# Cross-shelf zooplankton distributions in a dynamic western boundary system

Hayden Schilling1,2, Amandine Schaeffer3, Jason Everett2, Mark Baird4, Peter Yates1,2, Iain Suthers1,2

1Sydney Institute of Marine Science, Chowder Bay Road, Mosman, New South Wales, Australia

2School of Biological, Earth and Environmental Sciences, University of New South Wales, High Street, Kensington, New South Wales, Australia

3School of Mathematics and Statistics, University of New South Wales, High Street, Kensington, New South Wales, Australia

4Commonwealth Scientific and Industrial Research Organisation, Castray Esplanade, Battery Point, Tasmania, Australia

Corresponding author: Hayden.Schilling@sims.org.au

# Abstract

# Introduction

The link between physical and biological processes in the world's oceans is

well known (Denman and Gargett, 1995).

The has been visited on previous cruises (Roughan and Middleton, 2002,

2004).

Previous analyses had only the 5- 30 m is included. This was to ensure the data analysed is within the surface mixed layer and corresponds with remotely sensed observations (White 2018)

The differences in environmental conditions and drivers is ISW water mean that species are probably required to employ different habitat use strategies, and that species~environment relationships in ISW are likely to differ to those in mid/outer shelf. We have limited data on the drivers of productivity, plankton and zooplanktivory in ISW

(1) what is the spatial pattern

of larval abundance within the CBL, (2) are there

differences in larval assemblages close to shore (i.e.

are different larvae found inshore versus offshore

within the CBL), and (3) do time-dependent or spacede

pendent physical processes tend to dictate variability

in larval abundance?(Nickols et al. 2013)

* review of NBSS slopes (Sato et al. 2015, Dai et al. 2016)
* nice summary and refs of upwelling (drivers) and phyto blooms in (Armbrecht et al. 2015)
* The correlation between variation in upwelling and copepod biomasses in northern Chile suggested that population dynamics of copepods may depend on intensity of upwelling. Although the underlying mechanisms are unclear, and several hypotheses dealing with bottom-up or top down factors can be put forth, our findings suggest that upwelling intensity operates through an optimal window for copepod abundance and biomass and increasing upwelling in the last decade (2000–2008) may has been unfavorable for copepod populations.(Escribano et al. 2012)
* The parameters of the NBSS represent the inherent properties of zooplankton communities or marine ecosystems: a steeper slope of the NBSS indicates high productivity and low energy transfer efficiencies in marine ecosystems (Sprules and Munawar, 1986; Zhou, 2006); higher intercept values reflect higher primary production of a community (Marcolin et al., 2013; Zhou, 2006). Thus, analysis of the NBSS provides insight into the structure of marine ecosystems. (Dai et al. 2016). Size spectra were used as an indicator to examine zooplankton responses to upwelling and currents. (Dai et al. 2016)
* Understanding of physical and biological processes driven by the EAC, particularly in linking circulation to ecosystems, is limited (Suthers et al. 2011)
* Great example: (Sevadjian et al. 2014)
* The continental shelf off southeastern Australia (between 29 and 34 S) is relatively narrow, between 16 and 70 km (mean of 37 km) from the coastline to the 200m isobath. The dynamics on the shelf are influenced both by local coastal processes and the episodic intrusion of the large-scale East Australian Current (EAC) and its eddies (Fig. 1, Schaeffer et al., 2013, 2014a). The EAC is the western branch of the subtropical gyre in the South Pacific. It is a warm and dynamic poleward flowing current, encroaching on the continental shelf of southeastern Australia between around 18 S (Ridgeway and Godfrey, 1994) and usually 30.7–32.4 S (Cetina-Heredia et al., 2014) where it bifurcates eastward, forming the Tasman Front. Further south, eddies are shed (Everett et al., 2012), leading to high variability in the velocity field and water masses on the shelf (Schaeffer et al., 2014b; Schaeffer and Roughan, 2015).(Schaeffer et al. 2016)
* We tested several hypotheses: (1) Zooplankton abundances are higher in particle-rich, low temperature ( <22°C) upwell-ings than in particle poor, high-temperature (>22°C) upwellings. (2) Zooplankton concentrations are higher in and near upwelled water which moved onto the shelf earlier, than in water which was upwelled more recently. (3) In a vertically stratified water column zooplankton are most abundant at depths where particle (food) concentrations are highest (Paffenhofer et al. 1984)
* It can be deduced from first principles that patchiness of zooplankton results from the interaction of 3 phenomena. Population dynamics give rise to a local change in numbers of individuals, and those individuals are redistributed by the physical process of advection and the biological process of behavior. These 3 phenomena—population dynamics, advection and behavior— underlie the dynamics of patchiness at all length scales from meters (Davis et al. 1992) to thousands of kilometers (McGowan 1974). However, the one scale where all processes interact most strongly is dictated by that of population dynamics, the time scale of which is characterized by the time required to complete 1 generation, from egg to adulthood.(Huntley et al. 2000)
* Fronts such as CBL often coincide with a spike in phytoplankton (Mann 1991). Moreover, regions within a few kilometers from shore often have the highest abundance of larvae (Borges et al. 2007, Morgan et al. 2009, Shanks & Shearman 2009).
* Although the ecological importance of temperate inshore rocky reefs has been realised (Bennett et al. 2015), there is scarce information on the zooplankton that can support the majority of fish production in some cases (Champion et al. 2015, Truong et al. 2017).
* the inner shelf can be characterised as the the region offshore of the surf zone where the surface and bottom boundary layers converge and interact (Lentz 1994, Jacox and Edwards 2011, Kämpf 2016)
* Multiple mechanisms: wind-driven upwelling (Schaeffer et al. 2014), upwelling driven by the encroachment, acceleration due to shelf topography, or separation of the boundary current (Roughan and Middleton 2002, Ribbat 2018a)(Lopes et al. 2006)
  + increase in nutrient concentrations occurs downstream (Roughan and Middleton 2002, Armbrecht et al. 2015)
  + effects can propagate up the food chain e.g. to sharks (NSW example)
* In addition to potential physical differences be -tween the habitat of the inshore and offshore as -semblages, predation may be higher within the narrowband of inner CBL water than farther offshore.(Nickols et al. 2013).
* Inshore can be more productive (Bennett et al. 2015), more temperate (Suthers et al. 2011), high endemism (Malcolm et al. 2010), diff zooplankton assemblage (Morgan et al. 2009)
* Avoidance of surface waters by larvae can favor retention and de - crease offshore transport (Morgan et al. 2009b,c, Shanks & Shearman 2009, Morgan & Fisher 2010, Morgan et al. 2012) and there is mounting evidence that larval concentrations are high close to shore, even in areas of strong upwelling that are traditionally viewed as being recruitment-limited.(Nickols et al. 2013)
* The Intermittent Upwelling Hypothesis (IUH) posits that subsidies of larvae and phytoplankton to intertidal communities should vary unimodally along a gradient of upwelling from persistent upwelling to persistent downwelling with most subsidies occurring where upwelling is of intermediate strength and intermittent. Furthermore, the hypothesis states that larvae and phytoplankton are transported far offshore by strong, persistent upwelling and fail to subsidize nearshore communities, whereas weak upwelling or downwelling reduces nutrients for phytoplankton production limiting food for larvae and nearshore communities. We review studies conducted at sea and onshore and reanalyze published data to test the IUH and evaluate alternative hypotheses.(Shanks and Morgan 2018)
* How consistent are inshore-offshore gradients?
* Cross-shelf patterns in herbivores, invertivores, piscivores (Malcolm et al. 2010)
* (Lopes et al. 2006) reports a ‘typical’ inshore-offshore gradient in zooplankton diversity, although note that this is complicated by mesoscale eddies and fronts derived from the meandering of the Brazil Current.
  + Biomass maxima due to coastal zooplanktonic species are restricted to a rather narrow band influenced by CW, decreasing towards the outer shelf regardless of the season. Reviewed in (Lopes et al. 2006).
* example: clear cross shelf gradient, with an increasing contribution of large copepods, siphonophores, salps and euphausiids toward the ocean (Becker et al. 2018)
* Distinct ichthyoplankton assemblages characterised Kimberly inner shelf (Engraulidae and Gobiidae were dominant families), outer shelf / slope (mixed neritic and mesopelagic taxa) and oceanic waters (mesopelagic taxa, particularly Myctophidae, Gonostomatidae and Phosichthyidae), and were correlated with changes in environmental variables (water depth, seawater density, mixed layer depth and zooplankton). (Beckley et al. 2018)
* Higher proportions of diatoms (>20 μm) at stations located within the inner shelf water, whereas the EAC stations were dominated by smaller dinoflagellates and prochlorophytes that are indicative of tropical and EAC waters (Hassler et al. 2011) in (Henschke et al. 2011)
* Within the western Tasman Sea, the inner shelf water appears to be a favourable environment for swarms (Henschke et al. 2011)
* Peter to compare/contrast these some more…
* More on cross shelf gradients: size composition
  + Several studies have used the LOPC to report on plankton and particle distribution over large areas, particularly in the northern hemisphere (e.g., Basedow et al. 2010; Yamaguchi et al. 2014; Vandromme et al. 2014). In (Marcolin et al. 2015)
    - * abrupt changes in zooplankton abundance across the shelf (Sevadjian et al. 2014)
      * the horizontal distributions of each zooplankton group in this study showed distinct geographical patterns that were coupled with the different currents. The slope of the NBSS for each group ranged from −0.85 to −0.92, and no significant inter-group differences were observed (Dai et al. 2016)
      * zooplankton communities were classified into four groups, which basically coincided with the geographical patterns of different currents [size spectra] (Dai et al. 2016)
* Vertical distributions
  + Vertical stratification, mixing, and thin layers in ISW (Margaret et al. 2005, McManus et al. 2005, Henschke et al. 2011, Greer 2013, Henschke et al. 2015)
  + Upwelling can influence vertical distribution of plankton (Armbrecht et al., 2014, 2015) in (Archer et al. 2017)
    - (Greer 2013) showed that the vertical separation of predators and prey was related to predation avoidance by copepods
    - Given that shelf intrusions may not fill the whole vertical water column, the vertical position of zooplankton influences whether and how they are advected across the inner, mid and outer shelf (Morgan et al. 2009)
    - In the vertical, aggregations of multiple trophic levels often form in thin layers at pycnoclines, nutriclines, and photoclines in the water column (Sevadjian et al. 2014). Variability in the characteristics of thin layers is, in part, a function of the physical environment in which they occur [stratification](Sevadjian et al. 2014)
    - Effect of DO in Chesapeake Bay (Roman et al. 1993)
    - Another passive/active example on page 18 of (McGillicuddy 2016)
    - Zooplankton behaviorally mediate transport by physical processes, facilitating transport across the shelf and into the surf zone.(Morgan et al. 2018)
    - More on behaviour – vertical blah (Queiroga and Blanton 2004)
  + How are zooplankton communities distributed in ISW, what drives them, and how does this in turn influence higher trophic levels? See (Greer 2013)
  + Changes in size spectra (White 2018) have been shown however there is scarce data on how cross-shelf distribution patterns can be explained based on gradients in specific environmental variables. See (Armbrecht et al. 2015, Zeldis and Willis 2015, Becker et al. 2018)

# Methods

## Voyage details

The cruise took place at the beginning of the austral spring, in September 2004. At this time, the EAC had separated from the coast at approximately 31°S and formed a large pool of water at 33°S, 155°E, creating a counter-clockwise rotating warm core eddy (Fig X).

## Sampling

Five sections were sampled along constant latitude transects roughly perpendicular to the north NSW coast over a 6 day period in September 2004 using a CTD and a towed device called the Bunyip (a highly modi ed SeaSoar). During the CTD transects, florescence, temperature, salinity and oxygen were electronically measured, and nutrients (NO3, PO4, Si) and bottle oxygen taken at the surface, and, total depth of water allowing, at depths of 25, 50, 75, 100, 150, 200, 250, 400 and 500 m. Filtered particulate matter samples were taken at the surface of each of the CTD stations. The Bunyip varied between the surface and 120 m, and sampled temperature, salinity, and, using an optical plankton counter, the size distribution of particulate matter. Further sampling during this period using towed plankton nets will be reported in later publications. The shelf sampling was interupted 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) eastern Standard Time.

Diamond Head Section (31°45'S). The Bunyip undertook a transect between 1953-2201 on the 6th September in an easterly direction, followed by net tows in a westward direction. A CTD transect was then undertaken in a easterly direction on the 7th September from 0437-0838.

North Solitary Island Section (30°00'S). The Bunyip undertook a transect between 2134 on the 7th September and 0013 on the 8th in an easterly direction, followed by net tows in a westward direction. A CTD transect was then undertaken in an easterly direction on the 8th September from 1340 -2314.

Evans Head Section (29°00'S). A Bunyip transect was undertaken in an easterly direction from 1048-1243 on the 11th September. A CTD transect followed in an westward direction from 1317-2044 on the 11th September, and finally net tows.

Cape Byron Section (28°38'S). A Bunyip transect was undertaken in an easterly direction from 0805-1006 on the 12th September. No other sampling was undertaken at Cape Byron.

## Chlorophyll analysis

Water sampled for Chl a analysis was filtered through a 47 mm diameter, 1.2 µm glass fibre filter under low vacuum within 30 minutes of collection. Filters were then folded, blotted dry, wrapped in aluminium foil and stored at -20°C until analysis. Chl a concentration was calculated using the method of Jeffery and Humphrey (1975). The calibration curve of the CTD fluorometers is shown in Fig. 2 of Baird et al. (in prep.), where Fl = 4.66 [Chl a] +52.66, r2 = 0.73. Chl a is converted to phytoplankton biomass using 1 mmol N = 1.59 mg Chl a (Fasham et al., 1990).

Optical plankton counter

The optical plankton counter was mounted on the Bunyip, a CSIRO customised

towed device. The optical plankton counter (OPC) is a Focal Technologies

Corporation Model OPC-2T with a sampling aperture of 2 x 10 cm. The OPC records equivalent spherical diameters of particles that pass through the instrument in a 0.5 s interval. The particle sizes are recorded digitally into 4096 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 is based on distance measured, average 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. A 6 s interval provides the best resolution of spatial distribution of size distribution of the Tasman Sea waters with a biomass of ≈ 1-10 mmol N m-3. The biomass in the Coral Sea waters is so low that no sensible size-distribution data can be spatially resolved. Instead, size-distribution is averaged for the all Coral Sea water in a particular transect.

# Results

# Discussion

# References

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

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

Bennett, S., T. Wernberg, S. D. Connell, A. J. Hobday, C. R. Johnson, and E. S. Poloczanska. 2015. The ‘Great Southern Reef’: social, ecological and economic value of Australia’s neglected kelp forests %J Marine and Freshwater Research. **67**:47-56.

Champion, C., I. M. Suthers, and J. A. Smith. 2015. Zooplanktivory is a key process for fish production on a coastal artificial reef. Marine Ecology Progress Series **541**:1-14.

Dai, L., C. Li, G. Yang, and X. Sun. 2016. Zooplankton abundance, biovolume and size spectra at western boundary currents in the subtropical North Pacific during winter 2012. Journal of Marine Systems **155**:73-83.

Escribano, R., P. Hidalgo, M. Fuentes, and K. Donoso. 2012. Zooplankton time series in the coastal zone off Chile: Variation in upwelling and responses of the copepod community. Progress in Oceanography **97-100**:174-186.

Huntley, M. E., A. GonzÃÂ¡lez, Y. Zhu, M. Zhou, and X. Irigoien. 2000. Zooplankton dynamics in a mesoscale eddy-jet system off California. Marine Ecology Progress Series **201**:165-178.

Jacox, M. G., and C. A. Edwards. 2011. Effects of stratification and shelf slope on nutrient supply in coastal upwelling regions. **116**.

Kämpf, J. 2016. Upwelling systems of the world : a scientific journey to the most productive marine ecosystems. Switzerland : Springer.

Lentz, S. J. 1994. Current Dynamics over the Northern California Inner Shelf. **24**:2461-2478.

Lopes, R. M., M. Katsuragawa, J. F. Dias, M. A. Montú, J. H. Muelbert, C. Gorri, and F. P. Brandini. 2006. Zooplankton and ichthyoplankton distribution on the southern Brazilian shelf: an overview. 2006 **70**:14.

Malcolm, H. A., A. Jordan, and S. D. A. Smith. 2010. Biogeographical and cross-shelf patterns of reef fish assemblages in a transition zone. Marine Biodiversity **40**:181-193.

Mann, K. H. 1991. Dynamics of marine ecosystems : biological-physical interactions in the oceans.*in* J. R. N. Lazier, editor. Boston : Blackwell Scientific Publications, Boston.

McGillicuddy, D. J. 2016. Mechanisms of Physical-Biological-Biogeochemical Interaction at the Oceanic Mesoscale. Annu. Rev. Mar. Sci. **8**:125-159.

Morgan, S. G., J. L. Fisher, S. H. Miller, S. T. McAfee, and J. L. Largier. 2009. Nearshore larval retention in a region of strong upwelling and recruitment limitation. Ecology **90**:3489-3502.

Morgan, S. G., A. L. Shanks, J. H. MacMahan, A. J. H. M. Reniers, and F. Feddersen. 2018. Planktonic Subsidies to Surf-Zone and Intertidal Communities. Annu. Rev. Mar. Sci. **10**:345-369.

Nickols, K. J., S. H. Miller, B. Gaylord, S. G. Morgan, and J. L. Largier. 2013. Spatial differences in larval abundance within the coastal boundary layer impact supply to shoreline habitats. Marine Ecology Progress Series **494**:191-203.

Paffenhofer, G., B. T. Wester, and N. William. 1984. Zooplankton abundance in relation to state and type of intrusions onto the southeastern United States shelf during summer. Journal of Marine Research **42**:995-1017.

Queiroga, H., and J. Blanton. 2004. Interactions Between Behaviour and Physical Forcing in the Control of Horizontal Transport of Decapod Crustacean Larvae. Pages 107-214 Advances in Marine Biology. Academic Press.

Roman, M. R., A. L. Gauzens, W. K. Rhinehart, and J. R. White. 1993. Effects of low oxygen waters on Chesapeake Bay zooplankton. **38**:1603-1614.

Sato, K., K. Matsuno, D. Arima, Y. Abe, and A. Yamaguchi. 2015. Spatial and temporal changes in zooplankton abundance, biovolume, and size spectra in the neighboring waters of Japan: analyses using an optical plankton counter. Zoological Studies **54**:1-15.

Schaeffer, A., M. Roughan, E. Jones, and D. White. 2016. Physical and biogeochemical spatial scales of variability in the East Australian Current separation from shelf glider measurements. Biogeosciences **13**:1967-1975.

Sevadjian, J. C., M. A. McManus, J. Ryan, A. T. Greer, R. K. Cowen, and C. B. Woodson. 2014. Across-shore variability in plankton layering and abundance associated with physical forcing in Monterey Bay, California. Continental Shelf Research **72**:138-151.

Shanks, A. L., and S. G. Morgan. 2018. Testing the intermittent upwelling hypothesis: upwelling, downwelling, and subsidies to the intertidal zone. **88**:22-35.

Suthers, I. M., J. D. Everett, M. Roughan, J. W. Young, P. R. Oke, S. A. Condie, J. R. Hartog, A. J. Hobday, P. A. Thompson, K. Ridgway, M. E. Baird, C. S. Hassler, G. B. Brassington, M. Byrne, N. J. Holbrook, and H. A. Malcolm. 2011. The strengthening East Australian Current, its eddies and biological effects - an introduction and overview. Deep-Sea Research Part Ii-Topical Studies in Oceanography **58**:538-546.

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

White, Z. 2018. The spatial distribution of zooplankton production in the western Tasman Sea: A size-spectra approach. University of New South Wales, Sydney, Australia.