

Emiliana huxleyi
coccolith thinning in
the Mediterranean
Sea

K. J. S. Meier et al.

The role of ocean acidification in *Emiliana huxleyi* coccolith thinning in the Mediterranean Sea

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Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Abstract

Ocean acidification is a result of the uptake of anthropogenic CO₂ from the atmosphere into the ocean and has been identified as a major environmental and economic threat. The release of several thousands of petagrams of carbon over a few hundred years will overwhelm the capacity of the surface ocean reservoirs to absorb carbon. The recorded and anticipated changes in seawater carbonate chemistry will presumably affect the global oceanic carbonate production. Coccolithophores as the primary calcifying phytoplankton group, and especially *Emiliana huxleyi* as the most abundant species have shown a reduction of calcification at increased CO₂ concentrations for the majority of strains tested in culture experiments. A reduction of calcification is associated with a decrease in coccolith weight. However, the effect in monoclonal cultures is relatively small compared to the strong variability displayed in natural *E. huxleyi* communities, as these are a mix of genetically and sometimes morphologically distinct types. Average coccolith weight is likely influenced by the variability in seawater carbonate chemistry in different parts of the worlds' oceans and on glacial/interglacial time scales due to both physiological effects and morphotype selectivity. An effect of the ongoing ocean acidification on *E. huxleyi* calcification has so far not been documented in situ. Here, we analyze *E. huxleyi* coccolith weight from the NW Mediterranean Sea in a 12 yr sediment trap series, and surface sediment and sediment core samples using an automated recognition and analyzing software. Our findings clearly show (1) a continuous decrease in the average coccolith weight of *E. huxleyi* from 1993 to 2005, reaching levels below pre-industrial Holocene and industrial 20th century values recorded in the sedimentary record, and (2) seasonal variability in coccolith weight that is linked to the coccolithophore production. The observed long-term decrease in coccolith weight is most likely a result of the changes in the surface ocean carbonate system. Our results provide first indications of an in situ impact of ocean acidification on coccolithophore weight in a natural *E. huxleyi* population even in the highly alkaline Mediterranean Sea.

Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



1 Introduction

A key question in global climate change research is how the uptake of anthropogenic CO₂ from the atmosphere into the ocean will affect the ocean ecosystem in the near future (Bindoff et al., 2007; Kleypas et al., 2006; Kroeker et al., 2013). Model projections have shown that the global carbonate system will undergo substantial changes with a drastic decline in pH and calcium carbonate saturation by the end of the century (Orr et al., 2005; Zeebe, 2012). Calcifying organisms are most likely to be negatively affected by the process commonly called “ocean acidification” (OA), and a series of studies have demonstrated the sensitivity of calcification in response to OA for a variety of different organism groups (Kleypas, 1999; Lischka et al., 2011; Moy et al., 2009; Riebesell et al., 2000; van de Waal, 2013). Coccolithophores are the major calcifying phytoplankton group, and a reduction in coccolithophore calcium carbonate production would influence the global carbonate cycle and reduce organic carbon export (Gehlen et al., 2007; Wilson et al., 2012). Various culturing studies have demonstrated that the most abundant coccolithophore species *Emiliana huxleyi* reacts to increased CO₂ with a decrease in calcification, but the response is highly variable between strains (de Bodt et al., 2010; Langer et al., 2009; Riebesell et al., 2000). The genetic diversity among *E. huxleyi* (Read et al., 2013) even harbors a haplotype that can heavily calcify under elevated CO₂ and is environmentally restricted to high latitudes and upwelling regions (Beaufort et al., 2011; Smith et al., 2012). This haplotype is probably responsible for previous reports on an increase in *E. huxleyi* weight in response to ocean acidification (Beaufort et al., 2011; Grelaud et al., 2009; Iglesias-Rodriguez et al., 2008), but has not been reported from the Mediterranean thus far (Beaufort et al., 2011).

The in situ response to OA is more difficult to investigate, as physiological measurements on coccolithophore calcification are not feasible over extended time periods in the field. Coccolith weight increases under conditions that are favorable for coccolithophore calcification and therefore is an indicator for the calcification rate of the coccolithophore cell (Bach et al., 2012; Beaufort et al., 2011). A global study on

BGD

10, 19701–19730, 2013

Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

***Emiliana huxleyi*
coccolith thinning in
the Mediterranean
Sea**

K. J. S. Meier et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

the variations of coccolith weight over the natural range of CO₂ concentrations in the world's oceans has shown that coccolith weight decreases with increasing CO₂, and this effect can also be traced back in sedimentary archives of the last glaciation under natural CO₂ variations (Beaufort et al., 2011). In summary, coccolith weight decreases in laboratory experiments mimicking future OA scenarios, it decreases during periods of natural CO₂ increase during the last glacial termination, and it is nowadays lower in oceanic regions with naturally elevated CO₂ concentrations.

In this study we tested whether the ongoing ocean acidification has already affected the weight of *E. huxleyi* in the NW Mediterranean Sea. We carried out weight measurements on *E. huxleyi* coccoliths from a sediment trap series deployed in the Gulf of Lions from 1993 to 2005, and compared them to environmental data in order to determine which environmental factors may have driven changes in coccolithophore calcification. We also investigated sediment records from the region representing the 20th century and the Holocene (the last 10 000 yr) in order to test if coccolith weight has decreased since the beginning of the industrial period.

2 Site description

The Mediterranean Sea is known to be highly supersaturated with respect to carbonate throughout the entire basin from the surface to depth (Alvarez et al., 2013; Schneider et al., 2010, 2007). At the same time, it serves as a sink for anthropogenic CO₂, which is absorbed in the surface layers and transported into the deeper parts of the basin by mixing (Ait-Ameur and Goyet, 2006; Bethoux et al., 2005). The absolute values of anthropogenic carbon in the Mediterranean Sea are exceptionally high, and a decrease in pH between 0.061 and 0.148 since the pre-industrial era has been suggested (Schneider et al., 2010; Touratier and Goyet, 2011; Touratier et al., 2012). These unique oceanographic features make the Mediterranean a natural laboratory to study the effect of anthropogenic acidification on calcifying organisms.

Emiliana huxleyi
coccolith thinning in
the Mediterranean
Sea

K. J. S. Meier et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

A key area that combines all of these aspects is the northwestern part of the Mediterranean. A natural annual variation in $p\text{CO}_2$ driven mainly by temperature can be observed in the surface water column with the highest values occurring in the upper 50 m in summer under well-stratified conditions (Copin-Montégut et al., 2004). In winter the water column becomes unstable at temperatures below $\sim 13^\circ\text{C}$ and the surface water mixes with the underlying intermediate waters that are rich in dissolved inorganic carbon (DIC). This leads to an increase in $p\text{CO}_2$ in surface waters in autumn and early winter when biological production is low. However, mixing also brings nutrients into the photic zone resulting in phytoplankton blooms beginning in late winter and early spring, which lead to a $p\text{CO}_2$ decrease (Copin-Montégut and Bégovic, 2002; Copin-Montégut et al., 2004).

Long-term algal pigment observations at the DYFAMED site in the NW Mediterranean Sea have shown that haptophytes (including coccolithophores) are generally the dominant algal class throughout the year (Marty and Chiaverini, 2010; Marty et al., 2002). Production of haptophytes is highest in February/March and mostly takes place between 20 and 50 m water depth (Marty et al., 2002). This annual cycle is controlled by a seasonal change between nitrate limitation during winter and phosphate limitation during summer (Marty et al., 2002).

A prominent hydrological change has been observed in the NW Mediterranean Sea in 2006, with a warming of the deeper water masses due to mixing of the entire water column during winter (Marty and Chiaverini, 2010). This event was presumably preconditioned by drought years from 2003 to 2005, leading to a salinity increase and subsequently more intense mixing in winter. After these intense mixing events, nutrient levels were higher than usual, leading to diatoms becoming more abundant during the following spring blooms (Marty and Chiaverini, 2010).

3 Material and methods

The sediment trap material investigated here originates from the Gulf of Lions, NW Mediterranean Sea (43°02' N, 5°11' E, 1030 m water depth, Fig. 1). A sediment trap was continuously deployed over 6 month periods from 1993 to 2005 in the Planier Canyon at 500 m water depth and 530 m above bottom. No samples were available for the periods February–April 1994, June 1996 to January 1997, June–September 2000 and May–September 2004. The collected particles used here were filtered and picked to remove microzooplankton from the samples. The trap details and the description of the original sample processing have been published before (Heussner et al., 2006). Trap cups were filled with a formalin solution and neutralized with sodium borate, and pH was monitored before deployment and before processing to verify and ensure carbonate preservation.

Splits of the original sediment trap samples were brought into homogenous suspension in water. An aliquot representing between 0.2 and 2 mg of trap particles was taken from the suspension with a glass pipette and placed on a 47 mm diameter and 0.45 µm pore size cellulose nitrate filter. The filter was oven dried at 50 °C over night and embedded in Canada balsam on a glass slide to make the filter transparent.

All slides were analyzed with a polarizing microscope (LEICA DMRBE) with a 2 Megapixel Spot Insight camera. Routine checks on the assemblage showed that *E. huxleyi* dominated the assemblage throughout the record. 40 fields of view were taken automatically and analyzed with the automated recognition software SYRACO (Beaufort and Dollfus, 2004). Image analysis was performed on the output files for *Emiliana huxleyi* to obtain length and weight of the individual coccoliths. In total 35 602 coccoliths were identified. Only those data points within the inner fence of a box and whisker plot of coccolith length and weight were included in the analysis, i.e. values larger than 4.22 µm length and 12.28 pg weight were eliminated (1035 data points). For methodological details see previous studies (Beaufort, 2005; Beaufort et al., 2011, 2008).

BGD

10, 19701–19730, 2013

Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

***Emiliana huxleyi*
coccolith thinning in
the Mediterranean
Sea**

K. J. S. Meier et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

The selected surface and the Holocene sediment samples were collected during R/V *Meteor* cruise M40/4 (1998). Multicorer station #82 from the Gulf of Lions (42°18.51' N, 3°46.4' E, 1078 m water depth, 0–1 cm) spans approximately the last 40 to 80 yr, assuming approximate sedimentation rates of 0.1 to 0.15 cm yr⁻¹ (Miralles et al., 2005) and a bioturbation depth of 5–8 cm for the position. The gravity core station #87 taken near the Balears (38°59.28' N, 04°01.38' E, 1913 m water depth, 0–30 cm, sampled every cm) covers the time span of about 200 to 10 800 yr BP (Emeis et al., 2003). Smear slides were prepared using standard protocols, and coccolith measurements were carried out as described above.

Environmental data covering the time span of the analyzed trap samples were collected from the DYFAMED database (<http://www.obs-vlfr.fr/dyfBase/index.php>), the Ocean Productivity homepage (<http://www.science.oregonstate.edu/ocean.productivity/index.php>), and the OceanColor webpage (<http://oceancolor.gsfc.nasa.gov>). Detailed carbonate system parameters, temperature, salinity and nutrient measurements are only available for the DYFAMED site, which is located about 200 km east of the trap position (43°25' N, 7°52' E), i.e. upstream with respect to the general E–W circulation of the Northern Current along the slope (Fig. 1). It has been shown before that this data can be used for comparison with the sediment trap data (Heussner et al., 2006). Carbonate system measurements (i.e. alkalinity and DIC) are only available for the years 1998 to 2000 and 2003 to 2005. Data were obtained for the upper 200 m of the water column. Missing measurements were replaced with values obtained from linear regression of the measurements from above and below. [CO₂] and pH were calculated from the measured total alkalinity and dissolved inorganic carbon measurements with the CO₂SYS macro (Lewis and Wallace, 1998) using the CO₂ dissociation constants by Mehrbach et al. (1973) refit by Dickson and Millero (1987), KHSO₄ by Dickson (1990) and the seawater scale for pH. This data based on carbonate system measurements was then compared to theoretical carbonate system parameters calculated by the CO₂SYS macro as described above, by using atmospheric [CO₂] and alkalinity calculated from salinity (Schneider et al., 2007) for the entire timespan.

Primary productivity (npp) (Behrenfeld and Falkowski, 1997) and particulate inorganic carbon data (PIC) are derived from SeaWiFS satellite ocean color measurements taken as close as possible to the trap location (43° N, 5° 10' E, 10' resolution).

A singular spectrum analysis (SSA) was carried out on the coccolith weight and the environmental datasets in order to decompose trends from seasonal signals. For this, an evenly spaced time series without gaps (monthly values) was produced from the data. Monthly averages were calculated in those cases where traps were sampled twice in one month. Small gaps (1 to 3 months) were filled by linear interpolation between the values before and after the gap. Longer gaps were filled using the monthly averages from all years, in order to avoid the loss of the seasonal signal in the gap. These values were adjusted for the specific year, in order to compensate for colder or warmer years compared to the long-term average. For this, the difference between the actual measurement and the monthly average was calculated for the months before and after the gap. A linear interpolation between these two differences led to the adjustment values for the monthly averages.

4 Results and discussion

4.1 *E. huxleyi* coccolith weight and length

Seasonality and long-term trends are clearly shown in the weight and length of *E. huxleyi* coccoliths collected by the sediment trap investigated here (Fig. 2). The mean weight of *E. huxleyi* coccoliths shows maxima from February to May and minima from August to November during most parts of the record. The annual amplitude in average weight is about 1 pg. There are two periods in the record during which maxima occur twice a year. From 2001 to 2002, and from late 2004 to late 2005 maxima occur around January and June (Fig. 2a and b). Average coccolith length shows little seasonal variability with an amplitude of about 0.1 μm (Fig. 2c and d).

BGD

10, 19701–19730, 2013

Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

The inter-annual variability in weight and length of *E. huxleyi* is relatively small, but a long-term decrease can be observed from 1993 to 2005 (Fig. 2a and c), with a more pronounced decrease starting in 2001 and a further decrease only in weight from September 2004 onwards. Annual mean weight values decrease from about 5 pg in the first part of the record to less than 4 pg towards the end, equaling approximately a 20 % reduction in average weight (Fig. 2a and c). Annual mean length values show the same trend, but decrease only from 3.16 to 3.06 μm , which is a reduction of about 3 %. Theoretically, a reduction in length could be responsible for a decrease in weight without changing how well the coccolith is calcified. Coccolith weight has been shown to be approximately linearly correlated to the cube of coccolith length (Young and Ziveri, 2000). This means that a 3 % reduction in length (i.e. a reduction to 97 %) equals approximately a 9 % loss in weight ($0.97^3 \approx 0.91$), which is considerably less than the observed weight decrease of about 20 %. Therefore, coccolith weight decreases more than can be expected based on the length reduction, indicating that coccoliths become less calcified.

There are four intervals in the 1993–2005 trap deployment during which exceptionally low weight and length values of about 2 to 3 pg and less than 3 μm have been observed (Fig. 2). These are November 1993 to April 1994, June to November 2000, May to August 2004, and September to December 2005. As these extremely low measurements are not randomly spread over the record but last over periods of several months, it is likely that they represent a mechanism that leads to decreased coccolith weight. Carbonate dissolution during or after sample preparation is unlikely to have occurred, as all samples have been treated in the same way, and previous studies did not show a decrease in the carbonate content during these periods (Heussner et al., 2006). In most of these samples very few coccoliths were detected (Fig. 2), which suggests that *E. huxleyi* production could have been lower. The years 2000, 2004 and 2005 were characterized by intense mixing events during late winter (Marty and Chiaverini, 2010). In late winter and early spring of these years *E. huxleyi* is still abundant, but in the following months numbers decrease to a minimum (Fig. 2). As diatoms

Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

have a tendency to be more abundant during years following mixing events (Marty and Chiaverini, 2010), the decrease in *E. huxleyi* production may be related to a different phytoplankton community structure. In addition, in the years 2000 and 2004 coccolith weight changes from a one maximum per year to a two maxima per year signal after these coccolith-poor periods (Fig. 2). This may indicate, that the normal seasonal development of the *E. huxleyi* population was disturbed following intense winter mixing. The unusual seasonality can last for extended periods. After the change in late 2000 it took the system until 2003 before a normal seasonal signal established again in *E. huxleyi* weight (Fig. 2). The exact mechanism leading to these periods with extremely low coccolith weight and length values remains unclear, but it seems very likely that they represent exceptional phases that are different from the normal seasonal signal in the record. Therefore, measurements from these periods have been excluded from all analyses.

4.2 Sediment transport

Seasonal changes in sediment resuspension plays an important role in particle transfer on the Gulf of Lions margin (Canals et al., 2006; Heussner et al., 2006). In a previous multi sediment trap study including the trap investigated here, a linear increase of the carbonate content in the sediment trap material with increasing mass flux has been observed (Heussner et al., 2006). In the samples used here the influence of biological production on the sedimentation was shown to be highest compared to other settings in the Gulf of Lions (Heussner et al., 2006). This is likely because the trap was deployed in relatively shallow water (500 m water depth, mid-water column) and was located in the eastern part of the Gulf of Lions where the influence of resuspended material transported is smallest (Heussner et al., 2006). The lack of a linear relationship between total mass flux and the number of *E. huxleyi* coccoliths per gram of particles in our trap is shown in Fig. 3. This indicates that the majority of *E. huxleyi* coccoliths are likely to reflect the actual export production rather than resuspension, as has also been observed for silicoflagellates in the same trap (Rigual-Hernández et al., 2010).

4.3 Environmental controls

Oceanographic features of the NW Mediterranean Sea are well reflected in the weight and length of *E. huxleyi* coccoliths collected by the sediment trap investigated here (Fig. 4). Possible causes for the observed seasonal and long-term variations in *E. huxleyi* weight and length are changes in *E. huxleyi* production, morphotype selectivity related to environmental factors or changes in *E. huxleyi* calcification due to natural carbonate system variability (seasonal) or ocean acidification (long-term).

4.3.1 Seasonal variation in temperature, nutrients, salinity, and the carbonate system

Emiliana huxleyi coccolith weight and length have been shown to vary with different environmental parameters. The seasonal variability in temperature, salinity, nutrient concentration, and the carbonate system parameters is clearly expressed in both the raw measurements and the SSA extraction of the seasonal signal (Figs. 4 and 5).

E. huxleyi morphotypes show a distinct temperature preference in the NW Pacific, with a morphotype below 4.1 μm length preferentially found in warmer waters, and larger morphotypes characteristic of colder water masses (Hagino et al., 2005). In paleoceanographic studies, *E. huxleyi* coccoliths $> 4 \mu\text{m}$ are frequently used as a cold-water indicator (Flores et al., 2010). In our record there is no detectable seasonal variability in *E. huxleyi* length, and the vast majority of coccoliths measured here are below 4 μm in length, implying that the length variation observed in our data cannot result from *E. huxleyi* morphotype temperature selectivity. In addition, a direct influence of temperature on coccolith weight has not been found in culturing experiments (de Bodt et al., 2010) or to be statistically significant in a recently published global study (Beaufort et al., 2011). In our study, however, *E. huxleyi* coccolith weight has its maximum in February to May when temperatures are still relatively low, and decreases during summer when temperatures reach a maximum of about 16 to 20°C in the upper 40 m (Figs. 4 and 5). Therefore, the possibility that the temperature increase during the year

BGD

10, 19701–19730, 2013

Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



contributes to decreased average weight in *E. huxleyi* cannot be ruled out entirely. As mentioned above, the seasonal temperature variability also causes changes in the carbonate system (Copin-Montégut et al., 2004), which in turn could be responsible for coccolith calcification changes.

Salinity has been suggested to influence *E. huxleyi* morphometry, which has been consequently proposed as an indicator for past sea surface salinity (Bollmann et al., 2009; Fielding et al., 2009). However, a recent global survey has shown that the calcification state of *E. huxleyi* is not related to salinity (Beaufort et al., 2011), which is confirmed by our data. The salinity variability is too small (Figs. 4 and 5) to account for a substantial change in coccolith length (Bollmann et al., 2009), and therefore not one of the main factors controlling weight and length of *E. huxleyi* here.

Nutrient availability influences calcification in *E. huxleyi* in two ways: increased coccolith weight has been observed in cells grown under higher nutrient conditions and produced during coccolithophore blooms (Beaufort et al., 2007), but also under phosphate limitation despite slower growth (Kayano and Shiraiwa, 2009; Müller et al., 2008; Satoh et al., 2009). At the trap site both effects may play a role. Satellite derived primary production data shows a seasonal productivity cycle with maxima occurring in late winter/early spring, and phosphate limitation occurs in summer (Figs. 4 and 5). Absolute nutrient values are highest in winter (December to February) with about $6 \mu\text{molL}^{-1}$ nitrate and $0.2 \mu\text{molL}^{-1}$ phosphate, and then decrease to extremely low values in summer. The lower part of the photic zone also shows little seasonal variability but generally slightly higher values with up to $8 \mu\text{molL}^{-1}$ nitrate and $0.4 \mu\text{molL}^{-1}$ phosphate (Figs. 4 and 5). Coccolith weight of *E. huxleyi* shows a seasonal cycle that is in good accordance with the nutrient and productivity pattern (Figs. 4 and 5), whereas coccolith length shows no prominent seasonality. The general productivity pattern in the Gulf of Lions seems therefore to be responsible for an increase of *E. huxleyi* coccolith weight in February to May. If the P-limitation in summer has an effect, it is not strong enough to level out the seasonal signal in *E. huxleyi* weight, but may be one of the reasons for the reduced seasonal signal in *E. huxleyi* coccolith length. A less pronounced seasonality

BGD

10, 19701–19730, 2013

Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

***Emiliana huxleyi*
coccolith thinning in
the Mediterranean
Sea**

K. J. S. Meier et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

in nitrate and phosphate concentrations in 2001 and 2002 is paralleled by a reduced seasonal signal of *E. huxleyi* coccolith weight (Fig. 4), which is a further indication for the importance of nutrient supply for *E. huxleyi* calcification. Interestingly, the PIC data does not follow the productivity and coccolith weight trends (Fig. 4). As recently shown (Daniels et al., 2012) this may be due to suspended particles that are common in coastal regions.

A recently published conceptual model for the effects of the carbonate chemistry on coccolithophore calcification describes that calcification follows an optimum curve response to gradients in pH and dissolved inorganic carbon (DIC) (Krug et al., 2011). Calcification will decrease outside the optimum conditions, i.e. with decreasing pH and increasing DIC in the case of OA. An experimental design to test the effect of individual parameters of the carbonate system has confirmed that pH, $[\text{HCO}_3^-]$ and $[\text{CO}_3^{2-}]$ are the main factors controlling coccolith morphology and weight (Bach et al., 2012). $[\text{CO}_3^{2-}]$ was also the statistically most significant factor controlling coccolith weight in a global set of sediment and water samples (Beaufort et al., 2011).

In the data presented here, the seasonal signal can be observed on the carbonate system (e.g. $[\text{CO}_2]$, pH, $[\text{CO}_3^{2-}]$, calcite saturation) in the water column at the DYFAMED site (Figs. 4 and 5). The upper part (0–50 m water depth) shows stronger seasonal variability with elevated $[\text{CO}_2]$ and decreased $[\text{CO}_3^{2-}]$ in late winter and early spring. The lower part (70–200 m water depth) shows the opposite and weaker signal (Fig. 4). The upper and lower parts of the water column have similar $[\text{CO}_2]$ and $[\text{CO}_3^{2-}]$ values during winter and early spring when the water column is well mixed (Fig. 4). The temperature increases only in the upper 50 m of the water column during the year (Fig. 4) indicating stratified conditions in summer and autumn. This leads to a decrease in $[\text{CO}_2]$ and an increase in $[\text{CO}_3^{2-}]$ in the upper 50 m of the water column (Copin-Montégut and Bégovic, 2002), whereas the lower part is relatively stable. The largest average coccolith weight of *E. huxleyi* over the year is reached in February to May despite the elevated $[\text{CO}_2]$ and low $[\text{CO}_3^{2-}]$ values. As shown above, this is probably due to the increase in

coccolithophore production (Figs. 4 and 5), in agreement with the global survey published recently (Beaufort et al., 2011).

4.3.2 Long-term trends

The Mediterranean Sea has undergone acidification since the onset of human industrialisation, and the effect is largest in the NW Mediterranean Sea (up to 0.14 pH units, Touratier and Goyet, 2011; Touratier et al., 2012). Between the two time periods for which direct measurements of the carbonate system are available, [CO₂] increases about 1 μmol kg⁻¹, pH drops about 0.02 units, [CO₃²⁻] decreases by 7 μmol kg⁻¹, and the calcite saturation decreases by 0.14 units when comparing the time periods from 1998 to 2000 and 2003 to 2005 (Fig. 6). The calculated carbonate system parameters for the entire record are in the same range and show the same seasonal amplitude as the direct measurements (Fig. 4). The SSA analysis conducted on this data, coccolith weight and other environmental data reveals significant trends only for coccolith weight and the carbonate system parameters, whereas temperature, nutrients, and salinity present a limited variability (Fig. 7). Therefore, the most likely cause for the observed mass loss of *E. huxleyi* coccoliths is the observed change in surface water carbonate chemistry.

Further support for a reduction of coccolithophore calcification due to the influence of ocean acidification comes from the comparison of preindustrial Holocene and industrial 20th century records of coccolith weight with the sediment trap data. From 1994 to 2000, the scale of the observed weight variability in *E. huxleyi* coccoliths from the sediment trap is within the range of that recorded in pre-industrial Holocene sediments (Fig. 8). From 2001, annual averages lie in the range of the industrial surface sediments of the Gulf of Lions, that cover an approximate range of about 40–80 yr before the sampling in 1998. From 2004 they fall below these industrial average weight values (Fig. 8). Even if long-term sediment records that average over a considerable amount of time (40–80 yr in the industrial surface sediment, and a few hundred years in the Holocene record) may not be directly comparable to the interannual trend from the

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Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



sediment trap, two conclusions can be drawn: (1) coccolith weight is lower in sediments from the industrial period than in the pre-industrial Holocene, and (2) during recent years the average weight of *E. huxleyi* coccoliths has sunk to values unprecedented in the last 10 000 yr.

5 Conclusions

Our study demonstrates that long-term and seasonal variability in the average weight of *E. huxleyi* coccoliths in the Gulf of Lions has different causes. In the long-term run the seawater carbonate system displays the strongest change of all environmental parameters. Change in the surface water carbonate chemistry is the most likely parameter that has caused the decrease of *E. huxleyi* coccolith average weight below Holocene and industrial values in the western Mediterranean Sea. Productivity has a large influence on *E. huxleyi* weight on the seasonal scale, and future changes in the nutrient regime may have additional influence on CaCO₃ quota in coccolithophores. This study supports findings that have so far only been observed in laboratory experiments. Still it is only a first step in understanding what the effects of ocean acidification on coccolithophore calcification will be in the future. Recent evidence suggests resilience to lower pH environments for a genetically distinct type within the common species *E. huxleyi* (Beaufort et al., 2011; Read et al., 2013), indicating that the community response of coccolithophores to OA may be different from what can be observed in laboratory experiments on just one strain. Our study deals with a natural assemblage, and it is very likely that the coccoliths measured here represent more than just one genetic type within *E. huxleyi* (Read et al., 2013). This natural *E. huxleyi* assemblage shows a response to OA. This may be due to both physiological responses, i.e. a decrease in calcification, and morphotype selectivity within *E. huxleyi*. Future work should therefore try to disentangle these two processes of coccolithophore community calcification response to ocean acidification for reliable projections of the future global carbonate production.

Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

**Emiliana huxleyi
coccolith thinning in
the Mediterranean
Sea**

K. J. S. Meier et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

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Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)




[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

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Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

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Emiliana huxleyi
coccolith thinning in
the Mediterranean
Sea

K. J. S. Meier et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

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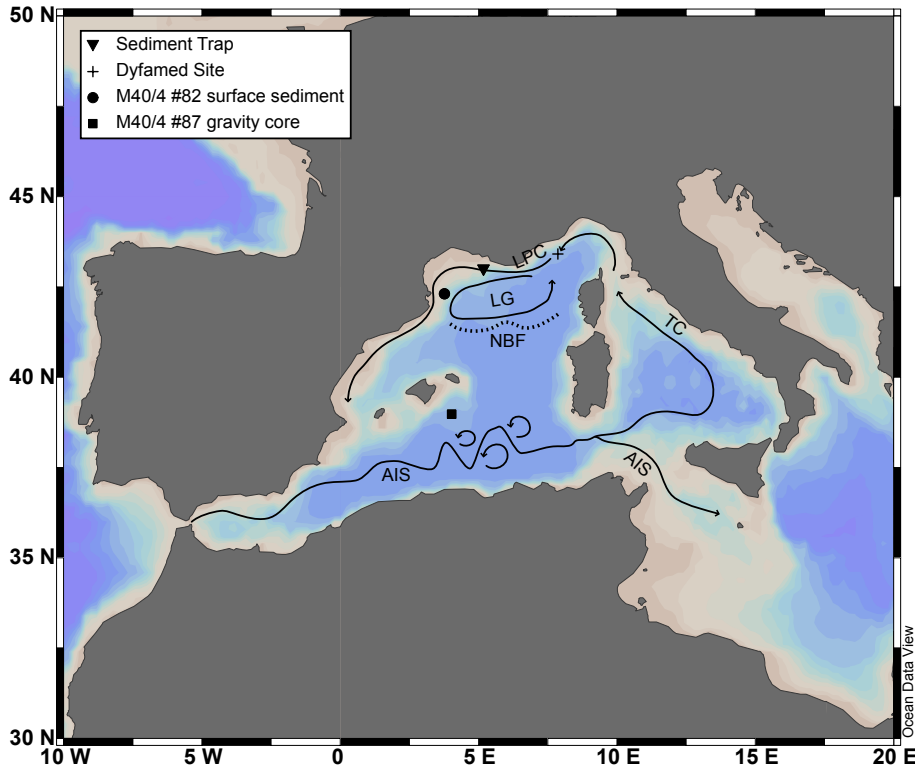


Fig. 1. Map of the NW Mediterranean Sea. Location of trap, Dyfamed Site, surface sediment sample, sediment core, and the major oceanographical currents and fronts (LPC: Liguro-Provençal Current (Northern Current), LG: Lion Gyre, AIS: Atlantic Ionian Stream, TC: Tyrrhenian Current, NBF: North Balearic Front). After Millot (1987) and Pinardi and Masetti (2000).

Emiliana huxleyi
coccolith thinning in
the Mediterranean
Sea

K. J. S. Meier et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



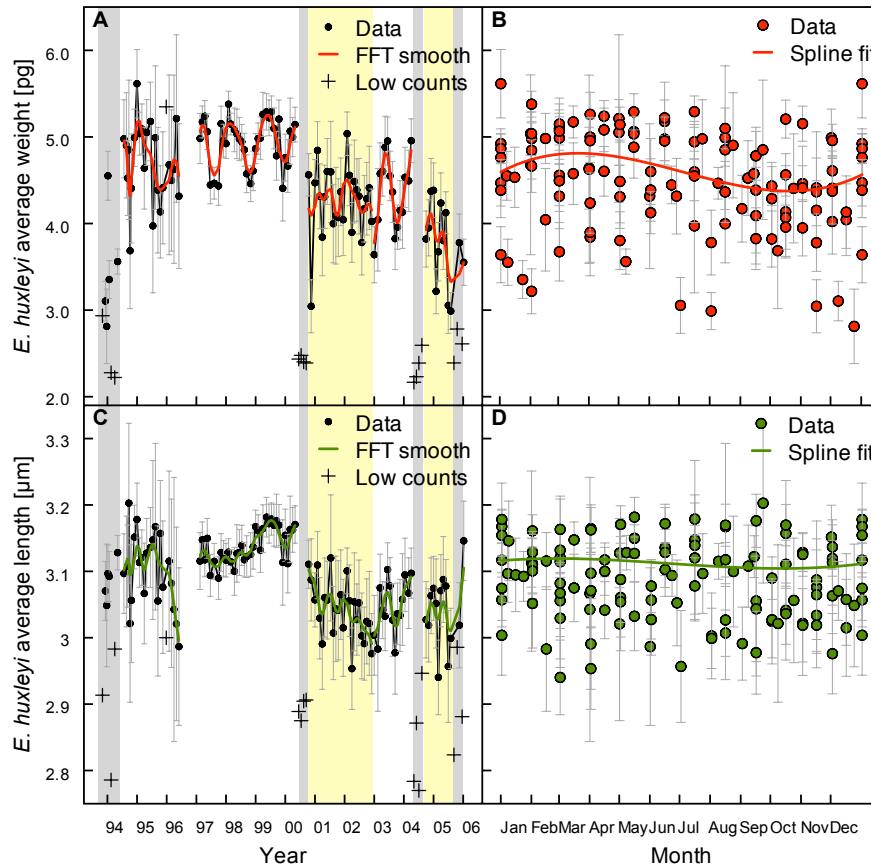


Fig. 2. *Emiliana huxleyi* mean coccolith length and weight over the sediment trap deployment period (A, C) and on a composite year (B, D). Long-term trends, seasonal variability, periods with extremely low average weight (grey shade), and periods with reduced/changed seasonality (yellow shade) are shown.

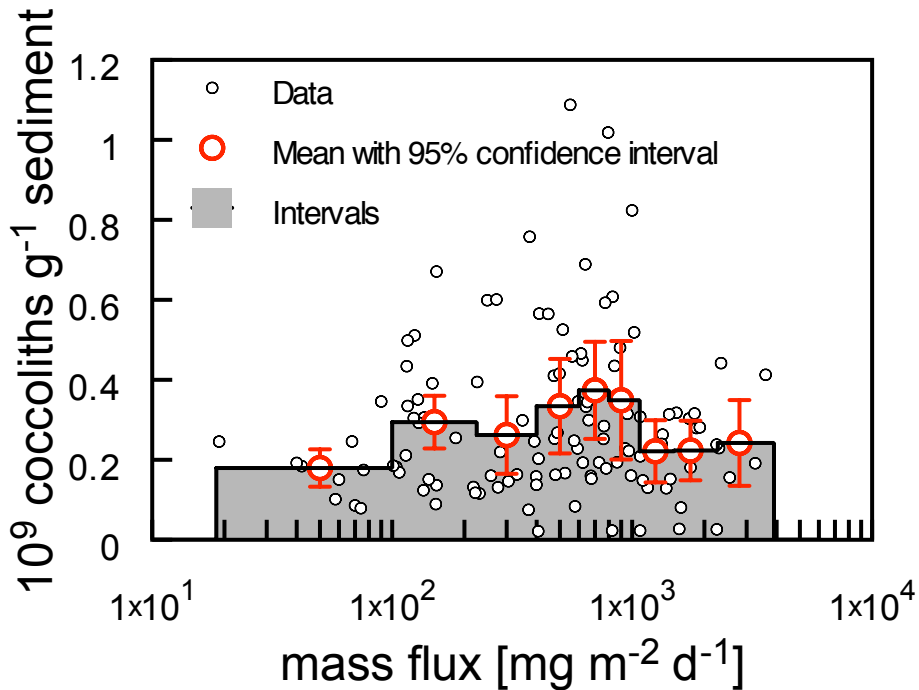


Fig. 3. *Emiliana huxleyi* coccolith concentration in trap material vs. total mass flux. Individual data points show a irregular scatter. Mean values within mass flux intervals show no increase with mass flux, indicating small influence of mass flux on coccolith weight.

Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

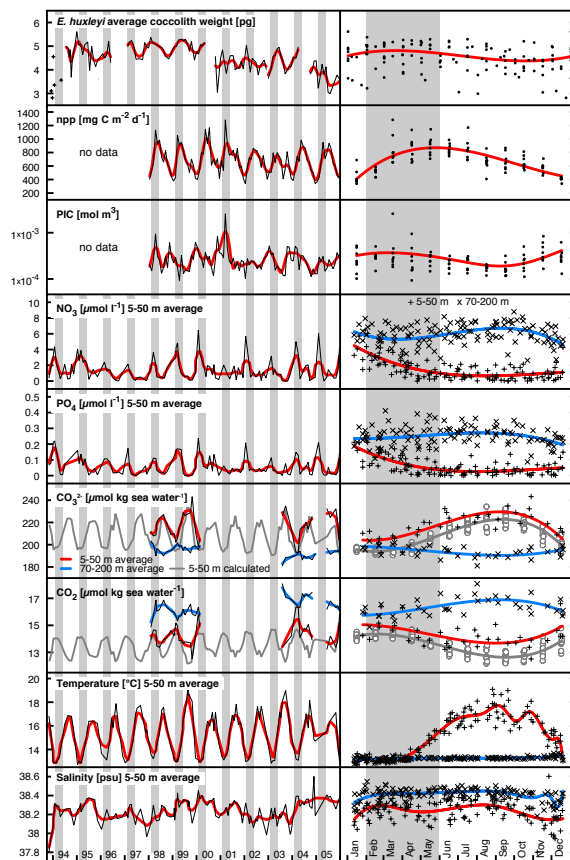


Fig. 4. *Emiliana huxleyi* coccolith weight vs. environmental data. Left: time period from 1993 to 2005 during which additional data was available. Thin lines represent original data, bold colored lines are fast Fourier transform smoothed data. Right: data as on the left plotted on a composite year, indicating seasonal trend. Bold lines represent spline fits. Grey bars indicate the time period from February to May.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

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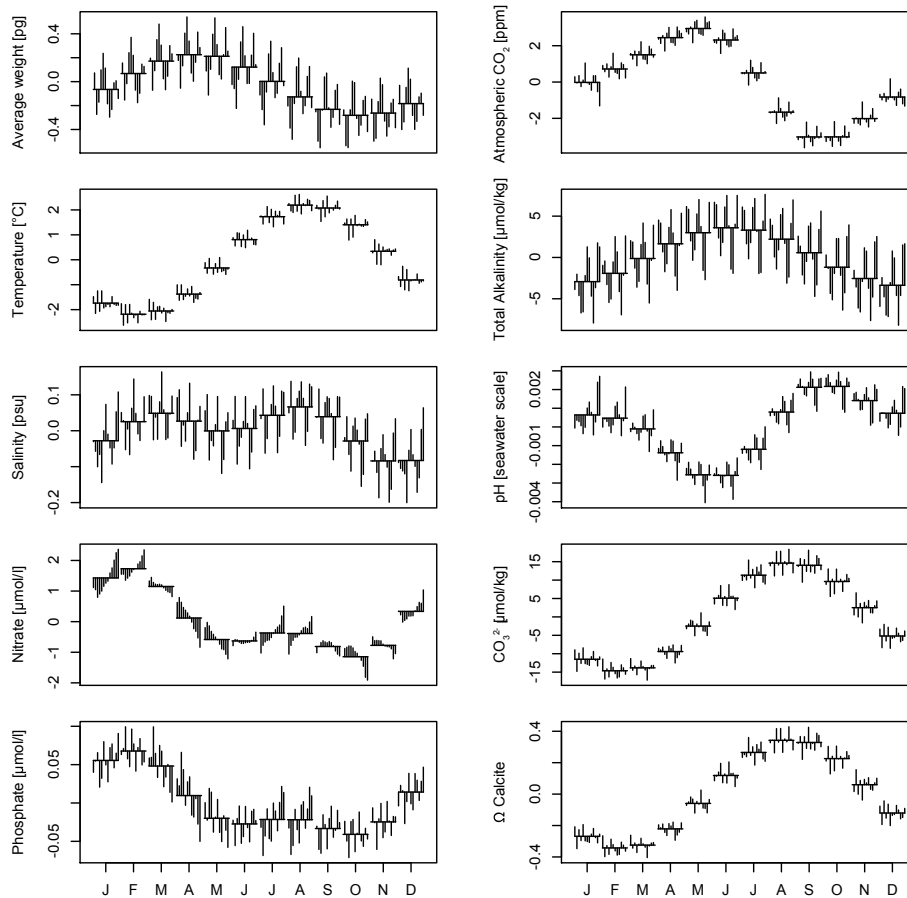


Fig. 5. Seasonal signal extracted from the weight and environmental data in Fig. 4 by a single spectrum analysis (SSA). Monthly averages and the deviation from the average for every year (bars) are shown.

Emiliana huxleyi coccolith thinning in the Mediterranean Sea

K. J. S. Meier et al.

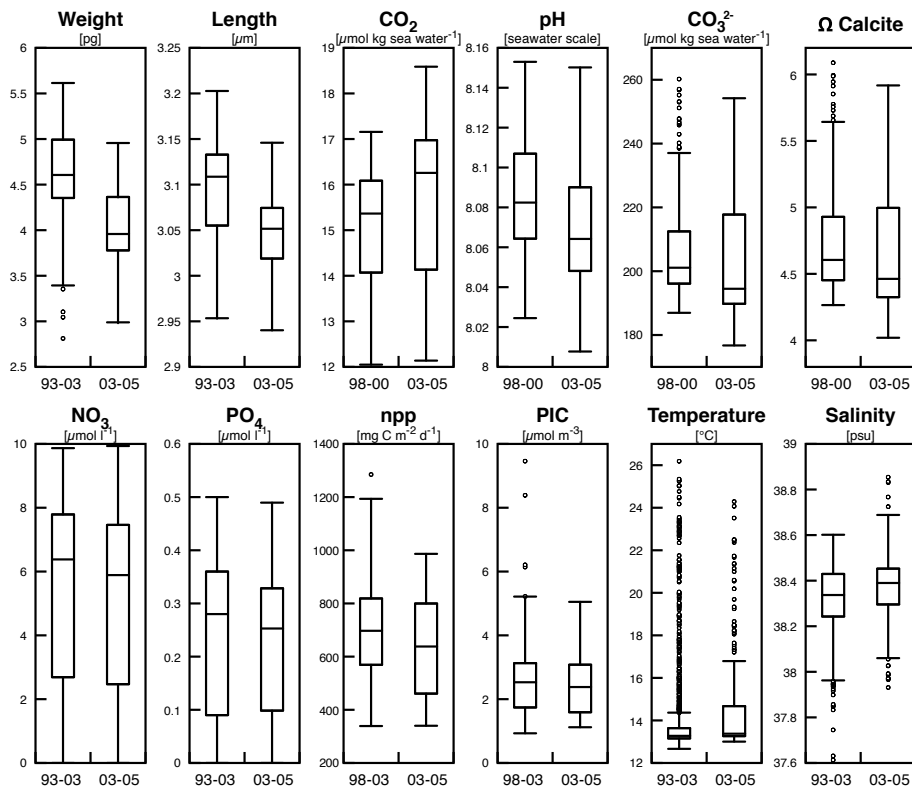


Fig. 6. Comparison of data from time periods before August 2003 with August 2003 to December 2005. Environmental data shown in Fig. 4 have been used in the box and whisker plots showing the quartiles of the data, with the median represented by the horizontal lines inside the boxes. Open circles indicate outliers.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)

[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

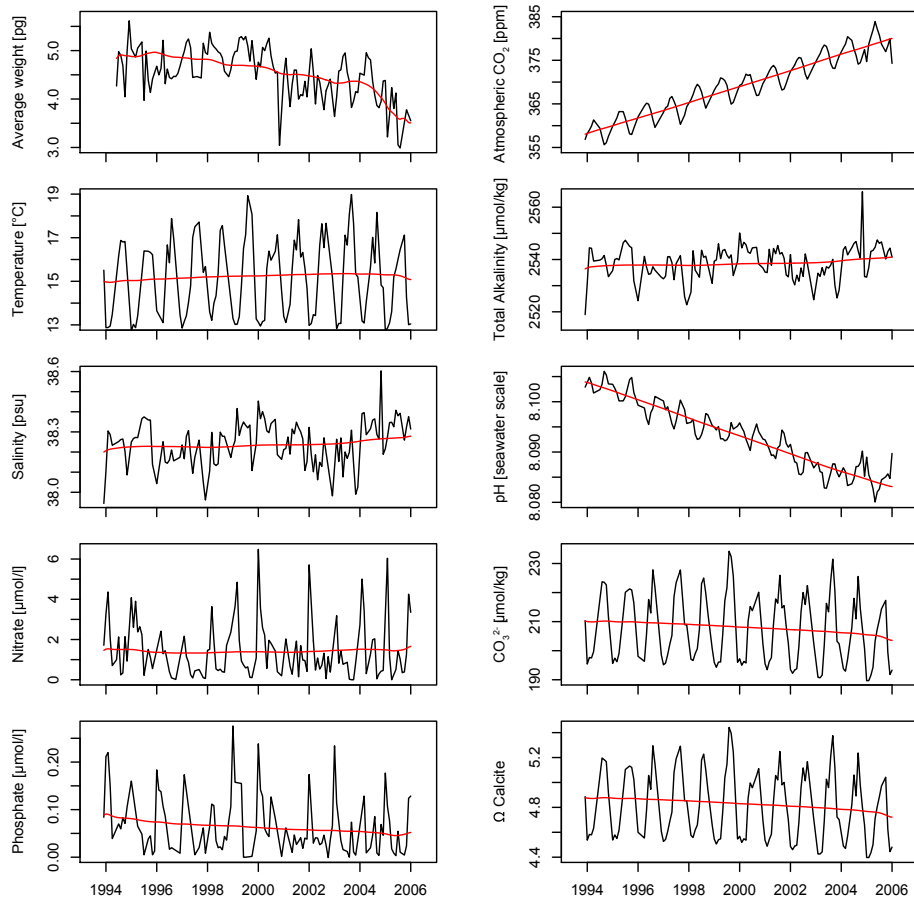


Fig. 7. Long-term trends in the environmental data from single spectrum analysis (SSA). Black lines show the evenly spaced dataset produced from the environmental measurements (see methods). Red lines indicate the trends from the SSA.

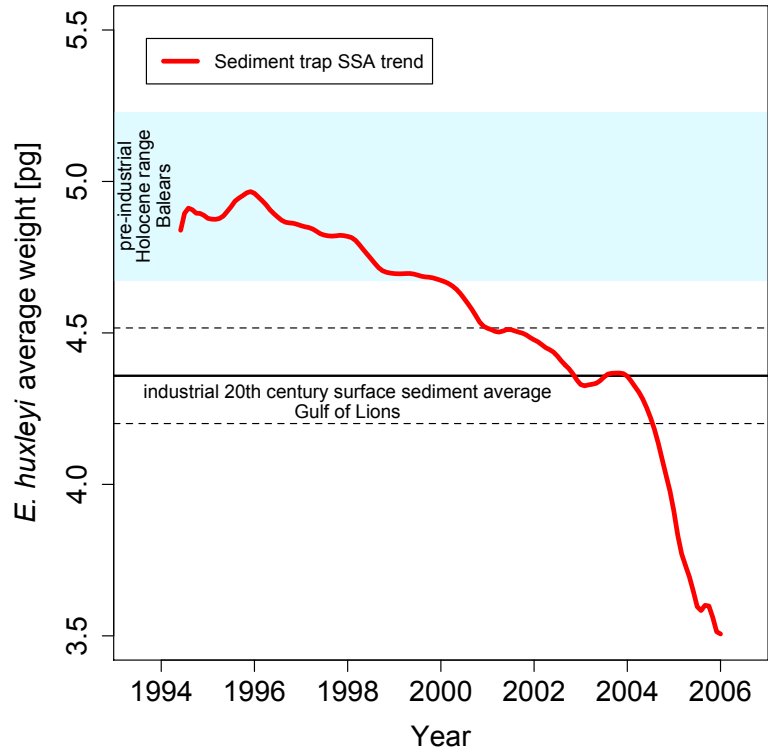


Fig. 8. Comparison of sediment trap with sediment data. *Emiliana huxleyi* SSA coccolith weight trend from the sediment trap in the Gulf of Lions in comparison with sediments from a 20th century industrial sediment surface (dashed lines indicating 95% confidence interval), and a pre-industrial Holocene sediment record (blue shaded area indicating range of average weight values) from the NW Mediterranean.

Emiliana huxleyi
coccolith thinning in
the Mediterranean
Sea

K. J. S. Meier et al.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

