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The influence of mesoscale physical structures in the phytoplankton taxonomic composition of the subsurface chlorophyll maximum off western Baja California

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ABSTRACT

The distribution of the subsurface chlorophyll maximum (SCM) layer, its taxonomic phytoplankton composition, and the maximum quantum efficiency of charge separation of PSII (F_v/F_m) was investigated in the west coast off Baja California during October 2003. SCM characteristics were described and related to the hydrographic regime and the mesoscale physical structures present during this period. Seven groups of phytoplankton were detected in the SCM based on chemotaxonomic analysis of pigment fingerprints: diatoms, haptophytes, pelagophytes, prasinophytes, cryptophytes, *Prochlorococcus* and cyanobacteria. The distribution of these groups was heterogeneous and closely related to the circulation patterns characterized by the interaction of subarctic and tropical water. Eddies and meanders were detected in the study area and these structures exerted a direct response in the depth, chlorophyll concentration, and photosynthetic competence of phytoplankton in the SCM. A cyclonic eddy characterized by a high chlorophyll concentration (1.6 mg m^{-3}) and high values of F_v/F_m, (0.52) was detected in the northern zone of the study area. In the central zone, a cyclonic eddy (1.2 mg m^{-3}); and other structure resembling a mode-water eddy was located northwest of Cedros Island. This structure presented the highest chlorophyll concentration (1.8 mg m^{-3}) and high F_v/F_m ($\sim$0.5). Chlorophyll concentration and the photosynthetic performance of the phytoplankton community was lower outside of these eddies. Cyanobacteria dominated the phytoplankton SCM community in these areas.

1. Introduction

In stratified waters there is an upper low-chlorophyll, nutrient-depleted mixed layer followed by a light-limited, nutricline-associated subsurface chlorophyll maximum (SCM, Herbland and Voituriez, 1979; Cullen, 1982). The SCM formation is linked to the availability of nutrients supplied from below for phytoplankton growth, but also this growth is limited by light supplied from above (Huisman et al., 2006).

Phytoplankton species adjust their physiology by modifying their cellular volume, carbon content, and chlorophyll concentration as mechanisms of acclimation in response to the environmental vertical heterogeneity in the water column (Furuya, 1990; Revelante and Gilmartin, 1995). Response to the vertical heterogeneity does not take place only at the cellular level; phytoplankton community differs between the mixed layer and the SCM. For example in oceanic regimes at temperate and tropical latitudes the mixed layer is dominated by small, coccoid picoplankton since they have a competitive advantage over larger cells for nutrient uptake (Chisholm, 1992). In contrast, autotrophic flagellates and diatoms (larger cells) are more abundant in the SCM than in the mixed layer (Eppley et al., 1988; Estrada et al., 1993; Brown et al., 2008).

The SCM community contributes significantly to the primary productivity of the water column, and any change in the taxonomic composition could be associated to changes in photosynthetic performance (Falkowski et al., 1991; Vaillancourt et al., 2003) and carbon fixation rates of the species present in this layer (McGillicuddy et al. 2007). In some regions, the SCM sustains an important fraction of the new production of the water column and represents an important source of carbon for the food web and for its exportation to deeper layers (Pollehne et al., 1993; Forest et al., 2008). Therefore, variation of biomass, species composition and size structure of the phytoplankton community within the SCM could modify the trophic pathways of the pelagic ecosystem (Legendre and Rassoulzadegan, 1996).

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The taxonomic composition in the SCM could change in response to regional and local hydrodynamic factors (Huisman et al., 2006). Temporal or transient physical processes, such as coastal upwelling, meanders, and eddies might have an impact of the taxonomic composition of the SCM (Olaizola et al., 1993; Bibby et al., 2008; Lu et al., 2010). The magnitude in community changes of the SCM will depend on the strength of the perturbation (Brown et al., 2008), and the background nutrient availability (Bibby et al., 2008; Mahaffey et al., 2008).

The west coast of Baja California is a productive marine system that is characterized by the presence of persistent physical structures and a marked seasonality in the pattern of winds and currents that generate a complex oceanographic regime (Espinosa-Carreón et al., 2004; Soto-Mardones et al., 2004; Jerónimo-Moreno and Gómez-Valdés, 2006). The SCM in the zone is a common and semi-permanent feature (Millán-Núñez et al., 1996); however, it is not known the response of this feature to the physical forcing in the zone. Given the importance of the SCM for the function of the pelagic ecosystem; here, we describe Chl *a* biomass and the contribution of different phytoplankton groups to this biomass in the SCM during October 2003 in the west coast of Baja California. These SCM characteristics were related to the oceanic physical structures observed during this period.

2. Methods

2.1. Hydrography

Hydrographic data and water samples were obtained during the IME1003 oceanographic campaign (10–31 October 2003) from the IMECOCAL (*Investigaciones Mexicanas de la Corriente de California*) research program. IMECOCAL sampling grid consist of ninety two stations located along the west coast of the Peninsula of Baja California (Fig. 1) that is a subset of the original CalCOFI sampling network (Gaxiola-Castro et al., 2008). At each station, temperature and salinity, were measured with a Seabird 19plus CTD profiler equipped with an ECO Wetlabs fluorometer (range 0.01–125 μg/l) for chlorophyll *a* (Chl *a*) estimation, and a dissolved oxygen (DO) Seabird 43 sensor for the measurement of dissolved oxygen in the water column.

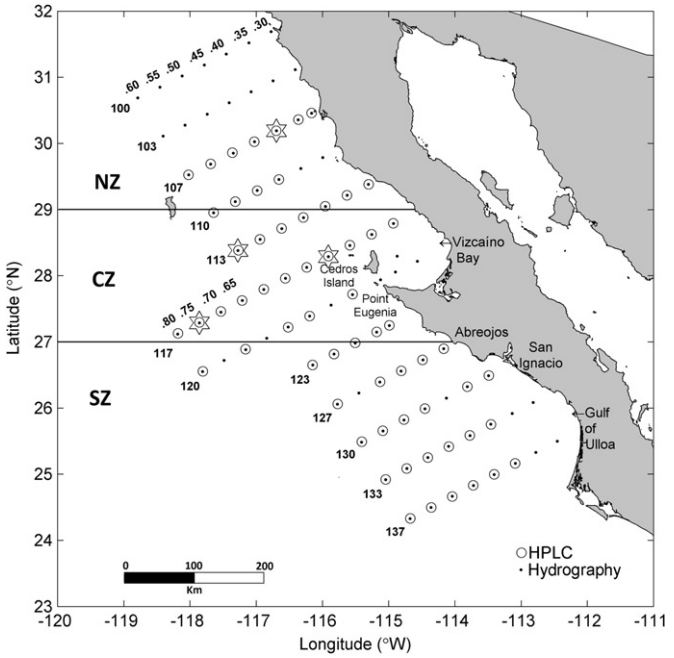

Fig. 1. Map of the IMECOCAL grid. Sampling stations are aligned in 12 transects perpendicular to the coast. Lines 100 and 103 were not sampled for HPLC pigment analysis and F_v/F_m measurements. Lines extending offshore the coast indicate a regional classification: NZ, northern zone; CZ, central zone; SZ, southern zone.

In 62 stations water samples from surface and from the SCM layer were collected for pigment analysis and measurement of the maximum photosystem II quantum efficiency of charge separation (F_v/F_m). The depth of the SCM was determined by the downward profile of the fluorescence signal. Temperature, salinity, oxygen concentration, chlorophyll, pigment concentration and F_v/F_m data were interpolated to a $0.05^\circ \times 0.05^\circ$ ($\sim 5 \times 5$ km) horizontal grid using a six-parameter objective mapping as described by Ochoa et al. (2001; 2003), but adapted to a horizontal domain instead of a vertical section. In each map we used large length scales of 2.5° (~ 250 km) to estimate the mean background, short length scales of $\sim 1.0^\circ$ (100 km) to map the anomalies, and signals-to-noise ratios of 0.1 for both scales. These scales are consistent with the optimum correlation scales reported by Jerónimo-Moreno and Gómez-Valdés (2005, 2006).

2.2. Photosynthetic pigments and taxonomic phytoplankton groups

Pigment quantification was done with the HPLC protocol of Van Heukelem and Thomas (2001) with modifications described in Almazán-Becerril and García-Mendoza (2008). Phytoplankton cells were filtered from 1 L water samples through 25 mm diameter GF/F filters. Filters were stored in liquid nitrogen until its analysis. Extraction of the pigments was done by mechanical disruption (Bead Beater, Biospec Inc.) of the filters with 0.5 mm diameter zirconia/glass beads in 1.5 mL pre-cooled 100% acetone. The homogenate was left for at least 2 h at –20°C in darkness. Cleaning of the samples was done by two centrifugation steps (15,000 $g \times 5$ min, 4 °C). The HPLC instrument was a Shimadzu AV−10 series equipped with a Zorbax Eclipse XDB-C8 reverse phase column (150 mm × 4.6 mm internal diameter, 3.5 − μm size particles). The absorption UV–vis detector (SPD 10AV) was set up at 436 nm. This protocol achieves baseline separation of Chl *a* and divinyl chlorophyll *a* (DVChl *a*), and was calibrated with 16 pigment standards (DHI Inc., Denmark): Chl c_1, peridinin (Per), 19'-butanyloxyfucoxanthin (19BF), 19'-hexanyloxyfucoxanthin (19HF), fucoxanthin (Fuc), neoxanthin (Neo), violaxanthin (Vio), Prasinoxanthin (Pras), diadinoxanthin (DDX), alloxanthin (Allo), zeaxanthin (Zea), lutein (Lut), Chl *b*, DVChl *a*, Chl *a* and *β*-carotene. The pigments were only identified by their retention time and the concentration was calculated by the area of peaks. Control of the equipment and peak area calculation was performed with a Shimadzu EZChrom Chromatography Data System (Shimadzu Scientific Instruments Inc., Columbia, MD, USA). Standard purity determination and the calibration protocol were as in Wright and Mantoura (1997). The relative contribution of different phytoplankton groups to total chlorophyll concentration (Chl *a* + DVChl *a* = TChl *a*), was estimated using the CHEMTAX program (Mackey et al., 1996).

The quality and validity of the estimated contribution of phytoplankton groups to TChl *a* derived from CHEMTAX analysis depends on adequate selection of the initial pigment to Chl *a* ratios (pigment:Chl *a*), on the number of taxa analyzed, and the consistency of the pigment data matrix (Mackey et al., 1996; Higgins et al., 2011). Pigments to Chl *a* ratios are not constant for each phytoplankton group since they depend on the photoacclimation characteristics of microalgae in response to environmental conditions (Goericke and Montoya, 1998). Low-light (LL) acclimated cells will have different pigment ratios than high-light (HL) acclimated organisms (Goericke and Montoya, 1998). A cluster analysis (Euclidian distance, simple linkage) was performed to the pigment data matrix to detect groups based in the