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Temporal and spatial patterns of microbial community biomass and composition in the Southern California Current Ecosystem

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ABSTRACT

As part of the California Current Ecosystem Long Term Ecological Research (CCE-LTER) Program, samples for epifluorescence microscopy and flow cytometry (FCM) were collected at ten 'cardinal' stations on the California Cooperative Oceanic Fisheries Investigations (CalCOFI) grid during 25 quarterly cruises from 2004 to 2010 to investigate the biomass, composition and size-structure of microbial communities within the southern CCE. Based on our results, we divided the region into offshore, and inshore northern and southern zones. Mixed-layer phytoplankton communities in the offshore had lower biomass ($16 \pm 2 \mu\text{g C L}^{-1}$; all errors represent the 95% confidence interval), smaller size-class cells and biomass was more stable over seasonal cycles. Offshore phytoplankton biomass peaked during the winter months. Mixed-layer phytoplankton communities in the northern and southern inshore zones had higher biomass (78 ± 22 and $32 \pm 9 \mu\text{g C L}^{-1}$, respectively), larger size-class cells and stronger seasonal biomass patterns. Inshore communities were often dominated by micro-size (20–200 μm) diatoms; however, autotrophic dinoflagellates dominated during late 2005 to early 2006, corresponding to a year of delayed upwelling in the northern CCE. Biomass trends in mid and deep euphotic zone samples were similar to those seen in the mixed-layer, but with declining biomass with depth, especially for larger size classes in the inshore regions. Mixed-layer ratios of autotrophic carbon to chlorophyll *a* (AC:Chl *a*) had a mean value of 51.5 ± 5.3 . Variability of nitracline depth, bin-averaged AC:Chl *a* in the mixed-layer ranged from 40 to 80 and from 22 to 35 for the deep euphotic zone, both with significant positive relationships to nitracline depth. Total living microbial carbon, including auto- and heterotrophs, consistently comprised about half of particulate organic carbon (POC).

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1. Introduction

The California Current Ecosystem (CCE) is a productive eastern boundary current system where nutrient delivery by coastal upwelling, wind stress curl and mesoscale eddies support high plankton production and standing stocks (Huyer, 1983; Legaard and Thomas, 2006; Rykaczewski and Checkley, 2008; Mantyla et al., 2008; Thomas et al., 2009). The main core of the California Current flows equatorward along the west coast of North America, and is defined by cool, low salinity subarctic water (Hickey, 1979; Lynn and Simpson, 1987). In the southern portion of the CCE Point Conception marks a transition zone, as the primary orientation of the coast line abruptly shifts from north-south to east-west, becoming the northern portion of the Santa Barbara Basin (SBB). A poleward flowing California Undercurrent originates in the eastern tropical Pacific, bringing warm, saline water from offshore

and the south and forming the Southern California eddy which is centered approximately near San Nicholas Island (Lynn and Simpson, 1987; Niiler et al., 1989; Bray et al., 1999). The interactions of these currents in the California Bight and offshore regions set up distinct floristic zones, defined by water masses and floral patterns, that can be used to split the region into northern and southern nearshore, and offshore regions (Hayward and Venrick, 1998; Venrick, 2002, 2009).

To better understand pelagic ecosystem dynamics of the southern CCE, extensive modeling and remote sensing studies have been conducted to determine processes controlling chlorophyll *a* concentrations, primary production, phytoplankton growth rates, biomass and carbon to chlorophyll *a* ratios (Eppley et al., 1985; Peláez and McGowan, 1986; Di Lorenzo et al., 2004; Gruber et al., 2006; Li et al., 2010; Kahru et al., 2012, this issue). However, the success of such studies depends highly on quality in situ measurements for parameterization, algorithm development and validation.

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has conducted routine assessments of ocean hydrography and biology on a spatially extensive sampling grid pattern in

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the southern CCE region since 1949. Aside from regular chlorophyll *a* analyses and occasional taxonomic studies based on visual microscopy and HPLC pigment analysis (Hayward and Venrick, 1998; Venrick, 1992, 2002, 2009, 2012; Goericke, 2011), detailed investigations of microbial community biomass and structure have not been a part of the CalCOFI program. Beginning in November 2004, the California Current Ecosystem, Long Term Ecological Research (CCE-LTER) program has augmented core CalCOFI measurements in this area, using advanced high-throughput digital epifluorescence microscopy and flow cytometry (FCM), to assess microbial community biomass, size-structure and taxonomic composition.

Here we present for the first time a detailed examination of carbon biomass, size-structure and composition of CCE microbial communities, sampled on quarterly CalCOFI cruises from 2004 through 2010. The goal of the study is to establish baseline measurements for the southern CCE, that are relevant for documenting and investigating climate change impacts in the region, and that will facilitate the development of ecosystem models and remote sensing algorithms that capture the natural variability in phytoplankton carbon biomass and functional group composition.

2. Materials and methods

2.1. Sample collection

We collected samples for analyses of microbial community abundance, biomass and composition during 25 quarterly CalCOFI cruises from November 2004 (cruise 200411) to November 2010 (cruise 201011). On each cruise, we sampled three depths with CTD rosette casts at each of 10 'cardinal' stations distributed onshore to offshore along Lines 80 and 90 of the standard CalCOFI grid pattern (Fig. 1). The locations of cardinal stations were selected so that at least two were located in each of the major floristic regions identified by Venrick (2002, 2009). The depths of sample collection were dependent upon the depth of the in vivo

fluorescence maximum: Type I stations (0–50 m fluorescence max) were sampled at 10 m as well as the middle and bottom shoulder of the fluorescence layer; Type II stations (50–80 m fluorescence max) were sampled at 10 m, 40 m and the fluorescence max; and Type III stations (80–120 m fluorescence max) were sampled at 10 m, 62 m and the fluorescence max. From each depth sampled, aliquots were taken directly from the Niskin bottles for plankton community analyses by flow cytometry (FCM) and epifluorescence microscopy, as well as for concentrations of dissolved nutrients, chlorophyll *a* (Chl *a*) and particulate organic carbon (POC) measurements made by the CalCOFI or CCE-LTER groups. Details of those methods are described below.

2.2. Analysis of eukaryotic nano- and microplankton by epifluorescence microscopy

Seawater samples (500 mL) for microscopical analysis were gently collected from the CTD and immediately preserved for slide preparation according to a modified protocol of Sherr and Sherr (1993). The samples were first preserved with 260 μL of alkaline Lugol's solution, immediately followed by 10 mL of buffered formalin and 500 μL of sodium thiosulfate, with gentle mixing between each addition. Preserved samples were shielded from light and left to rest at room temperature for 1 h. After the rest period, 1 mL of proflavin (0.33% w/v) was added and the samples were stored in the dark for an additional hour. Just prior to filtration, the preserved samples were stained with 1 mL of DAPI (0.01 mg mL^{-1}) and immediately transferred to the filtration manifold. A 50-mL aliquot (small volume, SV) of the sample was filtered through a 25-mm black polycarbonate filter with 0.8- μm pore size, and the remaining 450 mL aliquot (large volume, LV) was filtered through a 25-mm black polycarbonate filter with 8.0- μm pores. We placed a 10- μm pore size, 25-mm nylon backing filter under all polycarbonate filters to promote even cell distribution, and filtered the samples under gentle vacuum pressure (< 100 mm Hg). Each filter was then mounted onto glass slides with one drop of Type DF immersion oil and a No. 2 cover slip, and

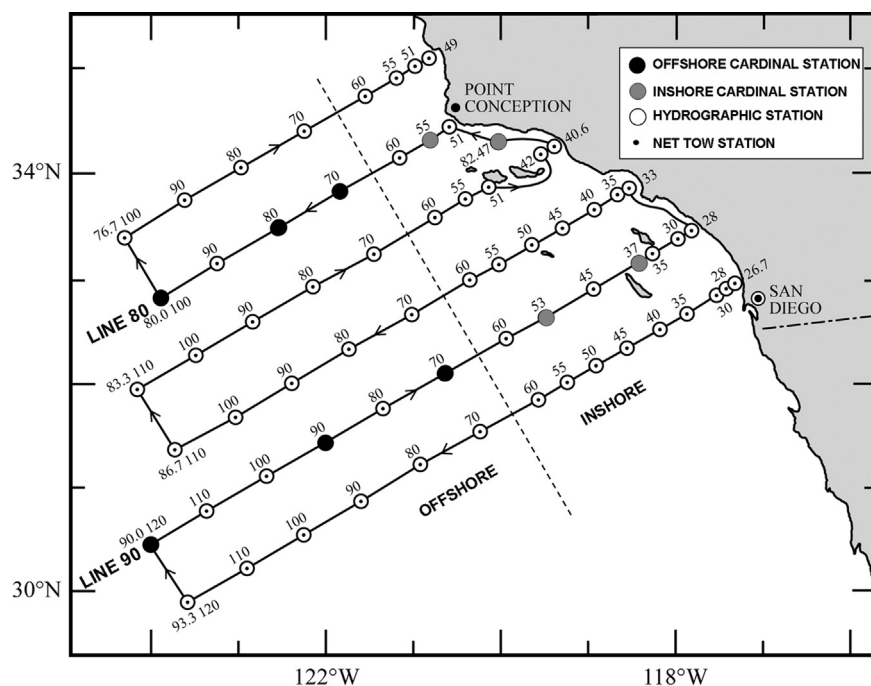


Fig. 1. Map of the CCE region showing the standard cruise tracks and station position of the CalCOFI sampling grid. The ten cardinal stations are depicted with filled in solid circles. Coastal cardinal stations are solid gray, offshore cardinal stations are solid black. Open circles are the other standard CalCOFI hydrographic stations. Map adapted from calcofi.org.

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