Marine Micropaleontology 77 (2010) 46–57

Contents lists available at ScienceDirect

Marine Micropaleontology

journal homepage: www.elsevier.com/locate/marmicro

Seasonal to interannual variability and geographic distribution of the silicoflagellate fluxes in the Western Mediterranean

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ARTICLE INFO

Article history:
Received 6 April 2010
Received in revised form 14 July 2010
Accepted 15 July 2010

Keywords:
Silicoflagellates
Sediment trap
Western Mediterranean
NAO
ENSO

ABSTRACT

A total of 337 samples collected from five sediment traps located in the Gulf of Lions, Catalan margin and the Alboran Sea have been analyzed in order to study the seasonal, interannual and geographical distributions of silicoflagellate fluxes in the Western Mediterranean. As a general trend, maximum fluxes of silicoflagellate skeletons always occurred during the spring bloom; i.e. during the winter–spring transition, while minimum fluxes were recorded during summer, characterised by a strong stratification and oligotrophic conditions. However, the sediment trap record of the Catalan margin did not exhibit any clear seasonal signal, probably owing to the fertilizing effect of the rivers Llobregat and Besos. Regarding interannual variability, no clear relationship between the NAO (North Atlantic Oscillation) and the silicoflagellate fluxes was found. In contrast, the silicoflagellate assemblages from the Alboran Sea and the Gulf of Lions responded with low fluxes and a delay in their annual maximum to the anomalous conditions elicited by the 1997–98 El Niño Event. Furthermore, the 2003 summer heat wave over the Western Mediterranean had similar repercussions on the silicoflagellate spring maximum 2004 in the Gulf of Lions. Three silicoflagellate species were identified in the samples, following the taxonomic concepts of Throndsen (1997): *Dictyocha fibula* (Ehrenberg), *Dictyocha speculum* (Ehrenberg) and *Octactis octonaria* (Ehrenberg) Hovasse 1946. *D. fibula* was cosmopolitan and the dominant species at all sites, always accounting for more than 80%. Moreover, its maximum fluxes were recorded in those sampling sites which were under the influence of high nutrient concentrations caused by the river input. *D. speculum* was only recorded in the northern locations, which suggests an affinity for colder water masses. In contrast, *O. octonaria* was restricted to the Alboran Sea stations, where temperatures reached the highest values and nutrients were scarcer.

1. Introduction

The silicoflagellates are a group of marine photosynthetic flagellates with a cosmopolitan distribution. They occur in all ocean environments but have a small contribution to the phytoplankton communities. Despite this, they can be a major component in coastal and estuarine waters (e.g. Jochem and Babenerd, 1989; Gómez and Gorsky, 2003). Silicoflagellates are generally considered as photosynthetic algae, however they have also been suggested to have mixotrophic behavior (Martini, 1977) and/or to contain symbiotic blue-green algae (Norris, 1967). Owing to their siliceous skeleton, silicoflagellates can be preserved in the sediment. Nevertheless, naked forms have also been described (Jochem and Babenerd, 1989; Moestrup and Thomsen, 1990; Henriksen et al., 1993). The taxonomy of this group has been based on the morphology of the siliceous skeleton of its representatives. However, as pointed out by Onodera and Takahashi (2005) this classification is in state of confusion due to its broad morphological variations in relation to environmental conditions (Van Valkenburg and Norris, 1970; Van Valkenburg, 1971a,b). The most recent literature (Throndsen, 1997) reports eight extant species grouped in three genera: *Dictyocha* Ehrenberg 1837, *Octactis* Schiller 1925 and *Mesocena* Ehrenberg 1843.

Traditionally, silicoflagellates have been used for biostratigraphic studies, mainly in high-latitude areas, where calcareous micro- and nannofossils are missing or not diagnosed (Perch-Nielsen, 1985). Additionally, they have been used as proxies for paleotemperature reconstructions across a wide range of latitudes in both hemispheres (Mandra and Mandra, 1970; Ciesielski and Weaver, 1974; Martini, 1977; Bukry, 1983; Schrader et al., 1986; Ciesielski and Case, 1989). The ratio between the "warm" genus *Dictyocha* spp. and the "cold"

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doi:10.1016/j.marmicro.2010.07.003

species *Dictyocha speculum* (synonymous with six-sided *Distephanus*) has been used to infer paleo-SST (Ciesielski and Weaver, 1974; Perch-Nielsen, 1985; Whitehead and Bohaty, 2003; Escutia et al., 2009). Silicoflagellates have also been suggested to be indicators of atmospheric and water mass variations e.g. studies on sediment traps registered changes in silicoflagellate fluxes in relation with El Niño events (Lange et al., 1997; Romero et al., 2001; Onodera and Takahashi, 2005), and as productivity indicators (e.g. Takahashi et al., 1989). Moreover, laboratory cultures of living silicoflagellates have shown that their growth rates are strongly influenced by environmental conditions, especially by temperature and salinity (Henriksen et al., 1993). Few authors have addressed the extant species of this cryptic group, however, some work has been done in our study area: the Western Mediterranean. Nival (1965) and Travers and Travers (1968) have described the seasonal distribution of silicoflagellates in Villefranche-sur-mer and the Gulf of Marseille respectively.

In this work, an array of five sediment traps set in three key areas (Fig. 1) of the Western Mediterranean was studied in order to record silicoflagellate information from different representative environments:

- Two sites in the Gulf of Lions (Fig. 1a): the Planier canyon station, considered as an oceanic station with lower influence of shelf-slope exchanges of particulate matter; and the Lacaze-Duthiers canyon station, with a higher input of particulate matter resuspended from the shelf and upper slope and affected by the fertilizing effect of the Rhône river plume.
- A third trap in the Foix canyon on the Catalan margin (Fig. 1b), characterised by sporadic inputs of particulate matter resuspended from the shelf and/or discharged by the Llobregat and Besos rivers.
- Two open sea sediment traps set within the influence of the two quasi-permanent anticyclonic gyres of the Alboran Sea (Fig. 1c).

In this sense, the present study attempts to complement current knowledge of the ecology and present distribution of silicoflagellates in the Western Mediterranean. Thus, the main objectives of this study were the following:

(1) To define the geographical distribution of the group;
(2) To characterize the annual and interannual variations of the silicoflagellate assemblages and their relationship with environmental conditions;
(3) To integrate the data recorded in the sediment traps in further paleoceanographic constructions.

2. Oceanographic setting

The Mediterranean Sea is a semi-enclosed basin that behaves as an antiestuarine circulation system: the surface waters enter through the Strait of Gibraltar from the Atlantic while deeper Mediterranean waters leave the basin (Bormans et al., 1986). The driving force of the general circulation has a thermohaline origin due to an excess of evaporation over precipitation and is controlled by the exchange of water through the Strait of Gibraltar.

The Mediterranean Sea is considered to be oligotrophic, however the Western Basin shows a number of hydrographic features that contribute to increasing its potential fertility (Estrada, 1996).

Here, three areas of the Western Mediterranean were considered; the Gulf of Lions, the Catalan margin, and the Alboran Sea (Fig. 1).

2.1. Gulf of Lions

From the hydrodynamic point of view, the Gulf of Lions can be considered a complex region (Millot, 1990). The general circulation in

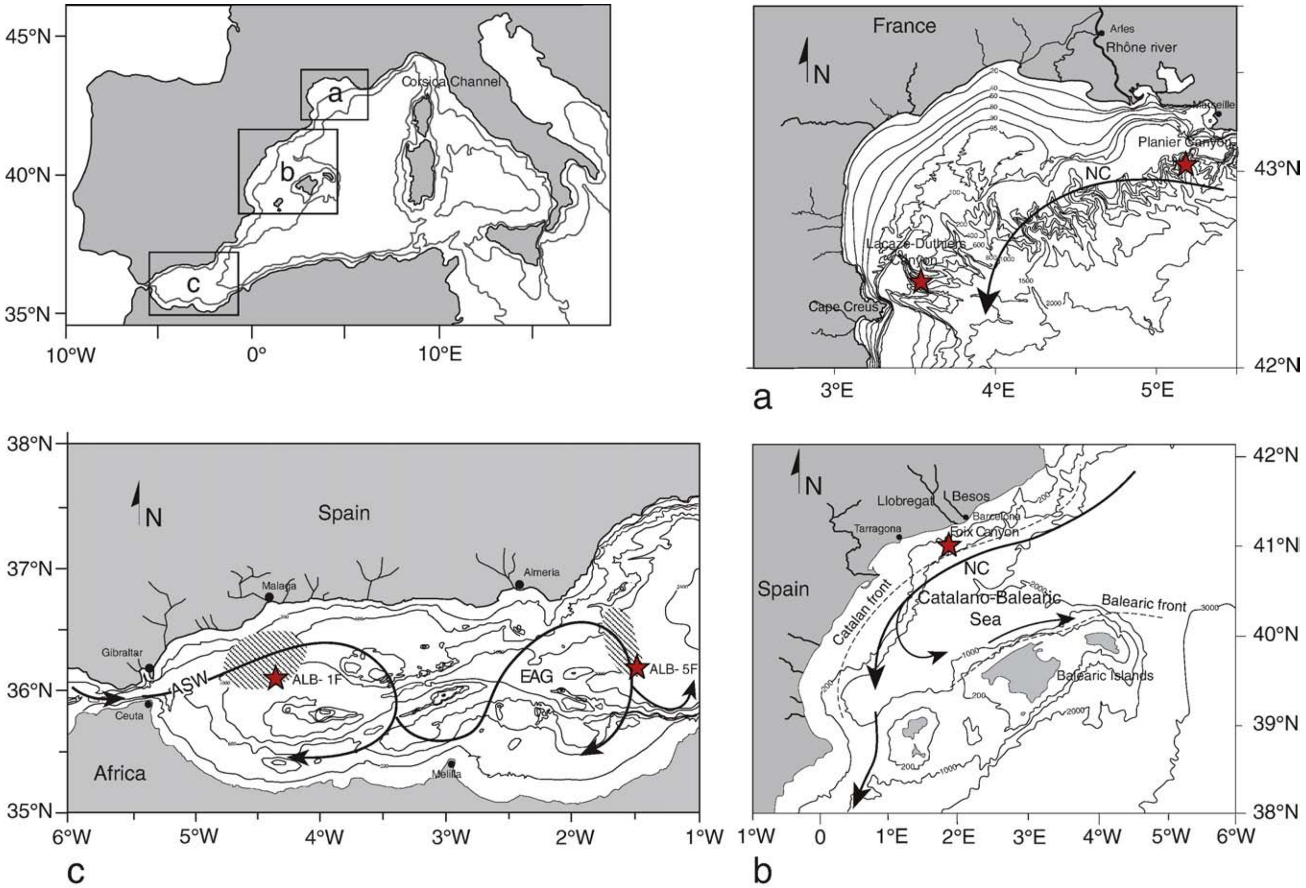


Fig. 1. Geographical setting of the sampling stations in the Western Mediterranean. The position of the sediment traps is represented with stars. Arrows represent the theoretical surface circulation. a. Gulf of Lions. b. Catalan margin. c. Alboran Sea. Dashed areas represent the northern border of the Western Alboran Gyre (WAG) and the Almeria–Oran Front (AOF).

this area is dominated by the Northern Current (NC), whose flux is directed to the south along the continental slope (Fig. 1a). Additionally, the Gulf of Lions is one of the few locations in the Mediterranean where dense-water formation takes place (Millot, 1990) and it is therefore a key area for the functioning of the thermohaline circulation in the Mediterranean. Dense-water formation occurs during winter when persistent, cold and dry northwesterlies (Mistral and Tramontana) cause heat losses and evaporation, that induce cooling and mixing of shelf waters that sink, overflow the shelf edge and cascade downslope (Béthoux et al., 2002). Dense-water formation shows important interannual variability, and in especially cold and dry years dense-water cascading may reach the bottom and erode the sea floor (Canals et al., 2006).

Regarding productivity, the Gulf of Lions can be considered as an exception to the general oligotrophy of the Mediterranean. The main mechanisms of nutrient supply in this area are the mesoscale variability of the Northern Current, the central divergence zone of the Liguro–Provençal Sea, and river runoff (Estrada, 1996), especially from the Rhône, which is one of the rivers with the highest flow to the Mediterranean area (Fig. 1a).

2.2. Catalan margin

The general circulation in this area is controlled by the Northern Current, which flows from the northeast to the southwest along the coast, between a permanent shelf-slope density front and the upper continental slope (Font et al., 1988) (Fig. 1b). The main nutrient enrichment mechanisms in this area are similar to those reported for the Gulf of Lions: the mesoscale variability of the Northern Current, which induces exchange of inorganic and organic elements between the ocean and the shelf, and the river input (Estrada, 1996). In particular, the plumes of the rivers Llobregat and Besos, which flow into the Catalano-Balearic Sea in its southern part (Fig. 1b), may affect the site studied. Both rivers flow through the large industrial belts of Barcelona and surrounding localities and receive agricultural, industrial and domestic wastes (Céspedes et al., 2005; Bosch et al., 1986).

2.3. Alboran Sea

The Alboran Sea can be considered a transition area between the Atlantic Ocean and the Mediterranean Sea. The pattern of circulation is intense, subject to strong seasonal variations related to fluctuations in the intensity of the water exchange through the Strait of Gibraltar. At the surface, the main oceanographic feature of the area is the entrance of a jet of Atlantic Surface Water (ASW) that forms two almost permanent anticyclonic gyres: the Western Alboran Gyre (WAG) and the Eastern Alboran Gyre (EAG) (Fig. 1c). Associated to the gyres, the Alboran Sea has two systems of high biological productivity as shown in Fig. 1c. For a detailed description of the physiography and oceanography of the Alboran Sea, see Parrilla and Kinder (1987).

In terms of sea surface productivity, the persistence of four main regimes is noticeable along the year: the winter bloom regime (November to March), the summer non-bloom regime (May to September), and two transition periods: from April to May, when thermal stratification starts, and October–November, coinciding with the highest wind variability and water column destratification (García-Gorriz and Carr, 2001).

3. Material and methods

3.1. Field experiments

The present study is a compilation of data from sediment trap samples recorded in different European (Euromarge-MB, MTP II-MATER and EUROSTRATAFORM) and French (PNEC: Programme National Environnement Côtier) projects performed in the Western Mediterranean.

All traps used were PPS3 Technicap sediment traps with a cylindrical–conical shape with a 0.4 m opening diameter (2.5 height/diameter aspect ratio for the cylindrical part) and equipped with 6 or 12 sampling cups (Heussner et al., 1990). Gaps in the temporal series were caused by mooring recovery periods or by problems in the functioning of the sediment traps.

In the Northwestern Mediterranean, three moorings were deployed at different locations (Fig. 1): one at the entrance of the Gulf of Lions, over the Planier Canyon (43.02° N, 5.18° E); one at the southwestern exit of the Gulf of Lions, over the Lacaze-Duthiers Canyon (43.02° N, 3.54° E) (Fig. 1a); and one in the Barcelona continental basin, over the Foix Canyon (41.04 N, 1.93 E) (Fig. 1b).

At the Planier and Lacaze-Duthiers sites, the moorings were deployed at a water depth of around 1000 m and they were equipped with two sediment traps at 500 and 30 m above the bottom (mab hereafter), paired with current meters (Heussner et al., 2006). Only the data from the sediment traps at 500 mab are reported in this work. The information recorded by these two sediment traps is especially relevant owing to the exceptional length of the time series: from October 1993 until January 2006. The sampling interval was set at 14 days until early 1997, and at 1 month from 1997 onwards (Table 1).

At the Foix Canyon station (Fig. 1b), the mooring was set at a water depth of 680 m and it was also equipped with two sediment traps at 530 and 30 mab (Puig and Palanques, 1998). Here, only the samples from the sediment trap at 530 mab were studied. In this experiment, the sampling period comprised one year, from April 1993 to May 1994, with a collection interval of 15–16 days (Table 1).

In the Alboran Sea two mooring lines were deployed: ALB-1F and ALB-5F (Fig. 1c). ALB-1F was set up on the continental slope at a depth of 1004 m and located at 36.01 N; 4.26 W while ALB-5F was deployed over the African continental margin at 2070 m depth and located at 35.91 N; 1.5 W (Fig. 1c). In both moorings, the sediment traps were set at 30 mab (Fabres et al., 2002; Sanchez-Vidal et al., 2005). The two moorings were deployed from July 1997 to May 1998 along three different periods. The sampling interval was set at 10–11 days for the whole period, except between April 20th and May 16th for ALB-1F, and between April 1st and May 22nd for ALB-5F, when the sampling interval was 3 days (Table 1).

Table 1
Summary of the main characteristics and environmental conditions of the 5 stations.

	Planier	Lacaze-Duthiers	Foix	ALB-5F	ALB-1F
Coordinates	43.02 N, 5.18 E	43.02 N, 3.54 E	41.04 N, 1.93 E	35.91 N, 1.5 W	36.01 N, 4.26 W
Depth (m)	1000	1000	680	2070	1004
Meters above botton (mab)	500	500	530	30	30
Sampling period	Oct 1993–Jan 2006	Oct 1993–Jan 2006	Apr 1993–May 1994	July 1997–May 1998	July 1997–May 1998
Sampling interval (days)	14 till Oct-94 and 30 till Jan-06	14 till Jan-97 and 30 till Jan-06	15	3–11	3–11
SST(°C)	12.35–26.22	11.82–26.55	12.82–26.42	15.81–24.69	15.12–23.88
Salinity	37.98–38.48	37.96–38.48	37.69–38.79	36.74–38.62	36.43–38.83
Chlorophyll-*a*	Available data (1997–2006)	Available data (1997–2006)	No data	Available data	Available data

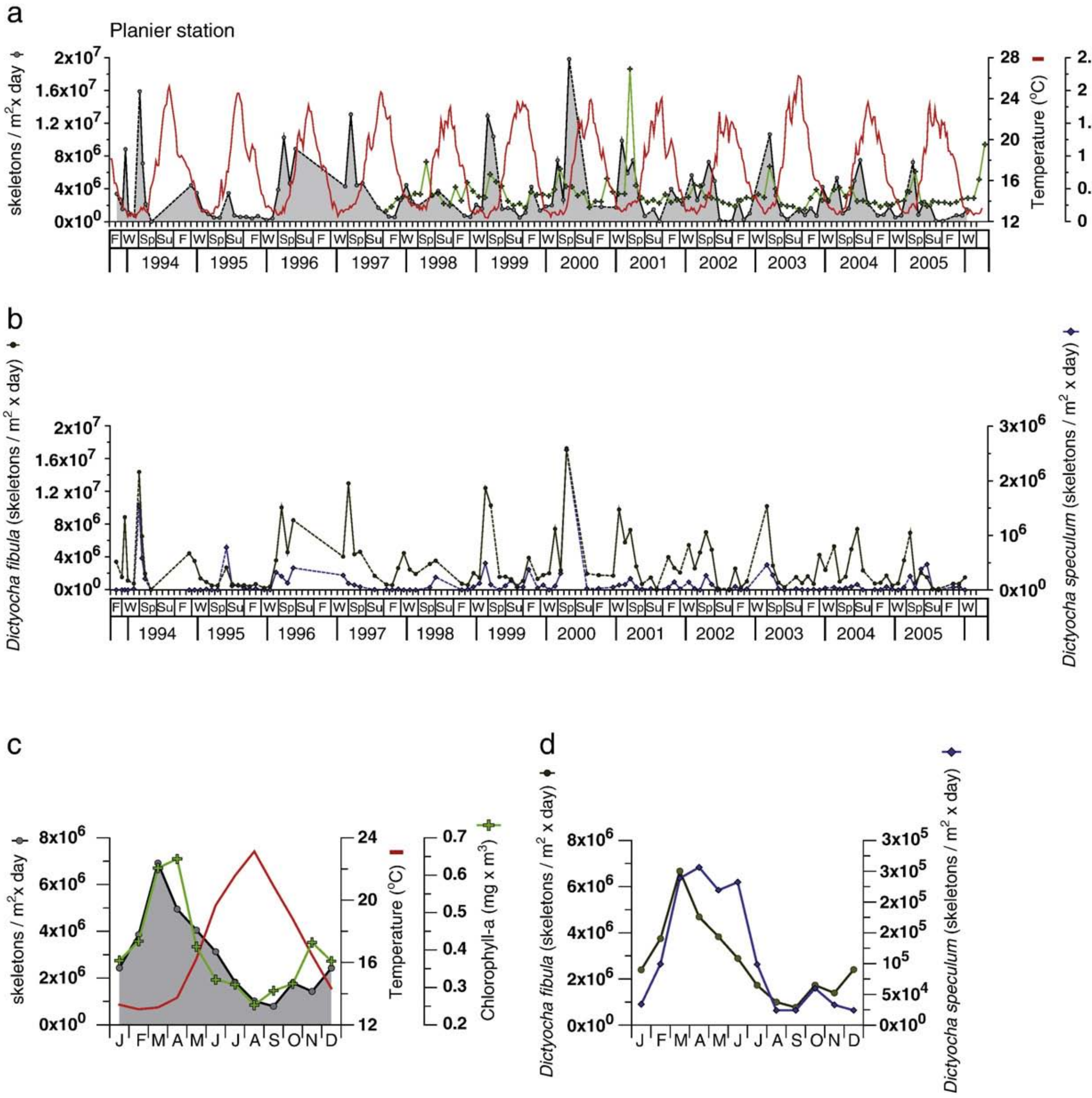


Fig. 2. Planier station. a. Total skeleton flux (skeletons/day × m^2), temperature (°C) and chlorophyll-*a* concentration (mg × m^3). b. *D. fibula* (squares) and *D. speculum* flux (skeletons day/m^2). Gaps in the time series are represented by a dotted line. The relative abundance of the different species and the SST are represented with solid lines. c. Composite year. Total skeleton flux (skeletons / day × m^2), temperature and chlorophyll-*a* concentration (mg × m^3). d. Composite year. *D. fibula* and *D. speculum* flux (skeletons / day × m^2).

3.2. General processing of the sediment traps

A detailed description of the PPS3 sediment trap and the sample processing used for this experiment can be found in Heussner et al. (1990). Here, we summarize a description of the treatment for siliceous microfossils analyses.

3.3. Specific treatment for siliceous microplankton

Different aliquots from the original samples were used for the micropaleontological analyses; although the most common was 1/8, other fractions were also used depending on availability, ranging from 1/64 to 3/4. The original samples were wet-sieved onto a 150 µm mesh in order to separate foraminifera larger than 150-µm from smaller diatoms, silicoflagellates and coccolithophores.

The samples studied were prepared with a standard decantation method according to the methodology proposed by Flores and Sierro (1997). Qualitative and quantitative analyses were performed at 1000 and 400 magnification, using a Nikon Eclipse 80i light microscope.

Owing to the high seasonal flux changes of this group, we detected some periods when almost no silicoflagellates were present in the water column and hence in the samples. The number of skeletons identified was usually higher than 100, but a compromise between the number of skeletons to be counted and the time spent analyzing them had to be accepted for some samples in which abundance was really low. In addition, diatom valves were counted in the Foix station samples. A minimum of 400 diatom specimens per sample was counted.

Silicoflagellate and total diatom fluxes are given as the number of skeletons or valves per day per square meter. In addition, an average year was calculated for the two 12-years-long sediment traps records of the Gulf of Lions. For this calculation, a flux value was assigned to each day of each collecting period. Then, all the days of the same month were placed in the same group and the flux average was estimated (Figs. 2 and 3).

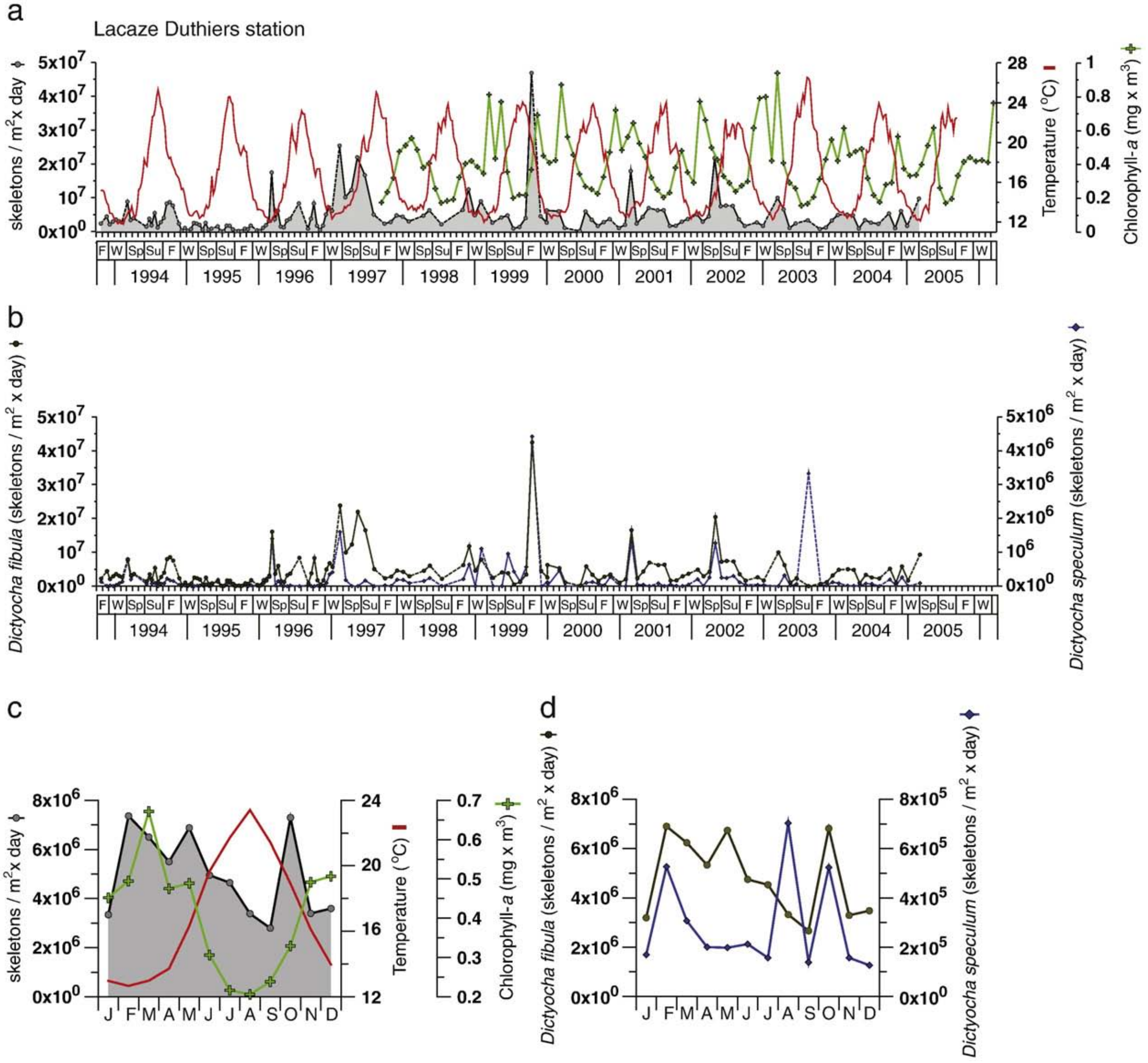


Fig. 3. Lacaze-Duthiers station. a. Total skeleton flux (skeletons / day × m^2), temperature (°C) and chlorophyll-*a* concentration (mg × m^3). b. *D. fibula* and *D. speculum* flux (skeletons / day × m^2). Gaps in the time series are represented by a dotted line. c. Composite year. Total skeleton flux (skeletons / day × m^2), temperature and chlorophyll-*a* concentration (mg × m^3). d. Composite year. *D. fibula* and *D. speculum* flux (skeletons / day × m^2).

3.4. Environmental variables

Weekly SSTs data from October 1993 until March 2006 were obtained using NOAA Optimum Interpolation Sea Surface Temperature Analysis (Reynolds et al., 2002). Monthly chlorophyll-*a* satellite data (since September 1997) were obtained from the NASA Giovanni programme (Acker and Leptoukh, 2007). General salinity values for each site were taken from MEDATLAS 2002. All this information is summarized in Table 1.

4. Results

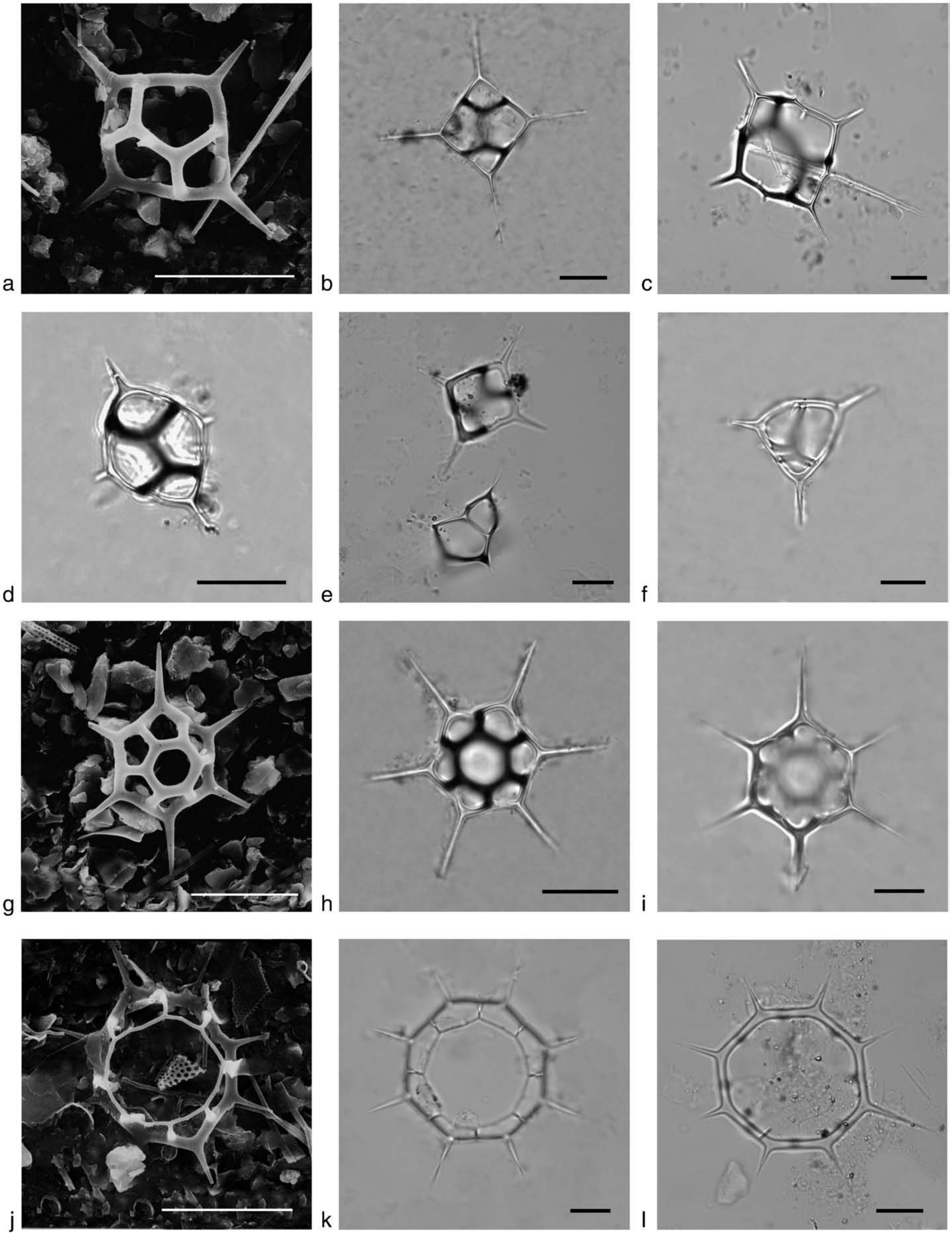
4.1. General considerations

Three silicoflagellate species were identified at the five stations of the Western Mediterranean: *Dictyocha fibula* (Ehrenberg), *D. speculum* (Ehrenberg) and *Octactis octonaria* (Ehrenberg) (Plate 1). *D. fibula* exhibited greater morphological and size variability than the others, although these variations were considered to be intraspecific (Plate 1). No remarkable morphological differences were found between seasons or locations in the samples studied. *D. speculum* and *O. octonaria* (Plate 1) showed more homogeneous skeletons with few aberrant specimens.

4.2. Gulf of Lions

Total silicoflagellate fluxes were one order of magnitude lower than diatom fluxes in both traps (Rigual-Hernández, unpublished data). At the Planier site, despite the time series exhibiting interannual variability, the observations for the composite year revealed a clearly unimodal trend (Fig. 2c and d). The highest fluxes were generally recorded in winter and spring and the minima in summer until the beginning of fall (Fig. 2c). The mean flux at the Planier station was

Plate 1. SEM and LM photos of the three silicoflagellate species found in the samples. a–f. *Dictyocha fibula* (Ehrenberg). SEM (a), LM (b–f). g–i *Dictyocha speculum* (Ehrenberg). SEM (g), LM (h,i). j–l. *Octactis octonaria* (Ehrenberg). SEM (j), LM (k,l). Scale bars: a, g, j = 20 μm; b–f, h, i, k, l = 10 μm.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2.89×10^{6} skeletons $m^{-2}\,d^{-1}$, while the maximum and minimum fluxes occurred in May 2000 (1.98×10^{7} skeletons $m^{-2}\,d^{-1}$) and August 2001 (6.69×10^{4} skeletons $m^{-2}\,d^{-1}$) (Fig. 2a) respectively.

The total silicoflagellate flux at the Lacaze-Duthiers site also exhibited interannual variability and a clear seasonal trend. The 12-year mean showed a trimodal distribution (Fig. 3c and d) with maximum values during February–March (winter–spring transition), a secondary maximum at the end of the spring (May), and a third peak in October, while minimum values were reached during summer and the beginning of fall. The mean flux at the Lacaze-Duthiers station was 4.97×10^{6} skeletons $m^{-2}\,d^{-1}$. The highest flux at this station was recorded in October 1999 (4.68×10^{7} skeletons $m^{-2}\,d^{-1}$), whereas the minimum was recorded in September 1995 (9.77×10^{4} skeletons $m^{-2}\,d^{-1}$) (Fig. 3a).

Regarding the composition of the silicoflagellate assemblage, *D. fibula* was by far the most abundant species, with a mean of 95.5% for both sites. *D. speculum* represented 4.3% of the assemblage for both stations, while only a handful of specimens of *O. octonaria* was identified in both records, affording a relative contribution of 0.08% for the Planier site and 0.18% for the Lacaze-Duthiers station. Owing to the scarce presence of *O. octonaria* in these two records, its relative abundance was considered negligible and hence it is not plotted in Figs. 2 and 3. The seasonal distribution of *D. fibula* and *D. speculum* was slightly different for both sampling sites: while at Planier *D. speculum* reached its maximum relative abundance in June (Fig. 2b and d), at Lacaze-Duthiers the maximum occurred during August (Fig. 3b and d).

4.3. Catalan margin

Silicoflagellate fluxes at Foix station were one order of magnitude lower than the diatom fluxes (Fig. 4a). Total silicoflagellate fluxes did not show any clear seasonal trend and paralleled those of diatoms (Fig. 4a). Total diatom fluxes (Fig. 4a) showed three remarkable maxima (April 1993, fall 1993 and February to April 1994) that were linked to relatively high silicoflagellate fluxes. The highest silicoflagellate fluxes were recorded during the first half of August 1993 (3.80×10^{7} skeletons $m^{-2}\,d^{-1}$), while minima were recorded during the winter and March of 1994 (Fig. 4a). The mean flux at this site was the highest of the five sediment trap records (6.36×10^{6} skeletons $m^{-2}\,d^{-1}$). Moreover, it is worth noting that the most important discharge pulses of the river Llobregat (Puig and Palanques, 1998) (Fig. 4a) were followed by relatively high silicoflagellate fluxes; i.e., in the spring and fall of 1993.

D. fibula represented 96.7% of the annual assemblage, the highest of the five records studied, while *D. speculum* represented 3.3% of the assemblage. During June 1993, *D. speculum* reached its highest relative abundance (17.6%) (Fig. 4b). No *O. octonaria* specimens were found in Foix record.

4.4. Alboran Sea

Total silicoflagellate fluxes were one order of magnitude lower than the diatom fluxes in both traps (Bárcena et al., 2004; Hernández-Almeida et al., submitted for publication). The ALB 1F total silicoflagellate flux exhibited a trimodal distribution, with a clear seasonal pattern (Fig. 5a). The maximum values were recorded in summer 1997 and winter 1997–98, but a third peak was recorded at the end of the spring 1998. The mean flux in ALB-1F was 3.05×10^{5} skeletons $m^{-2}\,d^{-1}$. In December 1997, the highest fluxes were recorded (1.05×10^{6} skeletons $m^{-2}\,d^{-1}$) while the lowest values were recorded during fall, the end of winter and the beginning of the summer in 1998.

ALB-5F also exhibited a trimodal distribution, but different from that seen for ALB-1F. The mean silicoflagellate flux at this site was 5.49×10^{5} skeletons $m^{-2}\,d^{-1}$. The maximum flux was recorded in May 1998 (2.35×10^{6} skeletons $m^{-2}\,d^{-1}$) and the minimum fluxes were recorded in October 1997 (2.52×10^{4} skeletons $m^{-2}\,d^{-1}$).

D. fibula was the dominant taxon at ALB-1F and Alb-5F (Fig. 5b and d), representing 81.69% and 88.8% of the annual assemblage, respectively. *D. speculum* relative abundance in the Alboran Sea stations was negligible, with only one specimen found in the whole record of Alb-1F and a relative abundance of 0.4% in Alb-5F. Because of these insignificant values, *D. speculum* is not plotted in Fig. 5. Regarding *O. octonaria*, its relative abundance reached the highest values of the study in the Alboran Sea stations, where it accounted for 16.74% in Alb-1F and 10.9% in Alb-5F (Fig. 5b and d).

5. Discussion

This study aims to shed new light on silicoflagellate ecology defining, at least in broad outlines, the seasonal, interannual, and geographic distribution of silicoflagellates in the Western Mediterranean.

5.1. Biological and physical processes controlling the seasonal changes of the silicoflagellate fluxes

The fluxes recorded at the two stations in the Gulf of Lions were markedly seasonal and reflected changes in the water column and atmosphere dynamics. In terms of input of particulate material, the Planier site is subject to less influence from the shelf, while the Lacaze-Duthiers site is more affected by the continental shelf and the Rhône river plume (Heussner et al., 2006) (Fig. 1a). The material recorded may be of diverse origin, such as shelf bottom and shelf break resuspended sediments, Rhône river material, and shelf and open-ocean pelagic biogenic material. Vertical transport and sediment resuspension are more important during winter periods when the hydrodynamics in the Gulf of Lions are more intense (i.e, currents, water mixing, and dense-water formation) (Millot, 1990). The silicoflagellate fluxes recorded by both sediment traps may be partially affected by the latter factors, although several lines of evidence suggest that the skeletons recorded by our sediment traps reflect silicoflagellate assemblages dwelling in the euphotic layer. First, previous studies on water samples from the NW Mediterranean (Nival, 1965; Travers and Travers, 1968; Gómez and Gorsky, 2003) have described a similar seasonal silicoflagellate distribution and assemblage composition to those observed in our investigation. In addition, the silicoflagellate flux annual maxima coincided with the highest annual chlorophyll-*a* values (Figs. 2c and 3c), which indicate that phytoplankton skeleton fluxes mirrored the phytoplankton community of the photic zone. Finally, both sediment traps were set at 500 mab, which hinders the recording of important amounts of resuspended sediments.

The nutrient-rich euphotic layer and solar radiation increase during the winter–spring transition (Leblanc et al., 2003) favour the development of the spring phytoplankton bloom (Bustillos-Guzmán et al., 1995; Marty et al., 2002), and hence of the silicoflagellate assemblages in both Planier and Lacaze-Duthiers stations. The low skeleton fluxes recorded during summer and the beginning of fall at both stations (Figs. 2 and 3) are due to the strong oligotrophy and stratification conditions of the water column (Leblanc et al., 2003).

The higher silicoflagellate fluxes at the Lacaze-Duthiers than at the Planier site (almost twice as high) (Fig. 3) seem to be elicited by the influence of the dilution zone of the Rhône plume, which enriches the southwestern part of the Gulf of Lions shelf with nutrients (Lefevre et al., 1997). This could be the cause of the silicoflagellate skeleton peak at the beginning of fall at the Lacaze-Duthiers site (Fig. 3c and d), when the Rhône River reaches its maximum discharge values (Heussner et al., 2006).

Previous studies in the NW Mediterranean (Nival, 1965; Travers and Travers, 1968; Gómez and Gorsky, 2003) have described that during summer *D. fibula* sinks to deeper and colder waters. Since *D. speculum* follows a similar annual cycle (Figs. 2 and 3), it is possible that it could have a similar kind of behavior and could sink to deeper

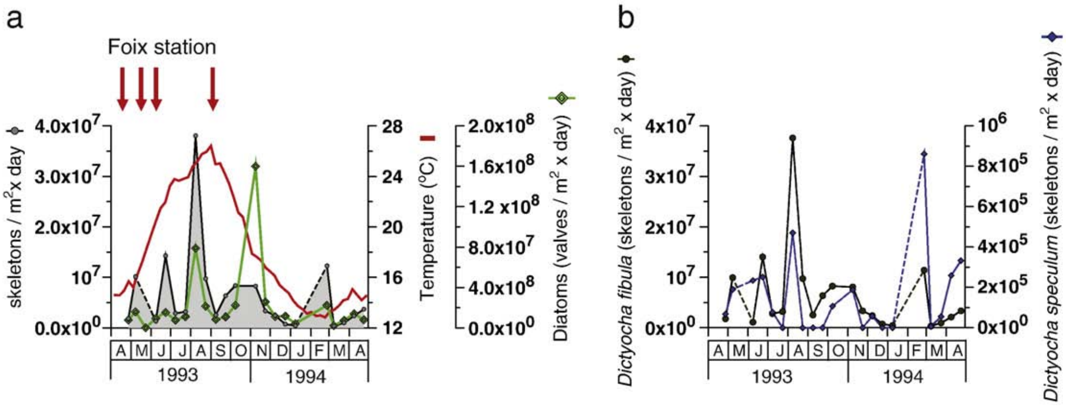

Fig. 4. Foix station. a. Total skeleton flux (skeletons / day × m^2), temperature (°C), total diatom flux (valves / day × m^2) and main river discharge events (red arrows). b. *D. fibula* and *D. speculum* flux (skeletons / day × m^2).

waters during the stratification period. Despite the low *D. speculum* fluxes, the relative abundance of this species increases during summer (up to 12%), suggesting a better adaptation of this taxon to oligotrophic conditions than *D. fibula*.

Regarding the Catalan margin, the Foix station does not exhibit a clear seasonal signal, probably due to the proximity of the Llobregat and Besos rivers (Fig. 1b) that could have influenced the plankton communities by means of nutrient and freshwater inputs along the collecting period. This, together with the fact that the Foix station is closest to the coast of the five sampling sites, seems to be the reason why the highest silicoflagellate fluxes of the five sampling locations were recorded at the Foix site. Owning to the similar distribution of diatom and silicoflagellate fluxes (Fig. 4a), both phytoplankton groups seem to respond to the same conditions of the water column. Little is known about the influence of river input on silicoflagellate populations, but Jochem and Babenerd (1989) described a progressive increase of the silicoflagellates assemblages in relation with the gradual eutrophication of the estuarine waters of the Kiel Bight. The absence of a clear seasonal pattern, together with the fact that the discharge pulses of the river Llobregat (Puig and Palanques, 1998) were often followed by relatively high silicoflagellate fluxes (Fig. 4a), suggests that the silicoflagellate skeleton fluxes recorded at the Foix station could have been determined by the river input. The plumes of the rivers Llobregat and Besos might have enhanced the growth of phytoplankton communities, and hence the silicoflagellate skeleton fluxes. In addition to this, it is worth noting that the highest

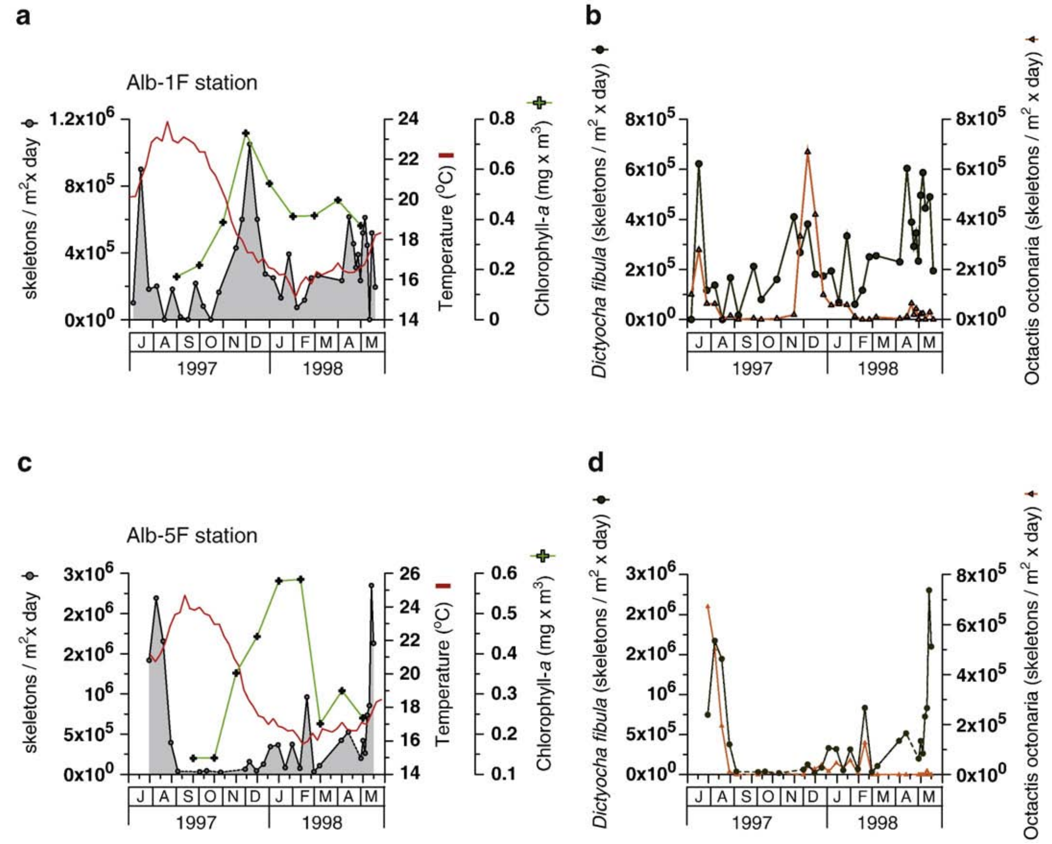

Fig. 5. Alboran Sea (ALB-1F and ALB-5F) stations. a. ALB-1F total skeleton flux (skeletons / day × m^2), temperature (°C) and chlorophyll-*a* concentration (mg × m^3). b. ALB-1F *D. fibula* and *O. octonaria* flux (skeletons / day × m^2). c. ALB-5F total skeleton flux (skeletons / day × m^2), temperature, and chlorophyll-*a* concentration (mg × m^3). d. ALB-5F *D. fibula* and *O. octonaria* flux (skeletons / day × m^2). Gaps in the time series are represented by a dotted line. c. Composite year.

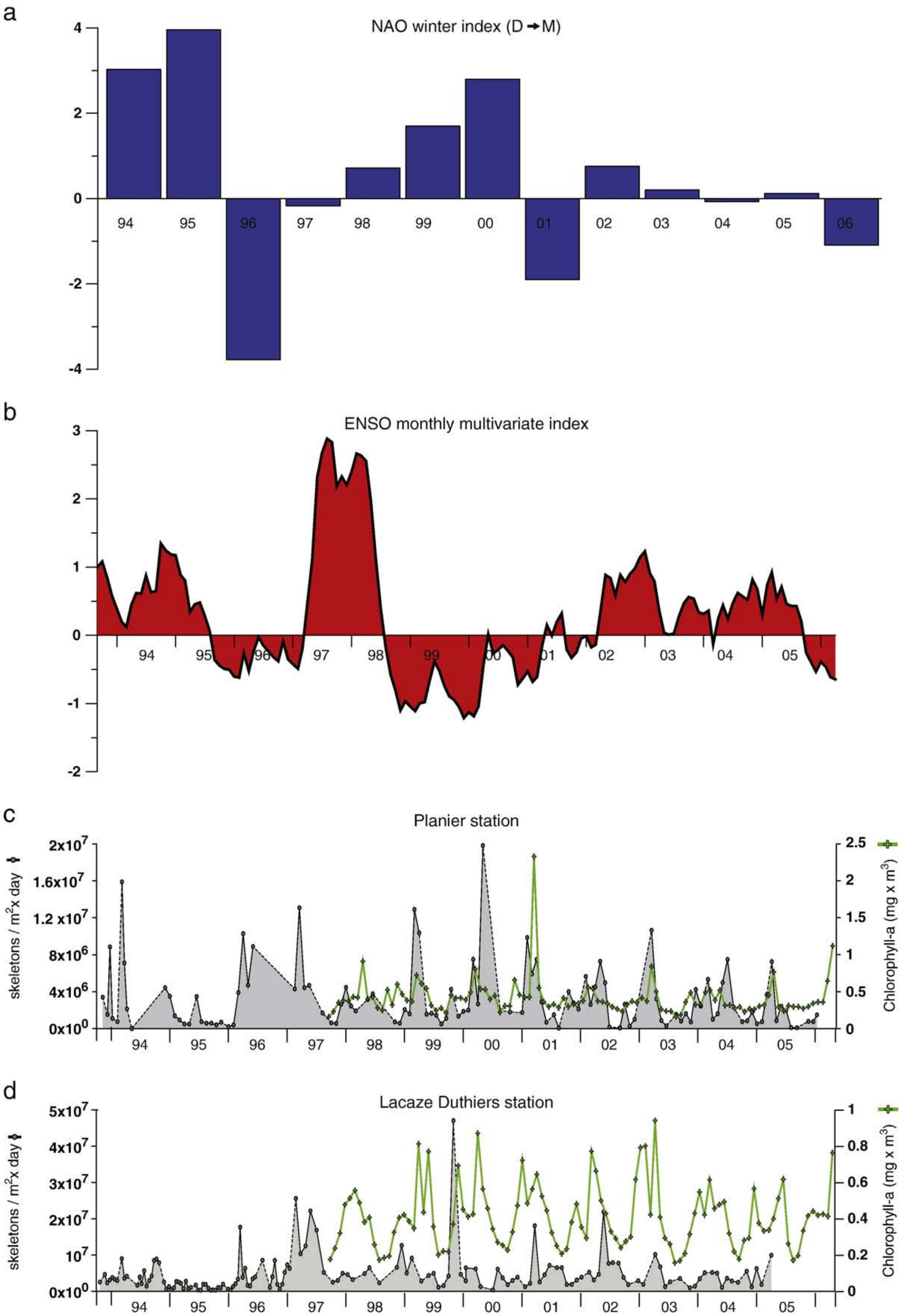

Fig. 6. a. NAO winter index. b. monthly multivariate ENSO index. c. Planier station total skeleton flux (skeletons/day × m^2) and chlorophyll-*a* concentration (mg × m^3). d. Lacaze-Duthiers station total skeleton flux (skeletons/day × m^2) and chlorophyll-*a* concentration (mg × m^3).

silicoflagellate fluxes of the whole record occurred during August, a period of strong stratification as indicated by the SSTs (Fig. 4), that can be used as a rough indicator of stratification (e.g. Martinez et al., 2009). We speculate that certain anthropogenic macro- or micro-nutrient inputs to any of the rivers could have triggered the massive growth of silicoflagellates during August, regardless of the river flow.

The sediment traps from the Alboran Sea were set in two systems of high biological productivity associated with the Western Alboran Gyre (WAG) and the Almeria–Oran density front (AOF) (Fig. 1), and were relatively less influenced by coastal inputs as compared to the other sampling sites. The lowest silicoflagellate fluxes of this study were recorded at the Alboran Sea stations, probably reflecting their location in the relatively open sea. Both silicoflagellate flux records exhibited a marked seasonality and responded to the same conditions as those observed by Bárcena et al. (2004) and Hernández-Almeida et al. (submitted for publication). At ALB 1F, the silicoflagellate skeleton pulses during the beginning of summer and fall 1997 (Fig. 5a and b) were related to the last steps of a high productivity period and to upwelling-favourable winds (Bárcena et al., 2004) respectively. Furthermore, the especially warm fall conditions of that year elicited a delay in the winter–spring bloom (García-Gorriz and Carr, 2001), and hence of the development of the silicoflagellate populations. Concerning the ALB 5F sediment trap (Fig. 5c and d), the similar distribution of the silicoflagellate fluxes to those found in ALB 1F suggest that both records respond to the same conditions. However, the 1997 fall silicoflagellate flux maximum was displaced to the winter, probably owning to the warmer temperatures in this area (Fig. 5c).

5.2. Impact of NAO and ENSO variability on silicoflagellate fluxes

Because the Gulf of Lions time series spanned more than one year we will focus on these two sediment traps to address interannual variability. The first point to be noted is that the maximum fluxes in both sediment traps did not always occur at the same time of year. The lower influence from the shelf, the Rhône, and dense-water formation events (Canals et al., 2006; Ulses et al., 2008) at the Planier site might explain their different behavior.

The climate of the Northern Basin (the Gulf of Lions and the Ligurian–Provencal Basin), as well as transport through the Corsica Channel (Fig. 1), is under the influence of the North Atlantic Oscillation (NAO), especially during winter (Fig. 6a) (Hurrell, 1995; Vignudelli et al., 1999). In the Northern Basin, negative NAO winter index values are associated with an intensification of heat losses to the atmosphere and with a consequent increase in water transport through the Corsica Channel, which feeds the Northern Current (Fig. 1a). Conversely, positive values of the NAO index mean that warmer and moister air masses are conveyed towards the Northwestern Mediterranean, leading to milder winters and a consequent decrease in the total amount of heat lost (Vignudelli et al., 1999). In their review of the interannual phytoplankton variability of the Northern Basin, Gómez and Gorsky (2003) pointed out that low or negative NAO indices are often associated with a remarkable spring diatom bloom, while positive values are associated with a lower spring bloom. Since the beginning of the chlorophyll-*a* record (September 1997), the most extreme negative winter NAO values occurred during 2001 and 2006 (Fig. 6). At the Planier site, the springs of 2001 and 2006 were coupled to remarkably high chlorophyll-*a* concentrations and elevated silicoflagellate fluxes, which reflect a positive response of the phytoplankton communities to the environmental conditions of those years (Fig. 6). In contrast, the spring chlorophyll-*a* values at Lacaze-Duthiers did not show anomalously high values during 2001 and 2006, although the silicoflagellate fluxes at this station were relatively high (Fig. 6). The different response of the phytoplankton community at the Lacaze-Duthiers station could be related to the influence of the Rhone plume and the particulate matter supply from the shelf and upper slope. Regarding the years with the most extreme positive NAO values (1999 and 2000) (Fig. 6a), both stations showed intermediate spring chlorophyll-*a* concentrations while silicoflagellate fluxes behaved differently: at the Planier site the silicoflagellates showed high fluxes, but relatively low silicoflagellate fluxes were recorded in Lacaze-Duthiers station (Fig. 6c and d). Therefore, although negative NAO values could be related to remarkable phytoplankton spring blooms in the Northern Basin, our silicoflagellate flux time series do not reveal a straightforward relationship with the winter state of the NAO, indicating that the process that generates silicoflagellate flux variability is not controlled by the NAO.

Another major source of climatic variability should be considered: the El Niño Southern Oscillation (ENSO). The ENSO (Fig. 6b) is the dominant mode throughout the tropical climate system and its major effects occur over the southern hemisphere. However, there is evidence that extreme ENSO events can modify the North Atlantic and European climate (Wanner et al., 1997). According to McPhaden (1999), the 1997–98 El Niño Event (Fig. 6b) was the strongest one of the last century and the author suggested that the major climatic impacts around the world were related to this event. This could be the case of the anomalously high summer and fall SSTs recorded in the Alboran Sea (Bárcena et al., 2004; Hernández-Almeida et al., submitted for publication) and the Gulf of Lions in 1997 (Figs. 5a, c, 6c and d). The winds at both locations were also unusually weak, favouring a strong water stratification that delayed the typical winter destratification and fertilization events, resulting in a weaker than usual winter–spring bloom regime (Bárcena et al., 2004; Rigual-Hernández et al. in prep.).

The anomalous warm conditions during the winter of 1997–98 in the Alboran Sea elicited a delay in the spring phytoplankton bloom until April–May (Bárcena et al., 2004), and hence in the silicoflagellates collected in both sediment traps. Something similar occurred in the Gulf of Lions: at the Planier site the spring bloom was also delayed until April and was linked to low silicoflagellate fluxes (Fig. 6c), while at the Lacaze-Duthiers station the bloom took place as in a normal year during the winter–spring transition (Fig. 6d). However, the chlorophyll-*a* values, as well as the silicoflagellate fluxes, were lower than in other years. Our observations coincide with those of Gómez and Gorsky (2003) for the NW Mediterranean, who described lower silicoflagellate concentrations and warmer temperatures during the winter of 1997–98 in comparison with 1998–99.

The 1997–98 El Niño Event also altered the silicoflagellate fluxes in other parts of the globe, such as in the North Pacific, where Onodera and Takahashi (2005) described changes in the silicoflagellate assemblage, or in the Santa Barbara Basin, where Lange et al. (2000) reported the lack of the annual fall–winter silicoflagellate peak.

Apart from the NAO and ENSO, other phenomena could also affect the silicoflagellate fluxes in the Western Mediterranean. In this sense, the 2003 summer heat wave over Western Europe and the Western Mediterranean Basin was coupled with an increase in air temperature

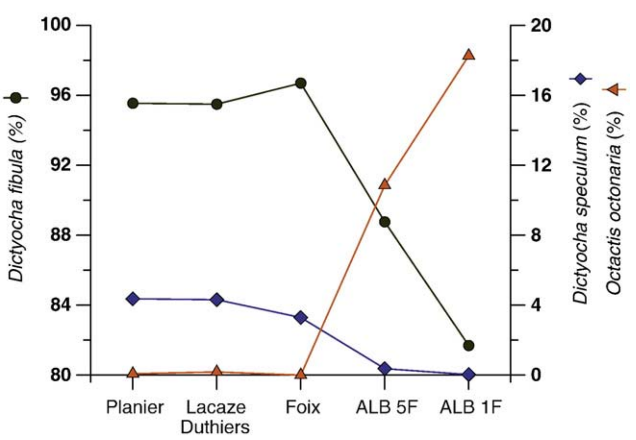

Fig. 7. Relative abundance of the three silicoflagellate taxa along a N–S transect from the Gulf of Lions to the Alboran Sea.

and a decrease in wind stress that affected the SSTs over the Western Mediterranean (Olita et al., 2007). During that year, the Planier and Lacaze-Duthiers stations recorded the highest summer SSTs of the record that probably contributed to reduce the spring chlorophyll-*a* productivity and the silicoflagellate fluxes (Figs. 2a and 3a) owned to the weaker winter mixing.

5.3. Geographic distribution of the Western Mediterranean silicoflagellates

The three areas studied in the Western Mediterranean show important differences in the composition of silicoflagellate assemblages (Fig. 7) that seem to be closely related to environmental factors, especially temperature.

D. fibula is a cosmopolitan species, and was the dominant species in all the assemblages (Fig. 7). Its fluxes are maximum during winter–spring periods and minimum during summer, when it probably sinks to deeper and colder water masses. *D. fibula* seems to be well adapted to a wide range of temperatures and to be especially sensitive to nutrient inputs, reaching its maximum fluxes in areas where the influence of a river is important (i.e. at the Lacaze-Duthiers and Foix stations).

The distribution of *D. speculum* however, is restricted to the Northern region (Gulf of Lions and the Catalan margin), being almost absent in the Alboran Sea. In fact the Northern region can be considered among the coldest areas in the Mediterranean, where annual SSTs range from 12 to 26 °C (Table 1). Using cultures, Henriksen et al. (1993) determined that the optimum growth of *D. speculum* occurs at temperatures between 11 and 15 °C at salinities of 30‰. Higher temperatures dramatically decrease the number of cell divisions. In nature, the skeleton-bearing and naked stages of *D. speculum* grows within similar temperature ranges, whereas the skeleton-bearing stage of *D. speculum* is generally found at higher salinities. In addition, these authors reported that salinities over 30‰ would reduce the optimal temperature range of this taxon. Taking into account that the salinity in the Mediterranean Sea is higher than the concentration used for the cultures (Table 1), the optimal growth temperature of *D. speculum* would be more restricted than for laboratory cultures. In our study, the restriction of *D. speculum* to higher latitudes (Fig. 7) suggests an affinity for relatively cold water masses. Its growth would be inhibited at the other regions where annual SSTs do not reach values below 15 °C; i.e., the Alboran Sea.

In contrast, the distribution of *O. octonaria* is restricted to the Alboran Sea (Fig. 7), where temperatures range between 15 and 24 °C (Table 1). The absence of significant relative abundances of this species in the coldest and most fertile sampling locations (Gulf of Lions and Catalan margin) (Fig. 7) suggests an affinity of *O. octonaria* for warmer and/or relatively oligotrophic water masses.

6. Conclusions

Silicoflagellate fluxes in the Western Mediterranean mirror the atmospheric and water column dynamics. Their fluxes are often maximum during the winter–spring transition, coinciding with the spring phytoplankton bloom. However, they seem to be especially sensitive to river input, showing their maximum fluxes and a less clear seasonal pattern at the stations affected by river plumes (e.g. the Lacaze-Duthiers and Foix stations). Of the three identified species found in the Western Mediterranean, *D. fibula* is the most widespread and abundant taxon, always accounting for more than 80% of the silicoflagellate assemblage in the five studied sites. The distribution of *D. speculum* and *O. octonaria* seem to be controlled by temperature. While *D. speculum* is restricted to the northern part of the Western Mediterranean Basin, where annual temperatures often drop to 12 °C during winter, *O. octonaria* is limited to the Alboran Sea stations, where annual minimum temperatures are never colder than 15 °C. Regarding interannual variability, the silicoflagellate fluxes do not show a straightforward relationship with the NAO winter index. However, the strong 1997–1998 ENSO event and the 2003 summer heat wave seem to have been the cause of the low silicoflagellate fluxes of the spring season of the following year, due to the higher winter temperatures and the delay of the spring phytoplankton bloom.

Acknowledgements

The authors wish to thank Nicole Delsaut and Joan Fabrés for their help and the preparation of the material supplied, as well as, Richard Jordan to put the electronic microscope at our disposal. Durrieu de Madron is greatly acknowledged for his assistance. The chlorophyll-*a* data used in this paper were produced with the Giovanni online data system, developed and maintained by the NASA GES DISC. This study has been performed thanks to funding from the Ministerio de Ciencia e Innovación Project GRACCIE (PROGRAMA CONSOLIDER-INGENIO 2010-CSD 2007-00067), CGL 2006-10593, CGL 2008-05560 and CGL 2009-08651 and the support from Junta de Castilla y León (Grupo GR34) and a MEC FPU grant awarded to Andrés S. Rigual-Hernández (AP2006-01992). Critical comments and suggestions from two anonymous reviewers helped greatly to improve the initial version of this work.

Appendix

The following descriptions of the three species identified (Fig. 1) are based on our observations and the descriptions of Throndsen (1997) and Hernández-Becerril and Bravo-Sierra (2005).

Dictyocha fibula Ehrenberg 1839

The siliceous skeleton size is 29–47 μm in width and 32–58 μm in length. The skeleton is square to rhomboid, with four radial spines and four “windows”. The apical bar (bridge) exhibits an apical spine in the middle. Four supporting spines are situated in the basal ring close to the junctions with the apical struts. This species exhibited more morphological variations than the other two taxa, such as variations in the size of the radial spines and in the shape of the basal ring, as well as the presence of different aberrant skeletons (e.g. Plate 1f).

Dictyocha speculum Ehrenberg 1839

The skeleton of *D. speculum* (size 26–31 μm in width, 30–43 μm in length) has a hexagonal basal ring with six radial spines. An apical ring is supported by six apical struts. All the components of the skeleton appear to have the same thickness. Six supporting spines are conspicuous in the basal ring. No remarkable morphological variations were found in the specimens studied.

Octactis octonaria (Ehrenberg) Hovasse 1946

The skeleton of this taxon has an octagonal basal ring with eight radial spines. The shape of the skeleton is approximately circular with a diameter of 48–61 μm. It exhibits an apical ring supported by 8 apical struts. The apical ring is thinner than the rest of the skeleton. The basal ring does not have supporting spines. The morphological variations of this skeleton were mainly caused by the absence of the apical ring (e.g. Plate 1l), which could be related to silica dissolution in the water column.

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