocity, were characterised by low zooplankton biomass with a GMS of ≈450 µm ESD (Figure 4) with a steep zooplankton size spectra slope of between -1 and -1.3 (Figure 5). The cooler water immediately inshore of the 21 °C isotherm had a high zooplankton biomass, shallower zooplankton size spectra slope (-0.9; Figure 5) with large particles (GMS 500 µm ESD; Figure 4)). Further inshore again (15 -17 km from the coastline), in water < 20 °C, biomass remained high (Figure 3), but the particles were smaller (GMS ≈430 µm ESD; Figure 4), resulting in a steeper zooplankton size spectra slope (≈-1.25; Figure 5).

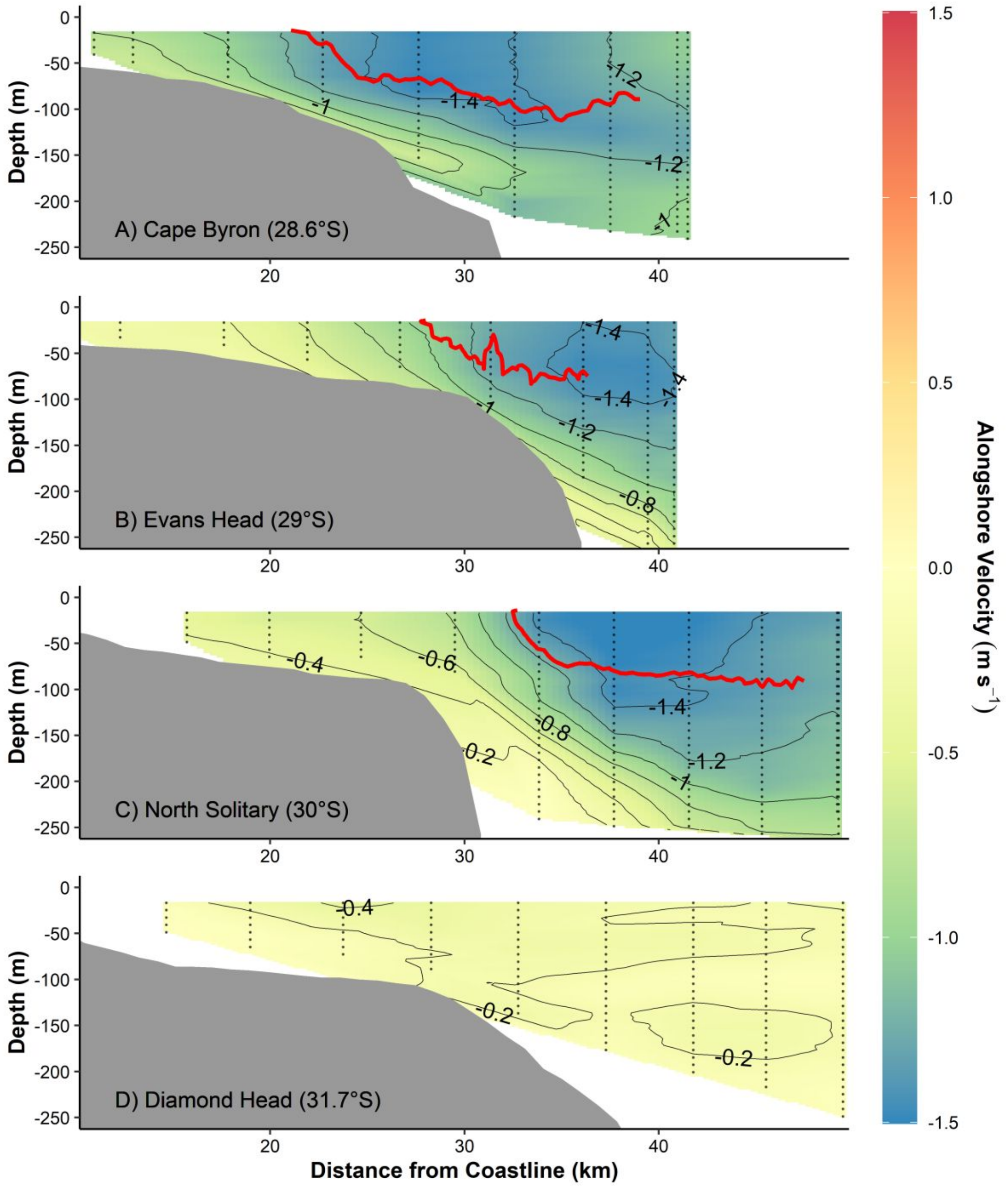

Figure 2 Alongshore velocity across the four cross shelf transects (Figure 1), from the vessel's Acoustic Doppler Current Profiler. Grey lines join areas of equal velocity. The red line shows the 21°C isotherm. Note the cooler water where there was no 21°C isotherm for Diamond Head.

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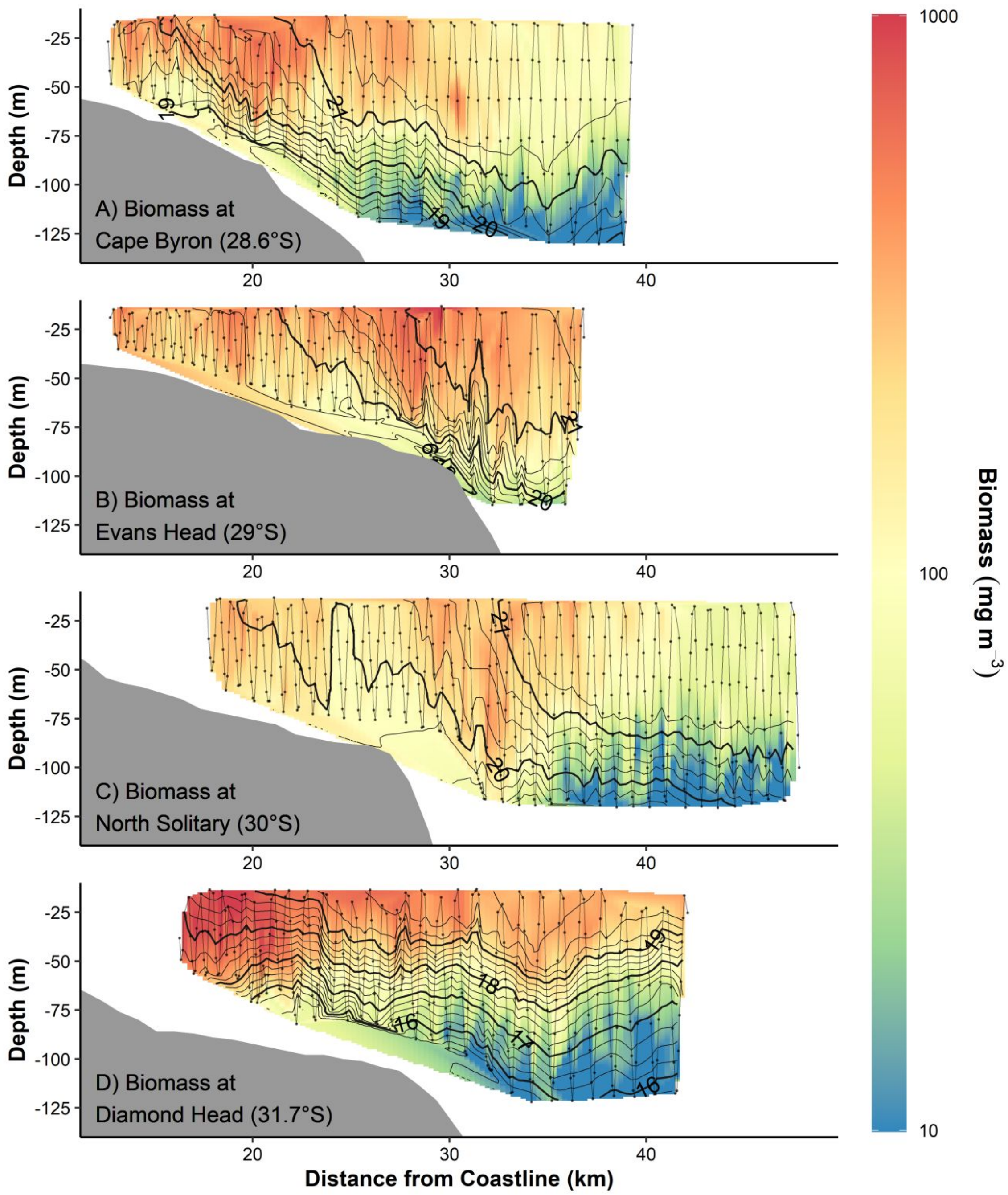

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284 **Figure 3** Zooplankton biomass (mg m^{-3}) distributions from the four cross shelf transects
285 (Figure 1). Transects were conducted from inshore to offshore with an undulating towed
286 body with the path shown by the grey line with midpoints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

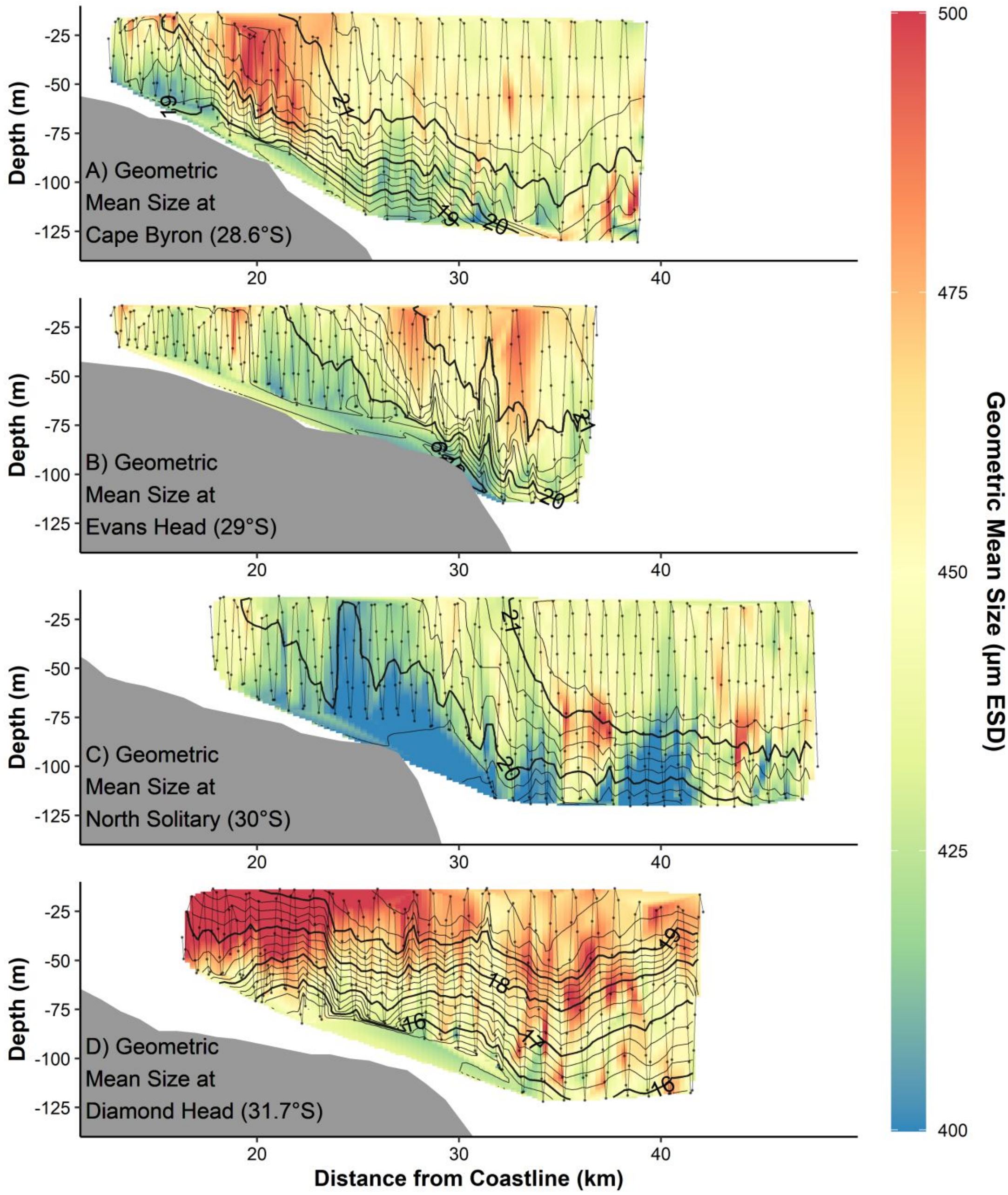


Figure 4 Geometric Mean Size (µm equivalent spherical diameter) of zooplankton from the four cross shelf transects (Figure 1). Transects were conducted from inshore to offshore with an undulating towed body with the path shown by the grey line with midpoints of each sample shown as dots. Temperature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

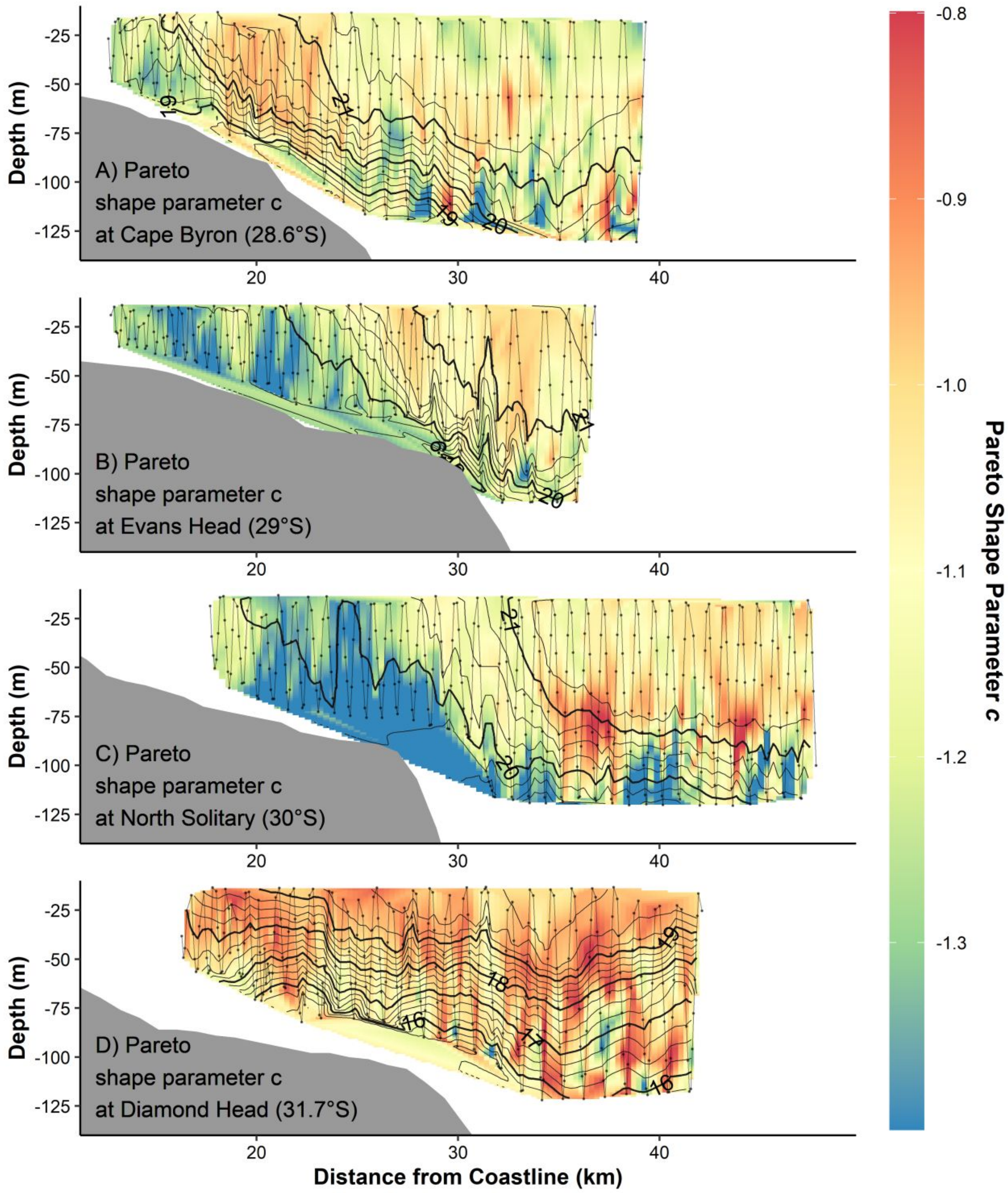


Figure 5 Interpolations of the shape parameter *c* from the Pareto distribution of zooplankton size from the four cross shelf transects (Figure 1). This is a robust estimate of the normalised biomass size spectrum slope (shown in Figure S7). Transects were conducted from inshore to offshore with an undulating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

Evans Head (29°S)

The transect slightly further south at Evans Head (29°S) did not go as far offshore as the other transects but was still largely influenced by the EAC which had a strong along-shore flow (1.47 m s^{-1}) centred 36.1 km from the coast, near the edge of the continental shelf (220 m seabed depth; 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 similar to the northern Cape Byron site (28.6° S).

The zooplankton community was strongly related to the water masses along the transect with strong relationships observed with temperature. 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). In the cool inshore waters < 20°C, there continued to be high zooplankton biomass (Figure 3), but the community had shifted towards smaller particles which resulted in a steeper *c* (< -1.3; Figures 4 & 5).

North Solitary (30°S)

The transect at North Solitary (30°S) showed the strongest evidence of current driven 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 3). The offshore portion of the transect continued to be dominated by the EAC which had a strong alongshore flow (1.59 m s^{-1}) centred 37.7 km offshore (310 m bathymetry;

Figure 2). The EAC had slight onshore movement, in offshore waters 100-150m below the surface (0.15 m s^{-1}; Figure S4).

The biomass of the zooplankton community generally decreased with distance offshore and with depth (Figures 3, S5 & S6). The EAC, particularly further offshore, contained low zooplankton biomass with a shallow pareto distribution shape parameter *c* (-0.9) and GMS of ~450 µm (Figures 3, 4 & 5). The 20 °C isotherm was a strong boundary for zooplankton communities with zooplankton in water < 20 °C having relatively low biomass and 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 4 & 5).

Diamond Head (31.75°S)

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

Reflecting the more homogenous water mass along this transect, the zooplankton community was not clearly related to water masses and are more likely due to physical location. Inshore, the zooplankton community was charactered by larger individuals (GMS ~500 µm ESD; Figure 4) and had higher overall biomass which declined steadily with distance offshore and with depth (Figures 3, S5 & S6). The pareto distribution shape parameter *c* of the community was shallow over the whole transect (≈-0.9; Figure 5).

Overall Patterns and Seasonal Changes in the EAC

Satellite altimetry showed throughout the year alongshore velocity varies at our transects by approximately 0.25 m s^{-1} with the more northern sites having the fastest overall flow (Figure 6). The velocity at all sites slows between April and August before peaking during September (the month our observations were taken) or October (except the southern Diamond Head site (31.8°S)) and remaining high until March corresponding to austral spring and summer. The southern Diamond Head site (31.8°S) showed a lag in the EAC influence, with alongshore flow peaking in December, remaining high until March.

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

Three distinct patterns in GMS were evident in our 4 transects. Cape Byron and Evans Head showed evidence of larger GMS around the front between the warm EAC and cooler inner shelf water (around the 21 °C isotherm; Figure 4). North Solitary showed evidence of uplift with the small GMS community from deep uplifted to the surface.

Diamond Head was very different with a more homogenous distribution of GMS although there was a trend of larger zooplankton inshore. The size structure of all sites was heavily related to the GMS with steeper zooplankton size spectra slopes in areas with smaller zooplankton (Figures 4 & 5). The Pareto *c* shape parameter was strongly correlated with the NBSS Slope but provided better coverage over the transects (r = 0.934, t_{535} = 60.362, p < 0.001, Figure S7).

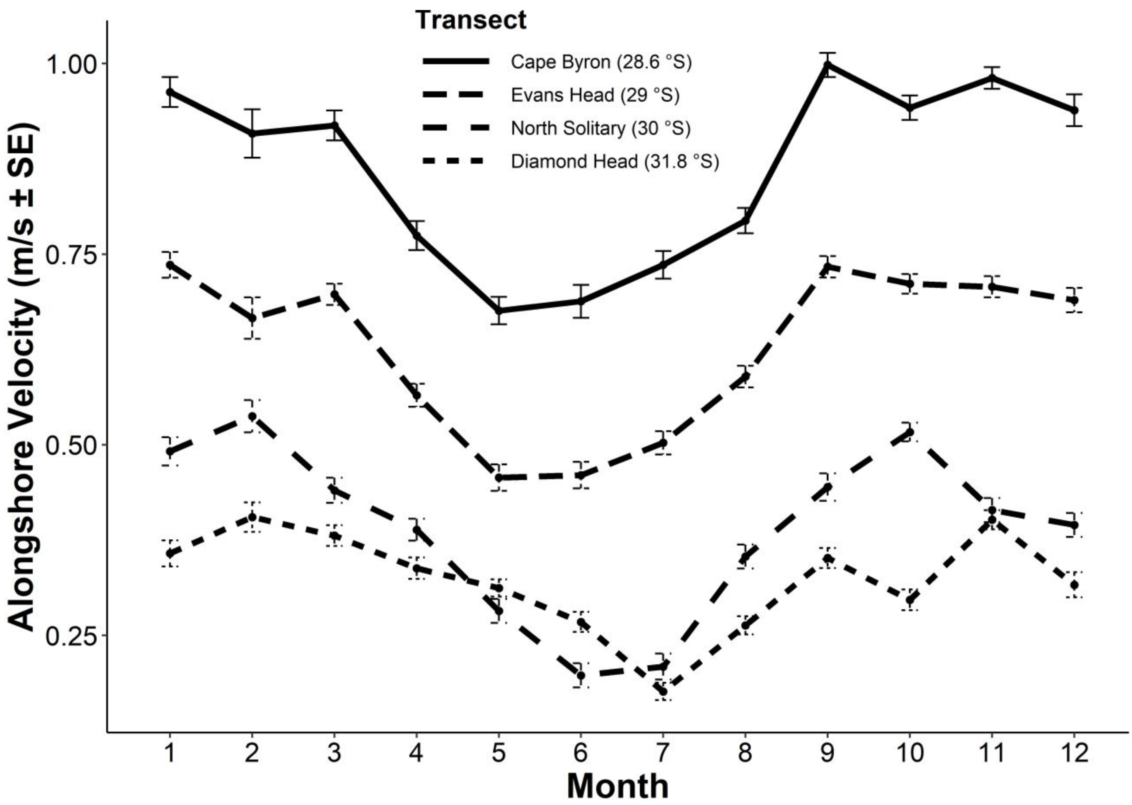
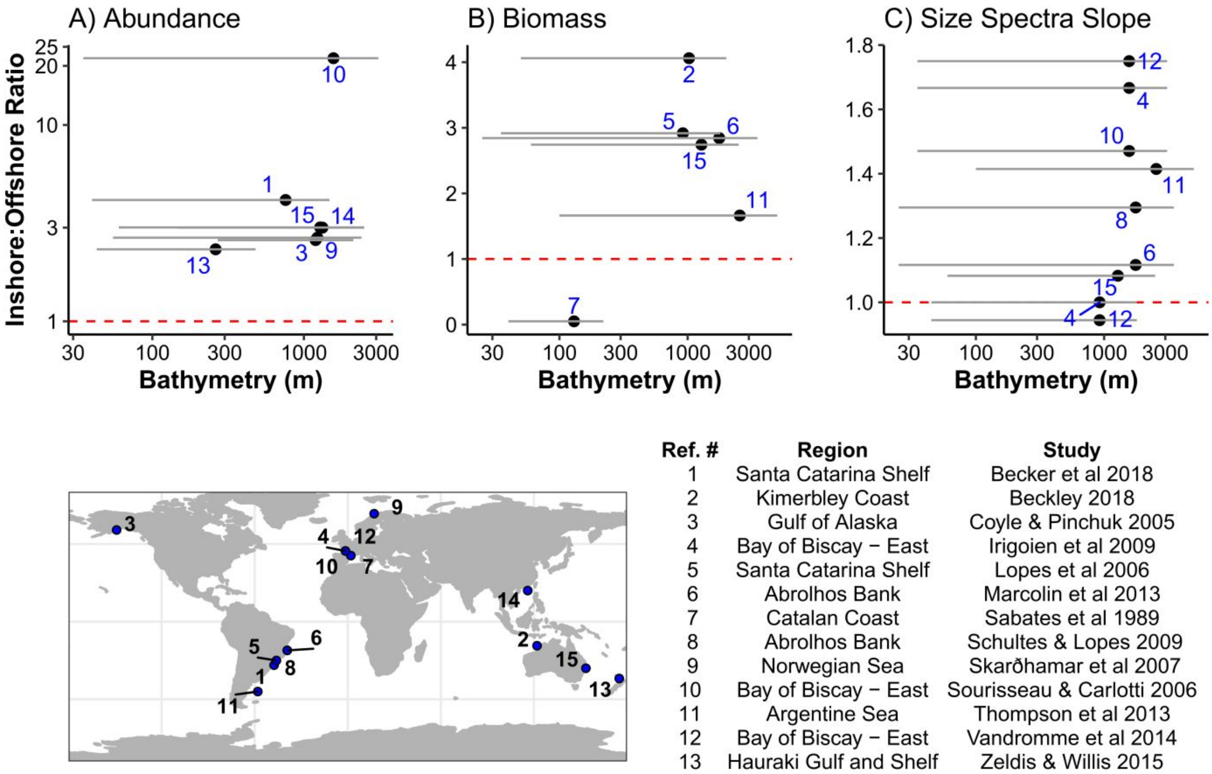


Figure 6 Seasonal changes in mean alongshore surface velocity at the Cape Byron (28.6°S), Evans Head (29°S), North Solitary Island (30°S) and Diamond Head (31.8°S) based upon 10 years of satellite altimetry data (2004 – 2013). Velocity data was downloaded for the eastern edge of each transect (Table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

Global Synthesis

15 studies quantified the cross-shelf changes in zooplankton (including this study), revealing a broad consensus (Figure 7; Table S1), even though many studies were not influenced by a western boundary current. Seven studies (including the current study) 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, five of six studies showed 1.5 – 4.1-fold greater biomass inshore compared with offshore (Figure 7; Table S1). The sixth study from the Western Mediterranean showed 20-fold higher biomass offshore compared to inshore values (Sabatès et al. 1989).

In terms of size structure, nine studies reported both inshore and offshore values with eight finding steeper zooplankton size spectra slopes in inshore areas compared with offshore areas (Figure 7, Table S1). The southern Bay of Biscay was unusual in having a marginally shallower inshore zooplankton size spectra slope compared to the offshore areas (Vandromme et al. 2014).



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

Figure 7 Summary of 14 previous studies investigating cross shelf patterns of zooplankton (#15 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 Spectra Slope. A ratio greater than 1 (red dashed line) means that the inshore region had a larger abundance/biomass or steeper size spectra slope. 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, and that not all studies are located in western boundary current influenced locations.

Discussion

This study highlights consistent declines in zooplankton biomass and altered size-structure horizontally and vertically across the narrow continental shelf off eastern Australia. These changes in the zooplankton community were observed both in data from the current study and in our global synthesis. We present these patterns as a consistent global trend in zooplankton communities across continental shelves (Figure 8). These cross-shelf trends are fundamentally important for understanding the productivity of coastal ecosystems and fisheries (Holland et al. 2020), and likely underpin the environmental and socio-economic value of temperate rocky reefs (Bennett et al. 2015). These trends in the zooplankton community are an outcome of cross-shelf flows and sporadic upwelling processes, driven by ocean currents and coastal winds, which are a focus for ocean observing programs around the world (Lynch et al. 2014). Western boundary currents are a particular focus for ocean observing as they have strengthened in recent decades (Wu et al. 2012) which could drive further upwelling and zooplankton biomass, resulting in stronger cross shelf gradients.

Peaks in zooplankton biomass coincided with the front between the continental shelf water and oligotrophic EAC water, where the interaction of water masses can create highly productive environments (e.g. Baird et al. 2008). Distinct from the warmer EAC, the cooler shelf water revealed a zooplankton community with higher biomass, smaller geometric mean size and steeper estimated normalised biomass size spectrum slope compared to the offshore community. These features together suggest higher productivity and increased predation on the continental shelf compared to the oceanic communities. During periods of low wind driven upwelling, as observed in this study, increased productivity driven by the uplift of the cooler water due to the western boundary current interacting with the sloping topography is likely an important driver for productivity through the supply of nutrients. As zooplankton are the basis of many coastal food webs, this consistent supply of nutrients is likely an important factor in the distribution and abundance of planktivorous fish found on continental shelves (Truong et al. 2017; Holland et al. 2020). By supporting the lower trophic level planktivorous fish, the production of zooplankton on continental shelves is likely a key supporting mechanism of continental shelf fisheries (Tilzey and Rowling 2001; Pauly et al. 2002; Bakun and Weeks 2008).

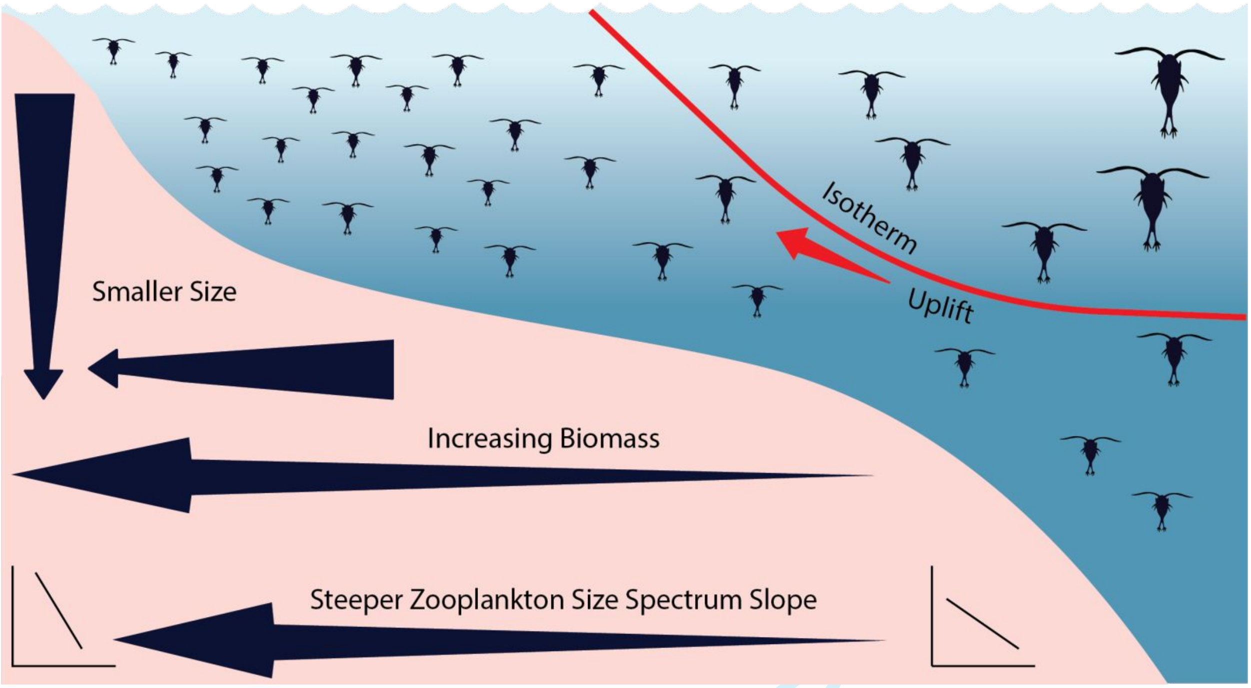


Figure 8 Conceptual diagram of the zooplankton community and how it changes over a continental shelf and with depth. Note all zooplankton are represented by copepods in this image. A steeper zooplankton size spectrum slope generally infers both increased production and predation.

Effects of the EAC on zooplankton

Off eastern Australia, the separation of the EAC from the coast forms a boundary between the northern oligotrophic waters, and the southern eutrophic Tasman Sea waters

(Oke et al. 2019). Offshore, this can separate the zooplankton communities (Baird et al. 2008) and is manifest in the abundance and diet of fish (Hobday and Hartmann 2006; Revill et al. 2009). On the continental shelf however, the influence of the EAC separation on the distribution of zooplankton and fish are less well known. The results of our current study demonstrate that along the three transects influenced by the EAC, current driven uplift onto the continental shelf (Roughan and Middleton 2002), promotes the higher biomass of phytoplankton (Everett et al. 2014), and therefore the higher zooplankton biomass. It is possible that closer inshore, we may have observed the effects of predation pressure from fish in the littoral zone, particularly on temperate reefs, removing larger plankton (Truong et al. 2017; Holland et al. 2020). Therefore a steeper zooplankton size spectra slope could arise not only from increased production of smaller zooplankton, but also by predation on larger zooplankton prey by planktivorous fish (Moore and Suthers 2006). This physically driven energy flow from nutrient to plankton to fish contributes to the highly productive fisheries often found in continental shelf areas (Pauly et al. 2002; Bakun and Weeks 2008).

Previous research on the biophysical properties of fronts in this region demonstrated an order of magnitude increase in the biovolume (a biomass proxy) of plankton in frontal regions (Baird et al. 2008). We also observed a clear increase in both zooplankton biomass and a steeper zooplankton size spectra slope at the boundary between the continental shelf water and warm EAC water. This increase in productivity around fronts may be a driver of previously observed relationships between fish abundance and frontal features (Fiedler and Bernard 1987; Reese et al. 2011).

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 with larger particles and a shallower zooplankton size spectra slope compared to the EAC influenced northern sites. The same pattern of decreasing biomass offshore, and with depth in the water column, existed, although the overall biomass was elevated and there was no front between water masses. In general, the Tasman Sea has an elevated nutrient concentration and higher zooplankton biomass compared to the oligotrophic EAC waters (Baird et al. 2008), however the cause of the declining biomass with distance offshore is uncertain. It is possible that the zooplankton are being retained on the continental shelf due to weak flow in the lee of the EAC separation (Everett et al. 2014). The larger geometric mean size and a shallower zooplankton size spectra slope suggest that the Tasman Sea dominated southern site potentially has low predation relative to the other transects as the biomass was the highest observed of all transects.

Uplift driven by the EAC will vary seasonally. The EAC is stronger in summer, and its width and separation latitude have a dominant period around 3 months (Mata et al. 2006; Archer et al. 2017). This may influence the various locations in this study differently. The location where the EAC separates from the coast also has a strong impact towards the south of our study region with separation driven upwelling and retention on the wider continental shelf identified as a key mechanism for productivity in this region (Suthers et al. 2011; Everett et al. 2014).

While this study provided high-resolution depth-resolved cross shelf transects, we were unable to sample in areas where the bathymetry was less than 50 m. This means that the inshore water masses which may be more heavily influenced by terrestrial inputs, waves, wind-driven vertical mixing, and interactions with the coastline were not sampled and may have differing patterns in terms of the zooplankton community. Nevertheless, our results are valid for most of the continental shelf.

Comparison to other studies

The current study showed a consistent decline in biomass horizontally (increasing distance from shore) and vertically (increasing depth in the water column) with the largest biomasses observed in the surface inner shelf waters. This was similar to almost all other comparable studies with the exception being the western Mediterranean which is not located in a boundary current system (Sabatès et al. 1989). In the northeast Atlantic, the declining pattern of biomass across the shelf was attributed to coastal nutrient inputs and long resident times of water masses over the shelf break (Sourisseau and Carlotti 2006; Irigoien et al. 2009; Vandromme et al. 2014). However, in the southwest Atlantic and the Brazilian Bight, the increase in inshore zooplankton biomass was attributed to bottom intrusions of cooler nutrient rich South Atlantic Central Water (Pereira Brandini et al. 2014). To the south, similar results were observed on the Abrolhos Bank where higher zooplankton biomass was observed on the continental shelf due to the Brazilian Current interacting with the sea-floor, generating uplift and eddies which increased mixing over the continental shelf (Marcolin et al. 2013). This process is comparable to the EAC interacting with the topography in our study region, which in turn generates uplift of cooler water onto the continental shelf (Roughan and Middleton 2002). The consistent observations of high zooplankton biomass and steeper zooplankton size-spectra slopes on continental shelves globally highlights the broad importance of the continental shelf regions, and more specifically the inner shelf regions. These regions of elevated zooplankton biomasses contribute to the coastal pelagic food webs which have been shown to support both reef ecosystems (Holland et al. 2020) and the larger pelagic ecosystems often targeted by the fishing industry (Tracey et al. 2013).

Steeper zooplankton size spectra slopes in inshore regions is another feature of zooplankton communities which is consistently observed. In some regions the areas of steepest slopes have been linked to estuarine-derived nutrients (Irigoien et al. 2009), which are exploited by nearshore planktonic communities while steep slopes occurring further offshore are observed to be more temporally consistent and potentially due to local circulation patterns and retention (Vandromme et al. 2014). In the current study, estuarine derived nutrients are unlikely to be important, as the study was undertaken along transects which began more than 10 km from the coast in a region with low terrestrial influences (Apte et al. 1998; Dai and Trenberth 2002). As continental shelfs are typically observed to have a steeper zooplankton size spectra slope and therefore higher predation and productivity (Figure 7), it suggests that there is increased benthopelagic coupling on the continental shelf as biomass moves through plankton into fish and then either to higher trophic levels or the benthos as fecal matter is deposited (Marcolin et al. 2013).

A prominent feature in the transects of the current study was the zooplankton community at the front between the warm EAC water and the cooler inshore waters. This community was shown to be high in biomass and have a steeper zooplankton size spectra slope, characteristic of a highly productive community. This is similar to the pattern previously observed in deeper waters to the south at the front between the EAC and Tasman Sea (Baird et al. 2008) and peaks in abundance near fronts observed in the southwest Atlantic (Becker et al. 2018). It has also been shown that in the Kuroshio Current, zooplankton are entrained from coastal areas and accumulate in frontal zones resulting in increased abundance (Yamamoto and Nishizawa 1986).

While none of the previous studies have examined the vertical structure of continental shelf zooplankton communities in the same detail as horizontal structure, a number of studies have made similar conclusions to that observed in the current study. In the south-east 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).

Our analysis of cross-shelf patterns in zooplankton communities globally reveals a consistent pattern (Figure 8). In regions where there is interaction of currents or other upwelling promoting mechanisms, there is higher zooplankton biomass and a steeper zooplankton size spectra slope inshore compared to off the continental shelf. This higher inshore biomass and steeper zooplankton size spectra slope is driven by larger numbers of smaller zooplankton utilising higher nutrient availability. With increased abundance and production of small zooplankton, biomass flows through to the larger size classes and higher trophic levels through predation. This is characteristic of a higher biomass and more productive ecosystem on the continental shelf as there is fast turnover of the smaller particles providing a constant food source for higher trophic levels. Within this cross-continental pattern 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).

Implications for the future

Most boundary currents are strengthening around the world (Zhou et al. 2010). In eastern Australia, climate change is driving substantial change in the EAC region with the flow strengthening by up to 35 % (Sun et al. 2012), and separation occurring further south

(Cetina-Heredia et al. 2014). The faster flowing EAC may result in increased uplift of cooler nutrient rich water onto the continental shelf via current driven uplift (Roughan and Middleton 2002) as demonstrated through the snapshot of transects in the current study which were heavily influenced by the EAC. It is unclear if this will offset the already declining growth rates in phytoplankton which have been caused by the greater influence of the warm oligotrophic EAC (Thompson et al. 2009). A decline in dinoflagellates has also been detected 120km further of this study region although there was no decline in overall phytoplankton abundance, suggesting a change in community assemblage (Ajani et al. 2014). With the EAC pushing further south before it separates from the coast (Cetina-Heredia et al. 2014), it may generate increased uplift and therefore nutrient supply (Oke and Middleton 2001) in regions which currently have low levels of current driven uplift. Further south the Tasman Sea waters generally have higher overall nutrient content compared to the oligotrophic warm waters.

While the distributions and patterns observed in the current study align with global observations, they are only a snapshot and it is possible that at other times of the year the patterns seen may vary from what we observed. Our analysis of seasonal influence by the EAC showed that while there are strong seasonal variations in alongshore current velocity due to the EAC (Figure 6), the velocities observed in our study reflect a large portion of the year in terms of the velocities at our transect locations. Despite this, the EAC is strengthening and the increasing water temperatures in the southeast Australian region are already impacting the zooplankton communities as the region becomes increasingly tropicalised (Kelly et al. 2016). At long term observing stations in the southeast Australian region, warming waters have resulted in a reduction in the spring phytoplankton bloom and > 60% decline phytoplankton growth during spring (Thompson et al. 2009). These changes may have significant effects on the overall distribution of zooplankton biomass, size structure and community composition on continental shelves as zooplankton are impacted across the globe in similar ways (Richardson 2008).

Conclusions

Our study is the first to look at high resolution vertical patterns of zooplankton across a continental shelf. Based upon the previous research into zooplankton distributions on continental shelves and the current study we suggest a general process for the distribution of zooplankton on continental shelves influenced by boundary currents. This heuristic model includes expectations for future studies to examine, such as the decline in zooplankton biomass with distance offshore and with depth in the water column. Continental shelf waters are more productive that offshore waters in general, and that western boundary currents drive productivity on the shelf through uplift of nutrient rich waters. Future studies could answer these questions with more sustained monitoring of cross-shelf patterns throughout the year which has not previously occurred with previous studies presenting only snapshots of cross-shelf patterns due to defined sampling seasons or irregular research voyages.

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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.

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Supplementary Material

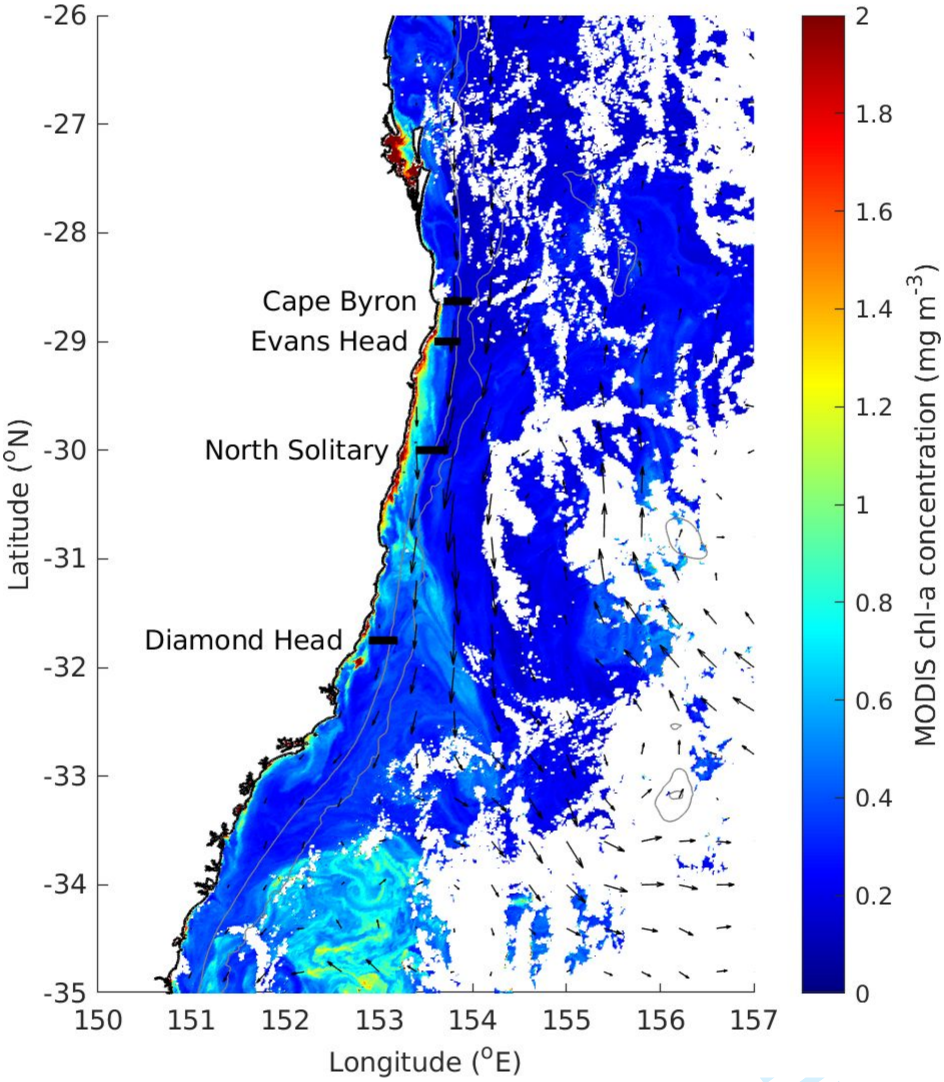

Figure S1 MODIS Chlorophyll *a* (mg m^{-3}) in the region during our study showing low amounts of Chlorophyll at all the transect sites (black lines) during our study.

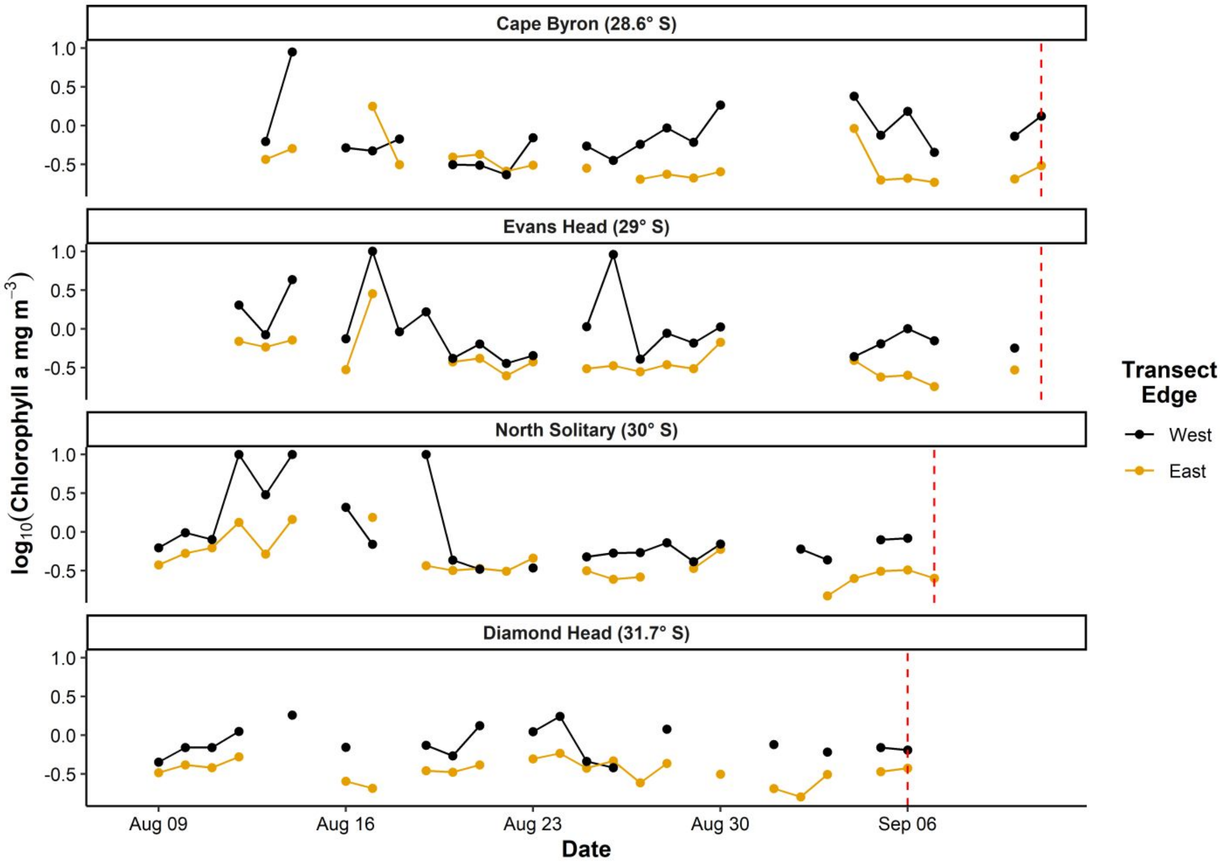

Figure S2 Satellite observed chlorophyll *a* in the month prior to each transect based upon a 10 x 10 km region around the western and eastern edges of each transect. Gaps are due to days with no data due to cloud cover. The vertical red line shows the day each transect was sampled.

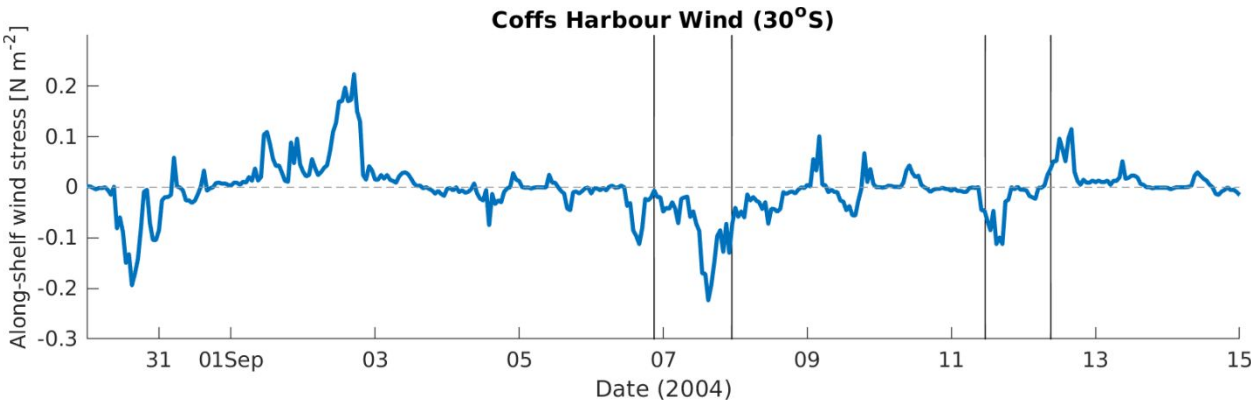

Figure S3 Time-series of along-shelf (northward) wind stress component calculated from the observed wind at Coffs Harbour (30° S, local time). Negative values show upwelling favourable winds. The vertical black lines show the times of the 4 transects in this study, in chronological order these were Diamond Head, North Solitary, Evans Head then Cape Byron.

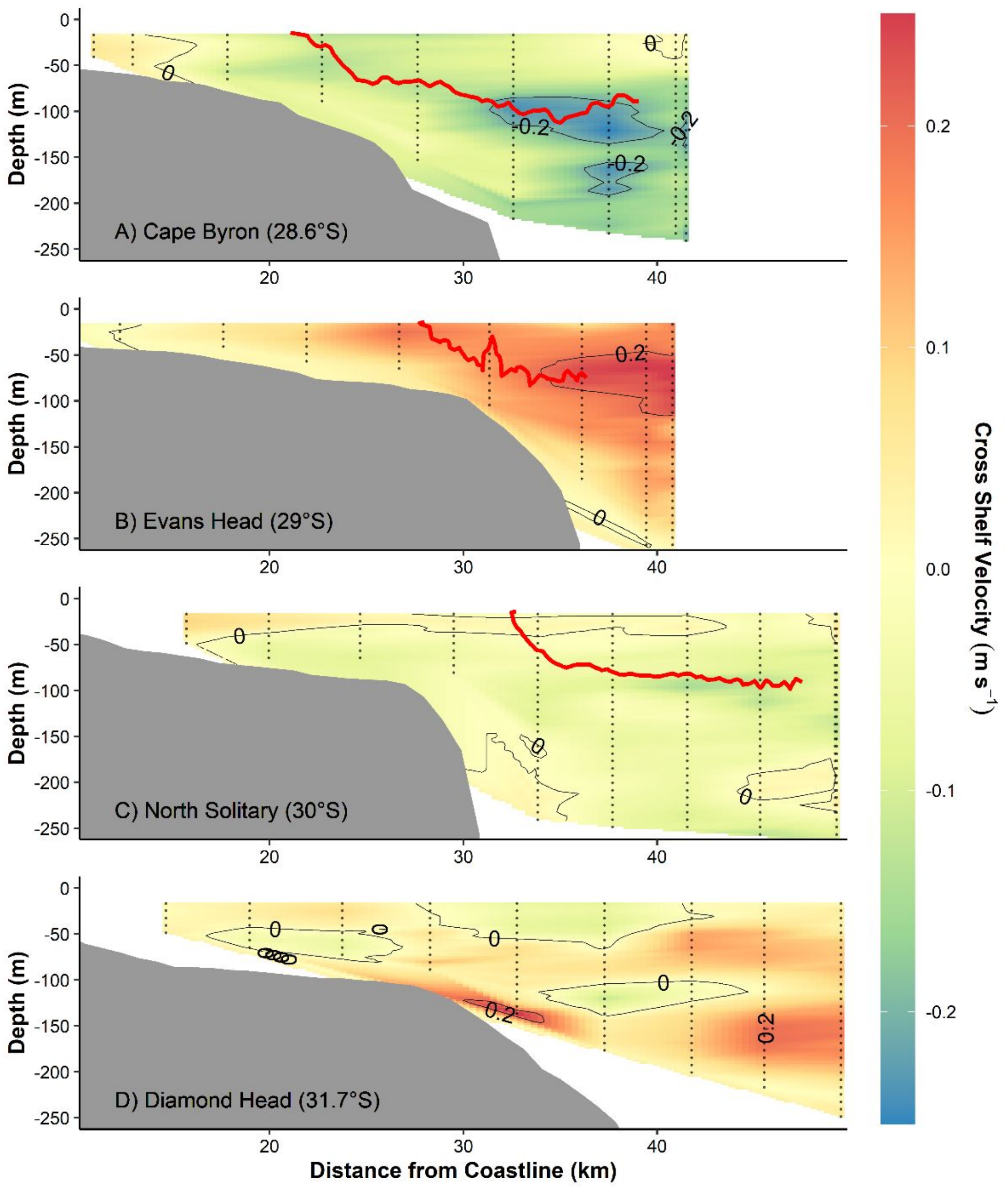

Figure S4 Cross-shelf velocity across the four cross shelf transects (Figure 1). Transects were conducted with an Acoustic Doppler Current Profiler during a CTD Transect. Grey lines join areas of equal velocity. The red line shows the 21°C isotherm based on the SeaSoar transect. Note there was no 21°C isotherm for Diamond Head.

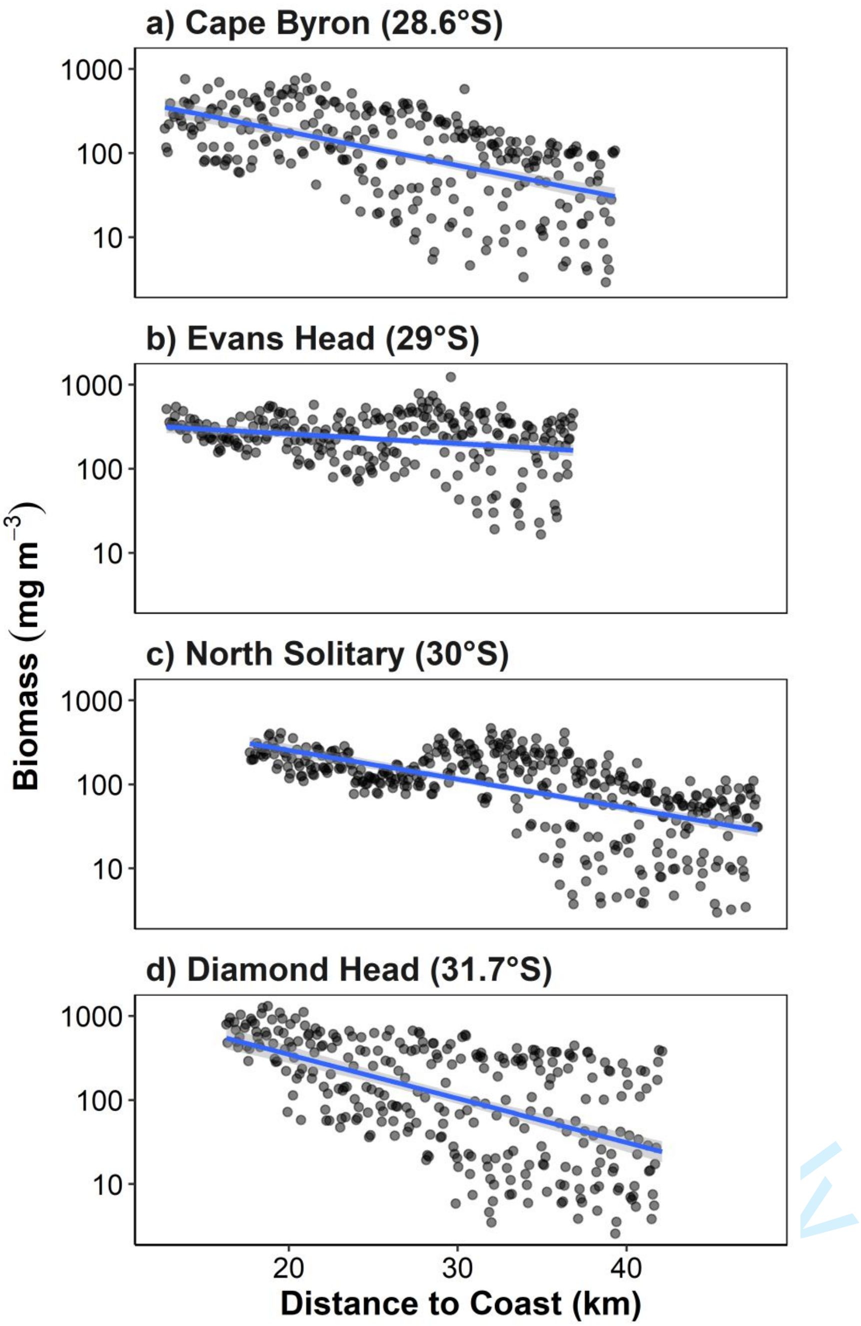

Figure S5 Biomass by distance from the coast for the four transects. Note the $\log_{10}$ transformed y-axis. Each dot represents a 6 s integration from the OPC mounted on the undulating towed body. Blue lines represent the linear trend line with the 95% confidence intervals shown in grey.

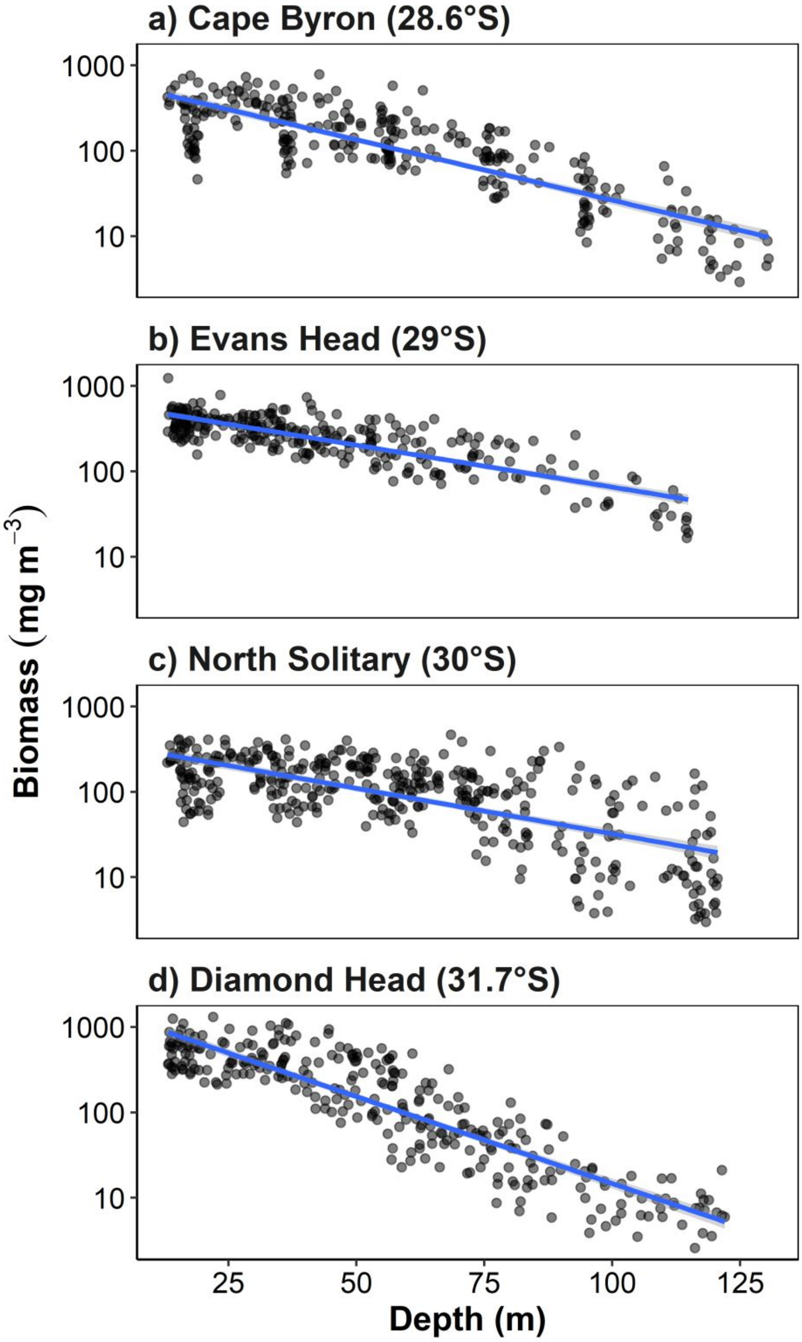

Figure S6 Biomass by sample depth for the four transects. Note the $\log_{10}$ transformed y-axis. Each dot represents a 6 s integration from the OPC mounted on the undulating towed body. Blue lines represent the linear trend line with the 95% confidence intervals shown in grey.

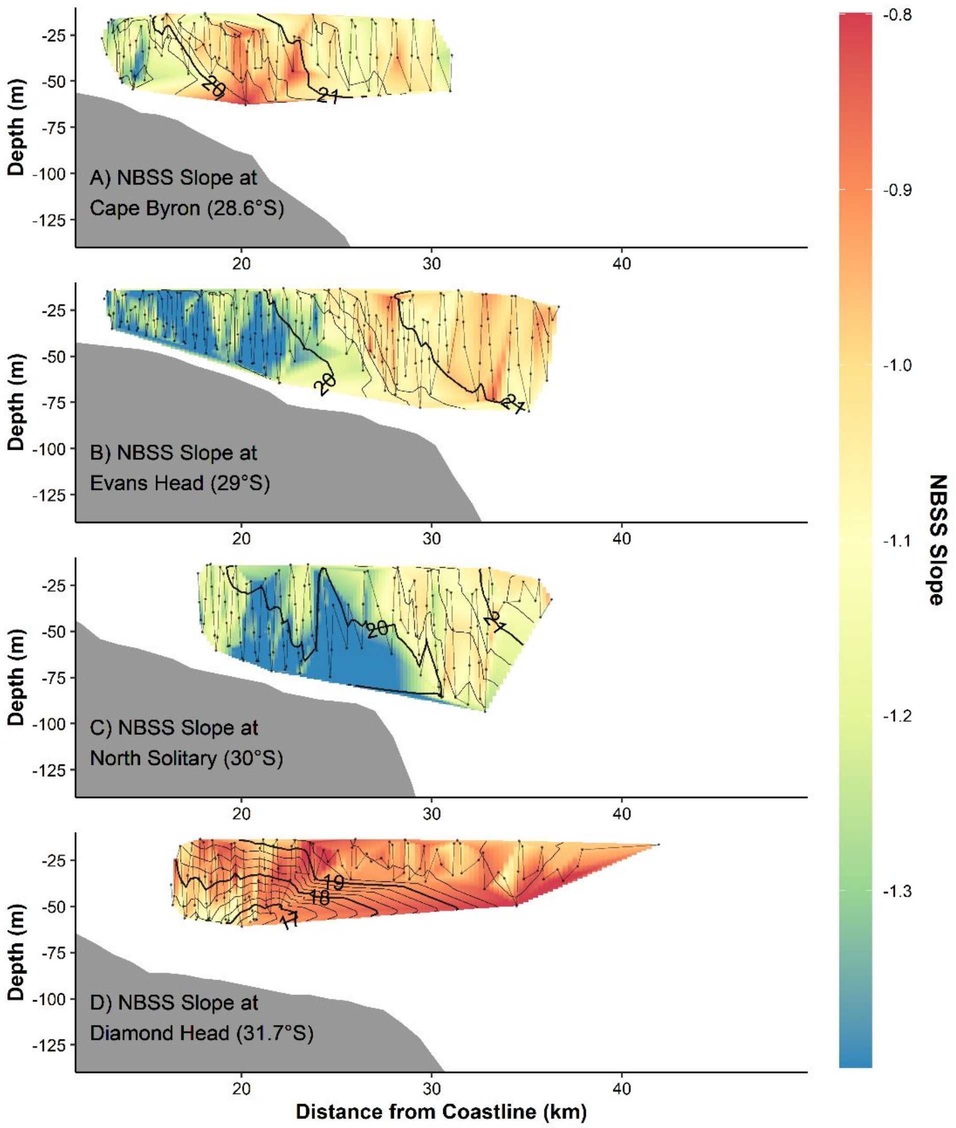

Figure S7 Interpolations of the zooplankton size spectra slope using the Normalised Biomass Size Spectrum (NBSS) method. Transects were conducted from inshore to offshore with an undulating towed body with the path shown by the grey line with midpoints of each sample shown as dots. Temperature (° C) isotherms are shown in black. The NBSS slope estimate was strongly correlated to the pareto *c* chape parameter (r = 0.934, t_{535} = 60.362, p < 0.001, Figure S7). Note the smaller coverage compared to the pareto *c* shape parameter due to the inability of the NBSS estimate to handle datapoints with few particles.

Table S1 Details of the additional studies used in the global summary of inshore-offshore zooplankton patterns. Empty cells represent no data.

Study (Fig 7 ref. #)	Region	Latitude (°)	Longitude (°)	Inshore Biomass (mg m^{-3})	Offshore Biomass (mg m^{-3})	Biomass Ratio	Inshore Abundance (ind. m^{-3})	Offshore Abundance (ind. m^{-3})	Abundance Ratio	Inshore NBSS Slope	Offshore NBSS Slope	NBSS Slope Ratio	Notes
Becker et al 2018 (#1)	Southwest Atlantic Santa Catarina shelf	-28	-47.5				2406	580	4.15				
Beckley 2018 (#2)	NW Australia	-15.5	122	1.34	0.33	4.06							biomass converted from ml m^{-3}
Coyle & Pinchuk 2005 (#3)	Gulf of Alaska	59	-149				267	103	2.60				
Irigoien et al 2009 (#4)	Bay of Biscay - East	45.5	-1.5							-1.25	-0.75	1.67	
Irigoien et al 2009 (#4)	Bay of Biscay - South	43.7	-2.5							-0.75	-0.75	1	
Lopes et al 2006 (#5)	Southern Brazilian Shelf	-25	-46	0.35	0.12	2.92							highest biomasses from intrusions
Marcolin et al 2013 (#6)	SE Atlantic - Abrolhos Bank	-18.5	-39	162.9	57.3	2.84				-0.96	-0.86	1.12	
Sabates et al 1989 (#7)	Western Mediterranean	42.5	2	5	100	0.05							strongly related to front.
Schultes & Lopes 2009 (#8)	SE Atlantic - Abrolhos Bank	-18.5	-39							-1.68	-1.3	1.29	
Skarðhamar et al 2007 (#9)	Northern Norway	69.5	17				2000	750	2.67				also high at front.
Sourisseau & Carlotti 2006 (#10)	Bay of Biscay - East	45.5	-1.5				17500	800	21.88	-1.25	-0.85	1.47	converted from ind. L^{-1}

Thompson et al 2013 (#11)	Southwest Atlantic	-45	58	47.9	28.8	1.66				-0.58	-0.41	1.42	non-linear slopes offshore, smaller particles inshore
Vandromme et al 2014 (#12)	Bay of Biscay - East	45.5	-1.5							-1.05	-0.6	1.75	
Vandromme et al 2014 (#12)	Bay of Biscay - South	43.7	-2.5							-0.85	-0.9	0.94	
Zeldis & Willis 2015 (#13)	New Zealand	-36.6	175				877	377	2.33				
Zhang et al 2019 (#14)	South China Sea	20	116				1500	500	3				
Schilling et al (This study #15)	Eastern Australia	-30	153.5	362	132	2.75	7037	2340	3.01	-1.18	-1.09	1.08	