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A local upwelling controls viral and microbial community structure in South Australian continental shelf waters

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ABSTRACT

Despite the increasing awareness of the role of viruses and heterotrophic bacteria in microbial dynamics and biogeochemical cycles, there is still a critical lack of information on their community composition and dynamics, especially in relation to upwellings. We investigated, within surface waters and the Deep Chlorophyll Max, the community composition and dynamics of flow cytometrically defined sub-populations of heterotrophic bacteria and virus-like particles in nearby water masses that were affected and unaffected by a localised wind-driven coastal upwelling. In contrast to previous studies we uniquely identified a 4-fold increase in total viral abundance and a decrease in bacterial abundance, from upwelled to offshore waters. Individual viral sub-populations were seen to correlate significantly to both bacterial populations and chlorophyll *a*, suggesting the possibility of individual viral populations infecting multiple host species rather than the often assumed single host species. The percentage of HDNA bacteria was high (84.3–93.4%) within upwelled waters, in accordance with the highest recorded values within an upwelling system, and decreased down to 35.5–42.6% away from the upwelling. Additionally, changes in the community composition of individual bacterial sub-populations suggest individual populations might be better adapted to distinct environments. We suggest that each flow cytometrically defined bacterial population may possess its own environmental niche where favourable conditions for that population result in an increase in abundance, cellular activity and productivity.

1. Introduction

Viruses and heterotrophic bacteria are critical components of the world's oceans ecosystems (Azam, 1998; Arrigo, 2005; Suttle, 2005). Heterotrophic bacteria play a significant role in the degradation of particulate organic carbon, the conversion of dissolved organic carbon into the particulate pool, and hence act as both remineralisers of organic carbon and trophic mediators (Azam et al., 1983; Cho and Azam, 1988; Gasol et al., 1997; del Giorgio and Cole, 1998). Viruses are the most common organisms in the marine environment (Fuhrman, 1999). Viruses are also a driving force in bacterial mortality (Bergh et al., 1989; Proctor and Fuhrman, 1990; Cochlen et al., 1993; Fuhrman, 1999; Suttle, 2005) and phytoplankton mortality (Evans et al., 2003; Brussaard et al., 2005; Baudoux et al., 2006). They potentially infect all organisms and influence various biogeochemical and ecological processes (Bergh et al., 1989; Proctor and Fuhrman, 1990; Fuhrman, 1999; Wommack and Colwell, 2000; Suttle, 2005), transforming carbon and nutrients from a particulate state into a dissolved state, a major step in global carbon cycling in the ocean (Suttle, 2005).

Aquatic microbial populations have been routinely identified and enumerated using flow cytometry for the past 15 years (Li et al., 1995; Marie et al., 1997; Lebaron et al., 2002; Seymour et al., 2005; Gasol et al., 2009). Heterotrophic bacteria have generally been classified into two distinct bacterial populations, containing cells with either a high- or low-nucleic acid content (HDNA/LDNA; Lebaron et al., 2001), which have nearly ubiquitously been reported in marine and freshwater systems (e.g. Gasol et al., 1999; Lebaron et al., 2002; Servais et al., 2003; Seymour et al., 2004, 2005). HDNA cells were thought to be active whilst smaller LDNA sub-populations were considered to be either inactive or dead (Li et al., 1995; Gasol et al., 1999; Lebaron et al., 2001; Servais et al., 2003). This has, however, recently been challenged (Zubkov et al., 2001; Longnecker et al., 2005; Bouvier et al., 2007; Wang

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et al., 2009); it has been shown that LDNA cells are also active (Bouvier et al., 2007) and retain their small size throughout their growth cycle (Wang et al., 2009). More specifically, in oligotrophic systems, whilst still having lower metabolic activities than HDNA cells, LDNA cells may play a larger role in heterotrophic processes than HDNA cells in eutrophic systems (Longnecker et al., 2005). Further investigation of these populations has resulted in a number of scenarios on the composition of HDNA and LDNA populations (Bouvier et al., 2007), with a possible movement of cells between HDNA and LDNA populations and cells that are distinctive to these populations (Bouvier et al., 2007). The composition of these populations is thought to be controlled by a number of biological mechanisms such as increasing DNA content during periods of high activity (Jellet et al., 1996), adaptive changes in genome size via DNA loss (Nilsson et al., 2005) and the replication and reduction during cell division (Lebaron and Joux, 1994). However, despite the increasing awareness of the role of viruses in microbial dynamics and biogeochemical cycles (Arrigo, 2005; Suttle, 2005), there is still a critical lack of information on the potential influence of viruses on the composition of HDNA and LDNA bacterial populations, and the related ecological implications.

Flow cytometric investigations of viruses and heterotrophic bacterial populations have been conducted over a wide range of environments (Lebaron et al., 2002, Seymour et al., 2004, 2005, 2007; Bouvier et al., 2007; Brussaard et al., 2008; Payet and Suttle, 2008; Schapira et al., 2009). However, assessments of viral and microbial dynamics in wind-driven coastal upwelling systems are still limited (Longnecker et al., 2005; Sherr et al., 2006; Alonso-Sáez et al., 2007a, 2007b), hence restricting our knowledge on the physical processes that may alter the composition of flow cytometrically defined populations. To our knowledge, only two recent studies have explored the effects of a localised upwelling event on viral abundance and microbial communities (He et al., 2009; Eissler et al., 2010). However, information on the dynamics of distinct viral and bacterial populations, as well as their potential relationship with one another are still lacking within coastal upwelling systems.

In this context, we used a sampling strategy specifically designed to investigate the abiotic and biotic properties of nearby water masses that are affected and unaffected by a localised wind-driven upwelling occurring in South Australian continental shelf waters. Therefore the objectives of this study were (i) to assess the spatial distribution of viral and bacterial communities in relation to the spatial dynamics of a wind-driven coastal upwelling, (ii) to investigate the composition of HDNA and LDNA heterotrophic bacterial populations in relation to the physical processes within the system and (iii) determine whether the dominance of specific heterotrophic bacterial populations may be influenced by viral abundance.

2. Materials and methods

2.1. Study site

Sampling took place on the South Australian continental shelf during an upwelling event occurring on the Bonney Coast (Fig. 1). The area is one of Australia's major upwelling systems and, uniquely, lies within a northern boundary current, the Flinders Current (Schahinger, 1987; Middleton and Platov, 2003; Middleton and Bye, 2007). In addition, the Bonney Coast continental shelf is characterized by the presence of the Murray canyons that are scattered along the South Australian continental shelf, a number of them such as the Bonney canyon being some of the largest canyons on Earth (Hill et al., 2005). More specifically, the Bonney canyon is one of the most significant canyons on the shelf and is located within the heart of South Australia's major upwelling system. The system is predominantly wind-driven, where persistent south-easterly winds move surface waters offshore via Ekman transport and are consequently replaced by cold, nutrient rich deep water. As a result the system is an area of high primary productivity, supporting valuable fishing grounds and feeding grounds for the threatened blue whale, *Balaenoptera musculus* (Butler et al., 2002; Kämpf et al., 2004).

2.2. Sampling procedures

Sampling was carried out onboard the R.V. *Southern Surveyor* from the 4th to the 16th February 2008 along three parallel transects, located to the west, centre and east of the Bonney canyon axis (Fig. 1). Five stations were sampled along each transect at bottom depths of approximately 100, 200, 500, 1000 and 1500 m (Fig. 1). Vertical profiles of temperature (T) and salinity (S) were carried out at each station using a Seabird SBE 911 plus CTD, which was also fitted with

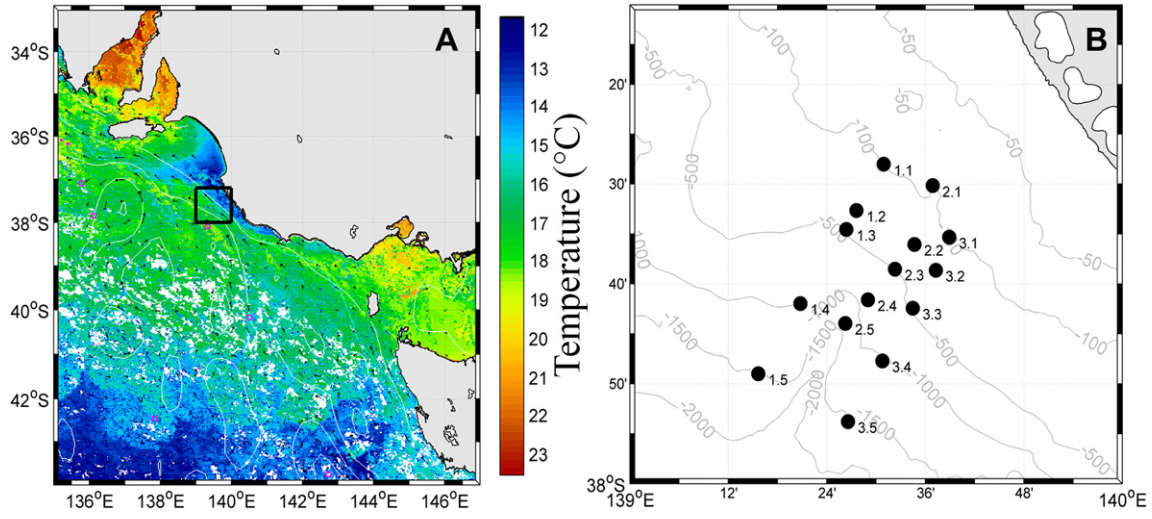

Fig. 1. Sea surface temperature (SST) off south-eastern Australia (A), where the black box represents the study area (B) with sampling transects and stations located to the west, centre and east of the axis of the Bonney Canyon. SST data sourced from the Commonwealth Scientific and Industrial research Organisation (CSIRO; http://www.marine.csiro.au/remotesensing/oceancurrents/).