Deep-Sea Research I 55 (2008) 1118–1130

Contents lists available at ScienceDirect

Deep-Sea Research I

journal homepage: www.elsevier.com/locate/dsri

Alkenone abundance and its relationship to the coccolithophore assemblage in Gulf of California surface waters

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ARTICLE INFO

Article history:
Received 28 November 2007
Received in revised form
9 April 2008
Accepted 29 April 2008
Available online 4 May 2008

Keywords:
Coccolithophores
Emiliania huxleyi
Gephyrocapsa oceanica
Alkenones
19′-hexanoyloxyfucoxanthin
Haptophytes
Gulf of California

ABSTRACT

Profiles of alkenone concentration, the abundance of the calcified alkenone-producing species *Emiliania huxleyi* and *Gephyrocapsa oceanica* as well as nutrient and phytoplankton pigment concentrations were measured through the euphotic zone in surface waters of the Gulf of California during cruises in two different summers (2004, 2005) and one winter (2005). As determined using a biomarker and pigment inventory approach, *E. huxleyi* and *G. oceanica*, always the most abundant coccolithophore species at all sampling sites and seasons, represented only a minor fraction of total haptophytes which themselves constituted only a minor fraction of the total phytoplankton community. In winter, alkenone concentration was highest at the surface and displayed relatively uniform values with depth throughout the nutrient-replete euphotic zone. In summer, it display a subsurface peak in nitrate-depleted waters situated just above the nitracline and the deep chlorophyll maximum layer (DCML), a feature found to be well-developed at most sites. Maximum biomarker abundance was comparable in the two seasons, although the putative alkenone-producing coccolithophore species were more abundant in winter than in summer. Estimates of cellular alkenone content for the combined abundance of *E. huxleyi* and *G. oceanica* at each sampling depth showed that cells residing in the nitrate-depleted upper euphotic zone in summer were typically more enriched than those residing in nutrient-replete waters found deeper in the euphotic zone or throughout the euphotic zone in winter. The former estimates were very similar to values documented in laboratory cultures of *E. huxleyi* harvested in a nutrient-depleted stationary growth phase and the latter to those harvested in an exponential growth phase, under the influence of incipient light limitation. Overall, our findings imply that calcifying forms of *E. huxleyi* and *G. oceanica* can account for the measured alkenone concentration at all sites and sampling times. Although the life history of these organisms is known to include non-calcifying stages, it is unnecessary to invoke such an explanation as the cause for the elevated alkenone content of cells from nutrient-depleted surface waters in summer.

1. Introduction

Oceanographic conditions in the Gulf of California (GoCAL) show characteristic seasonal contrasts. Strong, dry northerly winds in winter result in significant upwelling, focused primarily in the eastern gulf. Weak,

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doi:10.1016/j.dsr.2008.04.007

humid, southeasterly winds in summer yield far less intense, more episodic upwelling focused along the western side of the gulf (Roden, 1964) and stable, strongly stratified water column conditions throughout the central GoCAL basin (see discussion in White et al., 2007). This physical forcing of the system also leads to very large seasonal changes in sea-surface temperature (SST), from ~15 °C in winter to ⩾30 °C in summer. In fact, surface waters in winter are so well mixed that the complete euphotic zone (⩽50 m) is essentially isothermal (e.g. Ziveri and Thunell, 2000). In contrast, surface waters in summer are highly stratified thermally with a pronounced deep chlorophyll maximum layer (DCML) often developed at 25–30 m or deeper depending upon location (e.g., Goñi et al., 2001). The DCML lies within the dimly lit euphotic zone but below the depth represented by satellite-derived ocean color data (White et al., 2007). Ocean color shows large seasonal contrast, with highest detected chlorophyll concentration in winter (⩾2 mg m^{-3}) and lowest in summer (~0.25 mg m^{-3}) (see Fig. 3 in Ziveri and Thunell, 2000), reflecting a putative higher net primary production in surface waters in winter than in summer (e.g., Kahru et al., 2004).

Biogenic fluxes measured ~500 m below the sea surface in multiyear (1989–1996) sediment-trap time series from Guaymas Basin in the central GoCAL provide a record of export production from the euphotic zone (Thunell, 1998). Opal flux, primarily diatom-derived with minor contribution from silicoflagellates (Thunell et al., 1996), peaked in the late fall to early spring. In contrast, opal flux was lowest in summer while calcium carbonate flux, derived from combined foraminiferal and coccolithophore sources, was highest in the summer to early fall period. The record from a portion of this time series (July 1990–December 1992) showed that the coccolithophore export is dominated by two species, *Emiliania huxleyi* and *Geophyrocapsa oceanica*, which alternate on a seasonal and interannual basis (Ziveri and Thunell, 2000). Surprisingly, the time series record for organic carbon flux throughout the long, monthly resolved data set of Thunell (1998) showed no clear seasonal trend. This lack of seasonality implies that ecological processes affecting sedimentation in summer are as efficient in controlling organic matter export from the euphotic zone as those in winter. The ballasting effect of small carbonate particles (i.e., coccoliths) on sinking organic carbon (Ziveri et al., 2007) may provide some explanation for the apparent enhanced export efficiency for organic matter in summer.

Long-chain (C_{37-39}), di- and tri-unsaturated alkenones are produced by a limited suite of haptophytes and are believed to serve in the open ocean as biomarkers for two renowned coccolithophores, *E. huxley*i and *G. oceanica* (e.g., Conte et al., 1998; Volkman et al., 1995). Stratigraphic records for these biomarkers in sediments are acquired most notably for reconstructing changes in SST (Brassell et al., 1986; Muller et al., 1998) but also, in some cases, for reconstructing coccolithophore paleoproductivity (Schneider et al., 1996; Schulte et al., 1999; Villaneuva zet al., 1998). To date, comparison of quantitative results for alkenones and alkenone-producing haptophytes in the field has rarely been done. In particular, information is lacking on the amount of alkenones produced per cell by the coccolithophore community under different oceanographic conditions, on the depth range and seasonality of their production within the euphotic zone and on the mechanisms regulating their export to the seafloor. Knowledge gained by illuminating such details would almost certainly advance use of these biomarkers as paleoceanographic proxies.

Goñi et al. (2001) examined alkenone export flux in Guaymas Basin using a two-year (January 1996–October 1997) portion of the same sediment-trap time series examined by Thunell (1998) and Ziveri and Thunell (2000). Measured alkenone flux displayed a temporal pattern roughly paralleling that for total calcium carbonate (CC) (Goñi et al., 2001), with maximum values occurring in late spring to fall (May–June to November) and minimum values in winter. Although a correlation between alkenone and CC flux might be expected, it is likely not due to simple, direct cause-effect. In fact, CC captured in sediment traps like those employed by Goñi et al. (2001) can derive from more than just coccolithophores. Especially in the larger fraction, biogenic carbonate particles include a significant contribution from foraminiferal and pteropod sources (see Fig. 13 in Ziveri and Thunell, 2000).

No detailed information exists on the seasonal distribution of alkenone standing stock within the water column of the GoCAL, particularly in context with the distribution of *E. huxleyi* and *G. oceanica*. Consequently, we gathered such information on two summer cruises (2004, 2005) and one winter cruise (2005). Through analysis of a variety of chemical and ecological properties, results from our fieldwork show that: (1) *E. huxleyi* and *G. oceanica* are the most important contributors to the coccolithophore community year round in surface waters of the GoCAL but make up only a small fraction of the overall phytoplankton or haptophyte community; (2) the standing stock of these species in surface waters does not differ dramatically between summer and winter, although depth distributions in the euphotic zone are fundamentally dissimilar in these two seasons; (3) coccolith-bearing forms of *E. huxleyi* and subordinate *G. oceanica* are the dominant alkenone-producing haptophyte species year round in GoCAL surface waters; and (4) as a consequence of nutrient stress on the physiology of these organisms, alkenone-producing cells residing in nitrate-depleted surface waters of the GoCAL in summer contain much higher alkenone content than those residing in low-light, nutrient-replete deeper waters of the euphotic zone in summer or throughout the euphotic zone in winter.

2. Materials and methods

2.1. Cruises

Three cruises were conducted in the GoCAL aboard the *R/V* New Horizon: GoCAL1 (July–August 2004), GoCAL2 (February 2005) and GoCAL3 (July–August 2005). On all three cruises, one site was always sampled (Guaymas Basin, Station 2–27.5°N, 111.3°E). On the last summer cruise, three additional sites were sampled (Guaymas