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Contrasting oceanographic conditions and phytoplankton communities on the east and west coasts of Australia

P.A. Thompson [a,b,*], P. Bonham [a,b], A.M. Waite [c], L.A. Clementson [a,b], N. Cherukuru [d], C. Hassler [e], M.A. Doblin [e]

[a] *Marine and Atmospheric Research, GPO Box 1538, Hobart, TAS 7001, Australia*
[b] *Wealth from Oceans, National Research Flagship, Australia*
[c] *School of Environmental Systems Engineering, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia*
[d] *CSIRO Land and Water, GPO Box 1666, Canberra, ACT 2601, Australia*
[e] *Plant Functional Biology and Climate Change Cluster, Environmental Sciences, University of Technology, Sydney, PO Box 123, Broadway, NSW 2007, Australia*

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ABSTRACT

The composition and dynamics of the phytoplankton communities and hydrographic factors that control them are described for eastern and western Australia with a focus on the Eastern Australian Current (EAC) and Leeuwin Current (LC) between 27.5° and 34.5°S latitude. A total of 1685 samples collected from 1996 to 2010 and analysed for pigments by high performance liquid chromatography (HPLC) showed the average TChl*a* (monovinyl+divinyl chlorophyll *a*) concentration on the west coast to be 0.28 ± 0.16 μg L^{-1} while it was 0.58 ± 1.4 μg L^{-1} on the east coast. Both coasts showed significant decreases in the proportions of picoplankton and relatively more nanoplankton and microplankton with increasing latitude. On both coasts the phytoplankton biomass (by SeaWiFS) increased with the onset of winter. At higher latitudes (>27.5°S) the southeast coast developed a spring bloom (September) when the mean monthly, surface chlorophyll *a* (chl*a*) concentration (by SeaWiFS) was 48% greater than on the south west coast. In this southern region (27.5–34.5°S) *Synechococcus* was the dominant taxon with 60% of the total biomass in the southeast (SE) and 43% in the southwest (SW). Both the SE and SW regions had similar proportions of haptophytes; ~14% of the phytoplankton community. The SW coast had relatively more pelagophytes, prasinophytes, cryptophytes, chlorophytes and less bacillariophytes and dinophytes. These differences in phytoplankton biomass and community composition reflect the differences in seasonality of the 2 major boundary currents, the influence this has on the vertical stability of the water column and the average availability of nutrients in the euphotic zone. Seasonal variation in mixed layer depth and upwelling on the west coast appears to be suppressed by the Leeuwin Current. The long-term depth averaged (0–100 m) nitrate concentration on the west coast was only 14% of the average concentration on the east coast. Redfield ratios for NO_3:SiO_2:PO_4 were 6.5:11.9:1 on the east coast and 2.2:16.2:1 on the west coast. Thus new production (nitrate based) on the west coast was likely to be substantially more limited than on the eastcoast. Short term (hourly) rates of vertical mixing were greater on the east coast. The more stable water column on the west coast produced deeper subsurface chlorophyll *a* maxima with a 25% greater proportion of picoeukaryotes.

1. Introduction

Boundary currents can profoundly influence phytoplankton dynamics producing some of the world's richest zones of primary production, considerable phytoplankton biomass and substantial fisheries (Ryther, 1969; Bakun et al., 1982). Australia is the only continent with pole-ward flowing boundary currents along both coasts transporting warm, relatively nutrient poor waters southward (Fig. 1). Both coasts show rapid and significant, long term (~60 years) surface warming (Feng et al., 2003; Ridgway, 2007; Thompson et al., 2009) indicating the strengthening of these boundary currents. On Australia's west coast at 32°S the Leeuwin Current (LC) transports 2–3 Sverdrups ($1\ \mathrm{Sv} = 10^6\ \mathrm{m}^3\ \mathrm{s}^{-1}$) southward in summer rising to 5 Sv in winter (Feng et al., 2003). While on the east coast at 28°S the Eastern Australian Current (EAC) flow ranges from 7 Sv in winter rising to 16 Sv in summer (Ridgway and Godfrey, 1997). Most of the EAC turns abruptly east at ~32°S while about a third continues into the southern Tasman Sea, largely as a series of eddies (Ridgway and Godfrey, 1997). Upwelling has been

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[*] Corresponding author at: CSIRO Marine and Atmospheric Research, GPO Box 1538, Hobart, TAS 7001, Australia.
E-mail address: Peter.a.Thompson@csiro.au (P.A. Thompson).

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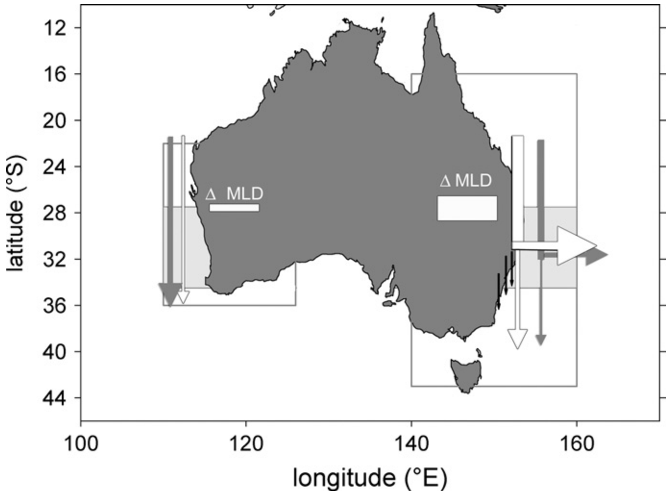

Fig. 1. A schematic showing the relative flow of the East Australian and the Leeuwin Currents, the study areas (boxes) with light grey boxes indicating the south east and southwest regions (27.5–34.5°S) used for a statistical comparison between the east and west coast phytoplankton communities. Arrows show relative magnitude of transport, dark arrow = winter. On the west coast the Leeuwin Current transports ~2 Sv in summer rising to 5 Sv in winter (Feng et al., 2003). On the east coast the Eastern Australian Current transports 7 Sv in winter rising to 16 Sv in summer (Ridgway and Godfrey, 1997). The EAC produces larger eddies and in N winds (small black arrows) can be induced to upwell (Rochford, 1975; Tranter et al., 1986; Cresswell, 1994; Gibbs et al., 1997; Oke and Middleton, 2001). At 28°S the annual amplitude in mixed layer depth is ~8 m on the west coast and ~27 m on the east coast (Condie and Dunn, 2006).

frequently reported to occur on the east coast at ~31°S (Rochford, 1975; Tranter et al., 1986; Cresswell, 1994; Gibbs et al., 1997; Oke and Middleton, 2001) and linked with coastal phytoplankton blooms (Humphrey, 1963; Hallegraeff and Reid, 1986; Pritchard et al., 2003).

Nutrient availability is a major factor influencing phytoplankton abundance (Yoder et al., 1993). The distributions of major nutrients in the Australian region was reviewed by Condie and Dunn (2006) and showed low concentrations at the surface throughout most of the year. The supply of nutrients to the euphotic zone is primarily dependent upon the depth, rate and temporal dynamics of vertical mixing. Vertical mixing can also a major determinant of phytoplankton irradiance, thus it is of fundamental importance to phytoplankton ecology. The temporal dynamics of vertical mixing and mixed layer depth (MLD) around Australia show the general pattern of an increase with increased latitude (Condie and Dunn, 2006) consistent with the global pattern (de Boyer Montégut et al., 2004). There are, however, significant east versus west coast differences in the annual amplitude of the MLD. Mixed layer depths are similar in summer (~20 m) and reach ~40 m in winter on the west coast. On the east coast winter MLD can exceed 80 m and are more spatially variable (de Boyer Montégut et al., 2004; Condie and Dunn, 2006). This deeper winter mixing must slow phytoplankton growth (Sverdrup, 1953) and create a different ecological niche (e.g. Margalef, 1978) on the east versus west coasts. If climate variability reduces vertical mixing (Falkowski and Oliver, 2007) then this east versus west comparison of the phytoplankton may give insights into long term community trends.

The effects of vertical mixing on phytoplankton ecology are determined by the temporal frequency of the mixing and by the capacity of phytoplankton to respond. These factors can be difficult to measure and assess but the presence of a subsurface chlorophyll maximum (SCM) is a good indicator of relatively long term (>1 month) water column stability (Cullen and Lewis, 1988; Cullen, 1990). In addition the ratio of the photoprotective pigments (diadinoxanthin+diatoxanthin) : chlorophyll *a* varies in response to irradiance and provides a reliable measure of vertical mixing rate and relative exposure to light over a time scale of hours (Claustre et al., 1994; Moline, 1998; Brunet et al., 2003). Therefore the vertical distributions of phytoplankton and their physiological characteristics can be used to compare the relative stability of the water column.

The biogeography of phytoplankton around Australia was extensively studied by Wood (1954, 1964a, 1964b) but the use of nets for sampling and analysis by light microscopy meant very poor discrimination of the smaller cells. More recent studies of Australian phytoplankton biogeography (e.g. Hallegraeff, 1981; Jeffrey and Hallegraeff, 1990) also relied heavily upon net samples although Hallegraeff and Jeffrey (1993) did report that up to 97% of the chlorophyll *a* was <15 μm in the northern tropics. Subsequent research has shown that up to 97% of the west coast phytoplankton biomass can be <5 μm in size (Thompson et al., 2007) while the majority of east coast phytoplankton can be <2 μm (Crosbie and Furnas, 2001; Sorokin and Sorokin, 2009) suggesting that a reappraisal of the phyto-biogeography that considers smaller taxa is needed. Small phytoplankton are well known to contribute significantly to phytoplankton biomass, particularly the prokaryotic cyanobacteria *Synechococcus* and Prochlorophyte *Prochlorococcus*, which are often reported to be the numerically dominant species in oligotrophic open waters (Olson et al., 1990). Unfortunately there are a very small number of quantitative cells counts of smaller taxa from Australian waters. In addition given the high likelihood of bias due to seasonality (Thompson and Waite, 2003; Brodie et al., 2007) it is improbable that an accurate biogeography could be constructed from these data. These small cells which often lack taxonomically useful morphological features for identification when observed by epifluorescence microscopy or conventional light microscopy can, fortunately, be estimated from phytoplankton pigments. We define 4 types of associations between pigments and taxa relevant to Australian waters (Table 1):

1. Pigments found within a narrow range of taxa and thus a limited range per cell, such as divinyl chlorophyll *a* (DVchl*a*) in *Prochlorococcus*, where the conversion to cell density can be relatively precise (after Morel et al., 1993).
2. Pigments, such as Zeaxanthin, that are found in more than one taxon but within some taxa the content per cell may be relatively constrained (e.g. *Synechococcus*).
3. Pigments that are highly constrained to a recognized taxon such as Peridinin (dinoflagellates), Alloxanthin (cryptophytes), Prasinoxanthin (prasinophytes), 19′-hexanoyloxyfucoxanthin (haptophytes) but with a wider range per cell.
4. Pigments that are found in a range of taxa, such as diadinoxanthin.

Where pigments are found across a range of taxa the conversion to taxonomic affiliation can be achieved using a various methods such as CHEMTAX which uses a steepest-descent algorithm to fit a matrix of expected pigment ratios from those taxa to the observations (Mackey et al., 1996).

This paper examines the spatial patterns of the phytoplankton along the east and west coasts of Australia. The primary goal was to investigate the roles of the predominant boundary currents on phytoplankton biogeography and ecology. This goal combined with the availability of data influenced the analyses that were undertaken. The primary approach was to pool pigment samples analysed by HPLC from a large number of cruises that took place from 1996 to 2010 and use these to investigate the patterns of phytoplankton distribution and to relate those to prevailing oceanographic conditions. In addition the ~10 years of SeaWiFS data were used to identify the major latitudinal and seasonal trends