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Seasonal production of organic-walled dinoflagellate cysts in an upwelling system: A sediment trap study from the Santa Barbara Basin, California

Manuel Bringué [a,*], Vera Pospelova [a], Dorothy Pak [b]

[a] School of Earth and Ocean Sciences, University of Victoria, PO Box 1700 STN CSC, Victoria, British Columbia, V8W 2Y2, Canada
[b] Marine Science Institute, University of California at Santa Barbara, Santa Barbara, CA 93106, USA

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ABSTRACT

Seasonal variations in dinoflagellate cyst fluxes and assemblage composition were investigated for the first time on the west coast of the United States of America. We analyzed the palynological content of an ~two year-long (May 1995 to March 1997) fortnightly sediment trap time series from the Santa Barbara Basin (SBB, off Southern California), a region characterized by seasonal upwelling and high levels of primary productivity. A total of 47 dinoflagellate cyst taxa were identified in the trap samples, with assemblages dominated by cysts produced by heterotrophic taxa. Multivariate analyses support that dinoflagellate cyst fluxes and assemblages are reliable indicators of primary productivity, and reflect sea surface temperature (SST) variations associated with upwelling in the SBB. In particular, *Brigantedinium* spp. are associated with active upwelling intervals (fluxes up to 127,430 cysts m^{-2} day^{-1} and up to 86.6% of the assemblage), when SST is lower, stratification is weaker and diatom production is maximal. Conversely, *Lingulodinium machaerophorum* indicates relaxed upwelling conditions (up to 9640 cysts m^{-2} day^{-1} and 29.9% of the assemblage) characterized by higher SST, stronger stratification and reduced primary productivity. *Selenopemphix undulata* is associated with colder SST in the region, whereas cyst type A abundances increase with higher SST. Thecae of potentially toxic dinoflagellates are also documented, such as *Lingulodinium polyedrum* and *Prorocentrum micans*, which are mainly recorded under conditions of higher SST and strong stratification, and *Dinophysis* spp. with higher fluxes between June and September of both 1995 and 1996.

1. Introduction

Dinoflagellates are one of the major phytoplankton groups, found in most aquatic environments, where they often account for substantial amounts of the planktonic biomass (e.g., Taylor, 1987; Dale, 2001). Over the past few decades, dinoflagellates have aroused considerable attention primarily due to their contribution to Harmful Algal Blooms (HAB) and their potential to serve as paleoenvironmental indicators (e.g., Hallegraeff, 1993; Dale, 1996). About half of them are autotrophic and as such, they directly contribute to primary productivity (Dale, 1996; Jacobson and Anderson, 1996). The other half are heterotrophs and feed mainly on diatoms and small flagellates, though mixotrophy (i.e., using both ways of feeding) is widespread among dinoflagellates (Jacobson and Anderson, 1986, 1996; Gaines and Elbrächter, 1987; Stoecker, 1999). Most dinoflagellates thrive in the euphotic zone since autotrophic taxa depend on light availability and heterotrophic taxa depend on the availability of their prey (e.g., Jacobson and Anderson, 1996). They use their two flagella to migrate and maintain their optimal position in the water column (Dale, 1996). However, approximately 13 to 16% of living dinoflagellates are meroplanktonic in that their life cycle includes a non-motile, resting cyst stage (e.g., Pfiester and Anderson, 1987; Taylor, 1987; Head, 1996). Unlike motile cells, the wall of most dinoflagellate cysts is made of organic polymers highly resistant to physical, chemical and biological degradations (e.g., Versteegh and Blokker, 2004) and are thus very well preserved in the sediments, whereas other microfossils of planktonic organisms such as diatoms, foraminifers and coccolithophorids are subject to dissolution due to the mineral composition of their cell coverings (e.g., de Vernal et al., 2001).

The distribution of dinoflagellate cysts in the sediments is determined primarily by the ecology of dinoflagellates, and can be influenced by transport processes such as water currents and sediment remobilization (e.g., Zonneveld et al., in press). In the northeastern (NE) Pacific, several studies have investigated the relationship between individual dinoflagellate cyst taxa in surface sediments and environmental parameters (Kumar and Patterson, 2002; Morquecho and Lechuga-Deveze, 2003; Radi and de Vernal, 2004; Radi et al., 2007; Pospelova et al., 2008; Vasquez-Bedoya et al., 2008; Krepakevich and Pospelova, 2010; Limoges et al., 2010; Bonnet et al., 2012). The most determinant factors controlling cyst distribution in the NE Pacific are considered primary productivity, sea-surface temperature (SST) and salinity (SSS) (e.g., Radi and de Vernal, 2004;

* Corresponding author.
E-mail address: mbringue@uvic.ca (M. Bringué).

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Radi et al., 2007; Pospelova et al., 2008). From Vancouver Island (Canada) to the tip of Baja California (Mexico), the west coast of North America lies under the influence of the California Current System, one of the most biologically productive areas of the world's ocean (Thomson, 1981; Antoine et al., 1996; Hickey, 1998). As an eastern boundary current, the California Current System is influenced by large-scale wind forcing that results from the relative positions and strength of the Aleutian Low and the North Pacific High atmospheric pressure systems (Thomson, 1981; Ware and Thomson, 2000; Bograd et al., 2002). Particularly in spring and summer, the North Pacific High strengthens, resulting in stronger northerly winds along the coast that increase Ekman transport of surface waters offshore and foster the upwelling of colder, nutrient-rich waters (e.g., Tabata, 1975; Thomson, 1981). In turn, enhanced primary productivity in areas influenced by upwelling supports vast populations of marine wildlife, including zooplankton, fish, seabirds and mammals (Ware and Thomson, 2005; Thompson et al., 2012).

In this study, we focus on documenting the seasonal production of dinoflagellate cysts in the Santa Barbara Basin (SBB), located at the northern end of the Southern California Bight, in relation to major environmental parameters. In particular, the SBB holds exceptional potential to document environmental change due to its location in the confluent region between cool waters upwelled north of the SBB and warmer waters of the Southern California Bight. Furthermore, the lack of oxygen in the SBB bottom waters and sediments fosters excellent preservation of dinoflagellate cysts in laminated sediments that serve as an excellent repository for high resolution records of past climate change (e.g., Emery, 1960; Hülsemann and Emery, 1961; Behl and Kennett, 1996; Field et al., 2006; Pospelova et al., 2006; Fisler and Hendy, 2008; Barron et al., 2010).

The seasonality of the production of each dinoflagellate cyst taxon can be investigated using sediment trap time-series (e.g., Montresor et al., 1998; Harland and Pudsey, 1999; Fujii and Matsuoka, 2006; Pospelova et al., 2010; Zonneveld et al., 2010; Price and Pospelova, 2011; and references therein). Indeed, in the vast majority of marine settings, surface sediment is deposited over several years and is subject to bioturbation. Surface sediment samples may thus reflect multiyear averages, rather than seasonal variations in dinoflagellate cyst production. Alternatively, sampling of microplankton from the upper water column allows direct comparison between motile dinoflagellates and environmental parameters. However, this technique seldom samples the entire photic zone and is temporally discontinuous (e.g., Dale, 1996, 2001). Particle-intercepting traps provide a means for continuous sampling of all sinking material over the entire deployment, allowing the determination of ecological and environmental conditions under which dinoflagellate cysts are produced. A few sediment trap studies using dinoflagellate cysts have been conducted in upwelling systems from the Arabian Sea (Zonneveld and Brummer, 2000), off the northwest African coast (Susek et al., 2005; Zonneveld et al., 2010) and in the Benguela upwelling system (Pitcher and Joyce, 2009). However, such studies are extremely rare in the North Pacific, in both open oceanic environments (Dale, 1992) and coastal settings (Ishikawa and Taniguchi, 1996; Morquecho and Lechuga-Deveze, 2004; Fujii and Matsuoka, 2006; Wang et al., 2007; Pospelova et al., 2010; Price and Pospelova, 2011). Here we report an ~two year-long fortnightly time-series of dinoflagellate cyst production in sediment trap samples collected in the SBB. This constitutes the first such effort carried out on the west coast of the United States of America.

Our objectives are to document seasonal variations in the production of dinoflagellate cyst taxa (including potentially toxic species) in the SBB, to identify environmental parameters controlling changes in dinoflagellate cyst production, and to compare the trap and surface sediment assemblages from the depositional center of the SBB. This will establish a basis for paleoenvironmental interpretations of laminated sedimentary sequences from the SBB by improving our knowledge of the specific ecology of dinoflagellate cysts in this area characterized by seasonal upwelling.

1.1. Environmental settings

The Santa Barbara Basin (SBB) is located off the coast of Southern California, in a zonally oriented channel bound to the south by the Northern Channel Islands (Fig. 1). It is 100 km long, 40 km wide and the central basin has a maximum depth of 590 m. Riverine input to the SBB is limited, the largest contributor being the Santa Clara River, with a drainage basin of approximately 4100 km^2 (Fan, 1976).

Water circulation in the SBB is restricted to the west by a sill (~475 m depth) between Point Conception and San Miguel Island, and the Anacapa Sill (230 m) to the east (Emery, 1960; Sholkovitz and Soutar, 1975). Oxygen depletion below sill depth inhibits bioturbation by macrobenthos (Emery and Hülsemann, 1961) and fosters the preservation of laminated sediments, with accumulation rates between 1 and 5 mm year^{-1} (Soutar and Crill, 1977; Schimmelmann et al., 1990; Barron et al., 2012).

The SBB is embedded within the California Current System (CCS), which includes the California Current, the Davidson Current and the northward California Undercurrent (Fig. 1B; Tabata, 1975; Hickey, 1998; Hickey and Banas, 2003). The California Current is an eastern boundary current that carries relatively cold, nutrient- and oxygen-rich subarctic waters southward off the Pacific coast of the USA, from the shelf break to a distance of about 1000 km from the coast (Hickey, 1998). South of Point Conception, a portion of the California Current turns shoreward and then poleward to form the Southern California Countercurrent or Southern California Eddy (Hickey, 1998).

The California Undercurrent originates in the eastern equatorial Pacific and flows northward over the continental slope as a relatively narrow (10–40 km), nearly continuous jet-like feature (Hickey, 1998; Hickey and Banas, 2003). It transports warmer, saline, phosphate-rich, and oxygen-poor water from the Baja Peninsula to the coast of British Columbia (Tabata, 1975; Reed and Halpern, 1976; Mysak, 1977; Hickey, 1998). During fall and winter, the Davidson Current flows northward over the continental shelf and slope from Point Conception to Vancouver Island, as an ~100 km-wide flow, strongest at the sea surface (Tabata, 1975; Hickey, 1998; Hickey and Banas, 2003).

Near-surface currents in the SBB are the result of interactions of CCS-scale flow and a cyclonic circulation of variable intensity within the channel (Fig. 1A; Hendershott and Winant, 1996; Harms and Winant, 1998; Winant et al., 2003). At subtidal frequencies, near-surface circulation in the SBB responds to both wind stress (generally upwelling favorable) and pressure gradients (directed poleward most of the year) along the channel. When the wind stress overwhelms the pressure gradient, the “upwelling” circulation pattern prevails and the mean flow is equatorward (Fig. 1C). If the pressure gradient dominates, the mean flow is poleward (“relaxation” pattern, Fig. 1D). When both wind stress and pressure gradient are strong, circulation is cyclonic in the SBB. In spring and summer, upwelling conditions prevail and the equatorward flow brings freshly upwelled water from north of Point Conception into the basin. In winter, wind stress and pressure gradient are commonly in the same direction and the flow is either equator- or poleward (Hendershott and Winant, 1996; Harms and Winant, 1998; Winant et al., 2003).

On interannual timescales, the El Niño–Southern Oscillation (ENSO) phenomenon is the major mode of climatic variability in the Pacific (e.g., Enfield, 1989). In the SBB, the impacts of strong El Niño events usually include positive SST anomalies, increased winter precipitations, damping of the upwelling and reduced primary productivity (e.g., Lange et al., 1987; Shipe et al., 2002). The studied period corresponds to an interval preceding the very strong El Niño event of 1997–98 (Passow et al., 2001; Pak and Kennett, 2002; Shipe et al., 2002; Pak et al., 2004). Since El Niño indices are very slightly