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**20th century
coccolithophores
assemblages in SBB
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Interactive Discussion

Coccolithophore response to climate and surface hydrography in Santa Barbara Basin, California, AD 1917–2004

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Abstract

The varved sedimentary AD 1917–2004 record from the depositional center of the Santa Barbara Basin (SBB, California) was analyzed with monthly to annual resolution to yield relative abundances of six coccolithophore species representing at least 96% of the coccolithophore assemblage. Seasonal/annual relative abundances respond to climatic and surface hydrographic conditions in the SBB, whereby (i) the three species *G. oceanica*, *H. carteri* and *F. profunda* are characteristic of the strength of the northward flowing warm California Counter Current, (ii) the two species *G. ericsonii* and *G. muellerae* are associated with the cold equatorward flowing California Current, (iii) and *E. huxleyi* appears to be endemic to the SBB. Spectral analyses on relative abundances of these species show that all are influenced by the El Niño Southern Oscillation (ENSO) and/or by the Pacific Decadal Oscillation (PDO). Increased relative abundances of *G. oceanica* and *H. carteri* are associated with warm ENSO events, *G. muellerae* responds to warm PDO events, and the abundance of *G. ericsonii* increases during cold PDO events. Morphometric parameters measured on *E. huxleyi*, *G. muellerae* and *G. oceanica* indicate increasing coccolithophore calcification from ~1917 until 2004 concomitant with rising pCO_2 and sea surface temperature in the region of the SBB.

1 Introduction

Coccolithophores are unicellular pelagic algae that represent a large part of the world ocean's nannophytoplankton and play a significant role in the carbon cycle as major producers of biogenic calcium carbonate. Coccolithophore assemblages are diagnostic for physical and chemical conditions in the photic zone, and therefore fossil coccolithophores in sediments can be used to reconstruct paleoecological and paleoceanographic conditions (Beaufort et al., 1997; Giraudeau et al., 1993; Kinkel et al., 2000; McIntyre and Be, 1967; Nederbragt et al., 2008; Okada and McIntyre, 1979;

Andruleit and Baumann, 1998) The inorganic fossil remains of coccolithophores consist of $<10\,\mu m$ calcareous plates called coccoliths. Their small size and large abundance make it possible to sample marine sediment cores at mm to sub-mm intervals with ultra-high resolution (Grelaud et al., 2008[1]).

5   This study analyzed coccolithophore assemblages in dated sediment cores from the deep center of the Santa Barbara Basin (SBB) on the North American Pacific margin in the interval from AD 1917 to 2004. The SBB region is hydrographically dominated by the California Current (CC) system, which in turn is modulated by Pacific climate conditions, especially by the El Niño Southern Oscillation (ENSO) and the Pacific Decadal

10 Oscillation (PDO). ENSO originates in the tropical Pacific and its warm/cold phases oscillate with a pseudo-frequency of 2 to 7–8 years, whereas warm/cold PDO transitions originate in the north Pacific at ~20° N and occur only every 20–30 years. The PDO is commonly described as a long-lived El Niño-like pattern affecting the north Pacific, since both ENSO and PDO exhibit some similar characteristics (Latif and Barnett,

15 1994; Mantua et al., 1997; Zhang et al., 1997).

    Reconstructions of ENSO and PDO prior to the twentieth century are difficult because they require well-dated high resolution proxy records of sufficient length. Nevertheless, several centuries-long reconstructions of ENSO and PDO have been reported. Paleo-ENSO records are based on the oxygen isotopic (δ^{18}O) composition of coralline

20 aragonite (Tudhope et al., 2001; Tudhope et al., 1995) or on the carbon isotopic (δ^{13}C) composition of stalagmite calcite (Frappier et al., 2002), as well as on tree ring data (D'Arrigo et al., 2005; Stahle et al., 1998). These records share a significant common variance and suggest that El Niño events of past centuries share a relatively consistent history (Jones and Mann, 2004). However, suitable coral cores and tree ring se-

25 quences are rare, relevant analytical methodologies are costly, and techniques require substantial amounts of sample material and effort.

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[1]Grelaud, M., Beaufort, L., Cuven, S., and Buchet, N.: Glacial to interglacial primary production and ENSO dynamics inferred from coccolithophores of the Santa Barbara Basin, Paleoceanography, 2007PA001578, submitted, 2008.

Surveys and studies on nannophytoplankton responses to the El Niño events of 1991–1992 and 1997–1998 in the Southern California Bight and in the SBB indicate that coccolithophores are influenced by El Niño (De Bernardi et al., 2005; Ziveri et al., 1995). Fossil coccolith assemblages can thus serve as a promising paleoceanographic proxy to highlight past El Niño variability, especially in laminated sediments with high resolution.

This study uses relative abundances of sedimentary coccoliths to constrain climatic and surface hydrographic settings of the SBB from ∼1917 until 2004. Indices of ENSO (Reynolds et al., 2002; Kaplan et al., 1998) and PDO (Mantua et al., 1997; Zhang et al., 1997) have been reconstructed back to the beginning of the 20th century based on instrumental and historic data. We compared our dated, high resolution SBB coccolith record against indices of ENSO and PDO to calibrate coccolith proxies for reconstructions of paleo-El Niño and paleo-PDO conditions in the SBB. Moreover, in the context of modern global warming and ocean acidification due to anthropogenic CO_2 release, we investigated the morphometry (size, weight) of selected species of the order Isochrysidales (i.e., *E. huxleyi*, *G. muellerae* and *G. oceanica*) to understand how calcification of coccolithophores is influenced by recent oceanographic global changes.

2   Materials and methods

2.1   Age model

Multicore 1MC-3 from the deep center of the SBB (34°13.41′ N, 120°01.53′ W) was retrieved in June 2004 during cruise BASIN 2004 (Fig. 1). Two parallel cylindrical cores A and B were retrieved from the multicore. We used the age model of core A (Huguet et al., 2007) to establish that of core B which was then sub-sampled with superior resolution. Briefly, we first measured the coccolith abundances in leftover sub-sectioned and freeze-dried sediment aliquots from core A that had been used by Huguet et al. (2007). The dating uncertainty for core A is ∼2 years below 1980

AD and ~1 year for younger sediment. We then subsampled the 25.6 cm long, wet sediment core B lengthwise every millimeter and measured coccolith abundances. The two coccolith data series from cores A (lower resolution) and B (higher resolution) were then correlated to each other. First, a correlation of the relative abundance patterns of the coccolithophore species *G. oceanica* matched cores A and B well between AD 1934 to 2004 (Fig. 2a), but less satisfactorily prior to AD 1934 (Fig. 2b). This correlation provided an approximate, preliminary age model for core B. Subsequently we fine-tuned the chronological relative abundance of *G. oceanica* of core B to the extended NINO3 index (Kaplan et al., 1998; Reynolds et al., 2002) (Fig. 2b), since earlier studies have shown that high abundances of *G. oceanica* are found during El Niño events (De Bernardi et al., 2005; Grelaud et al., 2008[1]). Finally, the chronology of the high-resolution data series from core B was further adjusted by linking peaks of relative abundance of *F. profunda* to instrumental monthly sea surface temperatures in the SBB, based on the fact that this species' growth is essentially limited to summer (Haidar and Thierstein, 2001; Grelaud et al., 2008[1]). The final age model for core B allows us to describe time-series with high resolution from 1917 to 2004, with a mean resolution of ~3 months.

2.2 Coccolith census

Smear slides were prepared for all samples of the two cores. 40 view fields from a light microscope (Leica DMRBE) with a 50x immersion oil objective were captured from each slide by a digital camera ("Spot insight"). Automatic image analysis of each frame resulted in recognition of coccolith species using SYRACO software (Beaufort and Dollfus, 2004; Dollfus and Beaufort, 1999). SYRACO is able to identify more than 96% of the coccolith assemblages, including the following six species that were enumerated in this study: *Emiliania huxleyi*, *Florisphaera profunda*, *Gephyrocapsa ericsonii*, *Gephyrocapsa muellerae*, *Gephyrocapsa oceanica,* and *Helicosphaera carteri*. A total of more than 600 individuals of these six species were typically counted in each sample. We applied a correction to the count of each species to compensate for SYRACO's

inclusion of non-coccolith specimens in the raw data. The final data and the influence of the correction are reproducible (Beaufort and Dollfus, 2004).

2.3 Coccolith weight estimate

It is possible to estimate the amount of coccolith calcite in a sample by weighing the <27 μm fraction (Broerse, 2000), but this semi-quantitative method relies on the assumption that the entire <27 μm fraction consists of coccolith calcite. This study uses images produced by SYRACO to estimate the individual weight of coccoliths (Beaufort, 2005) belonging to the order Isochrysidales (i.e., *E. huxleyi*, *G. ericsonii*, *G. muellerae,* and *G. oceanica*). The method relies on the brightness of calcitic grains when viewed in cross-polarized light. Brightness and color of an object in cross-polarized light depend on (i) the object's thickness in a range of 0 to 1.5 μm, (ii) its orientation, and (iii) its birefringence index, therefore making it common practice for nannopaleontologists to associate coccolith thickness with brightness. We converted the brightness of individual coccoliths into a number of pixels that was fed into a calibrated transfer function to indicate the amount of calcite (Beaufort, 2005).

2.4 Spectral analyses

We performed spectral analyses on the relative abundances of six species (Fig. 4c–h), the extended NINO3 index (Kaplan et al., 1998; Reynolds et al., 2002) (Fig. 4a), and the PDO index (Mantua et al., 1997; Zhang et al., 1997) (Fig. 4b). Redfit software (Schulz and Mudelsee, 2002) generated power spectra and associated 80% and 90% confidence intervals from our unevenly spaced data (Fig. 4). The resulting spectral coccolith data were then compared to those of the extended NINO3 and PDO indices by performing cross-spectral analyses. We used cross-spectral Blackman-Tukey methods in the Analyserie package (Paillard et al., 1996). The resulting coherency between cross-spectra is significant within a 90% confidence interval over a value of 0.672 (Fig. 4c–h).

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3 Results

3.1 Relative abundances of coccolith species

At least 96% of the SBB sedimentary coccolith assemblage is composed of *E. huxleyi*, *F. profunda*, *G. ericsonii*, *G. muellerae*, *G. oceanica*, and *H. carteri*. Other species present in SBB sediments, such as *Calcidiscus leptoporus*, *Coccolithus pelagicus* and *Umbilicosphaera sibogae* (De Bernardi et al., 2005) express insufficient relative abundances for the purpose of this study. *E. huxleyi*, *G. ericsonii* and *F. profunda* dominate the SBB coccolithophore assemblages and jointly account for almost 85–90% of all coccoliths (Fig. 3a), whereas *G. muellerae*, *G. oceanica* and *H. carteri* jointly represent only 8–10% of the assemblages (the six species are listed in decreasing order of relative abundance; Fig. 3a).

This study's data on *E. huxleyi* may include small placoliths of the genus *Reticulofenestra* and *Gephyrocapsa* that are not distinguished by automatic image analysis. However, comparative scanning electron microscopy (SEM) counts indicate that the resulting error is limited to a few % (Grelaud et al., 2008[1]). *E. huxleyi's* relative abundance of ~40% is dominating for the entire period covered in this study, with the exception of short episodes in 1966, 1970, 1980–1982, 2000, and 2004 when *F. profunda* becomes most abundant (Fig. 3a). *G. ericsonii* represents ~27% of the assemblages and is the second most abundant species in SBB sediment (Fig. 3a), being present at a relatively stable level throughout the record, with a slightly decreasing trend toward 2004. *F. profunda* is the third most abundant species representing 21% of the assemblages (Fig. 3a). Its relative abundance is stable from 1917 to ~1965, but exhibits occasional large peaks between ~1965 and 2004. Only 3.5% of the assemblages are contributed by *G. muellerae*, with an overall increasing trend from ~1917 to 2004. The relative abundances of *G. oceanica* are highly variable and account for 0.25 to 10.5% with a mean of 3% (Fig. 3a). Out of the six species counted, the lowest relative abundances from 0.4 to 3.9% are contributed by *H. carteri*, with a mean value of 1.6%. The abundances of these two last species are enhanced during strong El Niño events such as

in 1982–1983 and 1997–1998 (Fig. 3a).

3.2 Seasonality of coccolithophores inferred from varved SBB sediment

We evaluated the seasonality of the six selected coccolithophore species in core B by averaging each species' relative abundances for each season of each year during the period 1917–2004. The calculated decimals of the age model for each year are then used to evaluate the season. For example, 1917–1917.25 corresponds to winter 1917 (January to March), 1917.25–1917.5 corresponds to spring (April to June), 1917.5–1917.75 corresponds to summer (July to September) and 1917.75–1918 corresponds to fall (October to December). According to this definition, the four species *F. profunda*, *G. ericsonii*, *G. oceanica*, and *H. carteri* preferentially thrive during summer and fall (Fig. 3c), while *E. huxleyi* and *G. muellerae* bloom preferentially during winter and spring (Fig. 3c).

3.3 Spectral analyses

Spectral analyses of the extended NINO3 and PDO indices (Fig. 4a and b) were compared to those of the relative abundances of the six selected species using cross-spectral analyses (Fig. 4c–h). The three important ranges of frequencies are (i) the 2–7 yr pseudo-frequency of ENSO, (ii) the 20–30 yr PDO band, and (iii) the 50–70 yr very low frequency of the pentadecal band (Minobe, 2000). Frequencies commensurate with ENSO were expressed by the six species (Fig. 4c–h), PDO frequencies were found for *G. muellerae* and *G. ericsonii* (Fig. 4g–h), and spectral evidence for the pentadecal band was found for *E. huxleyi*, *F. profunda*, *G. oceanica*, and *H. carteri* (Fig. 4c–f).

3.4 Coccolith morphometry

Our automatic image analysis system used a calibrated algorithm to estimate the size (μm) and the weight in picogram (pg) of each recognized coccolith of the order

Isochrysidales. Size corresponds to a coccolith's largest diameter. For each sample we determined mean values of size and weight for the three species *E. huxleyi*, *G. muellerae*, and *G. oceanica* (Fig. 5a). The observed mean sizes and standard deviations fluctuate around 2.74±0.04 μm, 3.33±0.12 μm, and 3.96±0.13 μm, respectively, and are in agreement with observed sizes of coccolithophores (Young et al., 2003). Mean weights fluctuate around 3.41±0.6 pg, 7.96±1.9 pg, and 24.04 ±5.9 pg, respectively. Average contributions to Isochrysidales-produced calcite amount to 45% from *E. huxleyi*, ~22% from *G. oceanica*, and 17.5% from *G. muellerae*. Size and weight of coccoliths tend to increase between ~1917 and 2004 by (i) 0.5 % and 1.9 % for *G. muellerae*, (ii) 2.2% and 10.3% for *E. huxleyi*, and (iii) 2.7% and 22.1% for *G. oceanica*, respectively (Fig. 5a). Increases seem to have accelerated from the 70's to 2004 for *E. huxleyi* and *G. oceanica* (Fig. 5a). The mean weight of calcite of a coccolith belonging to the order Isochrysidales (i.e., the three species combined) increased from ~1917 until 2004 by more than 33% (Fig. 5B).

4 Discussion

4.1 Coccolith ecology in SBB inferred from sediment record

The SBB is hydrologically dominated by the California Current (CC) and the California Counter Current (CCC) (Hendershott and Winant, 1996). The equatorward cold CC enters the SBB from the west and supplies nutrients via injection of upwelled waters from off Point Arguello and Point Conception (Fig. 1). Seasonal differences in wind along the coast off Point Arguello limit strong upwelling mostly to summer and make upwelling more variable during winter (Dorman and Winant, 1995). The CC triggers a counter-clockwise circulation inside the SBB (Fig. 1) with maximum strength between spring and fall (Hendershott and Winant, 1996). The resulting cold SBB surface waters with moderately high concentrations of nutrients are favorable for coccolithophore species like *G. muellerae,* which prefer cold and moderately productive waters (Bollmann, 1997;

Flores et al., 1997; Knappertsbusch et al., 1997). We observed high abundances of *G. muellerae* from November to April (Fig. 3c) prior summer strong upwelling and when SST is coldest in the SBB. The dynamics of the CC may also influence the abundance of *G. ericsonii* that thrives in high nutrient environments (Takahashi and Okada, 2000)

5   between 13 and 22°C (Okada and McIntyre, 1979). We observed highest abundances of *G. ericsonii* during summer when upwelling is active and the SST stays relatively warm (Fig. 3c).

    The CCC originates from further south, enters the SBB from the east, and continues flowing northward (McLain and Thomas, 1983). The relatively warm and salty waters

10   of the CCC influence the SBB mostly from spring to fall and seem to be reduced during winter (Hendershott and Winant, 1996). The subtropical origin of the CCC favors warm coccolithophore species like *G. oceanica* and *H. carteri*. *G. oceanica* is found largely in tropical and subtropical seas (Andruleit et al., 2003; Andruleit et al., 2000; McIntyre et al., 1970) and prefers high nutrient environments such as upwelling areas

15   or continental shelves (Giraudeau, 1992; Houghton and Guptha, 1991; Mitchellinnes and Winter, 1987; Young, 1994). SST is the most important oceanographic parameter controlling the distribution of *G. oceanica* in the SBB (De Bernardi et al., 2005) triggering high abundances during the second half of spring, when SST rises during summer (Fig. 3c) and SBB surface waters are warm and rich in nutrients. The same

20   pattern is observed for *H. carteri* (Fig. 3c), which thrives in warm waters (Brand, 1994; McIntyre and Be, 1967) and shares ecological similarities with *G. oceanica* (Giraudeau, 1992). The CCC may also influence *F. profunda* which lives below the deep chlorophyll maximum in the lower photic zone in tropical to subtropical regions (Okada and Honjo, 1973). *F. profunda's* preference for stratified waters is well suited for the SBB during

25   summer (Kincaid et al., 2000; De Bernardi et al., 2005) when its highest abundance was observed (Fig. 3c).

    E. huxleyi is the most abundant and ubiquitous coccolithophore in modern oceans. Its strains tolerate large ranges of salinity and temperature and allow it to inhabit both the Red Sea (high salinity) and the Black Sea (low salinity). Its ability to grow in

eutrophic and oligotrophic waters testifies to this species' adaptation to a wide range of nutrient levels (Winter et al., 1994). The SBB sediment record indicates that *E. huxleyi* is still abundant during winter and early spring (Fig. 3c) when upwelling is absent or weak. Such behavior makes *E. huxleyi* an opportunistic species that is able to live in
5 cold and well mixed waters with low levels of nutrients.

The collective observations of this and earlier studies form the basis for dividing the six quantified species into three categories. (i) The CCC-controlled summer influence is best reflected by the response of *F. profunda*, *G. oceanica*, and *H. carteri*. (ii) The CC-controlled winter influence is witnessed by *G. muellerae*, and the CC-controlled
10 summer influence is expressed by *G. ericsonii*. (iii) *E. huxleyi* appears to be opportunistic and endemic to the SBB.

4.2 Influence of ENSO and PDO on SBB coccolithophores

The CC and the CCC are parts of the California Current system extending 1000 km from offshore Oregon to Baja California (Miller et al., 1999). The CC system is modu-
15 lated across various time scales by (i) ENSO with a pseudo-frequency of ∼2 to 7 yr, (ii) the PDO with a decadal-bidecadal frequency of ∼20 to 30 yr, and (iii) by pentadecadal variability of ∼50 to 75 years (Lluch-Belda et al., 2003; Minobe, 2000). Interannual temperature variability of SBB surface waters can be reduced to two opposite states that are expressed as warm and cold episodes. A warm phase is associated with a re-
20 duced CC and an intensification of the CCC. Warm phases tend to cause a northward migration of southern fauna (Lluch-Belda et al., 2003) and flora (e.g., diatoms (Thunell, 1998)), including coccolithophores. The opposite occurs during a cold phase when the CC is strengthened while the CCC weakens. The driving forces behind this variability of the CC system have geographically different origins. The PDO and the pentadecadal
25 oscillation modulate the CC system through the intensity and east-west position of the Aleutian Low (Miller and Schneider, 2000), whereas ENSO modulates the CC system through the intensity of the North Pacific High (Bograd and Lynn, 2001).

We performed spectral and cross-spectral analyses of our microfossil time-series
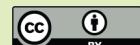
from six species in combination with the extended NINO3 and PDO indices to evaluate the hydrographic variability on different time scales and to explore the impact on SBB's coccolithophore community (Fig. 4). All examined time-series exhibit frequencies in the 2–7 yr ENSO band (Fig. 4c–h). The ENSO band can be divided into a sub-band of 2.5
5 to 3–4 yr that is generally associated with the duration of El Niño events and the alternation to La Niña conditions, whereas the sub-band of 3-4 to 7 yr relates more to the spacing between successive large El Niño events (Graham and White, 1988; Zebiak and Cane, 1987). The six coccolithophore time-series exhibit significant periodicities around 2.5 and 3–4 yr. Although this suggests that all species are influenced by ENSO,
10 the relationship of each species with ENSO depends mostly on its ecology. Thus, high abundances of warm species *G. oceanica* and *H. carteri* occur simultaneously with El Niño events as suggested by cross-spectral phases (Figs. 3a and 4c–d). This agrees with the observation that the CCC is enhanced during a warm event (Bograd and Lynn, 2001), allowing an extended northward advection of southern species (Lluch-Belda et
15 al., 2003) like *G. oceanica* and *H. carteri*. The same holds true for *F. profunda* (Figs. 3a and 4d), although this species may be slightly lagging behind El Niño. To the contrary, the abundances of *G. ericsonii* and *G. muellerae*, which are associated with a strong CC, are negatively correlated with warm events (Figs. 3a and 4e–f) when the CC in the SBB is temporarily weakened (Lluch-Belda et al., 2003). The same is true for the
20 dominant species *E. huxleyi* (Figs. 3a and 4a), suggesting that this species prefers CC rather than CCC water.

Spectral results from *E. huxleyi* and *F. profunda* indicate no significant response to strong El Niño events in the low-frequency ENSO sub-band of 3–4 to 7 yr (Fig. 4a–b). However, all four other species exhibit significant periodicities between 3 and 7 years
25 (Fig. 4c–f), reflecting an enhancement of their response patterns described above for normal El Niño / La Niña cycles. Cross-spectral phases confirm that *G. oceanica* and *H. carteri* are associated with warm water events, whereas *G. ericsonii* and *G. muellerae* prefer cold waters.

Cross-spectral analyses of the PDO index and the six microfossil time-series show

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that only the CC-associated species *G. ericsonii* and *G. muellerae* exhibit 20 to 30 yr periodicities corresponding to the PDO (Fig. 4g–h). Cross-spectral phases associate the PDO's cool phase with high abundances of *G. ericsonii*, and the PDO's warm phase with high abundances of *G. muellerae*. This pattern agrees with ecological observa-
5 tions of these two species in the California Borderland (Chavez et al., 2003) where low nutrient availability during warm phases favors *G. muellerae* which is associated to moderately productive waters. During cool phases, the region is characterized by higher nutrient availability favoring *G. ericsonii*. It seems that only species growing under the influence of the CC are affected by the PDO, suggesting an "equatorward"
10 expression of PDO variability in the SBB.

The spectral patterns of time-series from the four other species witness responses to a 50–58 yr component of pentadecadal variability (Fig. 4c–f). The same component is observed in the power spectra of the PDO (Fig. 4B). However, our 87 yr long record from AD ~1917 until 2004 does not cover two successive cycles and is thus too short
15 to lend statistical weight to this observation.

4.3   20th century warming and increasing calcification of coccoliths

Many studies have shown that 20th century warming affected the food chain at all trophic levels in the northeastern Pacific and particularly in the CC system, extending from marine algae (Tegner et al., 1996) to zooplankton (Brinton and Townsend, 2003;
20 Roemmich and McGowan, 1995) and fish (Mantua et al., 1997). Since the 1950s mean sea surface temperatures in some places off Southern California have increased by almost 1.5°C and caused an 80% reduction of macrozooplanktic biomass (Roemmich and McGowan, 1995). Regional abundances of tropical foraminifera species increased at the expense of temperate species (Field et al., 2006).
25 Even if relative abundances of some coccolithophores are sensitive enough to capture seasonal to decadal SBB regional oceanographic variability and trends, the approach may fail for monitoring global marine changes such as SST warming or ocean acidification linked to anthropogenic CO_2 release. We did not identify any increase of

the relative abundances of tropical coccolithophore species in SBB between ~1917 and 2004, especially during the last 30 years (Fig. 3a). The reverse is true for the cold species *G. muellerae* which did not exhibit a decrease of its relative abundances during the same period (Fig. 3a).

Our investigation of morphometric parameters of three species scrutinized the CC-associated species *G. muellerae*, the CCC-associated *G. oceanica*, and the SBB endemic species *E. huxleyi*. The average weight and size of each of the three species increased during the last century, although the rates of increase differed among the three species (Fig. 5). Increases in weight and size are largest for *G. oceanica* and *E. huxleyi* and smaller for *G. muellerae* (Fig. 5a), suggesting that SBB coccolithophore calcification experienced enhancement in waters of the CCC between ~1917 and 2004, whereas calcification changed little in waters deriving from the CC. After merging the data of the three species, a >33% increase in mean coccolith weight was determined for the order Isochrysidales over 87 years from ~1917 until 2004 (Fig. 5b).

A possible explanation for this increase is that older calcareous fossils in the deeper part of the core could have undergone slow dissolution. Increases in weight and size over time would thus be an artifact linked to better preservation of younger coccoliths. However, Beaufort et al. (2007) showed that during experimental acid attack the weight of cultured and fossil coccoliths did not change significantly in a range of pH going from 8.2 to 6.2, this range covering a large part of world ocean pH. They concluded that the weight of sedimentary coccoliths is roughly corresponding to the weight of the original coccosphere. The observed increases in size and weight of coccoliths in the SBB must therefore be based on stronger calcification in regional coccolithophores.

An alternate explanation is based on the influence of increasing SST on coccolithophore calcification, since the increases in size and weight occurred simultaneously with an ~0.7°C increase of the mean regional SST (Fig. 5b) between 1917 and 2004. Latitudinal variations in SST are responsible for the distribution of different morphological groups of the genus *Gephyrocapsa* in the Holocene world ocean (Bollmann, 1997), whereby the largest coccoliths of genus *Gephyrocapsa* are found in warm equatorial

oceans, while smaller specimens are found at higher latitudes in cooler waters. Similar conclusions were reached by Beaufort et al. (2008) who demonstrated that size and weight of coccolithophore species *E. huxleyi* and *G. oceanica* were larger in warmer surface waters from the southeastern Pacific Ocean in the Marquesas archipelago,
5 and became smaller in the cooler surface waters of the Peru-Chile upwelling region. The possible effect of increased calcification in a warming SBB is best expressed in *E. huxleyi* and *G. oceanic*, but remains inconclusive in SBB's record of *G. muellerae*.

The last century has witnessed an increasing net influx of atmospheric carbon dioxide into the world's oceans, a rising pCO_2 of surface waters, and under-saturation with
10 respect to aragonite, especially in the North American Pacific margin (Feely et al., 2008). Calcification in SBB's coccolithophores may be affected by acidification of surface waters overlying the Pacific North American continental shelf. Such conditions are expected to result in reduced coccolithophore calcification and a concomitant decrease in size and weight of coccoliths, as previously suggested in laboratory studies
15 on coccolithophore calcification (Zondervan et al., 2001; Sciandra et al., 2003; Riebesell et al., 2000) and under conditions of artificially increased pCO_2 in ocean waters (Delille et al., 2005). These studies controlled pCO_2 by adjusting pH (Riebesell et al., 2000; Zondervan et al., 2001) or by purging with CO_2-free, ambient, or CO_2-enriched air (Delille et al., 2005; Sciandra et al., 2003) and jointly arrived at the conclusion that
20 coccolithophore calcification is reduced under elevated pCO_2 conditions in seawater. In contrast, Iglesias-Rodriguez et al. (2008) cultured *E. huxleyi* under conditions of increasing pCO_2 by bubbling CO_2 in batch incubation experiments and demonstrated that increasing pCO_2 in seawater was compatible with an increase in coccolith weight. When the pH is controlled by CO_2 injection, rather than by acid addition (Riebesell et
25 al., 2000; Zondervan et al., 2001), the production of dissolved inorganic carbon (DIC) is greater and the production of bicarbonate HCO_3^-, which is the source of DIC for calcification in coccolithophores (Buitenhuis et al., 1999), is enhanced. The results from the laboratory culture experiments of Iglesias-Rodriguez et al. (2008) are corroborated by observations of a 40% increase in average coccolith weight across the last 220 years,

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as recorded in a box core from the subpolar North Atlantic (Iglesias-Rodriguez et al., 2008). The increases also compare well with our observed increase of >33% in mean weight of SBB Isochrysidales coccoliths. A continued future increase in pCO_2 of surface waters in the SBB, and by extension along the entire North American Pacific margin, would potentially increase the weight and size of microfossils from *E. huxleyi* and *G. oceanica*, but would exclude *G. muellerae* which seems to be unable to take advantage of increased pCO_2. It may be possible that the contrasting calcification response to increased pCO_2 by *G. muellerae* is based on physiological or biochemical differences, and that it shares characteristics with the subpolar species *Coccolithus pelagicus*, which has shown a negligible response to increased pCO_2 (Langer et al., 2006).

The available evidence is still insufficient to unambiguously differentiate the influence of SST on coccolithophore calcification from that of other sea surface water chemical properties, such as pCO_2, $[HCO_3^-]$, or alkalinity. However, our data suggest a link between modern oceanographic changes in SBB surface water properties and increased calcification of coccoliths. Enhanced biomineralization in coccolithophores (Fig. 5b) will transfer DIC out of the water column into carbonate that is subsequently buried in accumulating sediment. Every negative feedback in response to the anthropogenic rise in marine DIC will be appreciated.

5   Conclusions

(1) Automatic image analysis via SYRACO software quantified coccoliths' relative abundances along two sediment cores from a Santa Barbara Basin 2004 multicore and yielded reproducible and robust micropaleontological AD ∼1917–2004 time-series from six selected coccolithophore species.

(2) Core B allowed ultra-high sampling resolution and the reconstruction of seasonality of six coccolithophore species. Reconstructed seasonalities are in agreement with known climatic and surface hydrographic preferences of species in the modern Santa

Barbara Basin.

(3) Warm species thrive in summer when the northerly flowing California Counter Current warms the basin. The cold species *Gephyrocapsa muellerae* is preferentially found during winter when sea surface waters are coldest and low in nutrients. *Gephyrocapsa ericsonii* depends on high concentrations of nutrients and is found in summer when upwelling occurs off Point Conception. *Emiliania huxleyi* is opportunistic, ubiquitous, and able to live in cold and well mixed, nutrient-poor waters, primarily during winter.

(4) The abundances of warm water species are enhanced during strong El Niño events, such as in 1982–83 or 1997–98.

(5) Spectral analyses show that four out of six species respond to ENSO and PDO. High abundances of warm species *Gephyrocapsa oceanica* and *Helicosphaera carteri* are associated with El Niño, *Gephyrocapsa muellerae* and *Gephyrocapsa ericsonii* respond well to La Niña. Only two warm species are spectrally linked to the low frequency band of ENSO characterizing the time between successive strong El Niño events, e.g. between the events of 1982–1983, 1986–1987, 1991–92 and 1997–98. Relative abundances of *Gephyrocapsa oceanica* and *Helicosphaera carteri* can serve as paleo-El Niño indicators in Santa Barbara Basin.

(6) Only two species respond spectrally to the PDO, namely *Gephyrocapsa ericsonii* being associated with the PDO cold phase (high nutrient availability) and *Gephyrocapsa muellerae* with the PDO warm phase (low nutrient availability). Relative abundances of *Gephyrocapsa muellerae* and *Gephyrocapsa ericsonii* are useful paleo-PDO indicators in Santa Barbara Basin.

(7) *Emiliania huxleyi* and *Florisphaera profunda* are apparently unaffected by PDO but seem to respond to the classical El Niño / La Niña alternation.

(8) Examination of morphometry in three species showed that calcification of coccoliths in Santa Barbara Basin became enhanced from AD ~1917 until 2004. Intensification of calcification occurred in context with increasing SST and pCO_2 of surface water linked to anthropogenic release of CO_2, suggesting that coccolithophore calcification

in some species could be enhanced by further increases in greenhouse gas concentrations.

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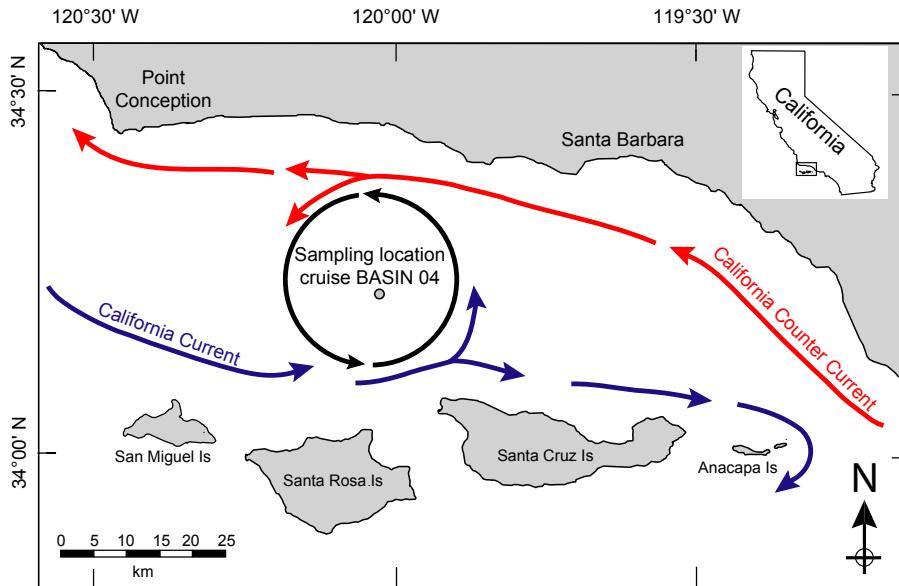
Fig. 1. Sampling location of multicore 1MC-3 during cruise BASIN 2004. Arrows denote flow directions of California Current (blue) and California Counter Current (red). Counterclockwise circulation inside the Santa Barbara Basin is indicated by black arrows.
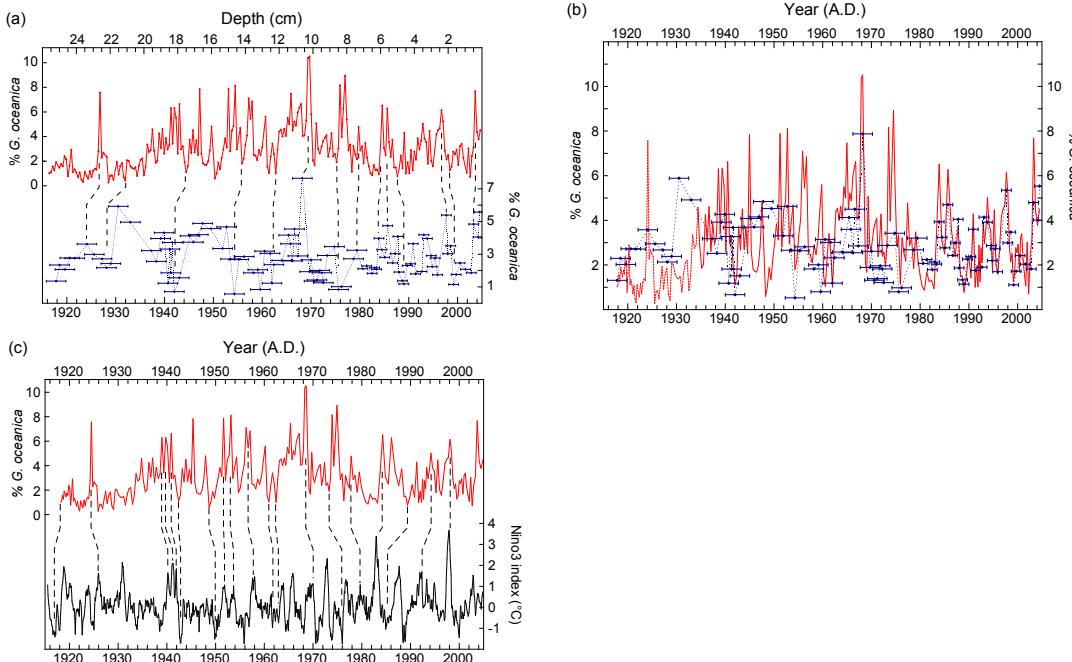
Fig. 2. Development of age model for core B from multicore 1MC-3, cruise BASIN 2004. **(a)** Correspondence between relative abundance records of *G. oceanica* in high-resolution core B (red, depth scale) and in low-resolution core A (dotted blue line, age scale). Error bars associated with core A denote the age uncertainty (1 yr after 1980 and 2 yr before 1980; Schimmelmann et al. (2006)). **(b)** Relative abundances of *G. oceanica* along core B (red) are adjusted to age model of core A (dotted blue line). **(c)** Relative abundance of *G. oceanica* in core B adjusted to extended NINO3 index (black) (Kaplan et al., 1998; Reynolds et al., 2002) (data available at http://iridl.ldeo.columbia.edu/SOURCES/.Indices/.nino/.EXTENDED/.NINO3/).
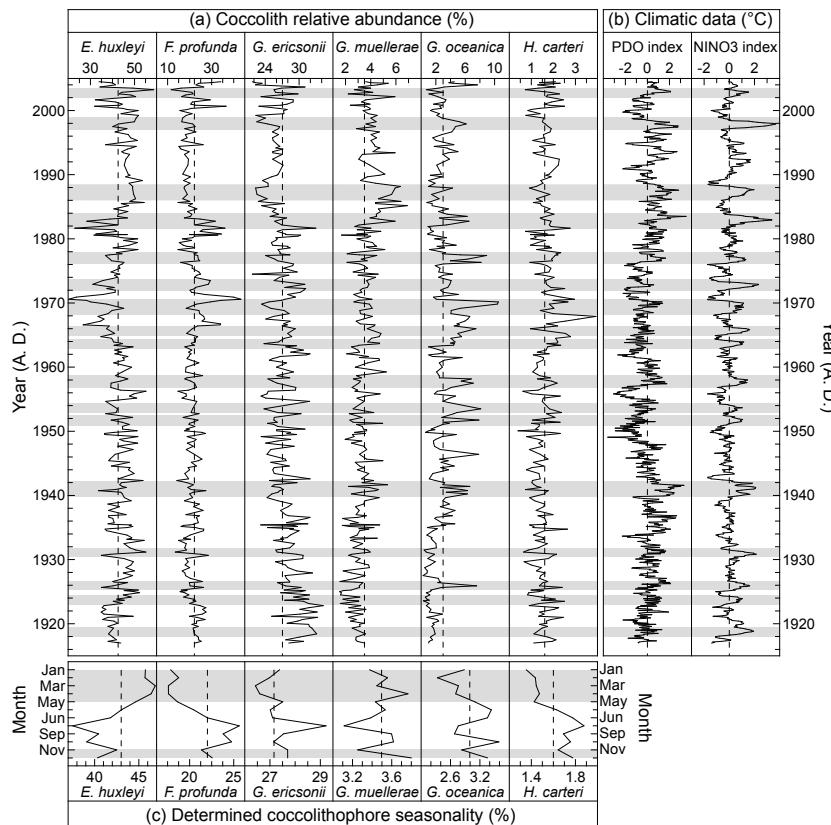
Fig. 3. **(a)** Relative abundances of six selected coccolithophore species in core B from multicore 1MC-3, cruise BASIN 2004. **(b)** PDO index (Mantua et al., 1997; Zhang et al., 1997) (data available at http://jisao.washington.edu/pdo/PDO.latest) and extended NINO3 index (Kaplan et al., 1998; Reynolds et al., 2002). **(c)** Reconstructed seasonality for the six selected coccolithophores species determined from the ultra-high resolution record of core B.
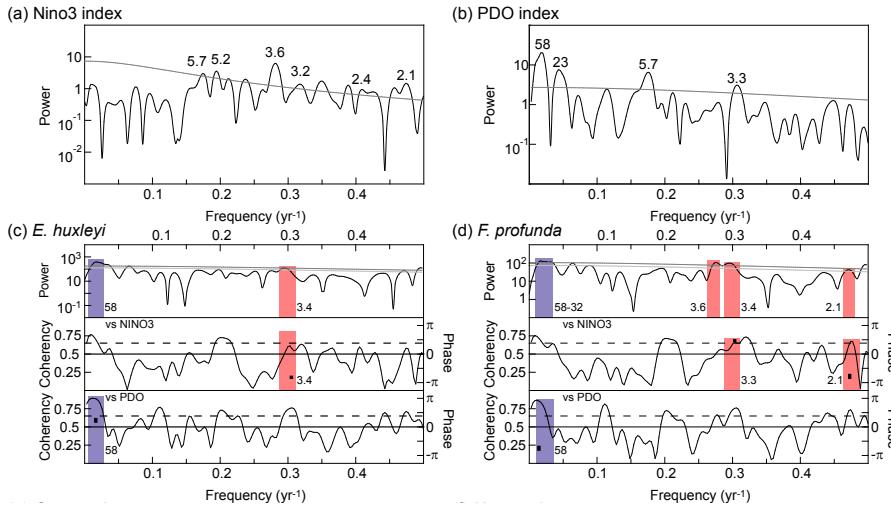
Fig. 4. Spectral analyses of the extended NINO3 **(a)** and PDO **(b)** indices (grey lines indicate 90% confidence intervals). **(c)** From top to bottom: Spectral analysis of % *E. huxleyi* (light grey line denotes 80% confidence interval; dark grey line denotes 90% confidence interval); cross-spectral analysis between % *E. huxleyi* and extended NINO3 index (coherency between spectra is denoted by black line; phase is indicated by black rectangles); cross-spectral analysis between % of *E. huxleyi* and PDO index (coherency between spectra is denoted by black line; phase is indicated by black rectangles). Here the coherency is significant at 90% over 0.672 (dashed line). Red bars represent significant frequencies in ENSO band common to % of *E. huxleyi* and extended NINO3 index. Blue bars represent significant frequencies in PDO band common to % of *E. huxleyi* and PDO. The same comments and settings apply to other panels pertaining to other species: (b) *F. profunda*. (c) *G. oceanica*. **(d)** *H. carteri*. **(e)** *G. ericsonii*. **(f)** *G. muellerae*.
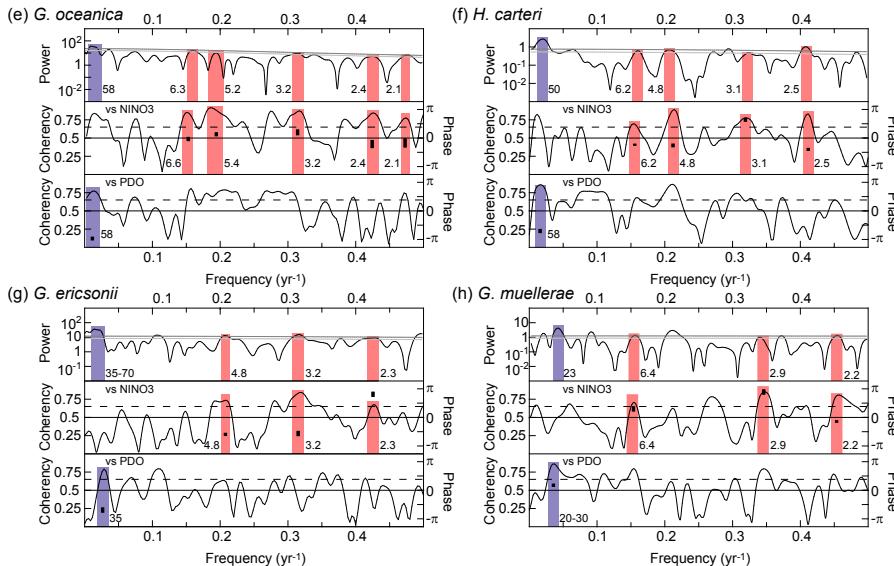
Fig. 4. Continued.
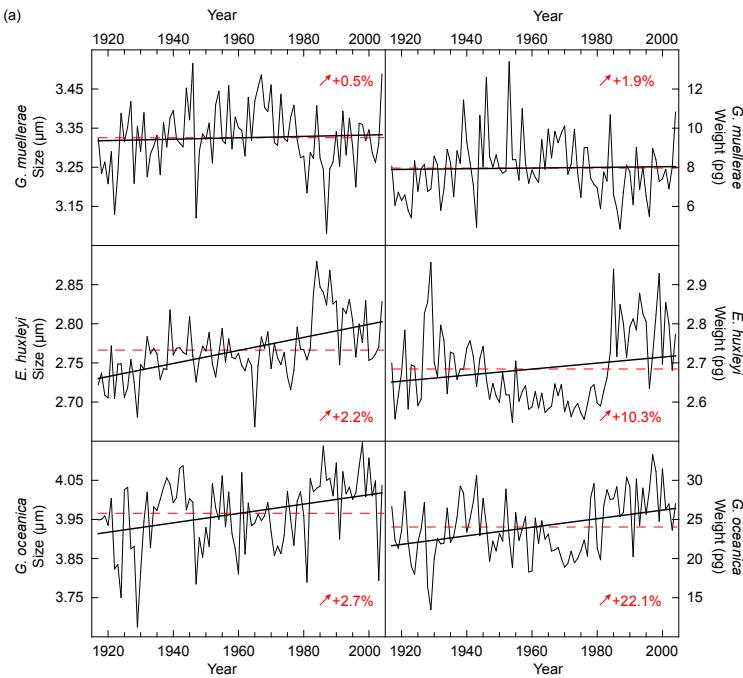
Fig. 5. **(a)** Annual mean coccolith size in μm (left part) and weight in pg (right part) of *G. muellerae*, *E. huxleyi* and *G. oceanica* (from top to bottom). **(b)** Mean weight of individual Isochrysidale coccoliths in pg and annual mean sea surface temperature of Santa Barbara Basin according to the reconstruction of global SST (Smith and Reynolds, 2003), and derived from the version of COADS release 2 (Woodruff et al., 1998), based on combined satellite and in situ instrumental data (Reynolds et al., 2002). Red dashed line represents the mean value of each series; thick black line corresponds to linear regression and indicates the general tendency of each parameter from AD ~1917 to 2004. Red arrows and associated numbers correspond to the % increase of each parameter between ~1917 and 2004.

Fig. 5. Continued.