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

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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 surface sea temperature (SST) variations associated with upwelling in the SBB. In particular, Brigi ntedinium 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 machae rophorum 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 Procorcentrum 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.

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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 palaeoenvironmental 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 dinoflagel lates 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; Morgancho 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;
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; Morquero and Lefugua-Deveez, 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 interpretation 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 km² (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), near continuously 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
negative with values of Nino3.4 index between $-0.847$ and $0.388$ (Trenberth and Stepaniak, 2001) and Multivariate El Niño Index between $-0.605$ and $0.481$ (Wolter and Timlin, 1993), we assume that the system was not (or only very mildly) affected by ENSO during the studied period.

2. Material and methods

2.1. Sediment trap deployment and environmental data

We analyzed sediment trap samples collected between May 20th, 1995 and March 13th, 1997, during the UCSB Santa Barbara Mooring Project (Passow et al., 2001; Pak and Kennett, 2002; Shipe et al., 2002; Pak et al., 2004). A Parflux Mark 7 GW-13 cone-shaped baffled sediment trap was deployed in the central portion of the basin (34° 15.33′ N/119° 56.29′ W; Fig. 1) at a depth of 470 m, 50 m above the sea floor. The trap was equipped with a 13-bottle carousel programed to rotate every 14 days (except 5 samples of 6 to 7 days). The trap was nearly continuously operational with some exceptions due to gaps between recovery and redeployment (every 6 months) and two clogged sample cups (Fig. 3), leading to gaps in the time series of up to ~2.5 months. The 500 ml collecting bottles were filled with a brine solution and 4% hexamine buffered formalin as an in situ preservative (Passow et al., 2001; Pak and Kennett, 2002; Shipe et al., 2002; Pak et al., 2004).

We also analyzed one sediment sample from core SBBC 0806-2202, collected in June 2008 at 34° 13.3′ N, 120° 01.7′ W (D. Field, pers. comm.). A chronology of the core (Barron et al., 2012) reveals that the sediment sample analyzed was deposited from 1994 to 1997.

Fortnightly water sampling of the upper 75 m above the mooring site was conducted to determine temperature, salinity and density, as well as chlorophyll a, nutrient concentrations, particulate organic carbon and nitrogen, and lithogenic and biogenic silica. Further environmental data used in this study include insolation and precipitation (Western Regional Climate Center; http://www.wrcc.dri.edu), runoff (U. S. Geological Survey; http://waterdata.usgs.gov/ca/nwis/sw) and wind (National Data Buoy Center; www.ndbc.noaa.gov), measured daily at stations in the vicinity of the mooring site (Fig. 1A). Previously published geochemical data, such as particulate organic carbon and
biogenic silica measured on sediment from the same trap samples, were also used (Shipe et al., 2002; Drs. Uta Passow and Alice Alldredge, pers. comm.).

2.2. Evolution of sea surface conditions during the study period

The strength and duration of upwelling constitute the dominant mode of variability in the SBB surface waters. Conductivity–Temperature–Depth (CTD) data collected fortnightly above the mooring site from May 20th, 1995 to March 13th, 1997 is presented in Fig. 2. Near-surface SST fluctuates between ~9 and 19 °C, with the lowest temperatures recorded from mid-January through late-July/ mid-August. The range in salinity values is rather small (~32.8 to 34.3) with maxima occurring simultaneously with lower SST. From this dataset, and in accordance with previous studies (Passow et al., 2001; Pak and Kennett, 2002; Pak et al., 2004), we define intervals of “active” and “relaxed upwelling” (Fig. 2B) as follows.

Intervals of “active upwelling” (mid-January to late-July/mid-August) are characterized by cooler SST and weaker stratification of the upper water column. CTD data and circulation patterns in the channel suggest that during these periods, freshly upwelled water from north of Point Conception is transported into the basin (e.g., Harms and Winant, 1998). We arbitrarily defined active upwelling phases as periods when the 13 °C isotherm reaches 25 m depth for more than one week.

During intervals of “relaxed upwelling” (approximately from August to mid-January), SST is more variable but generally warmer and stratification is stronger. Shorter, less intense upwelling events might occur during this phase (for instance, in early October 1996; Fig. 2). Surface circulation is dominated by the “relaxation” and “cyclonic” circulation patterns (Hendershot and Winant, 1996; Harms and Winant, 1998; Winant et al., 2003; Brzezinski and Washburn, 2011).

2.3. Palynological preparation

Splits of the sediment trap samples were processed in the Paleoenvironmental/Marine Palynology Laboratory at the University of Victoria. Organic-walled microfossils (also called palynomorphs) such as dinoflagellate cysts, microforaminiferal linings, pollen grains and spores, copepod eggs and tintinnid loricae were extracted using the palynological preparation described by Pospelova et al. (2005). Sediment samples were rinsed three times to remove salt residue, oven dried at 40 °C and weighed with an analytical balance. One calibrated tablet of Lycopodium clavatum was added to each sample in order to estimate cyst fluxes (Stockmarr, 1971; Mertens et al., 2009, 2012a). Samples were treated with room temperature 10% HCl to remove carbonates, rinsed with distilled water, presieved through a 120 μm mesh and retained on a 15 μm mesh to eliminate coarse and fine material. To remove silicates, the samples were exposed to room temperature 48% HF for up to three days, followed by a second 10% HCl treatment to eliminate precipitated fluorosilicates. Samples were then rinsed, gently sonicated for up to 30 s and collected on a 15 μm mesh. One or two drops of the residue were mounted in glycerine jelly between a slide and cover slip. Dinoflagellate cysts and other palynomorphs were identified and counted using a Nikon Eclipse 80i transmitting light microscope at 600× and 1000× magnifications. A minimum of 300 cysts per sample were counted, with an average of 346 cysts per sample. All samples and slides are stored at...
The dinoflagellate cyst nomenclature conforms to the paleontological taxonomy system given in Lentin and Williams (1993) and subsequent taxonomic descriptions provided by Lewis et al. (1984), Head (1996), Zonneveld (1997), Rochon et al. (1999), Head et al. (2001), Ellegaard et al. (2003), Matsuoka et al. (2009), Hoppenrath et al. (2010), Ribeiro et al. (2010), Verleye et al. (2011) and Mertens et al. (2012b). Cysts were identified to the species level whenever possible; however, some taxa were grouped together due to morphological similarities. In particular, Brigantedinium spp. include Brigantedinium carioense, Brigantedinium irregular, Brigantedinium simplex and other smooth round brown cysts since archeopyles were not always visible due to unfavorable orientations or folding. Impagidinium aculeatum, Impagidinium patulum and Impagidinium striatum are grouped with Impagidinium spp. as they occurred in very low number and they are usually associated with open oceanic settings. Table 1 provides a taxonomic listing of all dinoflagellate cysts recovered in this study, along with their thecal equivalents and autotrophic or heterotrophic affinity. Bright-field photomicrographs of selected dinoflagellate cysts are presented in Plates I, II and III.

Where cysts did not conform to any published description, cyst types were assigned. Cyst type A has been previously reported by Pospelova et al. (2006), Rady et al. (2007) and Pospelova et al. (2008) and is also illustrated in Pospelova et al. (2010), Krepacevich and Pospelova (2010), as well as in Price and Pospelova (2011). The cyst of Protoperidinium minutum corresponds to the description provided by Ribeiro et al. (2010), although the taxonomy within this group is complex and still under debate (Yamaguchi et al., 2011). Echinidinium cf. delicatum differs from Echinidinium delicatum sensu Zonneveld (1997) in that the processes tend to be slightly longer (up to 5 μm) and less numerous. Cyst type M (Plate II), a specific spiny brown taxon which accounted for 2.2% of the overall cyst assemblages in the trap samples, is reported for the first time. It is spherical with a body diameter of 29.5 μm (range of 24 to 35 μm, over 12 specimens measured). The cyst wall has a smooth to slightly thick, single-layered, non-tabular, acuminate, have a sub-circular base in cross section and taper distally. The processes are evenly distributed, with a very consistent length within each specimen, averaging 7.4 (6–9) μm. Further investigation (especially concerning the type and shape of the archeopyle) will be carried out in the near future to assign cyst type M1 to the proper genus.

A small type named cyst of cf. Biecheleria sp. (Plate III) may correspond to the cyst of Biecheleria baltica Moestrup et al. (2009) (previously Woloszyńska halophila sensu Kremp et al., 2005). This taxon is usually observed with cell content and has a body diameter ranging from 8 to 22 μm. It bears numerous, evenly distributed processes between 0.5 and 2 μm in length. Cyst of cf. Biecheleria sp. has not been included in cyst counts since many specimens were lost through sieving.

Cyst of ?Protoperidinium sp. A (Plate III) is a round brown cyst with an average body diameter of 30 μm (range of 28 to 35 μm over eight specimens measured). The cyst wall is very thin, single-layered, smooth to microgranular and pale brown in color. Our observations suggest that the saphophytic archeopyle is formed by the loss of the 2′, 3′ and 4′ apical paraplates. Cyst of ?Protoperidinium sp. A was not included in the cyst counts and statistical analyses because it is virtually absent from the fossil record in both our surface sediment assemblage (Fig. 4) and a 40 kyr-long sequence analyzed with the same protocol (Ocean Drilling Program [ODP] Hole 893A; Pospelova et al., 2006). It is possible that this taxon is a pellicle cyst (Bravo et al., 2008) and is also illustrated in Pospelova et al. (2010), Krepakevich et al. (2010), Radi et al. (2007) and Pospelova et al. (2006). It is possible that this taxon is a pellicle cyst (Bravo et al., 2008) and is also illustrated in Pospelova et al. (2010), Krepakevich et al. (2010), Radi et al. (2007) and Pospelova et al. (2006). It is possible that this taxon is a pellicle cyst (Bravo et al., 2008) and is also illustrated in Pospelova et al. (2010), Krepakevich et al. (2010), Radi et al. (2007) and Pospelova et al. (2006).
2010) produced by one of the many Protoperidinium species that thrive in the SBB surface waters.

2.5. Statistical analyses

Relationships between individual dinoflagellate cyst taxa and environmental parameters were investigated using multivariate statistical analyses. Detrended Correspondence Analyses (DCA) and Redundancy Analyses (RDA) were performed on dinoflagellate cyst relative abundances, using CANOCO 4.5 for Windows (ter Braak and Šmilauer, 2002). DCA was used first to determine the character of variability in cyst assemblages: if the length of the first gradient is greater than 2 standard deviations, we can assume a unimodal variation; a length smaller than 2 standard deviations indicates a linear variation (e.g., Lepš and Šmilauer, 2003). The length of the first gradient for cyst relative abundances (1.25 sd) indicates a linear variation, providing justification for the further use of Redundancy Analysis. RDA is a direct gradient analysis that summarizes relations between dinoflagellate cyst species and environmental parameters (Lepš and Šmilauer, 2003). Environmental variables were selected to avoid colinearity.
(detected by CANOCO). The significance of each environmental variable was determined using Monte Carlo testing, based on 9999 permutations restricted for a time series data structure. Environmental variables with a P-value less than 0.05 are considered to be significantly related to the cyst data. Statistical significance of the canonical axes was also determined using Monte Carlo tests, both individually and as a whole (Lepš and Šmilauer, 2003). No data transformation was applied; however, taxa that never exceeded 1% of the assemblages were excluded from multivariate analyses (see Table 1).

3. Results

3.1. Main palynomorphs and biogenic silica

Our analysis reveals that the most abundant palynomorphs in the trap samples are dinoflagellate cysts and thecae, pollen grains and spores, ciliates, copepod eggs and microforaminiferal linings (Fig. 3). Fluxes of dinoflagellate cysts averaged 73,700 cysts m\(^{-2}\) day\(^{-1}\) over the sampling period, with peak values up to 232,000 cysts m\(^{-2}\) day\(^{-1}\).
observed in July through September 1996. The ratio of cysts produced by heterotrophic over autotrophic taxa indicates a clear dominance of heterotrophs, especially during intervals of active upwelling when ratios average 59 (Fig. 3). Biogenic silica fluxes to the trap (Passow et al., 2001; Shipe et al., 2002) averaged 9 mmol m$^{-2}$ day$^{-1}$ throughout the time series. In the year 1995, biogenic silica fluxes decreased from ~20 mmol m$^{-2}$ day$^{-1}$ in July to ~3 mmol m$^{-2}$ day$^{-1}$ from October to December. In 1996, biogenic silica fluxes are more variable and three peaks with values >20 mmol m$^{-2}$ day$^{-1}$ are recorded in May, June and September (Fig. 3).

Ciliate fluxes to the trap varied between 24,700 and 179,200 specimens m$^{-2}$ day$^{-1}$, with slightly higher values recorded in July through September 1995 and January 1997 (Fig. 3). Fluxes of copepod eggs averaged 50,900 eggs m$^{-2}$ day$^{-1}$ over the sampling period, with higher values recorded 4 to 8 weeks after the end of the active upwelling interval (up to 272,000 eggs m$^{-2}$ day$^{-1}$ in

Plate III. Bright-field photomicrographs of selected dinoflagellate cysts and one microforaminiferal organic lining from the SBB. 1. Quinquecuspis concreta, UVic 10-37, slide 2, N48/0; dorsal surface. 2. Selenopemphix undulata, UVic 10-46, slide 2, S49/0; optical section. 3. Selenopemphix quanta, UVic 09-78, slide 3, B29/0; dorsal surface. 4. Cyst of Protoperidinium oblongum sensu Wall and Dale (1968; horned cyst type), UVic 10-38, slide 1, R43/4; dorsal view, optical section. 5. Votadinium calvum (= cyst of Protoperidinium oblongum sensu Wall and Dale, 1968; cordate cyst type), UVic 10-30, slide 1, S52/0; optical section. 6. Votadinium spinosum, UVic 09-78, slide 3, Y40/0; optical section. 7. Cyst of ?Protoperidinium sp. A, UVic 10-44, slide 1, O52/0, dorsal surface. 8. Cyst of Biecheleria sp., UVic 10-43, slide 2, R44/0; optical section, orientation uncertain. 9. Microforaminiferal organic lining, UVic 10-33, slide 1.
September 1995). Microforaminiferal lining fluxes were higher in June to September 1995 with peak values at 55,600 linings m$^{-2}$ day$^{-1}$, compared to values fluctuating only slightly around an average of 14,800 linings m$^{-2}$ day$^{-1}$ from October 1995 through March 1997 (Fig. 3). The benthic or planktonic nature of microforaminiferal linings is unknown (e.g., Traverse and Ginsburg, 1966; Stancliffe, 1989). Total fluxes of pollen grains and spores were higher (>50,000 grains m$^{-2}$ day$^{-1}$) from May to August 1995 and from April to July 1996, compared to a mean flux of 30,000 grains m$^{-2}$ day$^{-1}$ throughout the rest of the year (Fig. 3). Pollen and spore assemblages were dominated by non-bisaccate pollen (64.6%), while bisaccate pollen and spores accounted for 32.5% and 2.9%, respectively.

Several dinoflagellate thecae were recovered in the trap samples, including species of Dinophysis (D. acuminata, D. caudata, D. tripos, D. fortii, D. hastata, D. mitra, D. rudgei), Lingulodinium polyedrum, Prorocentrum micans, Prorocentrum lima, as well as species of Protoperidinium (P. brevipes, P. conicum, P. leonis, P. pellucidum, P. cf. oceanicum and P. cf. subsphaericum) and unidentified Diplopsalidaceae. Fluxes of thecae of potentially toxic taxa are presented in Fig. 3. Most thecae of L. polyedrum were recovered during conditions of relaxed upwelling, especially in...
September and October 1995 when fluxes reached 17,500 thecae m\(^{-2}\) day\(^{-1}\). The record of P. micans shows one pronounced, ~1-month-long occurrence per year, in September 1995 and September 1996, with fluxes up to 113,600 thecae m\(^{-2}\) day\(^{-1}\). Species of *Dinophysis* together were recorded in almost all samples, with higher fluxes (>5000 thecae m\(^{-2}\) day\(^{-1}\)) between June and September of both 1995 and 1996 (see Section 5).

3.2. Dinoflagellate cyst fluxes and assemblages

A total of 47 dinoflagellate cyst taxa were identified in the trap samples, including 32 taxa produced by heterotrophic dinoflagellates and 14 of autotrophic affinity (Table 1, Plates I, II and III). The number of cyst taxa per sample varied between 13 and 27, with an average of 20. Twelve taxa never exceeded 1% of the assemblages and are considered to be rare. Throughout the duration of the trap deployment, the total dinoflagellate cyst assemblage (Fig. 4) was dominated by *Brigantedinium* spp. (68.3%), accompanied by species of *Echinidinium* (15.2%) and *Lingulodinium machaerophorum* (4.3%). Within the genus *Echinidinium*, the dominant taxa were *E. cf. delicatum* (4.6%), *E. delicatum* (3.4%) and *Echinidinium acauleatum* (3.4%). Cyst type M1, *Selenopemphix quanta*, cyst type A and the cysts of *Polykrikos schwartzii* represented 2.4, 2.3, 2.2 and 1.2% of the total assemblage, respectively. Any other cyst taxon accounted for less than 1% of the total assemblage.

Fluxes and relative abundances of the major dinoflagellate cyst taxa during the trap deployment are presented in Fig. 5. Overall, the cyst assemblages are dominated by cysts produced by heterotrophic dinoflagellates (mainly *Brigantedinium* spp.), but autotrophic taxa such as *L. machaerophorum*, *Spiniferites ramosus* and *Spiniferites* spp. become more abundant under conditions of higher SST and/or relaxed upwelling.

Fluxes of *Brigantedinium* spp. vary from 14,350 to 127,430 cysts m\(^{-2}\) day\(^{-1}\), with an average of 46,050 cysts m\(^{-2}\) day\(^{-1}\). In general, fluxes of *Brigantedinium* spp. increase during active upwelling, and decrease during intervals of relaxed upwelling (Fig. 5). In terms of relative abundances, *Brigantedinium* spp. constitute on average 70.8% of the assemblages (and up to 86.6%) under active upwelling conditions and 57.1% under relaxed upwelling. *Selenopemphix undulata*, *Votadinium calvum*, *Selenopemphix nephrorides*, the cyst of *Archaeproperidinium saanichii* and cyst of *Protoperidinium americanum* also occur predominantly under active upwelling conditions. Conversely, *L. machaerophorum*, cyst type A, *E. cf. delicatum*, *S. ramosus*, *Spiniferites* spp. and the cysts of *P. schwartzii* show higher cyst fluxes and relative abundances during upwelling relaxation. Almost all taxa produced by autotrophic dinoflagellates are recorded with higher cyst fluxes and relative abundances during intervals of higher SST and relaxed upwelling, with the exception of *Impagidinium* spp. Since only a few specimens of *Impagidinium* spp. were recovered, we cannot infer any specific environmental conditions for these taxa. In particular, *L. machaerophorum* constitutes between ~10 and 30% of the assemblages between October and December 1995, when conditions of relaxed upwelling prevailed and SST was higher. *Votadinium spinosum*, the cyst of *P. minutum* sensu *Ribeiro et al.* (2010), *Quinquecuspis concreta*, *Dubridinium* spp., *Echinidinium zonellae* and *Echinidinium* spp. are present in almost all samples and show less pronounced variations. However, fluxes of *S. quanta*, *E. acauleatum* and *E. delicatum* were slightly higher after July 1996 compared to 1995, while most *Echinidinium granulatum* were recorded in 1995. For most cyst taxa, the highest proportion of cysts with cell content corresponds to the larger fluxes of the record (Fig. 5).

3.3. Multivariate analyses

The RDA performed on cyst relative abundances results in an ordination model that is statistically significant as a whole (*P* = 0.037; Fig. 6). The ordination of species, samples and environmental variables based on the first two axes explains 42.1% of the variance in the species data and 91.7% of the variance in the fitted species data. The first ordination axis, explaining 37.0% of the variance in the species data, is significantly and positively correlated with SST. The C/N ratio of the organic matter in the trap samples and precipitation over the SBB are positively (although not significantly) correlated with axis 1. SSS, biogenic silica, insolation and runoff of the Santa Clara River are negatively correlated with axis 1. Monte Carlo permutation tests indicate that the first axis is the only statistically significant axis (*P* = 0.037), whereas the second axis explains only 5.1%
of the variance, with a P-value of 0.577. Therefore, only gradients along the first ordination axis can be considered in the interpretation of species–environment relationships.

Ordination of “species” indicates that dinoflagellate cyst taxa with the lowest scores on RDA axis 1 are Brigantedinium spp. and S. undulata, and to a lesser extent V. calvum, S. nephroides and the cysts of A. saanichi (Fig. 6A). On the positive side of axis 1, L. machaerophorum has the highest score, followed by cyst type A, E. cf. delicatum, S. ramosus and Spiniferites spp. Ordination of sample scores (Fig. 6B) shows that almost all samples collected during intervals of active upwelling, when SST is lower, are located on the negative side of axis 1, whereas scores of samples corresponding to higher SST and relaxed upwelling conditions are positive. A separate RDA run on cyst fluxes indicated very similar results (not presented).

4. Discussion

This study documents dinoflagellate cyst production and seasonality in relationship with major environmental parameters in the SBB, on the west coast of the United States. It sheds light on the specific ecology of cyst-producing dinoflagellates, including potentially toxic taxa, providing detailed insights on their paleoenvironmental significance. It also documents seasonal trends in dinoflagellate cyst fluxes, as well as other palynomorphs including ciliates, copepod eggs, microforaminiferal linings and pollen and spores.

Most dinoflagellate cyst taxa identified in the sediment trap samples have been reported in previous studies from the SBB by Prauss (2002) and Pospelova et al. (2006). Prauss (2002) examined a sediment core spanning from 1883 to 1992 AD in which each sample
Echinidinium statistics. Lambda (\(\Lambda\)) is the variation explained by each environmental variable, considered independently (marginal effect), or considered after all variables already incorporated in the model (conditional effect). Statistically significant (P-value < 0.05) are highlighted in bold.

<table>
<thead>
<tr>
<th>Variable</th>
<th>(\Lambda)</th>
<th>Species-environment corr.</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>SST</td>
<td>0.32</td>
<td>0.780</td>
<td>0.007</td>
</tr>
<tr>
<td>bioSi</td>
<td>0.15</td>
<td>0.777</td>
<td>0.037</td>
</tr>
<tr>
<td>Insolation</td>
<td>0.08</td>
<td>0.514</td>
<td>0.033</td>
</tr>
<tr>
<td>C/N ratio</td>
<td>0.07</td>
<td>0.173</td>
<td>0.023</td>
</tr>
<tr>
<td>Runoff</td>
<td>0.02</td>
<td>0.722</td>
<td>0.033</td>
</tr>
</tbody>
</table>

Marginal effects

<table>
<thead>
<tr>
<th>Variable</th>
<th>(\Delta)</th>
<th>RDA axes summary</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>SST</td>
<td>0.32</td>
<td>0.051</td>
<td>1.000</td>
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<tr>
<td>bioSi</td>
<td>0.15</td>
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<td>Insolation</td>
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<tr>
<td>C/N ratio</td>
<td>0.07</td>
<td>0.222</td>
<td>0.033</td>
</tr>
<tr>
<td>Runoff</td>
<td>0.02</td>
<td>0.722</td>
<td>0.033</td>
</tr>
</tbody>
</table>

C. Marginal effects, conditional effects and summary of axes statistics. Lambda (\(\Lambda\)) is the variation explained by each environmental variable, considered independently (marginal effect), or considered after all variables already incorporated in the model (conditional effect). Statistically significant parameters (P-value < 0.05) are highlighted in bold.

Fig. 6. Redundancy Analysis performed on dinoflagellate cyst relative abundances. SST is the only statistically significant environmental variable (P-value < 0.05) and is shown as a solid arrow. Autotrophic taxa are plotted as empty circles and heterotrophic taxa as filled circles. SST: sea surface temperature; SSS: sea surface salinity; bioSi: biogenic silica. A. Ordination diagram showing “species” scores and environmental variables. B. Ordination of samples. C. Marginal effects, conditional effects and summary of axes statistics. Lambda (\(\Lambda\)) is the variation explained by each environmental variable, considered independently (marginal effect), or considered after all variables already incorporated in the model (conditional effect). Statistically significant parameters (P-value < 0.05) are highlighted in bold.

represents on average 3.7 years of sedimentation. Pospelova et al. (2006) analyzed the dinoflagellate cyst content from ODP Hole 893A for the past ~40 kyr at millennial-scale resolution. These studies document a number of taxa that were not encountered during the ~2 years of sediment trap deployment, namely Impagidinium pallidum, Impagidinium paradoxum, Impagidinium sphaericum, Nematosphaeropsis labyrinthus, Spiniferites bulbodeus, Spiniferites membranaceus, Tectatodiniumpellitum, Pyxidinopsis reticulata, cyst of Polykrikos kofacci, cyst of Gymnodinium spp., Islandinium brevispinosum, Lejeune cysta oliva and Trinovantidiniumapplanatum. In the present study, several cyst taxa are reported for the first time in the SBB, including I. patulum and Spiniferites pachydermus, as well as previously grouped or not identified round brown spiny cysts (Radi et al., 2013). These are E. delicatum, E. cf. delicatum, E. zonnewieidae, the cyst of P. minutum sensu Ribeiro et al. (2010), cyst of A. saanichi and cyst type M1.

4.1. Indicators of primary productivity and upwelling

The California Current System is an eastern boundary current associated with intense coastal upwelling and high levels of primary productivity with carbon export rates commonly over 300 g C m\(^{-2}\) year\(^{-1}\) (Antoine et al., 1996; Pospelova et al., 2008). In the SBB, Shipe and Brzezinski (2003) and Brzezinski and Washburn (2011) estimated seasonal primary production rates between 0.72 and 3.3 g C m\(^{-2}\) day\(^{-1}\) using the \(^{14}C\) and \(^{14}C\) tracer techniques, with rates almost 3 times higher in spring than during the rest of the year. Furthermore, Brzezinski and Washburn (2011) state that the first mode of an empirical orthogonal function of primary productivity at 5 m in the SBB accounts for 64% of the variance and describes seasonal productivity changes driven by coastal upwelling. Here we show that dinoflagellate cysts reflect the seasonal productivity signal (Fig. 7) and thus can be used as indicators of past upwelling history in the SBB.

Heterotrophic dinoflagellates are known to feed primarily on diatoms, small flagellates (including dinoflagellates and prasinophytes) and bacteria (e.g., Gaines and Taylor, 1984; Jacobson and Anderson, 1986; Taylor, 1987; Gribble et al., 2007). In our study, biogenic silica fluxes (Fig. 3) are used as a proxy for diatom production, since diatoms are major primary producers in coastal waters and they are the dominant producers of biogenic silica in the SBB (Shipe and Brzezinski, 2001; Shipe et al., 2002). We find that correlations between fluxes of biogenic silica and heterotrophic taxa are strongly positive and significant (\(R^2 = 0.616\); P = 0.000), whereas no significant correlation could be found between fluxes of biogenic silica and autotrophic taxa (Fig. 8). This observation supports that there is a causal relationship between heterotrophic dinoflagellates, in particular Protoperdinidaceae, and diatoms, which is consistent with earlier work (e.g., Fujii and Matsuoka, 2006; Pospelova et al., 2010; Zonneveld et al., 2010; Price and Pospelova, 2011). Thus, our data confirm the findings of Price and Pospelova (2011) that we can use heterotrophic, primarily Protoperdinidaceae, dinoflagellate cysts in sedimentary records to reconstruct past changes in diatom productivity in the region. It has been previously established that diatoms are the preferred prey for Protoperdinidaceae (e.g., Naustvoll, 2000).

In our sediment trap time-series, total dinoflagellate cyst fluxes increased during intervals of active upwelling, from ~25,000 cysts m\(^{-2}\) day\(^{-1}\) to values greater than 100,000 cysts m\(^{-2}\) day\(^{-1}\) at the transition to upwelling relaxation (in July 1995 and July through September 1996) and then decreased until the end of the relaxed upwelling intervals (Fig. 5). This trend was driven primarily by Brigantedinium spp. (Fig. 5), although several other heterotrophic taxa such as the cysts of P. americanum and S. quanta also tend to peak towards the end of active upwelling. Brigantedinium spp. represented up to 86.6% of the assemblages under active upwelling conditions, when nutrient supply is highest and SST is lower, but only 57.1% during intervals of relaxed upwelling. Thus, higher fluxes and relative abundances of heterotrophic taxa, particularly Brigantedinium spp., reflect active upwelling conditions.

Under conditions of relaxed upwelling, the dominance of Brigantedinium spp. in the cyst assemblages is diminished, predominantly in favor of the autotrophic L. machaerophorum (Fig. 7). Fluxes of L. machaerophorum were markedly higher and represented up to 29.9% of the cyst assemblages in fall and winter 1995, when SST was the highest, stratification was stronger and upwelling subsided (5). L. machaerophorum is considered an opportunistic species commonly encountered under a wide range of temperatures, salinities...
This sediment trap study provides insights on the ecology of the most dominant dinoflagellate cyst taxa in the region. As discussed above, the ecology of Brigantedinium spp. and Lingulodinium machaerophorum in the SBB is tied to SST and the state of upwelling. This observation becomes particularly relevant with regard to investigations of the evolution of past SST and upwelling history from the sediment record in the SBB and other areas characterized by seasonal upwelling.

**Lingulodinium polyedrum** (= motile stage of *L. machaerophorum*) has been extensively studied in southern Californian waters (e.g., Eppley and Harrison, 1975; Shipe et al., 2008) and worldwide (reviewed by Lewis and Hallett, 1997). *Lingulodinium polyedrum* is usually found in greater abundances in regions characterized by high nutrient levels, such as river mouths (e.g., Morzadec-Kerfourn, 1977; Zonneveld et al., 2009), some eutrophic fjords (e.g., Thorsen and Dale, 1997) and upwelling cells (e.g., Blasco, 1975). *Lingulodinium polyedrum* may swim to utilize nutrients below the pycnocline in stratified waters (Maclsaac, 1978; Lewis and Hallett, 1997; Smyady and Reynolds, 2003). Laboratory experiments show that temperatures of 10–12 °C are a minimum requirement in terms of growth rate (Meeson and Sweeney, 1982) and swimming speed (Hand et al., 1965; Kamykowski and McCollum, 1986). Sedimentary cyst records support that SST constitutes the primary controlling factor over the latitudinal distribution of *L. machaerophorum*, with summer temperatures of 10–12 °C as a lower limit (Dale, 1996; Lewis and Hallett, 1997; Marret and Zonneveld, 2003). In areas influenced by coastal upwelling, *L. machaerophorum* becomes one of the dominant cyst taxa in surface sediment assemblages where conditions of warmer (SST > 15 °C) and stratified waters prevail (Dale, 1996; Amorim et al., 2004;
upwelling conditions. In a study investigating the dinoflagellate cyst distribution in surface sediment from the northeastern Pacific, Pospelova et al. (2008) documented higher relative abundances of *Spiniferites* species south of the SBB, in the Southern California Bight down to the Baja Peninsula. The *Spiniferites* species clustered within the “warm water” taxa, in an ordination generated from canonical correspondence analysis (Pospelova et al., 2008). *Spiniferites* species have been previously associated with warmer SST in studies of dinoflagellate cysts in sediment cores from the SBB during the 20th century (Prauss, 2002) and over the last 40 kyr (Pospelova et al., 2006).

The highest cyst fluxes of *E. aculeatum* (up to ~20,450 cysts m$^{-2}$ day$^{-1}$) and *E. delicatum* (~18,350 cysts m$^{-2}$ day$^{-1}$) are recorded at the onset of upwelling relaxation. This particular interval is characterized by increasing SST and water column stratification, while both nutrient and biogenic silica concentrations decrease (Shipe et al., 2002).

Cyst type A has the second highest positive score on RDA axis 1, which is positively and significantly correlated with SST (Fig. 6). It has been previously documented in the northeastern Pacific from the Baja Peninsula up to the Seymour–Belize Inlets in British Columbia, Canada (Pospelova et al., 2006, 2008, 2010; Radi et al., 2007; Krepakevich and Pospelova, 2010; Price and Pospelova, 2011). Cyst type A seems to be systematically associated with warmer SST (Radi et al., 2007; Pospelova et al., 2008, 2010; Price and Pospelova, 2011) and higher surface productivity (Pospelova et al., 2008, 2010; Krepakevich and Pospelova, 2010; Price and Pospelova, 2011). In this study, the maximum fluxes of cyst type A were indeed recorded from mid-August through September 1996 (up to ~16,800 cysts m$^{-2}$ day$^{-1}$; Fig. 7), an interval characterized by the highest SST of the year (up to 17 °C at the surface). We conclude that cyst type A is associated with warmer SST in the region.

Finally, higher fluxes and relative abundances of *S. undulata* were recorded during cooler SST intervals of active upwelling (Figs. 5 and 7). However, occurrences of *S. undulata* were sporadic and fluxes were never maintained over periods longer than one month. This does not support enhanced primary productivity as a significant factor controlling the distribution and seasonality of this species. The present known distribution of *S. undulata* is restricted to the Pacific Ocean and ranges from cool temperate to sub-polar climates (Verleye et al., 2011). In the NE Pacific, the SBB lies at the southern limit of its area of distribution. In the sedimentary record of both ODP Hole 893A, from the SBB, and ODP Site 1233, off Chile, the maximal relative abundance of *S. undulata* was observed during the Last Glacial Maximum when SST was much cooler and the upwelling was weaker at both sites (Pospelova et al., 2006; Verleye et al., 2011). *S. undulata* can thus be used as an indicator of cold SST in the SBB.

### 4.3. Comparison with other sediment trap studies

In this study, we report dinoflagellate cyst fluxes averaging 73,700 cysts m$^{-2}$ day$^{-1}$ over the sampling period (peak at 232,000 cysts m$^{-2}$ day$^{-1}$ in July 1996) which reflect the highly productive nature of the SBB waters. The assemblages are dominated by cysts produced by heterotrophic dinoflagellates, particularly Protoperidinioid cysts, which is consistent with other sediment trap studies at sites characterized by high levels of primary productivity (Harland and Pudsey, 1999; Zonneveld and Brummer, 2000; Joyce and Pitcher, 2004; Susek et al., 2005; Fujii and Matsuoka, 2006; Pitcher and Joyce, 2009; Pospelova et al., 2010; Zonneveld et al., 2010; Price and Pospelova, 2011).

The dinoflagellate cyst fluxes observed in the SBB are within the range reported from other sediment trap studies conducted in areas characterized by intense upwelling (Pitcher and Joyce, 2009; Zonneveld et al., 2010). Zonneveld et al. (2010) report cyst fluxes about one order of magnitude lower off Cape Blanc (NW Africa), due to a trap location ~370 km from the nearest coast. Conversely,
Pitcher and Joyce (2009) estimated an average flux of 1.4 × 10^6 cysts m^-2 day^-1 (including calcareous cysts) from a trap deployed downstream of Cape Columbine, southern Bunguela upwelling system, at only ~3.5 km from the coastline. In comparison with other coastal sediment trap studies in the North Pacific, average cyst fluxes from the SBB are similar to values reported from the Straits of Georgia (Pospelova et al., 2010) and Bahía Concepción, Gulf of California (Morquecho and Lechuga-Deveze, 2004) whereas fluxes are about one order of magnitude lower than in highly productive Omura Bay, Japan (Fuji and Matsuoka, 2006) and Saanich Inlet, BC, Canada (Price and Pospelova, 2011). In general, the differences in flux magnitudes along the different settings can be attributed to an array of biotic and abiotic factors, including species composition, nutrient availability, stratification and freshwater influence. Distance to the shore is clearly a factor to consider when comparing sites under upwelling influence, the more coastal locations recording the highest cyst fluxes (e.g., Pospelova et al., 2008). In addition, the methods used to estimate dinoflagellate cyst fluxes should be taken into consideration when comparing studies (e.g., Mertens et al., 2009). Volumetric methods used by Morquecho and Lechuga-Deveze (2004), Fuji and Matsuoka (2006), Pitcher and Joyce (2009), and Zonneveld et al. (2010) usually lead to lower estimates of dinoflagellate cyst concentrations, compared to studies using the Lycopodium marker grain method (e.g., Pospelova et al., 2010; Price and Pospelova, 2011; and this study). Although dinoflagellate cyst production varies according to SST and upwelling in the SBB, it appears to be continuously high throughout the year compared to the other sediment trap studies mentioned above. This might be due to relatively high levels of nutrients maintained year round in the SBB, even during upwelling relaxation, with short upwelling events such as in October 1996 (Fig. 2), the advection of nutrient-rich waters by the California Undercurrent from the south (Hickey and Banas, 2003) and some minor contribution of river runoff during winter.

4.4. Comparison of dinoflagellate cyst assemblages in sediment trap and underlying sediments

With the presence of laminated sediments in the depositional center of the basin, it is possible to compare the cyst assemblages in sediments collected by the trap and deposited over the underlying sediments over very similar intervals (Fig. 4). The trap assemblage collected between May 1995 and March 1997 (Fig. 4B), and sediment accumulated between 1994 and 1997 are almost identical (Fig. 4C). All the taxa representing more than 0.1% of the total trap assemblage were recovered in the underlying sediments, with the exception of the pellicle cyst of ?Protoperidinium sp. A, a taxon that is not preserved in the sediments (Fig. 4A and 4B; Section 3.4). Thus, the assemblages captured by the trap reflect the accumulation of dinoflagellate cysts in the underlying sediments, and the ecological preferences of dinoflagellates determined on the basis of our trap assemblages are applicable for the interpretation of sedimentary sequences from the depositional center of the SBB.

4.5. Potentially toxic dinoflagellates

Occurrences of toxic dinoflagellates in the Southern California Bight have been reported for over 100 years (e.g., Torrey, 1902; Allen, 1941; Goodman et al., 1984; Shipe et al., 2008). The California Department of Public Health established a program that monitors levels of paralytic shellfish poisoning (PSP) toxins since 1929 and domoic acid since 1992, as well as occurrences of potentially toxic phytoplankton based on direct surface water sampling (e.g., Langlois, 2001). The California Cooperative Oceanic Fisheries Investigations (CalCOFI, http://calcofi.org) and Southern California Coastal Ocean Observing System (SCCOOS, http://www.scccoos.org) have also been sampling coastal waters since 1949 and 2004, respectively. However, relationships between harmful blooms and annual variations of oceanographic conditions are still poorly understood largely because blooms in the Southern California Bight have been sampled only occasionally (e.g., Shipe et al., 2008). Since sediment traps collect all sinking particles continuously, they provide a means for documenting microplanktonic communities by capturing even short span occurrences of individual taxa.

Several potentially toxic taxa were recovered in the sediment trap samples (Figs. 3 and 5). Their contribution to Harmful Algal Blooms (HAB) is due to oxygen depletion at night and during decay of the plankton and/or the production of toxins (e.g., Halloegraef, 1993). Lingulodinium machaerophorum is produced by the dinoflagellate L. polyedrum, known to produce yessotoxins (YTX; e.g., Paz et al., 2004). In particular, Armstrong and Kudela (2006) reported that two out of three isolates of L. polyedrum from Southern California contained YTX. In the SBB trap samples, higher fluxes of both L. polyedrum and L. machaerophorum are recorded during intervals of relaxed upwelling when SST is warmer and stratification is stronger. Operculodinium centrocarpum is the cyst of Protoceratium reticulatum, a species that can produce YTX (Paz et al., 2004). Although fluxes of O. centrocarpum never exceeded 520 cysts m^-2 day^-1 in our dataset, all occurrences were recorded during intervals of relaxed upwelling, mostly between August and October 1996.

Among species of Dinophysis involved in diarrhetic shellfish poisoning (e.g., Kat, 1983; Halloegraef, 1993), three were recorded in our SBB trap samples: D. acuminate, D. caudata and D. fortii (grouped with Dinophysis spp. in Fig. 3). Higher fluxes of thecae of Dinophysis spp. occurred between June and September 1995 (mostly D. caudata) and 1996. Our results show two very distinctive blooms of P. micans, a dinoflagellate possibly associated with human gastrointestinal illness (e.g., Kat, 1979). The blooms lasted for about one month and occurred in September of both 1995 and 1996 with fluxes up to 113,600 thecae m^-2 day^-1. This suggests that P. micans has an affinity for higher SST and stronger stratification, which is consistent with observations from Santa Monica Bay, about 120 km to the southeast (Shipe et al., 2008).

Finally, we report two dinoflagellates responsible for PSP toxin production in the SBB trap samples: cysts of Alexandrium spp. and cf. Polysphaeridium zoharyi (biological name: Pyrodinium bahamense), although too few specimens were observed to assess any ecological preference. Low numbers of cysts of Alexandrium spp. and cf. P. zoharyi can be explained by noting that during the trap deployment, PSP toxin levels detected in shellfish along the California coast were very low compared to the rest of the 1990s, with only a small peak above 600 pg/100 g in July/August 1996 (Langlois, 2001). In the sediment trap samples, few cysts of Alexandrium spp. were recorded in June through August 1996. Specimens of cf. P. zoharyi were identified in October 1995 and October through December 1996.

5. Conclusions

This work is the first sediment trap study to document seasonal dinoflagellate cyst production on the west coast of the United States. Our data provides insights on the specific ecology of dinoflagellates in the SBB and environmental preferences of cyst taxa in this area characterized by seasonal upwelling. We show that dinoflagellate cyst fluxes and assemblages are reliable indicators of primary productivity, and reflect SST variations associated with upwelling in the SBB. In particular, Brigantedinium spp. are associated with active upwelling intervals during which sea surface temperatures are lower, stratification is weaker and diatom production is maximal. Conversely, Lingulodinium machaerophorum indicates relaxed upwelling conditions characterized by higher sea surface temperatures, stronger stratification and reduced primary productivity. Selenopemphix undulata is associated with colder SST, whereas cyst type A indicates...
higher SST in the region. The strength and duration of upwelling are bound to pan-Pacific atmospheric and oceanic circulation patterns. We also document occurrences and ecological preferences of potentially toxic dinoflagellates such as Dinophysis spp., Lingulodinium polyedrum and Prorocentrum micans.

In the future, longer sediment trap time-series are needed to resolve year-to-year variations in this highly dynamic system, especially with regard to the possible effects of El Niño and La Niña events on dinoflagellate communities. Finally, this work lays the ground for future high resolution studies of downcore variations in dinoflagellate cyst assemblages from laminated sediment sequences in the Santa Barbara Basin.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.marmicro.2013.03.007. These data include a Google map of the area described in this article.

References
