



Composition and interannual variability of phytoplankton in a coastal upwelling region (Lisbon Bay, Portugal)

A. Silva ^{*}, S. Palma ¹, P.B. Oliveira ¹, M.T. Moita ¹

Instituto Nacional de Recursos Biológicos (INRB-IPIMAR), Av. Brasília s/n, 1449-006 Lisboa, Portugal

ARTICLE INFO

Article history:

Received 7 November 2008

Received in revised form 26 March 2009

Accepted 22 May 2009

Available online 23 June 2009

Keywords:

Phytoplankton succession

Time series

Diatoms

Coccolithophores

Dinoflagellates

Upwelling

ABSTRACT

From July 2001 to May 2005, at a fixed station located in Lisbon Bay (Cascais: 38° 41' N, 09° 24' W), surface seawater samples were collected on a weekly basis. We aimed to describe at different temporal scales, short-term to interannual, the phytoplankton community in relation to hydrographic conditions.

Maxima of the main phytoplankton groups varied according to the seasonality of upwelling/downwelling cycles and nutrient availability and were associated with particular hydrological mesoscale structures highlighted by satellite images. Short succession cycles were identified dependent on coastal upwelling events. Intermittent and weak pulses allowed the coexistence of species from different succession stages and groups, although having consecutive maxima. The interannual differences observed in the phytoplankton community, in Lisbon Bay, varied according to both the duration and strength of the upwelling events and to precipitation and Tagus river flow regimes.

Diatoms developed and were dominant, during spring–summer under prevailing upwelling conditions and silicon availability. Short upwelling pulses appeared to be unfavourable for diatoms maintenance. When upwelling weakened and SST increased due to onshore advection of warmer waters, coccolithophores dominated. This assemblage was the second most abundant during the study, in particular during the short transition period from upwelling (summer) to downwelling seasons (autumn) distributing in the largest range of hydrographical conditions between diatoms (maximum turbulence) during early spring and dinoflagellates (maximum stratification) during summer to further dominate during autumn and winter. Nitrites and nitrates seemed to favour greater developments of this group. Dinoflagellates peaked mainly during summer and were the less abundant through the four years due to the decrease of lasting convergence periods. Like coccolithophores, a preference for warmer waters emerged but this group seemed to have a narrow tolerance to turbulence and temperature changes.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

At the west coast of Portugal upwelling generally occurs seasonally, from April to September, under northerlies, while onshore advection of oceanic waters is observed during autumn and winter, when southerly winds begin to dominate and there is an intensification of waters flowing poleward (Fiúza et al., 1982; Haynes and Barton, 1990; Peliz et al., 2005). Episodes of reverse winds can occur during both seasons. Lisbon Bay is either influenced by the subtropical branch of the Eastern North Atlantic Central Water (ENACWst) as by Tagus river discharges, an import nutrient source especially during winter. North of the bay, an upwelling filament rooted at cape Roca (Fig. 1) recurrently occurs during the northerly wind periods (upwelling favourable), typically extending to the south and westward direction. However, at Lisbon Bay the structure of upwelling is complex since it represents an important coastline

discontinuity. This region is considered an upwelling shadow area where phytoplankton species can be accumulated through different retention mechanisms (Graham and Largier, 1997; Moita et al., 2003; Oliveira et al., 2009). Moita (2001), for this coast, identified upwelling as the major source of seasonal and spatial variability of phytoplankton. Primary production depends on incoming solar irradiance, temperature, nutrients and oligoelements and in upwelling systems is defined practically by the external energy made available (Margalef, 1978a). In shelf waters, phytoplankton production is primarily controlled by the interaction of water masses supplying different levels of nutrients to the euphotic zone (Ciotti et al., 1995) and by the alterations of the water column stability (Laubscher et al., 1993; Brandini et al., 2000). Thus, the development of a certain size structure of the phytoplankton community depends on the physical–chemical characteristics of the environment (Kiørboe, 1993).

The sampling site, Cascais (Fig. 1), is located at the northern side of Lisbon Bay and south of cape Roca. Here, phytoplankton is either influenced by upwelled waters of the Roca filament or by warmer and mature surrounding waters. The prevailing condition depends on the intensity and persistence of upwelling favourable winds and on the

^{*} Corresponding author. Tel.: +351 213027121; fax: +351 213015948.

E-mail address: amsilva@ipimar.pt (A. Silva).

¹ Tel.: +351 213027121; fax: +351 213015948.

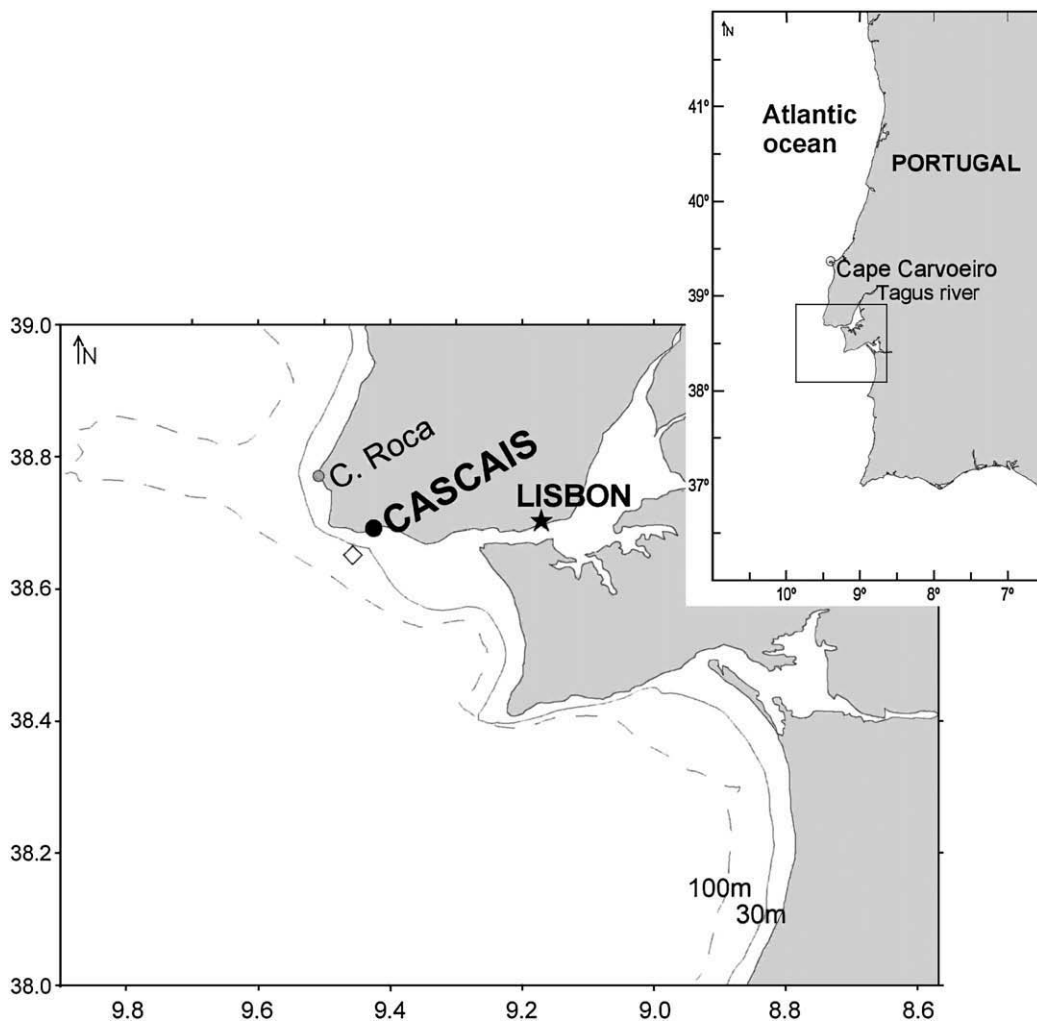


Fig. 1. Location of the sampling site – Lisbon Bay/Cascais (●) and validation station (◇), 4 km offshore.

offshelf mesoscale structures controlling the offshore extension and position of the upwelling filament. Weak upwelling conditions allow a larger influence of warmer and stratified waters into the bay.

The aim of this study, based on four years of weekly sampling, was the characterization of the dominant phytoplankton community (diatoms, dinoflagellates and coccolithophores) in relation to hydrological conditions from short-term to interannual scales of variability. Such data set will allow comprehensive observations on phytoplankton species succession and is original since rarely on Portuguese coastal waters, the three phytoplankton groups are studied simultaneously with sampling and observation methods focus on coccolithophores.

2. Materials and methods

2.1. Surveyed area and sampling strategy

From July 2001 to May 2005, at a fixed coastal station located in Lisbon Bay (Cascais: 38° 41' N, 09° 24' W) (Fig. 1), seawater samples were collected on a weekly basis, from surface, 1 h before high tide to minimize the direct influence of Tagus estuarine waters on the area. The surface samples were used for chlorophyll *a*, the fraction of chlorophyll *a* less than 20 μm , phytoplankton composition and nutrient determination. Temperature, salinity and depth were determined *in situ* with a Quanta CTD.

Daily wind data were obtained from the meteorological station of Cape Carvoeiro, located 50 km north of Cascais (Fig. 1).

2.2. Chlorophyll *a* and nutrient analyses

To evaluate the chlorophyll *a* concentration, 250 ml seawater samples were filtered and for chlorophyll *a* < 20 μm , the same volume was filtered through a 20 μm net placed on top of the filter (Whatman, 47 mm nitrate cellulose membrane with a 0.45 μm nominal pore size). Pigments were extracted with 90% acetone and determined on the Perkin-Elmer spectrofluorometer (Holm-Hansen et al., 1965).

The water for nutrient determination was filtered through a Millipore filter of 0.45 μm and stored at -4°C for subsequent analysis. Nitrites and nitrates ($\text{NO}_2^- + \text{NO}_3^-$), phosphates (HPO_4^{3-}) and silicon (SiO_4^{4-}) were determined using an autoanalyser “SKALAR” according to the methods of Technicon Industrial Systems (Grasshoff, 1983). The detection limit is 0.2 μM for silicon and 0.05 μM for nitrites + nitrates and phosphates.

2.3. Phytoplankton analyses

Phytoplankton samples were preserved with hexamethylenetetramine buffered formalin to a final concentration of 2% (Thronsdén, 1978). Phytoplankton species were identified and enumerated in subsamples of 50 ml by the Utermöhl technique (Hasle, 1978), using a Zeiss IM35 inverted microscope with phase contrast and bright field illumination. A magnification of 160 \times and 400 \times was used to analyse the phytoplankton assemblage with a detection limit of 40 cells l^{-1} and 2000 cells l^{-1} , respectively. When possible, the cells were identified to species level according to Hasle and Syvertsen (1996),

Dodge (1982) and Moita and Vilarinho (1999). Coccolithophores were separately identified and counted from water samples (750 or 1000 ml) filtered through a 47 mm nitrate cellulose membranes (Whatman) with a 0.45 μm nominal pore size. A strip of the filter was cut from the centre to the rim and slides were rendered transparent with a drop of Entellan mounting medium. Cocospheres were identified and counted until at a maximum of 300 cells of all taxa per sample (Fatela and Taborda, 2002) on an area of 2.2 mm^2 of the filter with a Zeiss optical microscope under cross-polarized light, at a magnification of 1250 \times . Depending on the overall abundance of cocospheres in the samples, counts ranged between 1 cell, corresponding to 73 cells l^{-1} and 300 cells equivalent to 22×10^3 cells l^{-1} . A scanning electron microscope (JEOL-5200) was used to complete the identifications of the coccolithophore assemblage. Species were identified following Young et al. (2003).

2.4. Data analysis

In order to validate the site, 10 supplementary surface samples were simultaneously collected once a month, 4 km offshore from the Cascais station. A Mann–Whitney *U*-test was performed with the 10 samples. The null hypothesis was that each pair of samples is drawn from a single community and therefore the medians are equal. The main phytoplankton groups were observed and quantified for the test and the *p*-level found for each pair was always above 0.1, meaning there was an overlap between the two distributions. The study site was then considered representative of the inner shelf community (Silva et al., 2008).

Based on the values of northward wind stress component a daily upwelling index was calculated (Bakun, 1973). A running average, with a window width of 7 days, was determined to allow a straight relation between data from different time scales (weekly sampling and daily upwelling index).

In order to reveal the internal structure of the data (species distribution through time) in a way which best explains the maximum variance, Principal Component Analysis (PCA) was performed using the software NTSYSpc version 2.02i from 1997 by Applied Biostatistics, Inc. The analysis constructs a new set of orthogonal coordinate axes such that the projection of points onto them has maximum variance. While defined in terms of variance and covariance, PCA was applied to standardized data since its scale dependent and the results are sensitive to the often arbitrary choices of units of measurement used in a study. As

data had a highly skewed distribution they were subject of a logarithmic transformation to restore normality in the distribution and equalize the variances and then standardized by subtracting the mean and dividing by the standard deviation. Thus, the centroid of the whole data set is zero and variance is unit. The species selected occurred at least in 20% of the samples during the four years and from the 209 taxa identified, 106 were excluded due to a relative low frequency.

Linear regressions were attempted, between the overall abundance of phytoplankton groups and each abiotic factor. No significant covariation was detected among parameters partly due to the wide range of temporal variability beneath. The highest correlations obtained were in accordance with field observations and were 0.2 ($n=197$, $p<0.05$) between coccolithophores and temperature, 0.3 ($p<0.01$) for diatoms versus Chl *a* and 0.4 ($n=197$, $p<0.01$) for total phytoplankton and Chl *a*.

The satellite-derived sea surface temperature (SST) maps were extracted from EUMETSAT's Ocean and Sea Ice Satellite Application Facility "Regional SST" product, available at 2-km resolution (CMS, 2005).

3. Results

3.1. Hydrography and nutrients

From 2001 until 2005 the upwelling conditions became more persistent, although less intense, usually higher than $-1000 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ and the number of days per year under northerlies increased (negative values in Fig. 2a). In 2004, there were more 55 days with upwelling conditions than in 2002. Conversely, the onshore advection periods of warmer oceanic waters were shorter over the years (upwelling index $>0 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$) to decreased in frequency and strength from late summer to winter seasons (Fig. 2a). Spring and summer defined the upwelling season while shorter periods of onshore advection were typically observed between mid-September and early December. The autumn and winter seasons, that are usually associated with southerlies, were recurrently dominated by persistent upwelling conditions and sometimes precipitation as in 2003 and 2004. In 2002, the upwelling and downwelling seasons were clearly distinguished but onwards the mild upwelling periods were longer, as observed in 2004.

The sea water temperature varied from seasonal to interannual time scales ranging between 11.5 $^{\circ}\text{C}$ in January 2003, under upwelling and precipitation conditions, and 20.4 $^{\circ}\text{C}$, observed in October 2002, the warmest autumn of the study period, under established convergence

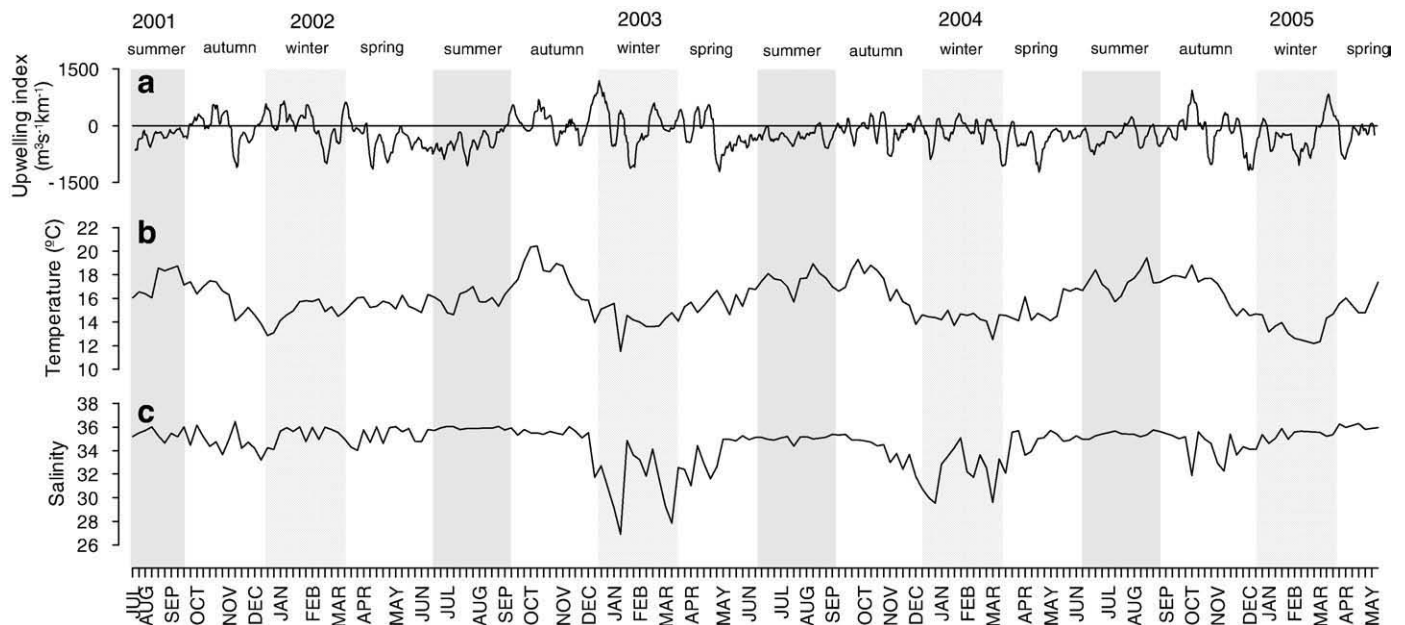


Fig. 2. Seasonal and interannual variability of upwelling index (a), temperature (b) and salinity (c), from July 2001 to May 2005.

Table 1
Seasonal average and interannual variability of phosphates, silicon and nitrites + nitrates.

($\mu\text{mol l}^{-1}$)	2001	2002	2003	2004	2005
Phosphates					
Winter	–	0.8	0.9	0.7	0.4
Spring	–	1.1	0.6	0.5	0.3
Summer	1.6	0.8	0.9	0.4	–
Autumn	3.0	0.8	1.0	0.8	–
Total	4.6	3.5	3.4	2.4	0.7
Silicon					
Winter	–	6.6	16.3	11.1	2.5
Spring	–	8.4	6.1	4.3	1.2
Summer	3.6	7.4	1.7	3.2	–
Autumn	13.9	8.2	8.8	5.6	–
Total	17.5	30.6	32.9	24.2	3.7
Nitrites + nitrates					
Winter	–	12.6	5.2	7.0	6.4
Spring	–	8.5	5.5	3.8	4.0
Summer	5.5	7.0	6.5	2.5	–
Autumn	10.0	7.3	6.0	5.8	–
Total	15.5	35.4	23.2	19.1	10.4

Grey squares indicate that sampling occurred during ~2.5 months.

(Fig. 2b). From spring to autumn seasons, SST increased ~1–1.5 °C and higher temperatures begin to be recorded earlier in the years. Summers were progressively warmer with longer periods above 17 °C. Summer 2003 in particular, had the warmer minima and higher temperatures earlier in the season. The reduced depth of the sampling site can lead to an overestimating of SST during summer. However, the raises recorded

were in agreement with other works for the area. According to Diaz et al. (2006), for the period 1991–2003, the summer 2003 (July and August) was exceptionally hot, especially in most of Western Europe. In Lisbon, the air temperature was ~4 °C higher in August 2003 than for the same period in 2002. These high temperatures influenced SST, with temperature anomalies of ~+1.5 °C in relation to the other summers. Additionally, the comparison between the SST distributions of July 2002 and 2004 showed that, despite the similar patterns of the cold upwelled water along the coast, there is a difference of more than 1 °C in the offshore temperatures, being higher in 2004, with a 15–20 day lag between the two years. It was observed that there was an increase in coastal temperatures during summer 2004 under downwelling conditions. The lowest SSTs were observed from late autumn until spring. Autumns had temperatures varying between 15 and 20 °C, with values decreasing towards winter temperatures that ranged from 12 °C to 15 °C. The winter periods became colder, with temperatures below 16 °C and the strongest differences were observed in 2003, apparently related to increments in precipitation due to an intensification of the SW winds (data on www.inag.pt and Silva et al., 2008). The rainfall regime and Tagus river flow strongly influenced salinity, especially from late autumn to winter as in 2003 and 2004, when the lowest values were recorded. During spring and early autumn values were relatively constant (around 35–35.5), usually higher than 34.5 (Fig. 2c). Salinity varied from 26.9 in January 2003 to 36.5 in October 2001. Higher salinities, as in 2002 reflected a drier year as in 2003, the longest period of intense precipitation was responsible for the subsequent strongest fluctuations in salinity.

Average nutrient concentrations per season and year are summarised in Table 1. Nutrient concentrations changed (Fig. 3), mainly

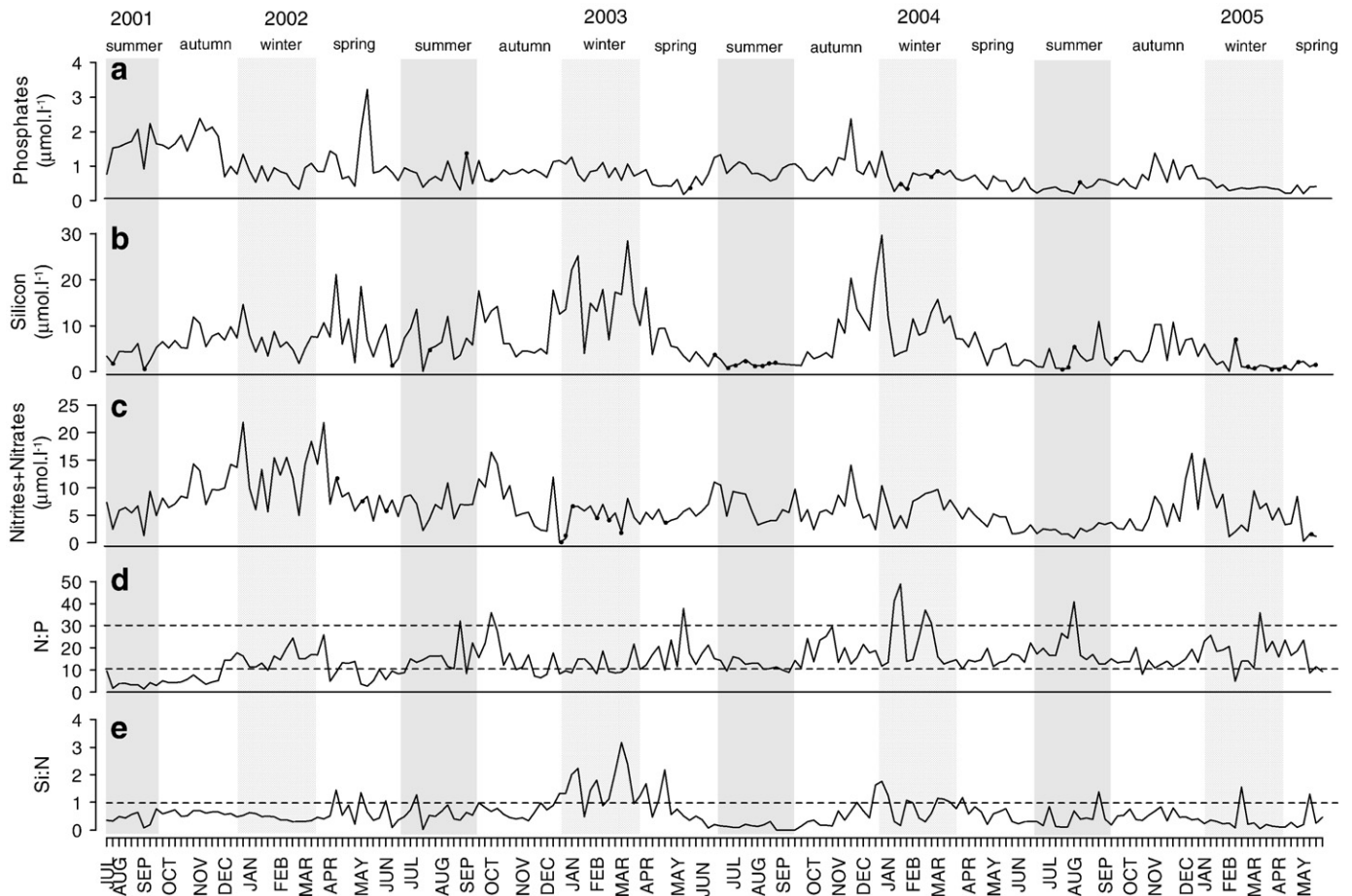


Fig. 3. Seasonal and interannual variability of phosphates (a), silicon (b), nitrites + nitrates (c), N:P ratios (d) and Si:N ratios (e) from July 2001 to May 2005. The dots (•) indicate nutrient limitation, according to Dortch and Whitlege (1992).

influenced by phytoplankton maxima causing exhaustion and by precipitation and runoff related to major inputs. Since the sampling site as a coastal location, nutrients were in general available. The highest values during autumn and early spring coincided with the lowest phytoplankton concentrations and were influenced by precipitation and runoff, especially as silicon is concerned. Conversely, the lowest nutrient concentrations, from late-spring until summer, were associated with phytoplankton consumption, sometimes until potential limitation, despite the persistency of upwelling as a nutrient supply. Concerning nutrient stoichiometry and according to [Dortch and Whitedge \(1992\)](#), from the 197 observed samples, limitation values were found 44 times ([Fig. 3d, e](#)). These two authors propose a combination between nutrient concentrations and ratios to access limitation. The measured phosphates ([Fig. 3a](#)) varied between 0.2 and $3.2 \mu\text{mol l}^{-1}$ (May 03–May 02), and were always available in 2001 and 2005 and limited one or two times in 2002–2003. During winter 2004 ([Fig. 3a, d](#)), potential limitation by phosphates ($\text{PO}_4^{3-} \leq 2$, $\text{N/P} > 30$ and $\text{Si/P} > 3$) occurred 8 times (4%). As for silicon ([Fig. 3b](#)), 2002 and 2003 presented the highest concentrations especially from autumn to spring while summer had minor concentrations. This nutrient ranged between 0.1 and $29.7 \mu\text{mol l}^{-1}$ (July 02–December 03). Potential limitation by silicon ($\text{SiO}_4^{4-} < 2$, $\text{Si/N} < 1$, $\text{Si/P} < 3$) was recorded 24 times (12%) through summer seasons (8× in 2003) and winter–spring 2005 (8×) ([Fig. 3b, e](#)). Silicon was in general available during 2001 and 2002 and particularly abundant after the rainy winters of 2003 and 2004 what possibly favoured the first diatom peaks recurrently observed through February months, the transition from winter to spring conditions. Nitrites and nitrates ([Fig. 3c](#)) were in general abundant especially during autumn–winter. Minima and maxima

were 0.06 and $21.9 \mu\text{mol l}^{-1}$ (December 02 and December 01). Nitrates potential limitation ($\text{DIN} \leq 1$, $\text{N/P} < 10$ and $\text{Si:N} > 1$) was observed 12 times (6%), during winter and spring in 2002 and 2003 ([Fig. 3d](#)).

3.2. Chlorophyll *a* and phytoplankton distribution

Chlorophyll *a* (Chl *a*) concentration presented minimum and maximum values of $0.1 \mu\text{g l}^{-1}$ (November 2001 and March 2005) and $5.3 \mu\text{g l}^{-1}$ (February 2005) respectively ([Fig. 4a](#)). Spring and summer were the two most productive seasons and the lower concentrations were usually during winter. This season, however, presented an increase in Chl *a* values since 2002 onwards, possibly related to the persistence of upwelling conditions. In average, during full years, the lowest Chl *a* concentrations were observed in 2002 while in 2004 they were the highest ([Table 2](#)).

The fraction of Chl *a* less than $20 \mu\text{m}$ increased along the years, especially during summer seasons (>50% of total Chl *a*) and was lower during winter and spring. Concentrations ranged from $0.01 \mu\text{g l}^{-1}$ in May 2002 (3% of total Chl *a*) to $3.96 \mu\text{g l}^{-1}$ in August 2001 (98% of total Chl *a*) ([Fig. 4a](#)).

Chlorophyll *a* reflected the major variations on phytoplankton biomass ($r^2 = 0.4$, $n = 197$, $p < 0.01$) that were influenced by the intensity and persistence of upwelling and downwelling events, changes in temperature and salinity and nutrient availability. Diatoms, coccolithophores and dinoflagellates ([Fig. 4](#)) represented more than 90% of cell counts. The remaining phytoplankton groups account less than 10% of total phytoplankton and were composed by small coccolithophores, small cryptophytes, chlorophytes, prasinophytes,

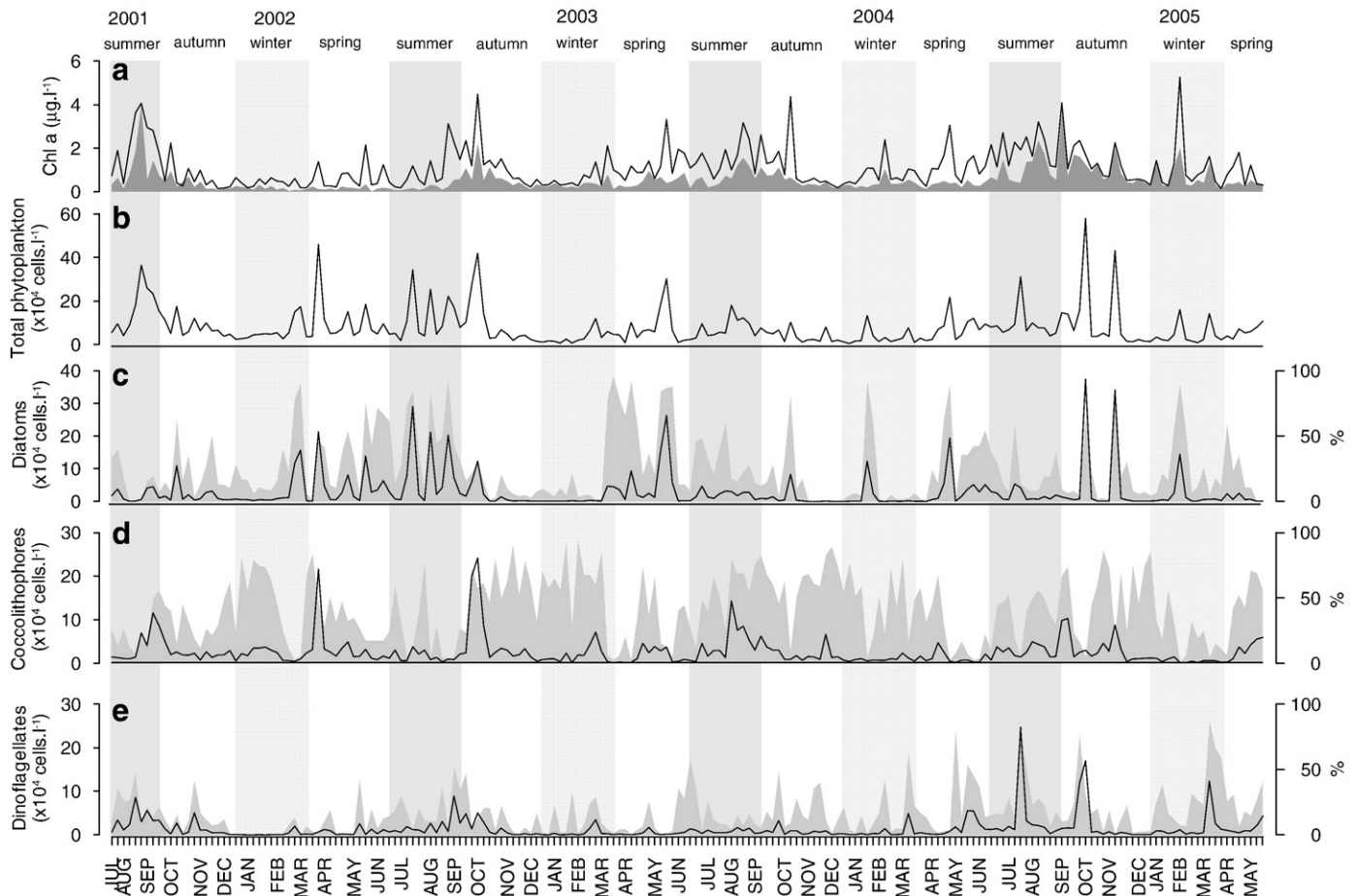


Fig. 4. Seasonal and interannual variability of Chl *a* (line) and Chl *a* below $20 \mu\text{m}$ (shadow) (a), total phytoplankton (b), diatoms (c), coccolithophores (d) and dinoflagellates (e), from July 2001 to May 2005.

Table 2
Seasonal average and interannual variability of Chl *a*, Chl *a* <20 μm and total phytoplankton, diatoms, coccolithophores and dinoflagellates.

(μmol l ⁻¹)	2001	2002	2003	2004	2005
Chl <i>a</i> (μg l⁻¹)					
Winter	–	0.4	0.7	0.9	1.2
Spring	–	0.7	1.3	1.4	0.7
Summer	2.3	1.1	1.6	2.1	–
Autumn	0.6	1.1	0.9	1.0	–
Total	2.9	3.3	4.5	5.4	1.9
Chl <i>a</i> <20μm (μg l⁻¹)					
Winter	–	0.2	0.3	0.4	0.7
Spring	–	0.2	0.5	0.5	0.3
Summer	1.2	0.3	0.8	1.3	–
Autumn	0.3	0.6	0.4	0.9	–
Total	1.5	1.3	2.0	3.1	1.0
Total phytoplankton (×10⁴ cells l⁻¹)					
Winter	–	78	44	40	51
Spring	–	150	98	107	49
Summer	150	160	101	120	–
Autumn	97	120	47	150	–
Total	247	508	290	417	100
Diatoms (×10⁴ cells l⁻¹)					
Winter	–	34	10	15	21
Spring	–	70	68	50	8
Summer	17	99	26	19	–
Autumn	24	23	11	76	–
Total	41	226	115	160	29
Coccolithophores (×10⁴ cells l⁻¹)					
Winter	–	28	23	11	7
Spring	–	49	22	20	24
Summer	38	22	63	48	–
Autumn	28	73	24	34	–
Total	66	172	132	113	31
Dinoflagellates (×10⁴ cells l⁻¹)					
Winter	–	4	6	8	18
Spring	–	9	6	22	14
Summer	31	29	10	42	–
Autumn	12	13	9	45	–
Total	43	55	31	117	32

Grey squares indicate that sampling occurred during ~2.5 months.

cyanobacteria and other not identified small algae. These groups were randomly observed and traced through the concentrations of Chl *a* <20 μm. The highest phytoplankton concentrations were observed in

Table 3
Diatoms, coccolithophores and dinoflagellates maxima (×10⁴ cells l⁻¹), dominant species, Chl *a* and Chl *a* <20 μm concentrations (μmol l⁻¹) during the period highlighted by the satellite images.

Date	18 July 2002	1 October 2002	19 July 2004
Physical conditions	Upwelling	Downwelling	Weak upwelling
Diatoms	29	12	4
Dinoflagellates	1	5	25
Coccolithophores	4	24	1.5
Dominant phytoplankton species (cell number)	<i>Pseudo-nitzschia</i> spp. (16)	<i>E. huxleyi</i> (9) <i>Gephyrocapsa</i> spp. (9)	<i>S. cf. trochoidea</i> (24)
Chl <i>a</i>	1.8	2.61	2.33
Chl <i>a</i> <20 μm	0.16	1.2	0.49
Satellite image – figure	5a	5b	5c

2002 and 2004 (508 × 10⁴ cells l⁻¹ in 2002 and 417 × 10⁴ cells l⁻¹ in 2004), mainly from spring to autumn while the lowest were during winter seasons as 40 × 10⁴ cells l⁻¹ in winter 2004 (Fig. 4b and Table 2).

Diatoms (Fig. 4c) represented the most abundant biomass source with several maxima from spring to early autumn and lower concentrations through late autumn to winter seasons (Table 2). During spring the group usually represented more than 80% of the phytoplankton community, contributing almost exclusively to Chl *a* (r² = 0.3, n = 197, p < 0.01). Diatoms were most abundant in 2002, during summer in particular, and the highest peak of the sampling period was observed in October 2004, 38 × 10⁴ cells l⁻¹ (65% of total phytoplankton). The assemblage was composed by 104 identified taxa dominated by *Chaetoceros* spp., *Thalassiosira* spp., *Pseudo-nitzschia* spp., *Skeletonema costatum*, *Asterionelopsis glacialis*, *Leptocylindrus danicus*, *Detonula pumila*, *Guinardia delicatula*, *Guinardia* spp., *Thalassionema nitzschoides* and *Cylindrotheca closterium* (Appendix A).

The satellite image from 13–18 July 2002 clearly shows the presence of colder waters (<15 °C) around cape Roca, defining an upwelling filament with a southward orientation (highlighted by white arrows in Fig. 5a). The phytoplankton community (PC) from day 18 was dominated by diatoms (85% of PA) being *Pseudo-nitzschia* spp. the main genus observed (Table 3). Coccolithophores and dinoflagellates presented very low concentrations (11% and 3% of PC, respectively) with a reduced number of species (2 species each).

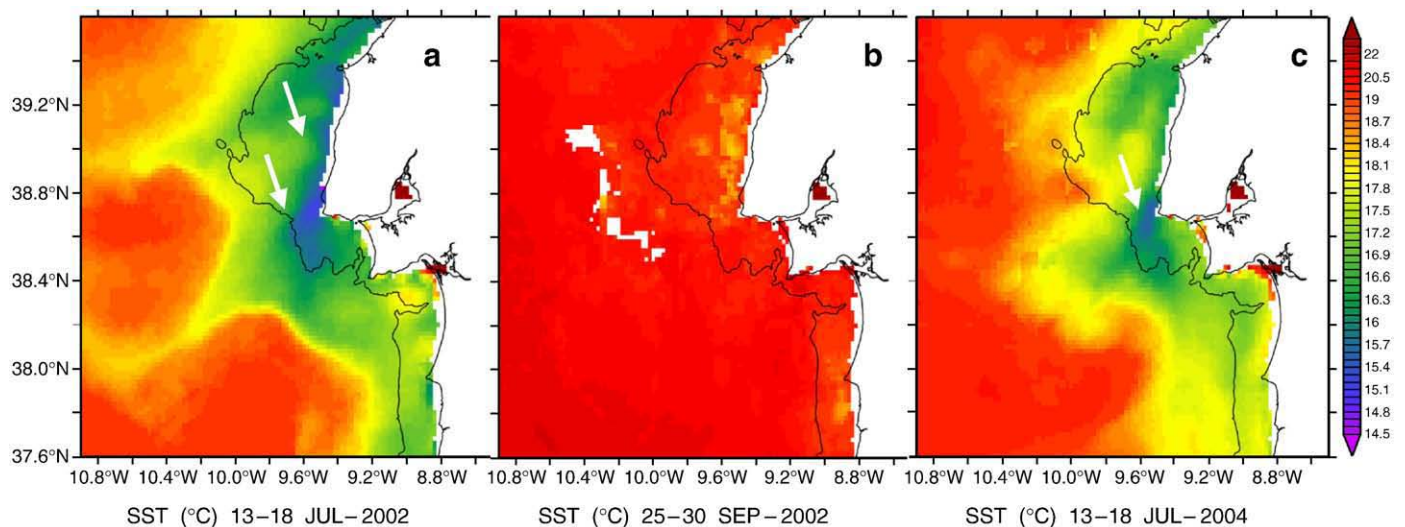


Fig. 5. Six-day average sea surface temperature (SST) derived from satellite data, previous to selected events of maxima concentration of diatoms (a), coccolithophores (b) and dinoflagellates (c). White arrows indicate the location of the upwelling filament.

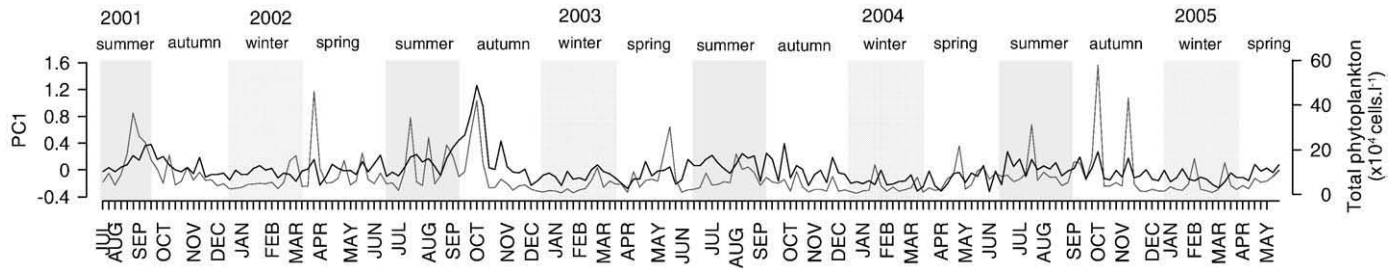


Fig. 6. Seasonal and interannual distribution of PC1 scores (black line) in relation to total phytoplankton (grey line).

Coccolithophores (Fig. 4d) reached major abundances in 2002, in particular during autumn, when the highest concentration was observed (24×10^4 cells l^{-1} in October 2002, 58% of PC). On the other hand coccolithophores recorded minor developments during winter seasons (Table 2) yet representing >90% of the phytoplankton community. Twenty two species were identified, being the assemblage dominated by *Emiliania huxleyi*, *Gephyrocapsa oceanica*, *Coronosphaera mediterranea*, *Calcidiscus quadriperforatus*, *Calcidiscus leptopus*, *Gephyrocapsa muelleriae*, *Helicosphaera carteri*, *Syracosphaera pulchra* and *Gephyrocapsa ericsonii* (Appendix A). The SST distribution (Fig. 5b) at the end of September 2002 showed that the prevailing downwelling conditions led to the onshore advection of the warm surface waters capping the remnants of the upwelled water at the end of the season. The coccolithophores *E. huxleyi* and *G. oceanica*

dominated the phytoplankton community (Table 3) and dinoflagellates attended in very low numbers (12% of total phytoplankton) but with a high species diversity (9 species present). The coccolithophore *S. pulchra* in particular, appeared for the first time during this year, in June 2004 onwards, dominating the coccolithophore assemblage, under mild upwelling conditions and the presence of offshore waters warmer than in July 2002. The species developed during a period characterized by low nitrates, a decreased in phosphates (N:P >11) and limited silicate (Si:N <1).

Dinoflagellates (Fig. 4e), the less abundant group, developed during summer–autumn and maximum abundances were observed in 2004. A peak (25×10^4 cells l^{-1}) occurred in July 2004 representing 79% of the phytoplankton community. The lowest concentrations were during winter and spring seasons (Table 2). From the 83 taxa

Table 4
Scores of phytoplankton species defined by the projection of PC1, PC2 and PC3.

Species	PC1	Species	PC2	Species	PC3
<i>Gymnodinium</i> spp.	Δ	<i>Thalassionema nitzschioides</i>	•	<i>Calcidiscus</i> spp.	+
<i>Diplopsalis</i> spp.	Δ	<i>Odontella</i> spp.	•	<i>Gephyrocapsa muelleriae</i>	+
<i>Coronosphaera mediterranea</i>	+	<i>Chaetoceros</i> spp.	•	<i>Gephyrocapsa ericsonii</i>	+
<i>Prorocentrum</i> spp.	Δ	<i>Guinardia</i> spp.	•	<i>Odontella</i> spp.	•
<i>Gephyrocapsa oceanica</i>	+	<i>Gramatophora</i> spp.	•	<i>Emiliania huxleyi</i>	+
<i>Protoperidinium diabolium</i>	Δ	<i>Pseudo-nitzschia</i> spp.	•	<i>Thalassiosira</i> spp.	•
<i>Skeletonema costatum</i>	•	<i>Guinardia cf. delicatula</i>	•	<i>Leptocylindrus danicus</i>	•
<i>Gyrodinium</i> spp.	Δ	<i>Leptocylindrus danicus</i>	•	<i>Coronosphaera mediterranea</i>	+
<i>Gephyrocapsa ericsonii</i>	+	<i>Skeletonema costatum</i>	•	<i>Gonyaulax</i> spp.	Δ
<i>Dinophysis cf. acuminata</i>	Δ	<i>Cylindrotheca closterium</i>	•	<i>Protoperidinium diabolium</i>	Δ
<i>Protoperidinium steinii</i>	Δ	<i>Detonula pumila</i>	•	<i>Gephyrocapsa oceanica</i>	+
<i>Gephyrocapsa muelleriae</i>	+	<i>Scripsiella cf. trochoidea</i>	Δ	<i>Dinophysis cf. acuminata</i>	Δ
<i>Ceratium furca</i>	Δ	<i>Thalassiosira</i> spp.	•	<i>Protoperidinium steinii</i>	Δ
<i>Gonyaulax</i> spp.	Δ	<i>Diploneis</i> spp.	•	<i>Gramatophora</i> spp.	•
<i>Thalassiosira</i> spp.	•	<i>Rhizosolenia</i> spp.	•	<i>Cylindrotheca closterium</i>	•
<i>Protoperidinium bipes</i>	Δ	<i>Licmophora</i> sp.	Δ	<i>Diploneis</i> spp.	•
<i>Cylindrotheca closterium</i>	•	<i>Protoperidinium diabolium</i>	Δ	<i>Thalassionema nitzschioides</i>	•
<i>Emiliania huxleyi</i>	+	<i>Gyrodinium</i> spp.	Δ	<i>Chaetoceros</i> spp.	•
<i>Protoperidinium</i> spp.	Δ	<i>Protoperidinium bipes</i>	Δ	<i>Protoperidinium bipes</i>	Δ
<i>Ceratium fusus</i>	Δ	<i>Prorocentrum</i> spp.	Δ	<i>Skeletonema costatum</i>	•
<i>Gramatophora</i> spp.	•	<i>Coronosphaera mediterranea</i>	+	<i>Dinophysis caudate</i>	Δ
<i>Rhizosolenia</i> spp.	•	<i>Protoperidinium steinii</i>	Δ	<i>Detonula pumila</i>	•
<i>Licmophora</i> spp.	•	<i>Diplopsalis</i> sp.	Δ	<i>Protoperidinium</i> spp.	Δ
<i>Scripsiella cf. trochoidea</i>	Δ	<i>Gephyrocapsa oceanica</i>	+	<i>Diplopsalis</i> sp.	Δ
<i>Paralia sulcata</i>	•	<i>Gonyaulax</i> spp.	Δ	<i>Guinardia cf. delicatula</i>	•
<i>Calcidiscus</i> spp.	+	<i>Dinophysis caudate</i>	Δ	<i>Prorocentrum</i> spp.	Δ
<i>Diploneis</i> spp.	•	<i>Protoperidinium</i> spp.	Δ	<i>Paralia sulcata</i>	•
<i>Guinardia cf. delicatula</i>	•	<i>Emiliania huxleyi</i>	+	<i>Scripsiella cf. trochoidea</i>	Δ
<i>Pseudo-nitzschia</i> spp.	•	<i>Gephyrocapsa muelleriae</i>	+	<i>Licmophora</i> sp.	•
<i>Dinophysis caudate</i>	Δ	<i>Gephyrocapsa ericsonii</i>	+	<i>Pseudo-nitzschia</i> spp.	•
<i>Ceratium</i> spp.	Δ	<i>Gymnodinium</i> spp.	Δ	<i>Ceratium</i> spp.	Δ
<i>Chaetoceros</i> spp.	•	<i>Calcidiscus</i> spp.	+	<i>Ceratium furca</i>	Δ
<i>Odontella</i> spp.	•	<i>Paralia sulcata</i>	•	<i>Gymnodinium</i> spp.	Δ
<i>Detonula pumila</i>	•	<i>Ceratium fusus</i>	Δ	<i>Gyrodinium</i> spp.	Δ
<i>Thalassionema nitzschioides</i>	•	<i>Ceratium furca</i>	Δ	<i>Rhizosolenia</i> spp.	•
<i>Leptocylindrus danicus</i>	•	<i>Dinophysis cf. acuminata</i>	Δ	<i>Ceratium fusus</i>	Δ
<i>Guinardia</i> spp.	•	<i>Ceratium</i> spp.	Δ	<i>Guinardia</i> spp.	•

Diatoms (•), coccolithophores (+) and dinoflagellates (empty Δ).

identified the assemblage was dominated by a permanent development of *Scropsiella* cf. *trochoidea* and in lower numbers by the species *Ceratium fusus*, *Prorocentrum micans*, *Ceratium furca* and several others included in the genus *Ceratium* spp., *Prorocentrum* spp., *Protoperidinium* spp., *Dinophysis* spp. and *Gymnodinium* spp. (Appendix A). The satellite data from 13–18 July 2004, the maxima period, showed prevailing mild upwelling conditions and the presence of colder waters (<15 °C) just in a small core around cape Roca (highlighted by a white arrow in Fig. 5c). *S. cf. trochoidea* dominated 95% of the dinoflagellate assemblage only represented by four species (Table 3). Diatoms and coccolithophores, with six identified species each (13% and 5% of PC, respectively) were observed in lower numbers.

3.3. Principal Component Analysis

The first 3 components explained 37% of the total variation within the data. The reduced variation explained was due to the low relative frequency used (20% with 93 species selected) and the wide range and heterogeneity of the temporal scales involved. However, the data was concentrated and phytoplankton grouped, revealing short-term and seasonal succession changes coherent with field observations.

The first component (PC1) accounted for as much of the variability in the data as possible and explained 15% of total variability within the data, positively correlated with all species. This relation is pointed out in Fig. 6 by the distribution of PC1 scores with total phytoplankton. PC1 separated two assemblages: the first correlated with the higher values of the component, included species with a regular attendance during summer, such as *Gymnodinium* spp., *Diplopsalis* spp., *C. mediterranea*, *Prorocentrum* spp., *G. oceanica*, *Protoperidinium diabolium* and *S. costatum* among others (Table 4). The second assemblage, correlated with lower values of PC1, developed during spring, when the second highest concentrations were observed, and was composed by *Guinardia* spp., *L. danicus*, *T. nitzschioides*, *D. pumila*, *Odontella* spp. and *Chaetoceros* spp. which attended as short peaks in this season, dominating the phytoplankton community.

Each succeeding component, PC2 and PC3 accounted for as much of the remaining variability as possible, explaining each one 11% of total variability within the data. PC2 was interpreted as a gradient between turbulence (positive values) and stratification (negative

values) while PC3 axis revealed a gradient between cold (positive values) and warm (negative values) waters (Fig. 7 and Table 4). The distribution of the main taxonomic groups along axis 2 and 3 simplified the underlying structure and allowed the definition of three distinct assemblages. One group, distributed in the positive scores of PC2 and along PC3, was composed by diatoms. The species most correlated with turbulence were small chain forming diatoms as *Thalassionema nitzschioides*, *Odontella* spp., *Chaetoceros* spp. and *Guinardia* spp. and as turbulence decrease, *Pseudo-nitzschia* spp., *G. delicatula*, *L. danicus*, *S. costatum*, *C. closterium* and *D. pumila* (Table 4) appeared. Some of these, like *Odontella* spp., *Diploneis* spp. or *Licmophora* spp., were never responsible by major diatom peaks but were recurrently observed in low numbers having a high global frequency in the samples.

Associated with the negative scores of PC2 and PC3, as stratification and temperature increased, the phytoplankton community was characterized in lower numbers by dinoflagellates as *C. fusus*, *P. micans*, *C. furca* and several others included in the genus *Ceratium* spp., *Prorocentrum* spp., *Protoperidinium* spp., *Dinophysis* spp. and *Gymnodinium* spp. It is interesting to notice the detachment from the other dinoflagellates of *Dinophysis acuminata*, a harmful algae species highly correlated with stratification but associated with colder waters. The dominant dinoflagellate *Scropsiella* cf. *trochoidea*, that opportunistically peak before upwelling pulses, was positively correlated with intermediate turbulence.

Between the two assemblages and detached by PC3, there was a third cluster, composed by coccolithophores. The coccolithophore assemblage distributed in the positive axis of PC3 and was represented by *Calcidiscus* spp., in colder waters, *G. muelleriae*, *G. ericsonii*, *E. huxleyi*, *G. oceanica* and *C. mediterranea*. This assemblage tolerated reduced turbulence and colder waters (11.5 °C). The opposite distribution of *Calcidiscus* genus, cold water taxa, and *Ceratium* species, warm water taxa, helped in the interpretation of axis 3 as a temperature gradient.

4. Discussion

During the four years the physical, chemical and biological parameters varied from short-term (upwelling event) to interannual

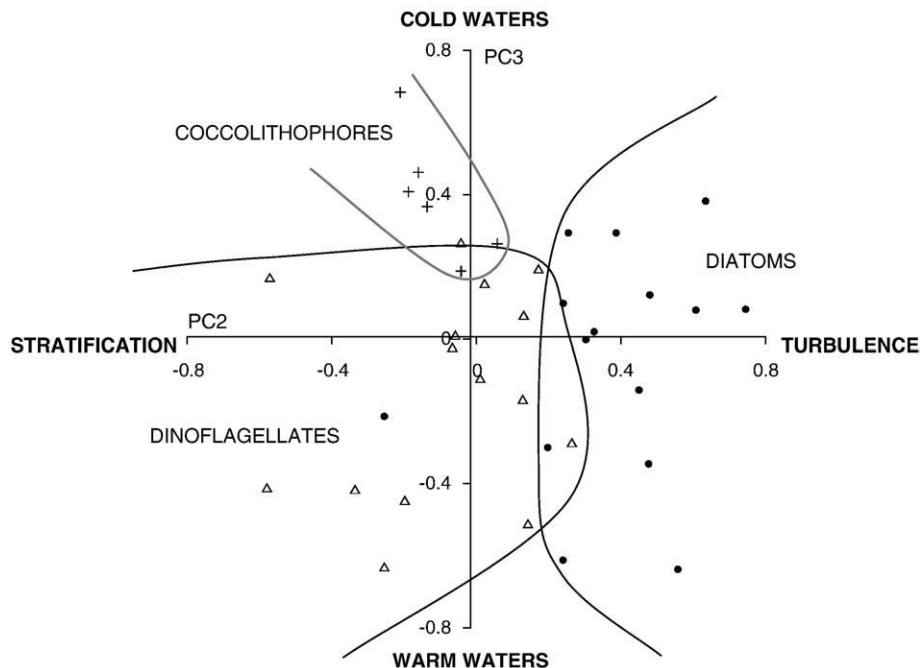


Fig. 7. Distribution of diatoms (•), coccolithophores (+) and dinoflagellates (empty Δ) in the space defined by the second (PC2) and third (PC3) components.

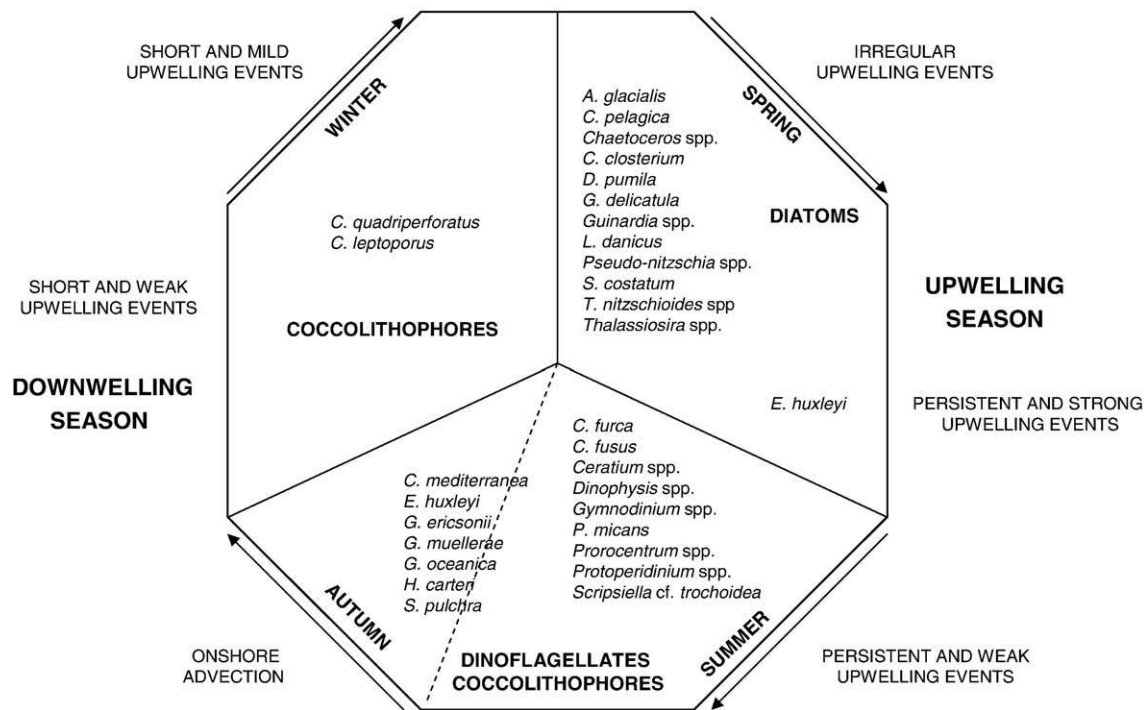


Fig. 8. Schematic representation of the seasonal distribution of phytoplankton groups and dominant species associated with the upwelling/downwelling cycle.

scales. It was possible to identify short succession cycles of diatoms, coccolithophores and dinoflagellates, dependent on coastal upwelling events (Fig. 8). They occurred along a gradient of a template of r versus K growth strategies, diatoms (r -selected) exploited well-mixed, turbulent, nutrient-rich conditions, while dinoflagellates (K -selected) dominated in stable, stratified waters with low nutrient concentrations, as previously described by several authors for upwelling regions (NW Africa: Margalef, 1978a,b; Estrada and Blasco, 1985; California current: Hutchings et al., 1995; Venrick, 1998; Ria de Vigo (NW Iberian Peninsula): Nogueira and Figueiras, 2005; North California: Lassiter et al., 2006). As evidenced by the distribution along the positive axis of PC2 (maximum turbulence), small chain and colonial diatoms within the genus *Chaetoceros* and *Thalassiosira*, *Asterionellopsis glacialis*, and *L. danicus*, were the first to react to turbulence (1st stage species in phytoplankton succession) and were followed by larger forms (2nd stage) like *Pseudo-nitzschia* spp., *D. pumila* and *Cerataulina pelagica*, after the upwelling peak, as conditions persisted. These diatoms are apparently well adapted to the turbulent, high-energy, nutrient-rich upwelling conditions as often noted in the literature (Margalef, 1978a,b; Estrada and Blasco, 1985; Chavez et al., 1991; Kobayashi and Takahashi, 2002). The *Chaetoceros* genus were always the main component of the population, when cell numbers were high together with other centric diatoms such as *Thalassiosira*, forming a functional group that fit with other upwelling studies (Blasco et al., 1981; Lassiter et al., 2006) and the Margalef paradigm of adaptation to upwelling conditions. Short upwelling pulses appeared to be unfavourable for the development of diatoms, maintaining the assemblage in the first stages of succession while persistency seemed to promote species succession. Associated with relaxation periods were third stage species like *Dinophysis*, *Protoperidinium*, *Ceratium* and other dinoflagellates. As for coccolithophores, distinct species were associated with particular hydrographic conditions but from an upwelling scale point of view a preference emerged for intermediate turbulence and nutrient regimes, between diatoms (maximum turbulence) and dinoflagellates (maximum stratification). In accordance with Margalef's model, Young (1994)

additionally related the ecological distribution of coccolithophores to their morphology, and found the lowest diversity and abundances both in strongly eutrophic environments and in extreme oligotrophic conditions, while the highest were in intermediate conditions. The placolith-bearing species dominated in nutrient-rich, turbulent environments such as upwelling areas, coastal and shelf seas, and constituted the main bloom-forming coccolithophores. These were recognised as early succession r -selected species, capable of a rapid growth, like *E. huxleyi* (Okada and Honjo, 1973; Honjo, 1977) and *Gephyrocapsa* spp. (Silva et al., 2008). The increasing cell numbers during the beginning of the upwelling season and under mild turbulent conditions suggested that *E. huxleyi* could be a 1st stage species in phytoplankton succession together with small chain diatoms, that prevailed if upwelling intensifies. The remaining coccolithophores included species showing a tendency towards weak r/K or K selection that decrease in abundance over the years due to shorter and less intense downwelling periods.

On Lisbon Bay, the seasonal pattern was typical of a temperate area with different phytoplankton groups peaking according to its particular abiotic preferences. Diatoms represented the most abundant biomass source with several maxima during persistent north-erlies and nutrient availability usual from spring and summer. Diatoms diversity remained similar over the years with species dominating according to the persistence of upwelling. The coccolithophores were the second most abundant group, peaking throughout the year. According to Silva et al. (2008, 2009), spring and summer were dominated by small and coastal coccolithophores as *E. huxleyi*, while larger and robust oceanic forms developed, during summer-autumn, in mature upwelled waters like *C. mediterranea* or were capable of dominating the phytoplankton assemblage during winter like *Calcidiscus* species (positively correlated with colder waters). Autumn was regarded as a short transition period (~1 month) from upwelling to downwelling seasons (Figueiras et al., 2002 for NW Iberia) when coastal turbulence is usually reduced but nutrients provided by upwelling are still available (Giraudeau et al., 1993; Kleijne, 1993; Ziveri et al., 1995). These conditions, where

coccolithophores were most favoured, promote the onshore advection of oceanic warmer waters into colder and nutrient enriched ones. Dinoflagellates were the less abundant group, usually having maxima during summer under warmer stratified conditions. The group seemed to have a narrow tolerance to changes in turbulence and temperature, in particular to winter conditions. Chavez et al. (1991) noted that dinoflagellates were never an important component of the phytoplankton community in the upwelling region just north of Bodega bay (Northern California) probably due to the persistency of upwelling related turbulent conditions. The only dinoflagellate positively correlated with stratified colder waters was *D. acuminata* that, according to Palma et al. (1997), is associated with colder and less salty waters with maxima observed further north in the Portuguese coast.

The seasonal biotic and abiotic differences observed resulted from distinct interannual upwelling/downwelling patterns, different precipitation regimes and nutrient concentrations. From 2001 until 2005 the upwelling conditions became more persistent and according to Bakun (1990) and Santos et al. (2005) for the Iberian margin and McGregor et al. (2007) for NW Africa, there has been a regional increase in coastal upwelling during the last decades of the 20th century. The intensification of northerlies observed earlier in the year can be one of the keys to explain the increase in biomass (Chl *a*) from 2001 onwards ($0.76 \mu\text{g l}^{-1}$). During 2002, the noticed distinction between upwelling and downwelling seasons and the availability of nutrients seemed to promote several phytoplankton maxima. The highest concentrations from the study were recorded in 2002 and characterized by diatoms, during a persistent and strong upwelling period, from spring to summer and by coccolithophores when convergence persisted, during the warmest autumn of the study. The satellite-derived and ocean colour data either supported the role of diatoms as proxies of upwelling conditions and the role of coccolithophores as tracers for the confluence of warmer offshore waters due to downwelling, as pointed out by Silva et al. (2008). Maxima of both groups interspersed with silicate and nitrate peaks, respectively, and were a possible reason to its subsequent reduction. Although the phytoplankton concentrations were maxima, total Chl *a* was the lowest from the study, mainly explained by the dominance of small chain diatoms, during spring–summer blooms and coccolithophores during autumn. A different picture was observed in 2003, when the SW winds promoting convergence conditions extended until May (late-spring) associated with longer rainy periods (winter–spring and late autumn onwards). Increments in precipitation and in Tagus river flow influenced the low salinity values and coincided with the main shifts in nutrient concentrations. Phytoplankton concentrations were in general low and maxima were observed later in the year, in contrast with 2002, restricted to late-spring–summer when upwelling intensified. Silicon was largely available during winter–spring, probably from a riverine origin, to be fully utilized by diatoms that seemed to be more turbulent and light dependent and less influenced by low salinities and temperatures. As northerlies intensified, the incoming solar radiation periods became longer and salinity and temperatures begin to rise, diatoms peak during late-spring causing silicon depletion during all summer when coccolithophores increased. In 2004, a year characterized by persistent although weak upwelling conditions, four phytoplankton peaks emerged, expressive but short in time. This year presented the next high phytoplankton concentrations and the highest total Chl *a* from the study, exactly the opposite from 2002. The presence of *D. pumila*, a large chain diatom, seemed to play a role in the inconsistency between lower cell counts and higher biomass levels once in 2002, when phytoplankton maxima was observed, the concentrations were explained by small chain diatoms and coccolithophores. Hence, particular attention should be given when interpreting Chl *a* values because opposite concentrations were found to be related with similar cell counts characterized by different floral compositions. These

results show the importance of microscope identifications in the interpretation of peaks. During 2004 the phytoplankton was dominated by diatoms and by dinoflagellates, instead of coccolithophores, with two short and significant peaks. Throughout this year was also observed an increase in the phytoplankton fraction $<20 \mu\text{m}$, the presence of large chain diatoms favoured by persistent turbulence and *Scropsiella* cf. *trochoidea*, an autotrophic opportunistic dinoflagellate abundant after upwelling peaks. The conditions highlighted by the satellite image from July 2004 promoted a mono-specific bloom of *S. cf. trochoidea*, what is not representative of the whole dinoflagellate preferences. The hypothesis of a local development of *S. cf. trochoidea* can be pointed out once this specie was always present in the samples and dominated the dinoflagellate assemblage. Ribeiro and Amorim (2008) observed in sediments from Lisbon Bay, a high percentage of cysts of *S. cf. trochoidea* and other species of the genus *Scropsiella*. The lower development of coccolithophores, during this summer–autumn, coincided with the absence of established convergence, with the lowest concentrations of nitrites and nitrates, important for calcification processes (Baumann et al., 2005), as well as with an overall decreased in phosphates and limiting silicates. Tyrrel and Merico (2004) pointed out low silicon conditions and N:P ratios between 6 and 11 as favourable conditions for coccolithophore development. The present data shows 2004 as the year when silicon was lower but N:P ratios were >11 . The coccolithophore *S. pulchra* peaked for the first time and dinoflagellates had maxima.

It is also important to highlight that phytoplankton community and its seasonal variability were not only dependent on physical–chemical process, but also represent the interaction of species specific net growth rates, combining variability of specific growth and loss rates (Domingues et al., 2005). For that reason, losses such as grazing, viral lysis and autolysis, could also explain part of the phytoplankton succession and should be evaluated in future studies.

5. Conclusions

The present study has provided a novel set of observations illustrating rapid changes (both short-term and seasonal) in phytoplankton size structure and community composition in Lisbon Bay coastal waters as a function to wind forcing and nutrient availability. Community changes were related to different scales of meteorological and hydrographic variability. Within the seasonal pattern, a series of short-term successions, from *r*-strategists towards *K*-strategists, was associated with hydrodynamic changes promoted by upwelling/relaxation events. At a seasonal scale, the succession was related to the annual cycle of mixing/stratification and high/low precipitation and runoff. Coccolithophores appeared as the most tolerant group, with species thriving in a remarkable variety of oceanographic conditions between diatoms upwelling favourable (spring–summer) and dinoflagellates thermal stratified affinities (summer) to further develop during autumn and winter. Short and weak upwelling pulses allowed the coexistence of the three groups although maxima were not coincident.

Acknowledgements

This work was partly funded by QCAIII-POPesca MARE “Caraterização ecológica da zona costeira- Plataforma Continental” and “Profit” (PDCTE/CTA/50386/2003) projects. We thank M. Falcão for performing all nutrient analysis and our colleagues A. Morais, T. Quintal and F. Quintela, for the weekly fieldwork support.

The satellite-derived sea surface temperature maps were obtained from the EUMETSAT’s Ocean and Sea Ice Satellite Application Facility, generated at CMS (Météo-France Satellite Meteorology Center, Lannion, Brittany, France) and distributed by IFREMER.

Appendix A

List of phytoplankton species observed during the sampling, separated in three major groups, diatoms, dinoflagellates and coccolithophores.

Diatoms	Dinoflagellates	Coccolithophores
<i>Acinoptychus senarius</i>	<i>Alexandrium</i> spp.	<i>Prorocentrum minimum</i>
<i>Acnantes</i> spp.	<i>Amphidoma caudatum</i>	<i>Prorocentrum scutellum</i>
<i>Amphiprora</i> spp.	<i>Ceratium candelabrum</i>	<i>Prorocentrum</i> spp.
<i>Amphora</i> spp.	<i>Ceratium furca</i>	<i>Prorocentrum triestinum</i>
<i>Asterionellopsis glacialis</i>	<i>Ceratium fusus</i>	<i>Protoceratium reticulatum</i>
<i>Asteromphalus flabellatus</i>	<i>Ceratium gibberum</i>	<i>Protoceratium spinulosum</i>
<i>Asteromphalus sarcophagus</i>	<i>Ceratium horridum</i>	<i>Protoperidinium aciculiferum</i>
<i>Asteromphalus</i> spp.	<i>Ceratium kofoidii</i>	<i>Protoperidinium bipes</i>
<i>Auricula</i> spp.	<i>Ceratium lineatum</i>	<i>Protoperidinium breve</i>
<i>Bacillaria paxillifera</i>	<i>Ceratium macroceros</i>	<i>Protoperidinium conicum</i>
<i>Bacteriastrium delicatulum</i>	<i>Ceratium complanata</i>	<i>Protoperidinium oceanicum</i>
<i>Bacteriastrium furcatum</i>	<i>Ceratium massiliense</i>	<i>Protoperidinium depressum</i>
<i>Bacteriastrium hyalinum</i>	<i>Ceratium minutum</i>	<i>Protoperidinium diabolum</i>
<i>Bacteriastrium</i> spp.	<i>Ceratium</i> spp.	<i>Protoperidinium divergens</i>
<i>Biddulphia alternans</i>	<i>Ceratium symetricum</i>	<i>Protoperidinium globolum</i>
<i>Biddulphia pulchella</i>	<i>Ceratium teres</i>	<i>Protoperidinium leonis</i>
<i>Biddulphia</i> spp.	<i>Ceratium triplos</i>	<i>Protoperidinium murrayi</i>
<i>Cerasterias cetauroides</i>	<i>Corythodinium</i> spp.	<i>Protoperidinium oceanicum</i>
<i>Cerataulina pelagica</i>	<i>Dinophysis acuta</i>	<i>Protoperidinium pellucidum</i>
<i>Chaetoceros curvisetus</i>	<i>Dinophysis caudate</i>	<i>Protoperidinium pentagonum</i>
<i>Chaetoceros danicus</i>	<i>Dinophysis cf. acuminata</i>	<i>Protoperidinium quinquecornu</i>
<i>Chaetoceros decipiens</i>	<i>Dinophysis dens</i>	<i>Protoperidinium</i> spp.
<i>Chaetoceros lorenzianus</i>	<i>Dinophysis diegensis</i>	<i>Protoperidinium steinii</i>
<i>Chaetoceros pseudocur/curv.</i>	<i>Dinophysis fortii</i>	<i>Pyrocystis elegans</i>
<i>Chaetoceros rostratus</i>	<i>Dinophysis imbricate</i>	<i>Pyrocystis lunula</i>
<i>Chaetoceros socialis</i>	<i>Dinophysis setigera</i>	<i>Pyrocystis</i> spp.
<i>Chaetoceros</i> spp.	<i>Rhizosolenia imbricate</i>	<i>Scripsiella cf. trochoidea</i>
<i>Cocconeis</i> spp.	<i>Rhizosolenia setigera</i>	<i>Thoracosphaera heimii</i>
<i>Corethron criophilum</i>	<i>Rhizosolenia</i> spp.	<i>Torodinium robustum</i>
<i>Coscinodiscus marginatus</i>	<i>Rhizosolenia styliiformis</i>	<i>Triadanium polyedricum</i>
<i>Coscinodiscus radiatus</i>	<i>Rhoicosigma</i> spp.	
<i>Coscinodiscus</i> spp.	<i>Skeletonema costatum</i>	
<i>Cylindrotheca closterium</i>	<i>Skeletonema</i> spp.	
<i>Dactyliosolen fragilissimus</i>	<i>Stephanopyxis palmeriana</i>	
<i>Dactyliosolen phuketensis</i>	<i>Stephanopyxis turris</i>	
<i>Detonula pumila</i>	<i>Stephanopyxis</i> spp.	
<i>Diploneis bombus</i>	<i>Streptotheca thamensis</i>	
<i>Diploneis</i> sp.	<i>Striatella unipunctata</i>	
<i>Ditylum brightwellii</i>	<i>Surirella</i> spp.	
<i>Eucampia cornuta</i>	<i>Synedra</i> spp.	
<i>Eucampia longicornis</i>	<i>Thalassionema bacilare</i>	
<i>Eucampia</i> spp.	<i>Thalassionema fraunfeldii</i>	
<i>Eucampia zoodiacus</i>	<i>Thalassionema nitzschioides</i>	
<i>Grammatophora marina</i>	<i>Thalassionema</i> spp.	
<i>Grammatophora</i> spp.	<i>Thalassiosira anguste-lineata</i>	
<i>Guinardia cf. delicatula</i>	<i>Thalassiosira eccentrica</i>	
<i>Guinardia cf. striata</i>	<i>Thalassiosira rotula</i>	
<i>Guinardia flaccida</i>	<i>Thalassiosira subtilis</i>	
<i>Guinardia</i> spp.	<i>Thalassiosira</i> spp.	
<i>Hemiaulus membranaceus</i>	<i>Thalassiotrix</i> spp.	
<i>Hemiaulus sinensis</i>	<i>Trachyneis aspera</i>	
<i>Lauderia annulata</i>		

References

- Bakun, A., 1973. Coastal upwelling indices, West Coast of North America 1946–71. NOAA Technical Report NMFs SSFR-671. In: U.S. Dept. of Commerce.
- Bakun, A., 1990. Global climate change and intensification of Coastal Ocean upwelling. *Science* 247, 198–201.
- Baumann, K.-H., Andruleit, H., Bockel, B., Geisen, M., Kinkel, H., 2005. The significance of extant coccolithophores as indicators of ocean water masses, surface water temperature, and palaeoproductivity: a review. *Palaeontologische Zeitschrift* 79 (1), 93–112.
- Blasco, D., Estrada, M., Jones, B.H., 1981. Short time variability of phytoplankton populations in upwelling regions – the example of Northwest Africa. In: Richards, F.A. (Ed.), Coastal Upwelling. AGU, Washington, DC, pp. 339–347.
- Brandini, F.P., Boltovskoy, D., Piola, A., Kocmur, S., Röttgers, R., Abreu, P.C., Lopes, R.M., 2000. Multiannual trends in fronts and distribution of nutrients and chlorophyll in the southwestern Atlantic (30–62°S). *Deep-Sea Research. Part 1* 47, 1015–1033.
- Chavez, F.P., Barber, R.T., Kosro, P.M., Huyer, A., Ramp, S.R., Stanton, T.P., Rojas de Mendiola, B., 1991. Horizontal transport and the distribution of nutrients in the coastal transition zone off northern California: effects on primary production, phytoplankton biomass and species composition. *Journal of Geophysical Research* 96, 14833–14848.
- Ciotti, A.M., Odebrecht, C., Fillmann, G., Möller Jr., O.O., 1995. Freshwater outflow and subtropical convergence influence on phytoplankton biomass on the southern Brazilian continental shelf. *Continental Shelf Research* 5 (14), 1737–1756.
- CMS (Centre de Météorologie Spatiale), 2005. North Atlantic regional sea surface temperature product manual. Météo-France Satellite Meteorology Center, Lannion, Brittany, France. SAF/OSI/MF/TEC/MA/ 124. http://www.osi.saf.org/biblio/docs/ss1_pmnrst_1_7.pdf.
- Díaz, J., García-Herrera, R., Trigo, R.M., Linares, C., Valente, M.A., Hernández, E., 2006. The impact of summer 2003 heat wave in Iberia: how should we measure it? *International Journal of Biometeorology* 50, 159–166.
- Dodge, J.D., 1982. Marine Dinoflagellates of the British Isles. Her Majesty's Stationary Office, London.
- Domingues, R.B., Barbosa, A., Galvão, H., 2005. Nutrients, light and phytoplankton succession in a temperate estuary (the Guadiana, south-western Iberia). *Estuarine, Coastal and Shelf Science* 64 (2–3), 249–260.
- Dortch, Q., Whitledge, T.E., 1992. Does nitrogen or silicon limit phytoplankton production in the Mississippi River filament and nearby regions? *Continental Shelf Research* 12, 1293–1309.

- Estrada, M., Blasco, D., 1985. In: Bas, C., Margalef, R., Rubias, P. (Eds.), *Phytoplankton Assemblages in Coastal Upwelling Areas*. In: International Symposium of Upwelling of W Africa, vol. 1. Instituto de Investigaciones Pesqueras, Barcelona, pp. 379–402.
- Fatela, F., Taborda, R., 2002. Confidence limits of species proportions in microfossil assemblages. *Marine Micropaleontology* 45, 169–174.
- Figueiras, F.G., Labarta, U., Fernández Reiriz, M.J., 2002. Coastal upwelling, primary production and mussel growth in the Rías Baixas of Galicia. *Hydrobiologia* 484 (1–3), 121–131.
- Fúza, A.F.G., Macedo, M.E., Guerreiro, M.R., 1982. Climatological space and time variation of the Portuguese coastal upwelling. *Oceanologica Acta* 5 (1), 31–40.
- Giraudeau, J., Monteiro, P.M.S., Nikodemus, K., 1993. Distribution and malformation of living coccolithophores in the northern Benguela system off Namibia. *Marine Micropaleontology* 22, 93–110.
- Graham, W.M., Largier, J.L., 1997. Upwelling shadows as nearshore retention sites: the example of northern Monterey Bay. *Continental Shelf Research* 17, 509–532.
- Grasshoff, K., 1983. In: Grasshoff, K., Ehrhardt, M., Kremling, K. (Eds.), *Methods of Seawater Analysis*. Verlag Chemie, New York, 419 pp.
- Hasle, G.R., 1978. *Phytoplankton manual: the inverted microscope method*. In: Sournia, A. (Ed.), *Monographs on Oceanic Methodology*. Unesco, Paris, pp. 88–96.
- Hasle, G.R., Syvertsen, E.E., 1996. Marine diatoms. In: Tomas, C.R. (Ed.), *Identifying Marine Diatoms and Dinoflagellates*. Academic Press, Inc., London, pp. 5–385.
- Haynes, R., Barton, E.D., 1990. A poleward flow along the Atlantic coast of the Iberian Peninsula. *Journal of Geophysical Research* 95, 11425–11441.
- Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W., Strickland, J.D.H., 1965. Fluorimetric determination of chlorophyll. *Journal du Conseil Permanent International pour l'Exploration de la Mer* 30 (1), 3–15.
- Honjo, S., 1977. Biogeography and provincialism of living coccolithophorids in the Pacific Ocean. In: Ramsey, A.T.S. (Ed.), *Oceanic Micropaleontology*. Academic Press, London, pp. 951–972.
- Hutchings, L., Pitcher, G.C., Probyn, T.A., Bailey, G.W., 1995. The chemical and biological consequences of coastal upwelling. In: Summerhayes, C.P., Emeis, K.-C., Angel, M.V., Smith, R.L., Zeitschel, B. (Eds.), *Upwelling in the Oceans; Modern Processes and Ancient Records*. Wiley, New York, pp. 65–81.
- Kjørboe, T., 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Advanced Marine Biology* 29, 1–73.
- Kleijne, A., 1993. *Morphology, Taxonomy and Distribution of extant coccolithophorids (calcareous nannoplankton)*. Ph.D Thesis, Vrije Universiteit Amsterdam.
- Kobayashi, F., Takahashi, K., 2002. Distribution of diatoms along equatorial transect in the western and central Pacific during the 1999 La Niña conditions. *Deep-Sea Research*, II 49, 2801–2821.
- Lassiter, A.M., Wilkerson, F.P., Dugdale, R.C., Hogue, V.E., 2006. Phytoplankton assemblages in the CoOP-WEST coastal upwelling area. *Deep-Sea Research*, II 53, 3063–3077.
- Laubscher, R.K., Perissinotto, R., McQuaid, C.D., 1993. Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. *Polar Biology* 13 (7), 471–481.
- Margalef, R., 1978a. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta* 1 (4), 493–509.
- Margalef, R., 1978b. Phytoplankton communities in upwelling areas. The example of NW Africa. *Oecologia Aquatica* 3, 97–132.
- McGregor, H.V., Dima, M., Fisher, H.W., Mulitza, S., 2007. Rapid 20th-century increased in coastal upwelling off Northwest Africa. *Science* 315, 637–639.
- Moita, M.T., 2001. *Structure, variability and dynamics of phytoplankton from the Portuguese continental coast*. Ph.D. Thesis. University of Lisbon, Lisbon, unpublished (<http://ipimar-iniap.ipimar.pt/>).
- Moita, M.T., Vilarinho, M.G., 1999. Checklist of phytoplankton species off Portugal: 70 years (1929–1998) of studies. *Portugaliae Acta Biologica. Série B* 18, 5–50.
- Moita, M.T., Oliveira, P.B., Mendes, J.C., Palma, A.S., 2003. Distribution of chlorophyll a and *Gymnodinium catenatum* associated with coastal upwelling plumes off central Portugal. *Acta Oecologica* 24, S125–S132.
- Nogueira, E., Figueiras, F.G., 2005. The microplankton succession in the Ría de Vigo revisited: species assemblages and the role of weather-induced, hydrodynamic variability. *Journal of Marine Systems* 54, 139–155.
- Okada, H., Honjo, S., 1973. The distribution of oceanic coccolithophorids in the Pacific. *Deep-Sea Research* 20, 355–374.
- Oliveira, P., Nolasco, R., Dubert, J., Moita, T., Peliz, A., 2009. Surface temperature, chlorophyll and advection patterns during a summer upwelling event off central Portugal. *Continental Shelf Research* 29 (5–6), 759–774.
- Palma, A.S., Vilarinho, M.G., Moita, M.T., 1997. Interannual trends in the longshore variation of dinofysis off Portuguese coast. Harmful algae. In: Reguera, B., Blanco, J., Fernández, M.L., Wyatt, T. (Eds.), *Xunta de Galicia and Intergovernmental Oceanographic Commission of Unesco, Santiago de Compostela, Spain*, pp. 124–127.
- Peliz, A., Dubert, J., Santos, A.M.P., Oliveira, P.B., Le Cann, B., 2005. Winter upper ocean circulation in the Western Iberian Basin – fronts, eddies and poleward flows: an overview. *Deep-Sea Research*, I 52, 621–646.
- Ribeiro, S., Amorim, A., 2008. Environmental drivers of temporal succession in recent dinoflagellate cyst assemblages from a coastal site in the North-East Atlantic (Lisbon Bay, Portugal). *Marine Micropaleontology* 68 (1–2), 156–178.
- Santos, A.M.P., Kazmin, A.S., Peliz, A., 2005. Decadal changes in the Canary upwelling system as revealed by satellite observations: their impact on productivity. *Journal of Marine Research* 63 (2), 359–379.
- Silva, A., Palma, S., Moita, M.T., 2008. Coccolithophores in the upwelling waters of Portugal: four years of weekly distribution in Lisbon Bay. *Continental Shelf Research* 28, 2601–2613.
- Silva, A., Palma, S., Oliveira, P.B., Moita, M.T., 2009. *Calcidiscus quadriperforatus* and *Calcidiscus leptoporus* as oceanographic tracers in Lisbon Bay (Portugal). *Estuarine, Coastal and Shelf Science* 81, 333–344.
- Thronsen, J., 1978. *Phytoplankton manual: preservation and storage*. In: Sournia, A. (Ed.), *Monographs on Oceanic Methodology*. Unesco, Paris, pp. 69–75.
- Tyrrel, T., Merico, A., 2004. *Emiliania huxleyi*: bloom observations and the conditions that induce them. In: Thierstein, H.R., Young, J.R. (Eds.), *Coccolithophores, from Molecular Processes to Global Impact*. Springer-Verlag Heidelberg, Germany, pp. 75–98.
- Venrick, E.L., 1998. Spring in the California Current: the distribution of phytoplankton species, April 1993 and April 1998. *Marine Ecology. Progress Series* 167, 73–88.
- Young, J., 1994. Function of coccoliths. In: Winter, A., Siesser, W.G. (Eds.), *Coccolithophores*. Cambridge University Press, Cambridge, pp. 63–82.
- Young, J., Geisen, M., Cros, L., Kleijne, A., Sprengel, C., Probert, I., Ostergaard, J., 2003. A guide to extant coccolithophore taxonomy. *Journal of Nannoplankton Research, Special Issue* 1, 123.
- Ziveri, P., Thunell, R., Rio, D., 1995. Export production of coccolithophores in an upwelling region: results from San Pedro Basin, Southern California Borderlands. *Marine Micropaleontology* 24, 335–358.