

Influence of phytoplankton cell-size on the biogeochemical cycle of carbon.

Introduction

Because of the dynamic nature of marine systems and because our climate is continually changing, it is increasingly important to rely on fast and efficient methods to measure marine primary productivity (MPP). However, the overwhelming majority of MPP studies have been reported in the northern hemisphere with very few studies reporting measures in Australia (Chavez, Messié & Pennington 2011; Cloern, Foster & Kleckner 2014; Everett & Doblin 2015). As a consequence our understanding of Australia's MPP can be very biased.

Australia's eastern coastline has started to show the effects of climate change at a rather fast pace. The western boundary current of the South Pacific, the East Australian Current (EAC), shows a warming trend, which is affecting the eastern coast of Australia and Tasmania (Holbrook & Bindoff 1997; Holbrook et al. 2011), transporting warm, low nutrient, tropical water to these mid-latitude regions (Matear et al. 2013). As a consequence, the Tasman Sea is warming and becoming saltier (Ridgway 2007). Observed changes in temperature, among other changes in the water column (e.g. salinity, stratification), are expected to have important implications in biological processes (Thompson et al. 2009; Thompson et al. 2011). There is evidence that the strengthening of the EAC has altered phytoplankton diversity in this region over the last 60 years, with tropical species expanding into southerly waters (Thompson et al. 2015).

As Australia's marine ecosystem continue to change it is important to understand how these changes can affect their functioning. One of the ways to get the most information from MPP measures relies on utilizing a size-based approach (Klauschies et al. 2012). Although estimating size-fractionated characteristics of phytoplankton communities is not practical (including MPP), this data provides valuable information on the phytoplankton community and the ecosystem that harbours it (Beardall et al. 2009; Finkel 2007; Finkel et al. 2009). Size distribution of phytoplankton assemblages has been suggested as a major biological feature in the functioning of pelagic food webs, consequently affecting the rate of carbon export and dissolved nutrients from the upper ocean to the ocean interior (Finkel et al. 2009; Marañón et al. 2001). Furthermore, phytoplankton cell size can be linked to expected time of residence in the water column, nutrients uptake, growth rates, and grazing by herbivores (Rodriguez & Guerrero 1994).

As phytoplankton cell-size has been linked to MPP and other important biological process in the ocean (food webs), a growing number of studies employ size to explain distribution of phytoplankton in time and space and use this distribution to model biogeochemical processes (Acevedo-Trejos et al. 2015; Brewin, Hardman-Mountford & Hirata 2011; Marañón 2015). However, most of the models rely on data from studies carried out in the northern hemisphere and some of these are carried out from indirect measures. It is therefore important to carry out long-term direct MPP measures and test existing hypotheses of phytoplankton cell-size in Australian waters.

In my thesis I first describe an annual study of MPP in Port Hacking a marine station 6 km southeast of Sydney, Australia. This study was designed to determine the underlying factors that impact changes in MPP, including changes in average cell-size of the community. In order to determine the role of different phytoplankton size classes in MPP a second study was implemented. Size-fractionated carbon assimilation, biomass, and chlorophyll-*a* were measured during a seasonal transition (June to December 2015). The sampling strategy was devised after studying results from the annual MPP study, the months where higher MPP were chosen for sampling. The Final study was carried out in Sydney Harbour, this study aimed at determining changes in MPP of different size-classes following an extreme rain event.

Chapt 1 PH100 time series description of c-uptake and what drives production

Satellites provide databases covering a large array of space and time; as a consequence they provide comprehensive data sets for Global and large-scale models of MPP. In order for these models to be validated, satellite products need to be corroborated with direct measures of MPP. However, only 4 coastal stations and two open ocean station have a long time records of *in situ* MPP measures (Chavez, Messié & Pennington 2011). These long-term data bases fall short of representing the 30 biogeographic oceanic provinces that were proposed in 2009 by UNESCO, which are based on changes in environmental conditions, including temperature and MPP (Briones, Rice & Ardron 2009). What's more, most of these stations together with the majority of MPP measures reported in scientific journals have been carried out in the northern hemisphere.

In Australian waters most of the measures of MPP have been carried out in oceanographic expeditions (Burford & Rothlisberg 1999; Furnas 2007; Harris et al. 1987; Koslow et al. 2008), in short-term studies (Hanson, Pattiaratchi & Waite 2005), or estimated indirectly using pigments and ocean colour (Doblin et al. 2011; Mackey et al. 1997; Moore & Abbott 2000). These estimates have provided valuable information on the functioning of Australian marine ecosystems. But, since most direct measures of MPP have been short (often limited to 2 weeks) in comparison to many oceanographic cycles, and many of these come from

indirect measurements, their results can have significant biases (Binswanger 1974; Campbell et al. 2002).

In order to account for long trends in marine waters, the Integrated Marine Observing System (IMOS) is managing the task of keeping a continuous record of different parameters in key marine coastal stations around Australia (<https://imos.aodn.org.au>). IMOS records rely on the monthly assessment of different stations in Australia; which include monthly physicochemical profiles of the water column, and the chemical and biological composition analyses of samples at discrete depths (e.g. pigment composition and dissolved nutrients, among others), as well as the continuing logging of temperature, salinity and current velocity using mooring devices. Each of these parameters provides important information on the mechanics of Australian ecosystems. However, IMOS does not measure MPP as part of their monthly assessment of the stations, which is the key parameter that links the response of phytoplankton communities to changes in the water column.

This study has focused on studying MPP in Port Hacking 100 m deep station (PH100), over the course of one year. The monthly sampling of this station is currently managed by IMOS. The time-series data available for PH100, that has been studied for over 60 years, has provided an understanding of patterns related to the seasonality of the station (Roughan & Morris 2011; Schaeffer, Roughan & Morris 2013), which is heavily associated to the East Australian Current (EAC). This is the first long-term assessment of MPP that has been carried out in this station or anywhere in Australia.

This study aims to document temporal and depth-related changes in MPP. The pigment composition of the phytoplankton communities was used to study changes in physiology (Barlow et al. 2004), diversity (Jeffrey & Hallegraeff 1987; Jeffrey, Wright & Zapata 2011; Nair et al. 2008) and average size (Brewin et al. 2010; Brewin et al. 2014; Bricaud et al. 2004; Uitz et al. 2010; Vidussi et al. 2001).

By studying an annual cycle of MPP we provided a data set that can help improve existing models that use pigments and satellite products as indirect measure of MPP. We were able to document changes in the water column and the phytoplankton community. In particular we observed lower carbon assimilation during winter and autumn with primary production dominated by smaller cell-size phytoplankton. These communities had a higher ratio of photoprotective carotenoids to photosynthetic carotenoids (PPC:PSC). The spring and summer months when C assimilation was highest, phytoplankton communities were dominated by larger size phytoplankton with lower PPC:PSC ratios. However, when carbon assimilation was standardised to total chlorophyll-*a* or total pigment, there was no difference in Photosynthetic Efficiency between

phytoplankton communities dominated by small or large cell-size. This observations suggests that a higher proportion of PPC in communities dominated by small cells does not necessarily translates in lower production per unit of pigment.

Chapt 2 PH100 size-fractionated study.

As our planet's climate continues to become warmer, small phytoplankton cells are expected to dominate the ocean (Peter & Sommer 2012, 2013). It is therefore becoming increasingly important to understand the size structure of phytoplankton communities and its implication on the ecosystem. Field studies have shown that areas with high nutrient inflows are more productive and their biomass is dominated by larger size phytoplankton (e.g. chain forming diatoms or large dinoflagellates). On the other hand, oligotrophic regions tend to be less productive, and their biomass is dominated by smaller phytoplankton (e.g. cyanobacteria and picophytoplankton).

In order to standardise MPP measure some studies use chlorophyll-*a* as a proxy for phytoplankton biomass, however chl-*a* content per cell is known to change with cell-size, and with light and nutrient supplies, which adds a significant amount of bias to size-fractionated studies (Finkel et al. 2009; Verdy, Follows & Flierl 2009; Yoshiyama & Klausmeier 2008). To better account for the environmental differences between ecosystems and times of sampling, recent studies have standardised size-fractionated MPP measures using estimated measures of phytoplankton biomass (based on biovolumes and cell counts). A review of these studies by Marañón (2015) proposed that the relationship between size and standardised measures of carbon uptake (in unites of time^{-1}) is best represented by a unimodal curve with phytoplankton of intermediate size presenting optimal values. These results have been explained by trade-offs of resource utilisation based on characteristics of cells of different sizes (Cermeño et al. 2006; López-Sandoval et al. 2014).

The mechanism explained by Marañón (2015) is meant to be independent of taxonomy. But the same environmental pressures that have fostered the wide range of size-classes (over than 9 orders of magnitude) (Beardall et al. 2009; Finkel et al. 2009; Marañón 2015), have fostered a great taxonomic diversity (Not et al. 2012), with phytoplankton counting with representative in most eukaryotic groups. The relationship between phytoplankton cell-size and diversity has been described before. Some studies have shown that it follows an unimodal curve, with maximum diversity observed at intermediate sizes (Finkel et al. 2009), while other studies have shown this relationship to vary with the type of resources in the ecosystem (Acevedo-Trejos et al. 2015; Cermeño & Figueiras 2008; Cermeno et al. 2008).

To test the relationship between diversity, MPP and size, we measured ^{14}C uptake, chlorophyll-*a* and phytoplankton biomass for 4 size-classes of phytoplankton during a period of 6 months (June to December 2015) at 6 discrete depths (0-75 m). We compared these biological measures to diversity obtained from 16s and 18s analyses. After the construction of operational taxonomic units, the taxonomic profile of the samples will be further categorised using the V9 metabarcoding data set from Tara (<http://taraoceans.sbroscoff.fr/EukDiv>), which allows for the discrimination of basic trophic modes (e.g. photo vs heterotroph) and infer size-classes. By studying all these features over a seasonal transition we set to observe how contrasting changes in the water column could influence the relationships between diversity, MPP and size. These measures were carried out at Port Hacking 100 m station (PH100), after a yearly study of MPP, which allowed to identify the best time to carry this study.

Preliminary results show that small size-classes are dominating in terms of biomass and carbon assimilation during all the study period. Biomass of large size-classes peak in December but this increase in biomass did not translate in higher *c* assimilation compared to the other sampling months. Our results also show a decrease in growth rate with size following a power rule for all the sampling months. This data set provides the characterization of different size-classes over time, such as changes in C:Chl-*a* ratios (among other parameters) during a seasonal transition.

Chapt 3 Primary productivity and changes in the size structure of the phytoplankton community in Sydney Harbour after a storm event.

Being at the heart of a metropolitan area, Sydney Harbour has been exposed to significant quantities of pollutants including heavy metals, some of which have accumulated in the sediments (Birch 1996; Birch 2011; Davis & Birch 2010; Hedge et al. 2014). Improved management of Sydney Harbour has assisted in decreasing pollution sources. Currently, storm water inflows are one of the major sources of contamination (Hedge et al. 2014). Apart from directing high concentration of nutrients and pollutants into the estuary, storm water from extreme rain events have a higher potential to resuspend historically accumulated contaminants that rest in the sediments surface layers (Davis & Birch 2010). These extreme events, which are becoming more intense as a result of climate change (i.e. higher precipitations in shorter time intervals than previously observed) (Allan & Soden 2008; Cai et al. 2014; Coumou & Rahmstorf 2012; Rahmstorf & Coumou 2011; Webster et al. 2005), can exacerbate the stress on the ecosystem caused by human activity in Sydney Harbour.

As a consequence of these extreme rain events, estuaries can rapidly fluctuate between low and high nutrients concentrations in the timeframe of hours. These drastic changes in nutrients are often accompanied by introduction of pollutants, allochthonous OM, and reduce light availability for long periods of time. These

variations in the water column can significantly alter phytoplankton structure (i.e. shifts in species composition and phytoplankton size-classes) and the functioning of the ecosystem. For example, many estuarine ecosystems with high nutrient input have been observed to present low carbon uptake after extreme rain events due to the low light availability in the system caused by plumes (Kocum, Underwood & Nedwell 2002).

The last measures of MPP in Sydney Harbour were carried out more than 40 years ago (1975) (Revelante & Gilmartin 1978) after the implementation of remediation measures in area. The study, accounted for one sampling event carried out during a dry period. It allowed to establish patterns of size-fractionated production and diversity along different areas of the estuary. But since no follow-up studies were carried out since, it is not possible to know how relevant these findings remain or if the remediation measured implemented then have continued to make a difference in MPP and the size structure of phytoplankton populations.

In this study we set to investigate how inputs from stormwater runoff (>100 mm in 72 h) influence phytoplankton c-uptake in an urbanised system with a legacy of heavy metal contamination. To determine the underlying contributors to c-uptake, we measured the size-fractionated uptake for three different phytoplankton size-populations. In order to capture dynamic changes that occur after the rain events we measured different physicochemical parameters in the water column and biological parameters of the phytoplankton populations at high-resolution intervals. The water samples were collected from 4 different locations with large points of discharge into Sydney Harbour and covering different types of habitats with different retention characteristics. Two locations were poorly-flushed embayment ecosystems and two were well-flushed channels. Finally, based on the data available at the moment and our results, we proposed an ecological mechanism of the response of phytoplankton populations to rain events in Sydney Harbour.

During the duration of the study, the stations closer to the head of the estuary showed a higher biological response and higher changes in the water column (i.e. salinity, nutrient, chl-*a*, MPP). We observed a bloom only at Parramatta River 3 days after the rain event; this bloom was likely caused because Parramatta River is the station closer to the head of the estuary. The short duration of this bloom might be due to the low retention characteristic of the station. With the exception of Parramatta River, MPP remained relatively unchanged. However, a shift in the relative proportion of the size classes responsible for C assimilation was observed consistently across all station. A similar pattern was observed for size-fractionated chl-*a*. Small size phytoplankton contributed to at least 50 % of total MPP with the exception of day 3 after the rain event, where it contributed only 10 % of MPP.

Discussion.

1. Time series provides MPP data in NSW
2. Size fractionated study provides information on the structure of phytoplankton population and importance of each size class on production.
3. Recent study of phytoplankton production in Sydney Harbour and the role of different size classes after a rain event.
4. Important to focus on the role of small size phytoplankton.
5. Interaction between size-classes and not just succession of populations seems to play a role in MPP.

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