Cross-shelf patterns in zooplankton characteristics in a western boundary current region

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**NOTES:**

**Figures aren’t finalised. Some have minor details to fix, including interpolations**

* Figures 7 & 8 show strong patterns but they are really just repeats of Figures 3 which I think are better because they show the depth and distance from coast at the same time which I think is important. I think we should remove F7 and F8 – thoughts?
* Iain previously asked for a quantitative summary and plot of previous work (section 2.5) which looked at changes in biomass/abundance across continental shelves. I have not included this in this version because it is not finished and I’m unsure of the value of adding this information as it was already included as a table in Marcolin (2013) where they identified it may not be appropriate to compare all the studies.

Abstract

Zooplankton are the basis for many pelagic ecosystems, yet it is largely unknown how the zooplankton community varies horizontally and vertically across continental shelves, particularly in areas influenced by strong boundary currents. Western boundary currents are known to influence continental shelf waters through a variety of physical mechanisms including uplift which have the potential to influence the planktonic community. Using an optical plankton counter and CTD mounted on an undulating towed body in waters off the east Australian continental shelf, we show that zooplankton biomass tends to be highest inshore with a decline in biomass with both increasing distance from shore and depth in the water column. Within uplift influenced zones, the inner shelf zooplankton communities tended to be smaller and more productive, as determined by smaller geometric mean sizes and steeper normalised biomass size spectrum slopes observed in transects influenced by the East Australian Current. This study presents the first high-resolution depth-resolved profiles of the zooplankton community across a continental shelf (what did they show). The patterns observed in this study align with previous research on zooplankton distributions on continental shelves suggesting that globally inner continental shelf regions appear to be more productive and support high biomasses of zooplankton compared to offshore, particularly where uplift may be a common occurrence. This may be a driver of the highly productive fisheries which are often found on continental shelfs.

1 Introduction

Western boundary currents (WBCs) are fast-flowing currents which transport warm salty water from the tropics to the poles. As they flow along continental boundaries they generally inhibit cross-shelf transport due to their strong along-shore flows (Roughan et al. 2011). At a more local scale, WBCs interact with the continental shelves to generate eddies, fronts and upwelling that often increase transport across the shelf (Malan et al. 2020). By increasing uplift of cold water on the continental shelf (Schaeffer et al 2013), WBCs contribute to production through the supply of nutrients normally found in cooler deeper water (Pereira Brandini et al. 2014).

Within uplift dominated systems such as WBCs, zooplankton have been shown to have important keystone roles (Libralato et al. 2006). These roles include transferring energy to fish (Marquis et al. 2011; Champion et al. 2015) as well as linking the benthic and pelagic zones. Zooplankton support up to 53 % of fish biomass on temperate coastal reefs (Truong et al. 2017). Predator-prey interactions among zooplankton are usually driven by body size within coastal pelagic ecosystems, (Barnes et al. 2010). By focusing on the size distribution of the zooplankton community, complex species-specific dynamics can be simplified. One method of analyzing community size structure is the normalized biomass size spectrum, which uses simple metrics to quantify a community (Kerr and Dickie 2001). Using a linear fit of normalized biomasses in logarithmically equal size bins, the structure of the zooplankton community is quantified, with a general overall slope of -1 observed in the open sea (Sheldon, 1972; Baird et al. 2008). A steeper slope with a large fraction of small particles generally infers higher production while a shallow slope often represents lower predation and less ‘top-down’ pressure (Moore and Suthers 2006; Blanchard et al. 2017).

Zooplankton are not distributed uniformly across continental shelves with oceanographic features a key factor in their distribution (REF). The distribution of zooplankton is the result of a number of factors including physical mechanisms such as transport and retention, biological factors including prey availability and predator abundance as well as behaviour of the zooplankton (Huntley et al. 2000). In the southeast Atlantic it was shown that the zooplankton community on the continental shelf had higher biomass and a steeper Normalised Biomass Size Spectrum (NBSS) slope compared to the offshore oceanic stations which were typically more vertically stratified (Marcolin et al. 2013). This is similar to northeast Atlantic where high zooplankton biomasses and steeper NBSS were found in some but not all inshore regions with the majority of high productivity areas located along the French coastline with productivity and biomass decreasing in offshore areas (Sourisseau and Carlotti 2006; Irigoien et al. 2009; Vandromme et al. 2014). This onshore-offshore gradient in biomass has also been observed in the southwest Atlantic where it was identified that vertical distributions of zooplankton on the continental shelf are likely related to water masses (Pereira Brandini et al. 2014). Despite exploration of spatial patterns in zooplankton, few studies have examined patterns of zooplankton with depth on continental shelves. Off New York, during late summer it was observed that vertical zooplankton abundance was strongly influenced by water mass with distinct zooplankton communities driven by a strong thermocline (Turner and Dagg 1983). This is contrasted by a winter study on the Abrolhos Bank where, on the shelf, copepod abundance peaked near the surface (20 – 40m) and decreased with depth (Marcolin et al. 2015). Recently it has been suggested that light availability and predation by fish are significant drivers of zooplankton depth distributions (Aarflot et al. 2019).

The East Australian Current (EAC) is a baroclinic jet which forms between 10 and 20 °S when the South Equatorial Current diverges against the Australian coast. The southward flowing component, the EAC, flows at approximately 0.5 – 1 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 had significant impact on shelf circulation (Schaeffer et al. 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, composition and distribution (Armbrecht et al. 2014; Armbrecht et al. 2015). Phytoplankton and nutrients are a key energy source for zooplankton, and can strongly influence zooplankton communities (REF). Despite this, there is little information on how WBCs influence the depth distribution of zooplankton on continental shelves around the world and no analyses of zooplankton distribution in the EAC continental shelf region. This study will investigate cross shelf and depth stratified patterns of zooplankton on the east Australian continental shelf. We aim to:

2. Materials and Methods

*2.1 Voyage details*

From 2nd – 13th September 2004, a research voyage on the on the RV Southern Surveyor was undertaken from Sydney, Australia to Brisbane, Australia. 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 anti-cyclonic warm-core eddy forming off the coast at approximately 33 °S, 155 °E (Figure 1).

*2.2 Sampling*

Four constant latitude transects were sampled roughly perpendicular to the north NSW coast over a seven-day period (6th – 12th September; Table 1) using a towed device called the Bunyip (a highly modified SeaSoar). The Bunyip was towed from inshore to offshore and undulated between 10 and 120 m depth. Mounted on the Bunyip was a XXCTDXX and an Optical Plankton Counter (OPC; Herman 1992) to measure temperature, salinity and the size distribution of particulate matter. The ship was also equipped with an ADCP which continuously monitored the velocity of water beneath the vessel with alongshore velocity of currents calculated by rotating the U and V vectors to account for the angle of the coastline at each location. The shelf sampling was interrupted on the 8-10th September to undertake a wake study around North Solitary Island (29°55'S, 153°23'E) which will be reported elsewhere. All times reported are local (Sydney) Australian Eastern Standard Time.

*2.3 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 a 0.5 s interval. The particle sizes were recorded digitally using 4096 size bins, corresponding within the operating range of the instrument to bins with a 5 and 15 µm width.

The volume of flow through the sample region was based on distance measured, averaged over a 6 s interval. The choice of time interval is a trade-off between a larger time period to obtain a higher particle count to accurately obtain the estimate of the size distribution, and a shorter time period to provide better spatial resolution. The spatial averaging is along the instrument trajectory. As the instrument moves vertically at approximately 1 m s-1, a long period averaging most affects vertical resolution. We found a 6 s interval provides the best possible vertical and horizontal resolution (~ 6 m vertically) of the size distribution of the Tasman Sea waters with a biomass of ≈ 1-10 mmol N m-3.

To quantify the zooplankton community, several metrics were calculated for each interval of our transects. These included total biomass (mg m-3), geometric mean size (µm ESD) and an estimate of the normalised biomass size spectrum (NBSS) slope. As traditional NBSS slope estimates can be biased by size bins containing zero particles, particularly when smaller volumes are filtered such as in this study, we used the Pareto distribution to estimate the NBSS slopes along the zooplankton transects. The shape parameter *c* of the Pareto distribution is highly correlated to the slope of the NBSS and is a more robust estimate of the NBSS slope when there are size bins containing no particles (Vidondo et al. 1997; Suthers et al. 2006). The Pareto distribution has a probability density function (pdf) defined as:

where *s* is the size of the particle (such as the weight class, *w)*, and *c* and *k* are the distribution’s shape and scale parameters, respectively (Vidondo et al. 1997). An efficient estimator of –*c* is the slope of the logarithm of the probability that a particle of random volume *W* will exceed a size *w*, log10 Prob(*W* ≥ *w*), against log10 *w*. The slope of the NBSS is an unbiased, although inefficient estimator of –*c* (Vidondo et al. 1997). As a result, within the limitations of our data, and their conformity to the Pareto distribution, the slope of the NBSS should approximately equal the slope of log10 Prob(*W* ≥ *w*) regressed against log10(*w*). 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. In this paper we will present the Pareto shape parameter as an estimate of the NBSS slope as it has been used successfully in this region previously to spatially resolve the size distribution of particles (Baird et al. 2008). SOME OF THIS paragraph may be unnecessary but was from one of the other Baird papers and I’m not really sure about how best to explain the pareto.

*2.4 Other Environmental Data*

To investigate environment conditions leading up to 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. MODIS data were retrieved for 5x5 pixels (~25 km2) surrounding the western and eastern edges of each transect, for the month prior to the day of sampling.

To investigate the seasonal variation of the EAC strength in the region of our transects, 10 years (2004 – 2013) of satellite altimeter data were obtained from the IMOS Data Portal (<http://imos.aodn.org.au/imos/>) for each of our transects. The alongshore velocity was calculated based upon the coastline and the mean and standard deviation for each month calculated. The assumption being that faster alongshore velocity would be due to increased influence of the EAC. Bathymetry data was sourced from GEBCO (GEBCO Bathymetric Compilation Group 2019).

*2.5 A global context* **(Still to finish) – OR NOT DO?**

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 X studies which investigated changes in zooplankton communities over continental shelves and if possible from each study we extracted inshore and offshore values for biomass, abundance and the NBSS slope. From each study we extracted a maximum of one inshore-offshore per 1 latitude of sampling with the data restricted to spring/early summer to reduce seasonal influences as this is when the majority of studies were undertaken.

Specific details on quantifying needed

3 Results

*3.1 Regional Oceanography*

The three northern most sites (north of 30°S) all crossed from cool inshore waters into warm (>21 °C) EAC water (Figure 1). This is contrasted by the southern transect (Diamond Head 31.75°S) transect which was located south of the separation zone in cooler (<19.5 °C) waters and did not cross into EAC waters. All transects showed low chlorophyll levels (<1.4 mg m-3) peaking at the surface which was representative of the previous month of low chlorophyll-a at these locations (Figure S1). There were negligible effects of wind on circulation in the 3 days prior to the transects.

*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 southward flow (1.50 m s-1) centred over the 200 m isobath (27.6 km offshore). As a result, most of the continental shelf was flooded by warm EAC water (Figure 2). The shipboard ADCP showed slight onshore movement of the EAC (not shown) which increased offshore and with depth (up to 0.26 m s-1). 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.

Along the northern transect, 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) observed at the surface ~20 km from the coastline, just inshore of the 21 °C isotherm. This 21 °C isotherm appears to be a strong delineator of both zooplankton biomass and the NBSS slope. The EAC waters warmer than 21°C were characterised by low zooplankton biomass with a geometric mean size of ~450 µm with a slope of the NBSS between -1 and -1.3. The cooler water immediately inshore of the 21°C isotherm had a high zooplankton biomass, shallower Pareto slope (-0.9) with large particles (geometric mean size 500 µm). Further inshore again (15 -17 km from the coastline), in water < 20 °C, biomass remained high, but the particles were smaller (~430 µm), resulting in a steeper NBSS slope (~-1.25).

*3.3 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 southward flow (1.47 m s-1) centred further offshore at 36.1 km from the coast, near the edge of the continental shelf (220 m seabed depth; Figure 2). The EAC had a slight offshore movement (0.27 m s-1) which increased with distance offshore. 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.

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 geometric mean size of ~450 µm to that observed at the northern Cape Byron transect but had a higher biomass and shallower NBSS Slope (~-1; Figures 3, 4 & 5). In the cool inshore waters < 20°C, there continued to be high zooplankton biomass, but the community had shifted towards smaller particles which resulted in a steep NBSS slope (< -1.3; Figure 5).

*3.4 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 southward flow (1.59 m s-1) centred 37.7 km offshore (310 m bathymetry) with the EAC having slight onshore movement, offshore and at depth (0.15 m s-1; Figure 2).

The biomass of the zooplankton community generally decreased with distance offshore and with depth. The EAC, particularly further offshore, contained low zooplankton biomass with a shallow NBSS slope (-0.9) and geometric mean size of ~450 µm. 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 geometric mean size (~400µm) resulting in a steeper NBSS slope (< -1.3). This was particularly evident where the 20°C isotherm reach the surface ~24 km from the coastline (Figures 4 & 5).

*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 as such was characterised by a more homogeneous water mass. Within the transect the, alongshore velocities are 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. 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 et al. 2015).

Reflecting the more homogenous water mass along this transect, the zooplankton community was not related to water masses and changes can be more attributed to physical location. Inshore, the zooplankton community was charactered by larger individuals (g.m ~500 µm) and had higher overall biomass which declined steadily with distance offshore and with depth (Figures 3 & 4). The NBSS slope of the community was shallow and steady over the whole transect (~-0.9; Figure 5).

*3.6 Overall Patterns and Seasonal Changes in the EAC*

Satellite altimetry showed throughout the year alongshore velocity varies at all of 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 in peaking during September or October and remaining high until March in austral spring and summer.

Both EAC-influenced transects (three northern ones) and transects south of the EAC (Diamond Head) showed that the highest zooplankton biomasses were observed in the inner shelf waters with general declines offshore and with depth (Figures 7 & 8). The Evans Head and North Solitary transects also showed elevated biomass levels (~700 mg m-3)at the outer edge of the continental shelf around the 21 °C isotherm at a front between the EAC and continental shelf water. 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.

Two distinct patterns in Geometric Mean Size (GMS) were evident in our 4 transects. Cape Byron and Diamond Head had a larger GMS towards the coast (> 475 µm ESD) with the GMS declining offshore. Evans Head and North Solitary showed a small increase in GMS around the 21 °C isobar which formed a front between the EAC and coastal waters. All sites also showed a general decline in GMS with depth. Patterns in GMS were also reflected in the NBSS slope with steeper slopes generally observed in areas with a smaller GMS.

4. Discussion

The declines in zooplankton biomass and altered size-structure across the continental shelf highlight the importance of understanding the interaction of physical and biological processes across the continental shelf. Distinct from the fast flowing EAC water mass, the cooler inner shelf water revealed a zooplankton community with higher biomass, smaller geometric mean size and steeper 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. This increased productivity driven by the uplift of the cooler water is likely an important driver for fisheries on the continental shelf region.

*4.1 Effects of the EAC on Zooplankton*

Western Boundary Current regions have complex circulation (REF, REF) with cascading effects onto the biological communities (REF). In this region, the separation of the EAC from coast (REF) is known to act as boundary between the northern oligotrophic waters, and southern eutrophic Tasman Sea waters (Suthers et al 2011). Offshore this can influence the zooplankton communities (Baird et al., 2008) and the distribution of fish diets and abundances (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 shown here demonstrate that along the three transects to the north of the separation zone, current driven uplift of cooler nutrient rich water onto the continental shelf (Roughan and Middleton 2002) drives higher zooplankton productivity in the form of increased biomass and steeper slopes. EXPAND ON SOME RESULTS HERE – VERTICAL AND HORIZONTAL PATTERNS.

In contrast, the southern transect (Diamond Head; 31.75° S) was dominated by Tasman Sea water with larger particles and a shallower NBSS slope compared to the EAC influenced northern sites. The same pattern of decreasing biomass offshore, and with depth, existed, however the overall biomass was elevated which was most likely influenced by uplift generated by the separation of the EAC to the north (Roughan and Middleton 2002).. The Tasman Sea is known to have elevated nutrient content and generally hold larger amounts of zooplankton compared to the oligotrophic EAC waters (Baird et al. 2008), explaining the high biomass overall but the cause of the declining gradient 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) or it is possible that there are more nutrients closer to shore due to anthropogenic inputs. The larger geometric mean size and a shallower NBSS 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.

Seasonally the influence of the EAC as an uplift mechanism will vary. Over a year, the EAC is stronger in summer, and its width and separation latitude have a dominant period around 3 months (Archer et al 2017, Mata et al 2006 ). This will influence the various locations of the transects in this study differently. The most northern site (Cape Byron 28°S) is also the most exposed, located off a headland pushing directly out into the EAC. This results in the EAC regularly flooding the continental shelf in this region, removing any continental shelf water that may have been retained. Further south where the coastline is more angled, the EAC does not flood the continental shelf but the seasonal strengthening of the flow is likely to drive changes in the strength of uplift generated with the location where the EAC separates from the coast having 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).

*4.2 Comparison to other studies*

All sites in this study showed there was a decline in biomass with both increasing distance from shore and depth with the largest biomasses observed in the upper inner shelf waters. A similar pattern occurs on continental shelves in the southeast Atlantic, northeast Atlantic and southwest Atlantic which all showed have higher biomasses inshore compared to the offshore locations. While the northeast Atlantic pattern was attributed to variable hydrology and topography, particularly over the shelf break (Sourisseau and Carlotti 2006; Irigoien et al. 2009; Vandromme et al. 2014), in the southeast Atlantic and the Brazilian Bight, this increase in inshore plankton concentrations was attributed to bottom intrusions of cooler nutrient rich South Atlantic Central Water (Pereira Brandini et al. 2014). Slightly to the south, similar results were observed on the Abrolhos Bank with larger zooplankton biomasses observed on the continental shelf, attributed to the Brazilian Current interacting with the topography, 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 which in turn generates uplift of cooler water onto the continental shelf. The consistent observations of high zooplankton biomass and steeper NBSS slopes inshore 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 and the larger pelagic ecosystems often targeted by the fishing industry.

Steeper NBSS slopes in inshore regions is another feature of zooplankton communities which has been previously noted. In the Bay of Biscay, the steeper NBSS slope in inshore regions is a regular occurrence, particularly on the French continental shelf (Sourisseau and Carlotti 2006; Vandromme et al. 2014). The areas of steepest slopes have been linked to estuarine influences resulting in regions of increased nutrients which are exploited by planktonic communities in this region while the steep slopes slighter further offshore are observed to be more temporally consistent and potentially due to local circulation patterns and retention (Vandromme et al. 2014). In the south-east Atlantic, continental shelf sites have been characterised by steeper, more productive NBSS slopes compared to oceanic slopes attributed to mixing on the continental shelf generated by the interaction between the topography of the Abrolhos Bank, the Brazilian Current and bottom intrusions (upwelling) of nutrient-rich South Atlantic Central Water resulting in increased benthopelagic coupling on the continental shelf and different energy sources and food availability for lower trophic levels between communities (Marcolin et al. 2013).

While none of the previous sites have examined continental shelf zooplankton communities by depth in the same detail as across the continental shelves, a number have made similar observations to that observed in the current study. In the south-east Atlantic, a higher biomass of plankton was found above the pycnocline attributed to the increased chlorophyll 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). Focusing above the thermocline, abundance generally peaked at 20 – 30 m depth, which aligns with the current study.

When the current study is viewed in conjunction with previous studies of zooplankton communities across continental shelves globally, a consistent pattern emerges (Figure 9). In regions where there is interaction of currents or other upwelling promoting mechanisms, there is higher zooplankton biomass inshore compared to off the continental shelf. This higher inshore biomass is driven by larger numbers of smaller zooplankton. Combining the higher biomass and smaller geometric mean sizes of particles in the inshore region there is a gradient from steeper NBSS slopes to shallower slopes with distance offshore. Within this cross-continental pattern of zooplankton, biomass and mean size also tend to decline with depth.

*4.3 Implication for the future* **(DO I NEED THIS SECTION?)**

Globally many boundary currents are strengthening. 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). With the EAC pushing further south before it separates from the coast, it may generate increased uplift in regions which currently have low levels of current driven uplift. On the other hand, the increasing water temperatures in the southeast Australian region are already impacting the zooplankton communities as the region becomes increasingly tropicalised, forcing some species to shift southward as they reach thermal limits or change their reproductive patterns (Kelly et al. 2016). 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).

*4.4 Limitations*

This study was based upon a single voyage which completed targeted cross-shelf transects to investigate the zooplankton communities in upwelling favourable regions. This means that the distributions observed in these transects represent 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 we sampled during the peak season of EAC flow, the alongshore velocities observed in our study are reflective of a large portion of the year. Despite this, our observed inshore-offshore gradient in zooplankton biomass and NBSS slopes did match those seen in other continental shelf regions around the world which supports the idea that the patterns we observed are representative of larger temporal and spatial scales. While our study is the first to look at high resolution depth patterns of zooplankton across a continental shelf, due to limitations of the Bunyip, it did not sample in areas where the bathymetry was less than 50 m. This means that the true inshore water masses which may be heavily influenced by waves, wind-driven vertical mixing, and interactions with the shore were not sampled and these areas may have differing patterns in terms of the zooplankton community.

5 Conclusions

This study provides the insights in to both the depth and spatial patterns of zooplankton communities across a continental shelf. By comparing zooplankton communities in the EAC influenced region with the more southern region which is not influenced by the EAC we showed how current driven uplift creates a highly productive inner-shelf water zooplankton community. It is likely that this is reflective of other WBCsystems where similar horizontal patterns of zooplankton biomass have been observed. Based upon the previous research into zooplankton distributions on continental shelves and the current study we would like to propose a general model for the distribution of zooplankton on continental shelves influenced by boundary currents. This model includes a number of hypotheses for future studies to test. 1) Zooplankton biomass declines with distance offshore and with depth. 2) Continental shelf waters are more productive that offshore waters, and 3) Western boundary currents drive productivity on the shelf through uplift. Future studies could answer these questions with more sustained monitoring of cross-shelf patterns throughout the year which has not previously occurred with all previous studies presenting only snapshots of cross-shelf patterns due to defined sampling seasons or irregular research voyages.

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Tables

Table 1 Summary of the four transects undertaken using the Bunyip with attached optical plankton counter and CTD.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Transect** | **Start Longitude**  **(° E)** | **Start Latitude**  **(° S)** | **End Longitude**  **(° E)** | **End Latitude**  **(° S)** | **Start Time (Local)** | **End Time (Local)** |
| Cape Byron | 153.7039 | 28.6328 | 153.9808 | 28.6332 | 12/09/2004 8:11 | 12/09/2004 9:59 |
| Evans Head | 153.6110 | 28.9973 | 153.8583 | 29.0024 | 11/09/2004 10:55 | 11/09/2004 12:36 |
| North Solitary | 153.4115 | 29.9978 | 153.7255 | 29.9972 | 7/09/2004 21:41 | 8/09/2004 0:05 |
| Diamond Head | 152.9126 | 31.7521 | 153.1905 | 31.7470 | 6/09/2004 20:00 | 6/09/2004 21:53 |

**Figures**

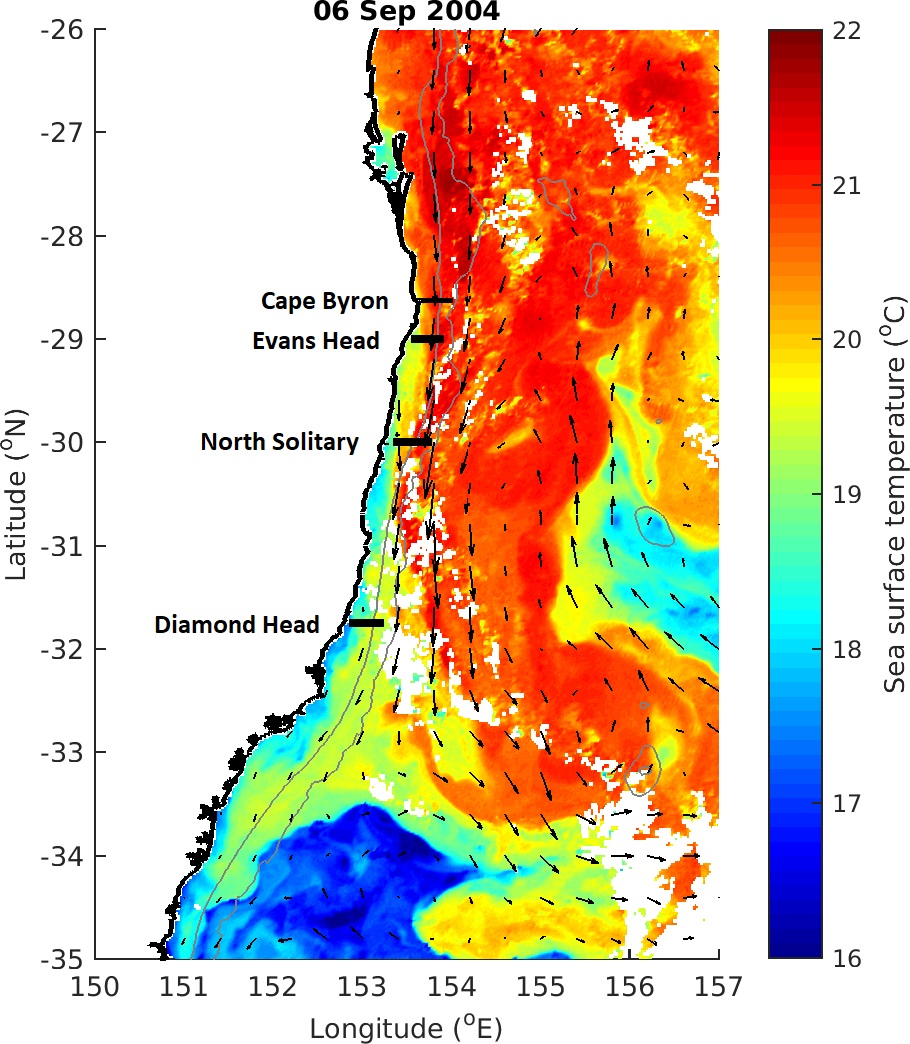


Figure 1 Locations of the four cross shelf sections which were sampled in September 2004. The sea-surface temperature for 6th September 2004 is shown in colour with velocity arrows from satellite altimetry shown with black arrows. ISOBATHS? 200 and 1000m?

A close up of a map

Description automatically generated

Figure 2 Alongshore 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. NEED TO Fix the interpolation issues and redo to match other plots.

A close up of a map

Description automatically generated

**Figure 3** Zooplankton biomass (mg m-3) distributions from the four cross shelf transects (Figure 1). Transe**c**ts were conducted form 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 the log transformed colour scale.

A close up of a map

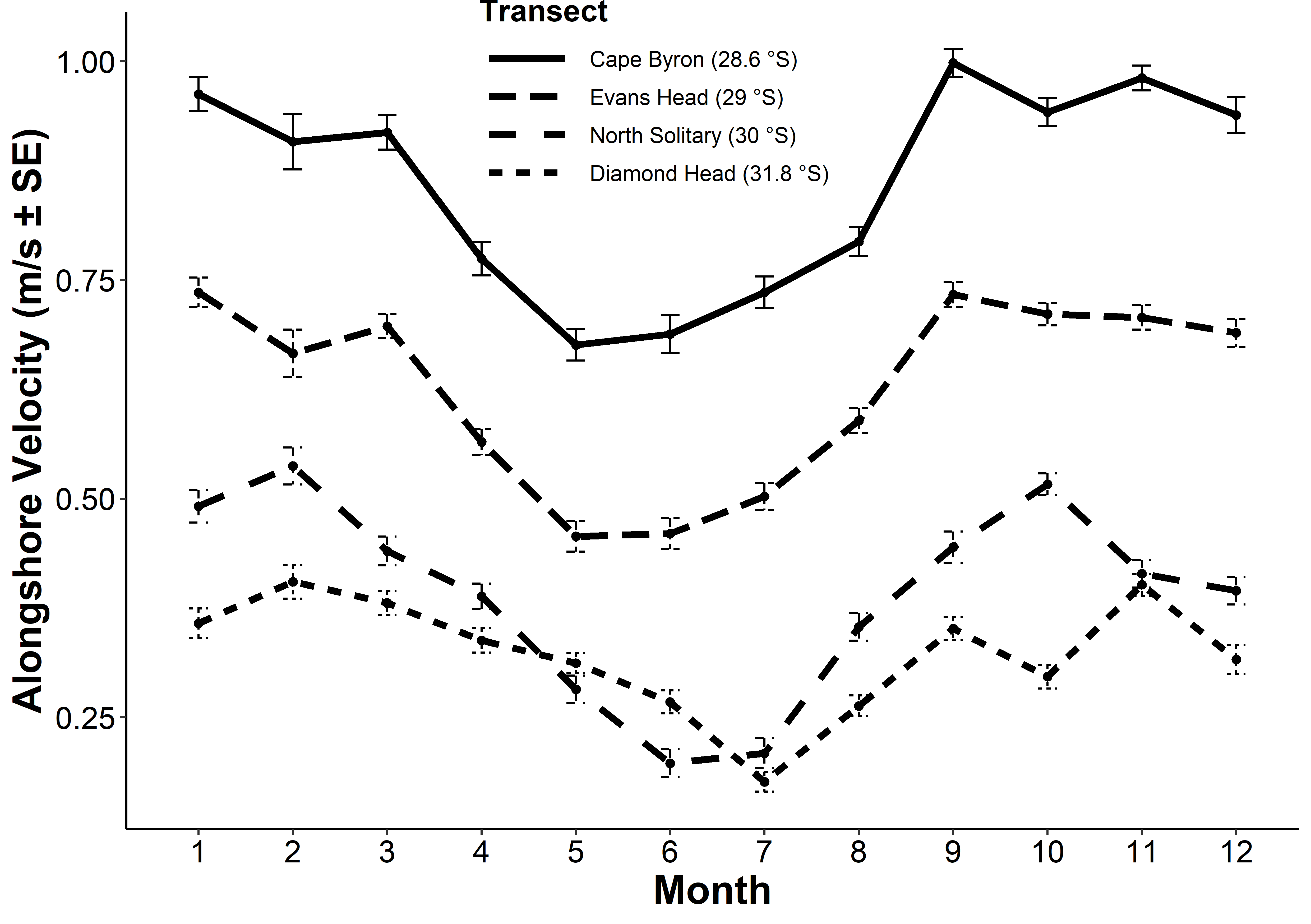
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**Figure 4** Geometric Mean Size (µm equivalent spherical diameter) of zooplankton from the four cross shelf transects (Figure 1). Transects were conducted form inshore to offshore with an undulating towed body with the path shown by the grey line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

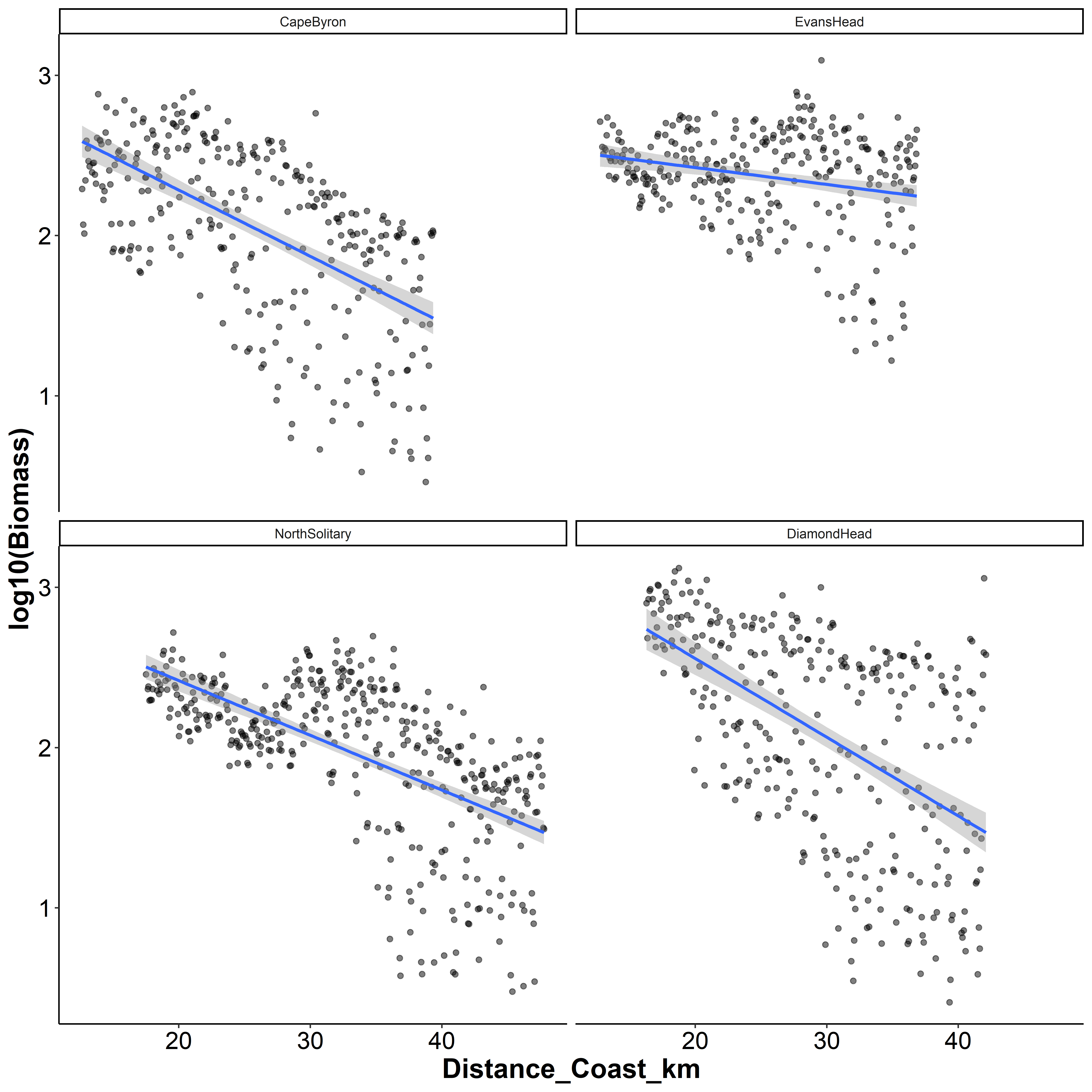
A close up of a map

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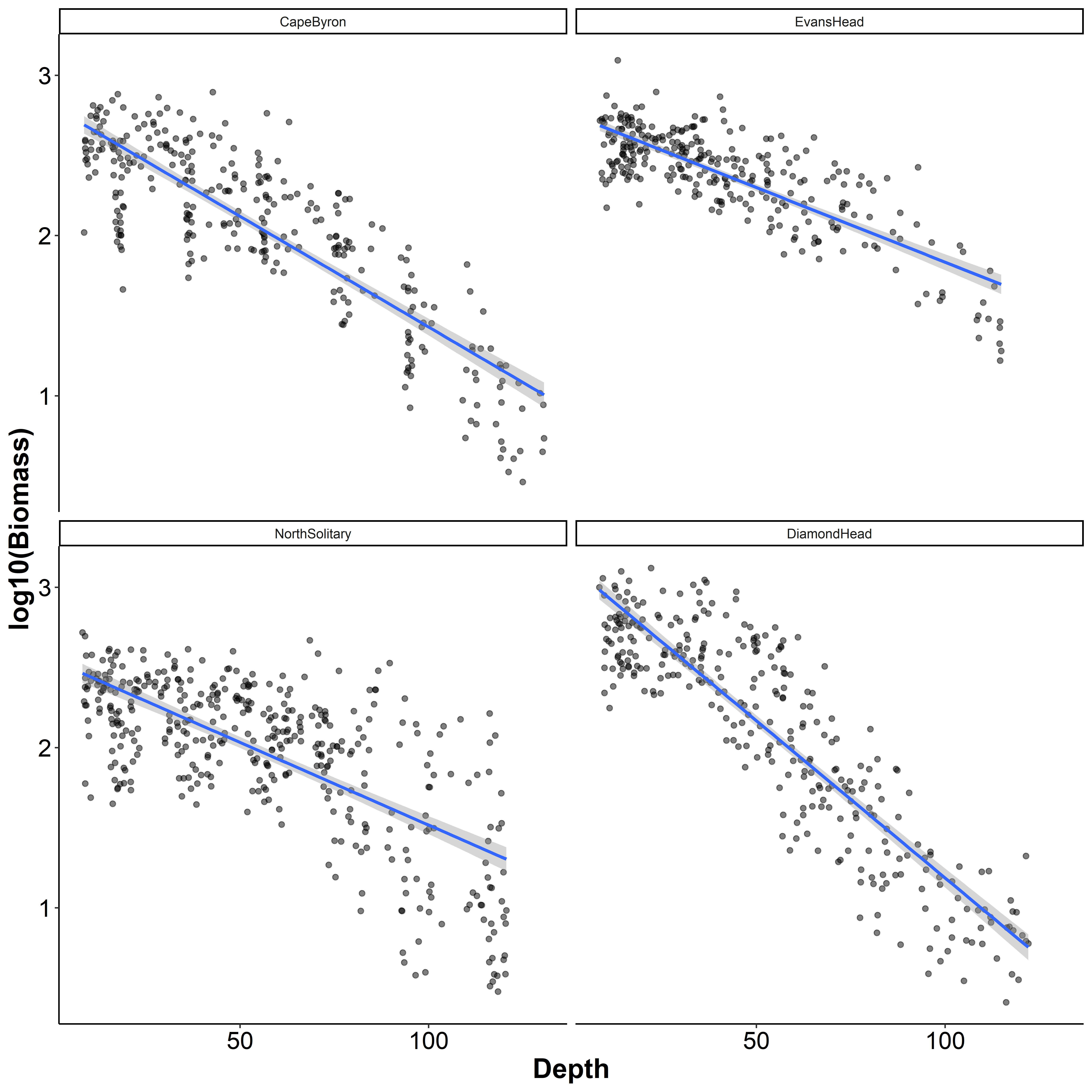
**Figure 5** Interpolations of the Normalised Biomass Size Spectrum slope, estimated using the Pareto method from the four cross shelf transects (Figure 1). Transects were conducted form inshore to offshore with an undulating towed body with the path shown by the grey line with midpoints of each sample shown as dots. Temperature (° C) isotherms are shown in black. Note the log transformed colour scale.



**Figure 6** Seasonal changes in alongshore velocity at the four transects based upon satellite altimetry.

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**Figure 7** Log10(Biomass) by distance from the coast for the four transects. Each dot represents a 6 s integration from the OPC mounted on the undulating towed body.



**/Figure 8** Log10(Biomass) by sample depth for the four transects. Each dot represents a 6 s integration from the OPC mounted on the undulating towed body.



**Figure 9** Idealised concept 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.

**Supplementary Material**

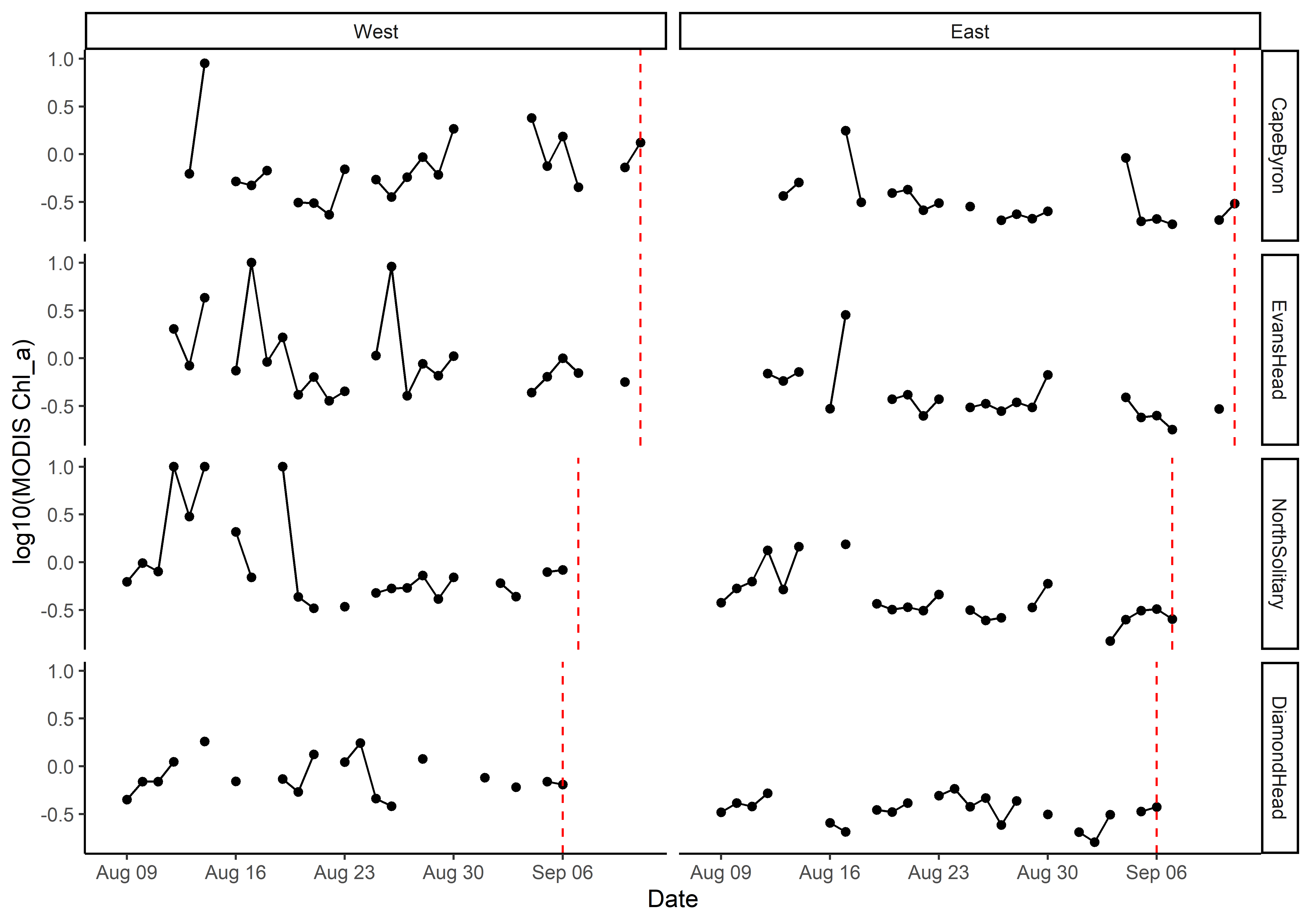


Figure S1. Satellite observed chlorophyll *a* in the month prior to each transect based upon a 5 x 5 km region around the western and eastern edges of each transect. Gaps are due to days with no data due to cloud cover. The vertical red line shows the day each transect was sampled.

To do – Tidy up plot labels etc.

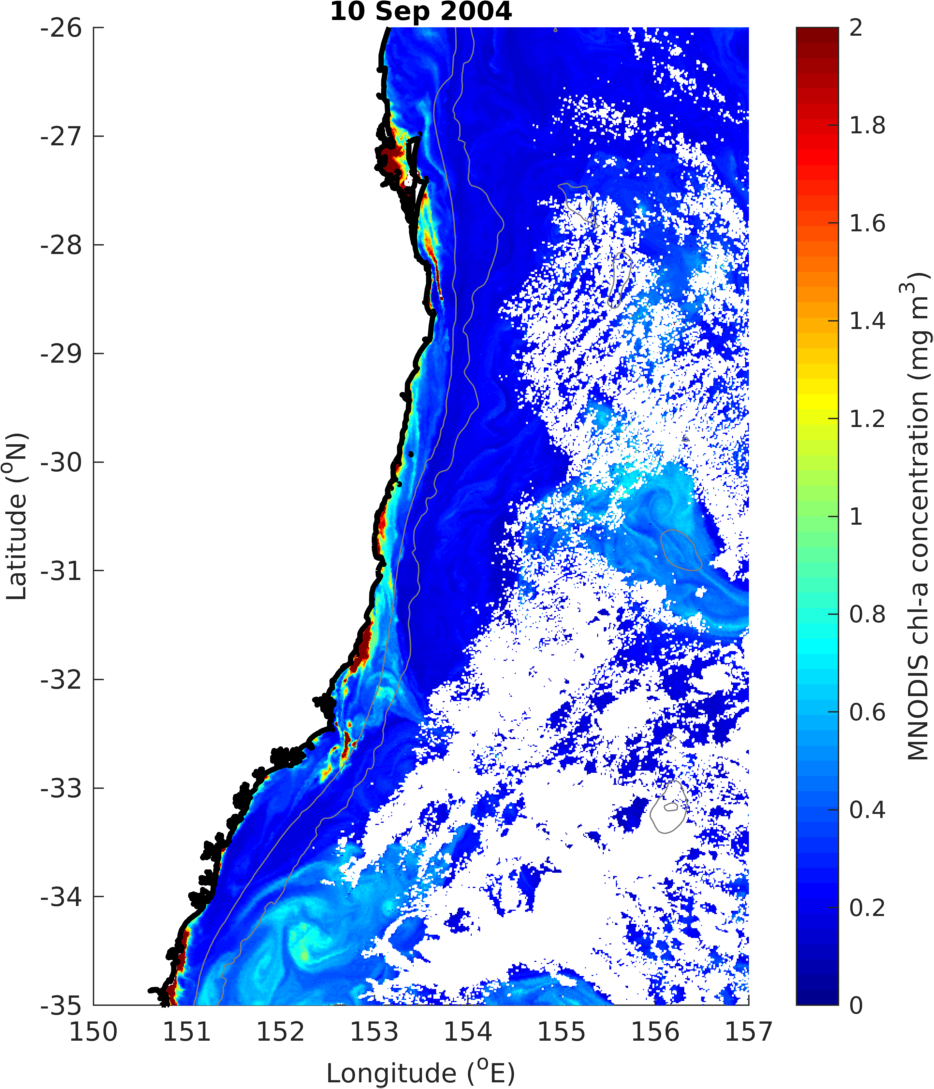
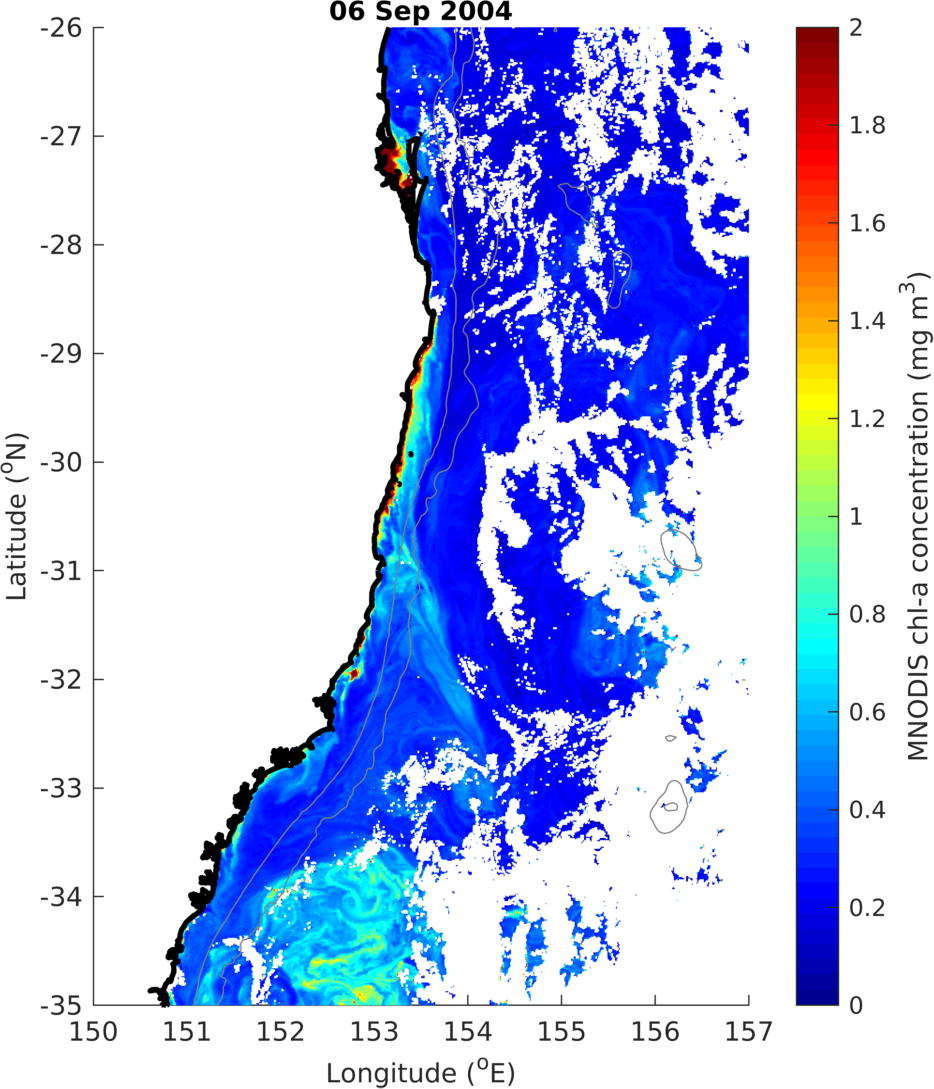


Figure S2 MODIS Chlorophyll *a* in the study region on the 6th and 10th of September showing no big upwelling at the Diamond Head site.