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Shifts in picophytoplankton community structure influenced by changing upwelling conditions

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The influence of upwelling events on the structure of picophytoplankton communities was assessed at the annual scale from a station within the South Australian shelf region. In this region, local (wind) and global (La Niña/El Niño–Southern Oscillation) hydroclimatic conditions affect the development of upwelling over the austral summer. Using flow cytometry, changes in picophytoplankton community structure were investigated in relation to the properties of the water column when the nature and strength of upwelling event differed for the upwelling seasons of 2008, 2009, and 2010. In 2008, strong upwelling favorable southeasterlies were responsible for extensive upwelling and the dominance of picoeukaryotes. Alternatively, in 2009, the observed dominance of *Prochlorococcus* reflected the presence of oligotrophic conditions whilst southeasterlies were replaced by downwelling favorable northwesterlies that likely prohibited the full development of upwelling. In 2010, whilst southeasterlies remained relatively weak, particularly cold and low saline upwelled waters indicated enhanced upwelling events. This weak local wind field together with the occurrence of El Niño explained the observation of shallow upwelled waters below the warm surface layer and subsequent enhanced stratification. These conditions led to the dominance of *Synechococcus* in surface and fluorescence maximum depths, but of *Prochlorococcus* in bottom upwelled waters. The tight association between upwelling and stratification, i.e. whether upwelled waters reach shallower depths and/or mix with those of the surface as a result of variable climatic conditions, was suggested as the process driving the vertical heterogeneity of picophytoplankton populations. This study brings valuable information for changing picophytoplankton community structure with potential future changing hydroclimatic forcing.

1. Introduction

Picophytoplankton (i.e. photoautrophic cells less than 2 μm in diameter; Sieburth et al., 1978) largely contribute to total phytoplankton abundance, biomass, and production in the ocean (Chisholm et al., 1992; Vaquer et al., 1996; Partensky et al., 1999; Agawin et al., 2000; Marañón et al., 2001; Morán, 2007). They include three major groups that are *Prochlorococcus*, *Synechococcus*, and picoeukaryotes, which can in turn be subdivided into distinct ecotypes or strains (Rocap et al., 2002; Rodríguez et al., 2005; Worden and Not, 2008). Because each of these groups are characterized by distinct physiological and ecological properties (Partensky et al., 1999; Veldhuis et al., 2005), understanding the variability in the relative importance of *Prochlorococcus*, *Synechococcus*, and picoeukaryotes is crucial to understand the fate of carbon and energy fluxes within and between ecosystems.

Current knowledge on picophytoplankton community structure in coastal upwelling systems is sparse (Hall and Vincent, 1990; Partensky et al., 1996; Sherr et al., 2005; Reul et al., 2006; Echevarría et al., 2009; Linacre et al., 2010; Daneri et al., 2012; van Dongen-Vogels et al., 2011) largely due to the fact that these nutrient-enriched systems are typically seen as larger phytoplankton (>20 μm) dominated systems (e.g. Herrera and Escribano, 2006; Teixeira et al., 2011). Various studies have previously reported changes in the relative contribution of distinct phytoplankton size classes in terms of both abundances and primary production for coastal upwelling systems (e.g. Iriarte and González, 2004;

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Herrera and Escribano, 2006; Cermeño et al., 2006). Despites this lack of information on the dynamic of picophytoplankton communities, picophytoplankton could be important for nutrient and carbon transfer to higher trophic levels in such dynamic regions (e.g. Vargas et al., 2007; Morales and Anabalón, 2012). Past and recent studies have nevertheless recorded the dominance of *Synechococcus*, or picoeukaryotes, in surface waters of coastal regions influenced by upwelling, although more typically being reported to growth within the diluted upwelled surface waters advected offshore (Hall and Vincent, 1990; Partensky et al., 1996; Sherr et al., 2005; Echevarría et al., 2009). Upwelling coastal waters involving the uplift of deep cold nutrient-rich waters toward the surface would be hostile to *Prochlorococcus*, known to dominate in warm (>20 °C) oligotrophic open oceanic waters, having limited growth below 12 °C (Partensky et al., 1999). Recent studies have however showed that distinct ecotypes of *Prochlorococcus* have their optimal growth rates at distinct temperatures with relatively higher cell abundances (c.a. 10^4 cells mL^{-1}) of low light adapted ecotypes in relatively cold environments (<15 °C) in contrasted to that of high light-adapted ecotypes being more restricted to warm oligotrophic waters (e.g. South East Atlantic, Zwirglmaier et al., 2008; Jameson et al., 2010, North West Atlantic, Zinser et al., 2007). The abundances dynamic of diverse picophytoplankton populations has only been recently investigated in South Australian continental shelf waters where their high spatial and temporal variability in abundances reflected the complex hydrodynamic of the shelf region, involving localized upwelling and downwelling events (van Dongen-Vogels et al., 2011). Taken together these patterns indicate that varying upwelling conditions are likely to influence picophytoplankton community structure.

Summer upwelling events within the South Australian continental shelf waters could be important to sustain the productivity of the highly valuable fisheries of the region (Ward et al., 2006; van Ruth et al., 2010). During summer, southeasterly upwelling favorable winds and Ekman transport force cold (<16 °C) and low saline (<35.7) waters of the northern boundary current, the Flinders Current, onto the shelf through the du Couedic Canyon, located south off Kangaroo Island (KI, Fig. 1). The physical dynamic of the summer upwelling season has previously been reviewed by Middleton and Bye (2007a, b) and involve the occurrence of single to multiple upwelling events by pulse, each event potentially followed by intermittent periods of relaxation, mixing, or downwelling processes (Middleton and Platov, 2003; Kaempf et al., 2004; Middleton and Bye, 2007a, b; van Ruth et al., 2010). Due to the width of the shelf, upwelled waters typically remain below the surface and have previously been observed to slowly (c.a. 0.1 cm s^{-1}) advected northwestward along the 100 m isobath of the shelf region (Middleton and Bye, 2007a, b; van Dongen-Vogels et al., 2011). The prevailing hydroclimatic conditions such as the alongshore wind and La Niña/El Niño Southern Oscillation (ENSO) may, however, strongly affect the depth at which deep waters are upwelled and the structure of the water column (Middleton and Bye, 2007a, b; Middleton et al., 2007). The high inter-annual variability in phytoplankton community structure and production previously observed may hence be ultimately controlled by local and large scale changes in hydroclimatic forcing (van Ruth et al., 2010; van Dongen-Vogels et al., 2011). In this context, the present study focuses on changes in picophytoplankton community structure at a single station located directly on the path of the upwelled plume for three distinct upwelling events that occurred in the summer of 2008, 2009, and

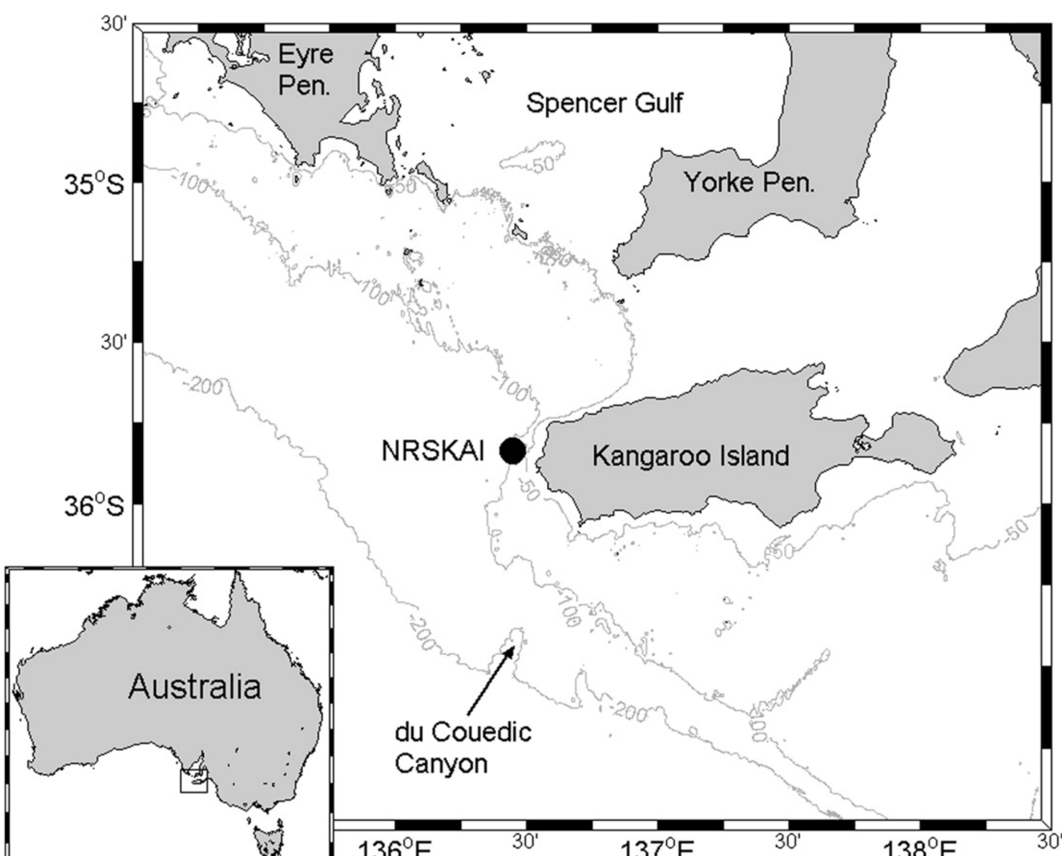

Fig. 1. Map of the South Australian continental shelf region showing the national reference station located off Kangaroo Island (NRSKAI) and the du Couedic Canyon from which waters of the Flinders Current are upwelled over the austral summer.