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A recurrent and localized dinoflagellate bloom in a Mediterranean beach

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Abstract. A recurrent, prolonged and singular bloom of *Alexandrium taylori* Balech in an open beach (La Fosca, Spain, NW Mediterranean) is described. *Alexandrium taylori* appears at several places along a wide area of the NW Mediterranean (Costa Brava) during the summer, reaching concentrations up to 10^5 cells l^{-1}, but it only proliferates persistently, massively (densities $>10^6$ cells l^{-1}) and recurrently during August in La Fosca beach. The *A.taylori* bloom can be considered a manifestation of large-scale proliferation in a restricted area, where coupling between resting cysts in the sediment and bloom outbreak is not a major factor compared to the interaction of local environmental conditions with the planktonic organism's life history. From observations of environmental conditions (the environmental window) and the multiscale spatio-temporal distributions and life history of *A.taylori*, we describe the bloom dynamics and answer some critical questions about the different phases of the bloom. Some of these answers are: (i) the source of the *A.taylori* population is widespread offshore and is not located directly at the beach; (ii) high cell densities are reached and maintained with a moderate *in situ* growth and low loss rates; (iii) temporary cysts act as a reserve of the population.

Introduction

The increase in toxic, noxious or harmful algal blooms (HABs) that is apparently occurring worldwide (Anderson, 1989; Smayda, 1990, 1997; Hallegraef, 1993) has also been seen in the NW Mediterranean, where there have been numerous descriptions of dinoflagellate blooms in the last 50 years. This especially includes species in the genus *Alexandrium* (Margalef, 1957, 1969; Halim, 1960; Margalef and Estrada, 1987; Delgado *et al.*, 1990; Montresor *et al.*, 1990; Garcés, 1998), some of which are known to cause paralytic shellfish poisoning (PSP).

Although critical factors for bloom formation have been described for some species (Seliger *et al.*, 1970; Anderson and Morel, 1979; Tyler and Seliger, 1981; Franks and Anderson, 1992b; Figueiras, 1994), we have only a crude understanding of the ecophysiological mechanisms that promote and maintain harmful algal blooms. From recent reviews (Anderson, 1997, 1998), some outbreaks of *Alexandrium* episodes can be classified as large-scale coastal blooms associated with major oceanographic processes such as coastal currents, tidal fronts, etc. Some source populations originate from widely distributed germinating resting cysts, with emergence controlled by an endogenous clock that restricts germination to a seasonal window irrespective of the external environment (Anderson and Keafer, 1987). The other *Alexandrium* bloom model is that of small-scale, localized populations in areas such as salt ponds, embayments and estuaries. These blooms originate from isolated and autochthonous cyst seedbeds, with no input of cells from coastal waters (Anderson and Wall, 1978; Anderson and Morel, 1979). Blooms in those areas have very tight linkage in time and space to benthic resting cyst populations. However, blooms in such waters can also be a manifestation of large-scale blooms, where coupling between resting cysts in the sediment and bloom outbreak is not direct, and depends mainly on the interaction of local environmental conditions and organism behaviour (e.g. specific strategies, life histories). In this genus, autecological features are often dominated by life cycle transformations and their effect on bloom dynamics (Anderson *et al.*, 1983; Wyatt and Jenkinson, 1997; Anderson, 1998). The life histories of most *Alexandrium* species involve an alternation between asexual (vegetative cells) and sexual reproduction (resting cysts).

This paper focuses on the autecological underlying features of an *Alexandrium* bloom that can be considered unusual because of its particular characteristics; we analyse the distribution pattern of *Alexandrium taylori* and environmental conditions at different spatio-temporal scales (from regional to local scales). The association of this species with massive proliferations has not been described previously and only recently have the phases of its life history been described (Garcés *et al.*, 1998; Giacobbe and Yang, 1999). The *A.taylori* bloom develops into a small and limited patch of high biomass (~10 000 m^2 of 10^5–10^6 cells l^{-1}) that causes water discoloration (up to 20 μg l^{-1} of chlorophyll *a*) and is noticeable for 2 months. These features are an exception rather than the rule, since *Alexandrium* blooms are often reflected in moderate biomass levels and are not particularly long lasting (Wyatt and Jenkinson, 1997). This allows us to discover more about the specific diversity of this genus with respect to ecological requirements.

Background and study area

The presence of intensely green–brown-coloured water at La Fosca, between mid-July and mid-September, which coincides with the greatest influx of tourists, has been reported since 1982 and has caused great problems for the Spanish Government (evident deterioration in the quality of water). Discoloration of the water is apparent from late morning and mid-day until the evening, although the water appears quite clear in the early morning. The incidence is greater during years characterized by calm weather. With wind and high sea movement, the patch is not visible; it can only be seen after 3–4 days of calm. Problems arise due to the distinct deterioration in the quality of the water, which the people in the area associate with sewage discharges. This led to extensive monitoring of water quality, but no evidence of sewage has been found in 7 years. No explanation of the phenomenon was found until the cause of the water discoloration was described as a non-toxic dinoflagellate bloom of *A.taylori* Balech (Delgado *et al.*, 1997). *Alexandrium taylori* does not appear to be mentioned in the Mediterranean prior to its identification at La Fosca. Some information about *A.taylori* is available from previous work (Garcés *et al.*, 1998). Vegetative cells of *A.taylori* are free swimming and show marked diel vertical migration. In addition to the motile vegetative form, *A.taylori* has two benthic forms: a resting cyst and a temporary cyst. Apparently, temporary cysts are not a consequence of stress conditions and could be considered as a stage of the natural life cycle. The *in situ* growth rate was measured and the total population growth was the result of division by both vegetative cells (0.4–0.5 day^{-1}), and germination and division of temporary cysts (0.14 day^{-1}).

The study area was located from 41°50′N, 3°E to 42°30′N, 3°E on the Costa Brava (NW Mediterranean) and especially at La Fosca beach (Figure 1). The dimensions of La Fosca beach are 525 × 300 m (approximately rectangular) with the opening pointing towards the SE. Average and maximum depths are 3 and 7 m, respectively, with a gentle uniform slope between 2 and 7 m. The mean size of sediment at La Fosca ranges from 0.467 to 0.286 mm, with 98% of clear sand. The beach is divided into two areas separated by the Roca Negra, which stretches 30 m into the sea (La Fosca and St Esteve beaches).

Method

Spatio-temporal sampling

The study was performed at several spatio-temporal scales.

Coastal monitoring station in La Fosca

A fixed point (1 m depth) on the beach (station A) was sampled every 3–4 days during summers of 1995–1998. The parameters measured were salinity, temperature and nutrients. The cell quantification involved vegetative cell counts and temporary cysts in the sediment (only 1996). Surface water samples and sediment were taken at the same time of the day (between 13 and 17 h).

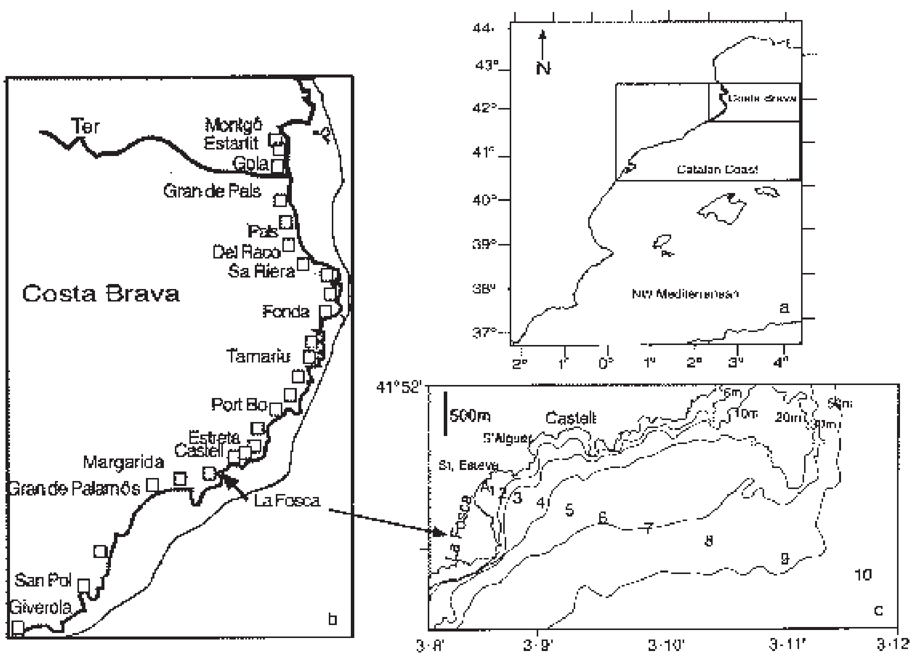

Fig. 1. Study area. Sampled beaches along the Costa Brava. La Fosca, stations 1–10 comprise the across-shelf section sampled in 1995. Point A is a fixed station sampled from the beach in the 4 years of this study.

Cruises in La Fosca beach

Inshore–offshore transects in La Fosca. Three cruises were conducted aboard the vessel 'Mar blau' during the summer months of 1995. An across-shelf section with 10 sampling stations (until 4 km from the coast) was made from 3 to 70 m depth (Figure 1c). CTD profiles were obtained and water samples were taken with Niskin bottles for cell counts and nutrient analysis.

Small-scale distribution. A total of 10–20 sampling stations (points inshore within the area of La Fosca and Castell) were chosen to analyse organism distribution in relationship to the temperature of La Fosca on 7 and 21 July 1995, and 20 August 1996.

Middle-scale sampling along the Costa Brava

Eighteen beaches were selected in the surroundings of La Fosca beach to delimit organism distribution. Temperature measurements and water samples were taken at the surface (between 13 and 17 h) once a week during the summer of 1996. The temperature anomaly of La Fosca has been calculated in relation to its surroundings [temperature of La Fosca (°C) minus the average temperature of the 18 beaches selected].

Monthly environmental measurements (physical parameters and nutrient analysis)

These measurements involved several coastal monitoring stations (1 m depth) along the Catalan coast during two annual cycles (including station A of La Fosca beach). Surface nutrient, salinity and chlorophyll *a* measurements of 22 stations that comprise the monitoring in the Costa Brava were presented to situate La Fosca beach in a regional framework. Sediment and surface water samples in La Fosca were also taken for cell counts.

The general procedure for identifying and quantifying *A.taylori* involved the collection and fixation of water samples (150 ml) in formaldehyde (1% final concentration), sedimentation of a subsample in 50 ml settling chambers and counting cells in an appropriate area (Throndsen, 1995) using an inverted Nikon microscope. Nutrient samples were frozen immediately and concentrations of nitrate, nitrite, ammonia, phosphate and silicate were measured following the Strickland and Parsons (1968) method. The chlorophyll concentration (Chl *a*) was measured using the Yentsch and Menzel (1963) fluorometric method, after filtering 50 ml water samples in a GF/F filter.

For sediment samples, the samples (50 g of sediment) were fixed in formaldehyde (1% final concentration) and a subsample (10 g) was sonicated for 5 min, and washed and filtered with sea water through a 60 μm screen. From the final suspension, 10 ml were examined at ×40 magnification in settling chambers with an inverted microscope. The vegetative cells and temporary cysts were distinguished by observing the cells with a well-defined thecal plate (Garcés *et al.*, 1998) with the specific staining of calcofluor (Fritz and Triemer, 1985)

Results

La Fosca beach in a regional framework (results from two annual cycles on a monthly basis)

Salinity was constant and high in the southern part of the Costa Brava, including La Fosca beach (Figure 2), since there were no river water discharges. Seasonal variations occurred within the normal values for coastal waters: from values of 37.6 p.s.u. at the beginning of the summer to 38.0 p.s.u. during September. Low salinity in the northern part of the area was due to direct river discharges mainly in autumn and spring. The range of pigment values (Chl *a*) was low (Figure 3); only the area influenced by river discharges showed values >2 µg l^{-1}. Concentrations of inorganic nutrients (Figure 4) showed an inverse pattern to salinity (relatively high values localized at the stations of minimum salinity). Values on the Costa Brava were low, and La Fosca was characterized by even lower inorganic nutrients, being particularly poor in silicate.

No vegetative cells or temporary cysts were found in these monthly samples along the annual cycle until the beginning of July, when middle-scale sampling at weekly frequency began.

Middle-scale sampling along the Costa Brava (weekly basis during summer months)

The average daily surface water temperature on the Costa Brava (18 beaches selected in the surroundings of La Fosca beach) from the end of May 1996 to the end of September 1996 is shown in Figure 3. From the first week of July until the end of August, the temperature rose from 21°C to almost 25°C; after this period, the temperature fell quickly to 18°C in 1 month. In the same figure, the temperature anomaly of La Fosca is presented and a tendency for positive values from June to mid-August was evident. It is important to note that the highest average temperature coincided with the maximum positive anomaly of La Fosca (+3.5°C). When the average temperature began to fall (end of August and September), the pattern was clearly reversed and La Fosca had a negative anomaly. Cell density of *A.taylori* is shown in Table I. The first week of July marked the beginning of the appearance of *A.taylori* in some locations. In August, densities of 10^5 cells l^{-1} were found in three main areas, near La Fosca beach, Gola-Pals and St Pol, although maximum cell densities (10^6 cells l^{-1}) were always observed at La Fosca. In early September, *A.taylori* populations disappeared from all the sampled beaches, except La Fosca, where the presence of the organism densities was found for another 3 weeks.

Coastal monitoring station in La Fosca over 4 years

The surface water temperature together with *A.taylori* cell densities at La Fosca in the 3–4 day basis during the four summers (1995–98) of the studied period and nutrient concentrations in the summer of 1996 are presented in Figures 5 and 6, respectively. Surface temperature ranged from 22 to 27°C during

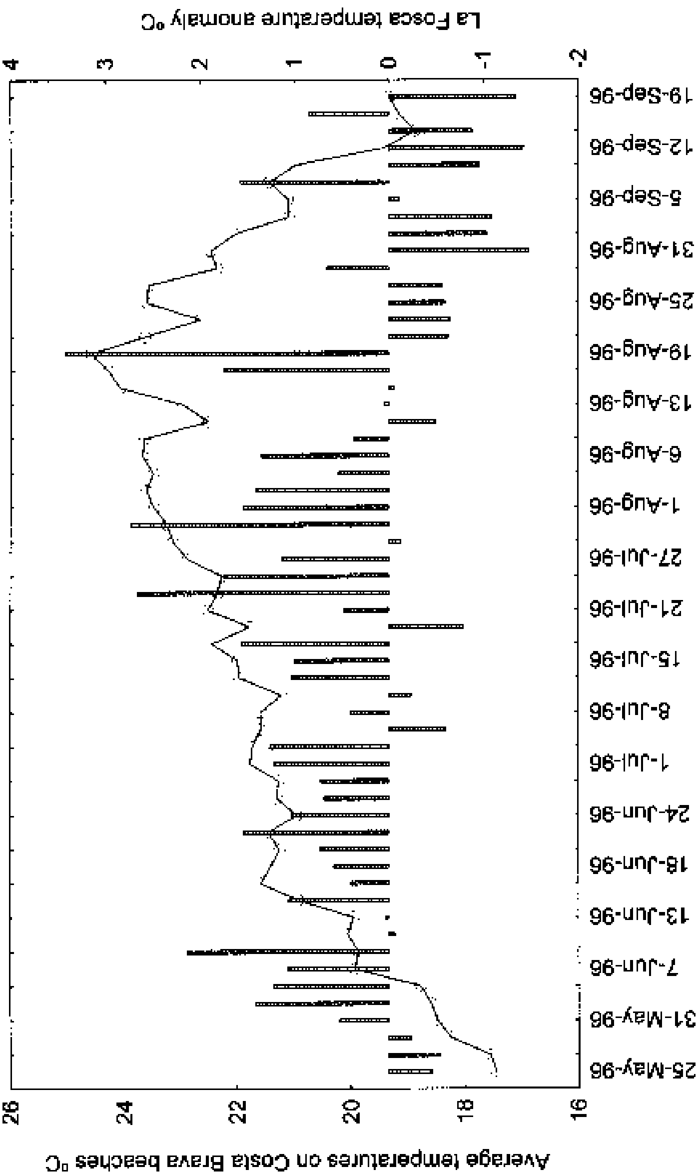

Fig. 2. Average surface water temperatures on the Costa Brava (17 beaches, line) and temperature anomaly of La Fosca (bars) on a daily basis from the end of May to September 1996. Anomaly = average Costa Brava surface water temperature – La Fosca surface water temperature.

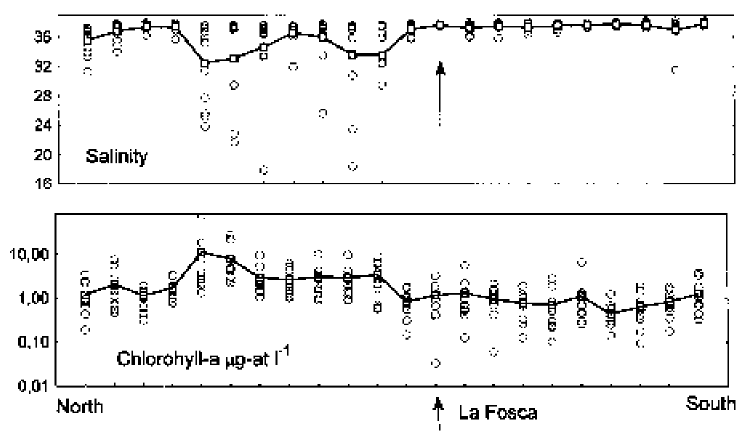

Fig. 3. Surface salinity and chlorophyll *a* from north to south along the Costa Brava (n = 22 beaches) over 10 months in 1996. Lines are the average values. La Fosca is indicated by an arrow.

July–September. From the third week of July until late August, temperatures did not fall below 24°C in any year (Figure 5). The increase in temperature occurred during July and the decrease started in late August. Surface nutrients were within the range of the annual cycle values shown in Figure 4. However, some isolated maximum values were detected in August. Cell densities varied between 10^3 and 10^4 cells l^{-1}, during the first week of July. An increase from 10^4 to 10^5 cells l^{-1} coincided with the water temperature increase for that month. Population densities $>10^5$ cells l^{-1} were maintained during August (temperatures >24°C) with variations between 10^5 and 10^6 cells l^{-1}. Discoloration of the water was observed with cell concentrations $>5 \times 10^5$ cells l^{-1}, which corresponds to up to 20 µg l^{-1} of Chl *a* (Garcés, 1998; Garcés *et al.*, 1998). An apparent decrease in cell densities occurred from the third week of August, coinciding with the decrease in water temperature. No cells were found during mid–late September.

In Figure 7, vegetative cell and temporary cyst densities, together with surface water temperature, are presented for the summer of 1996. At the beginning of July, when cell densities were $<10^3$ cysts g^{-1}, temporary cyst densities were already at 10^4 cysts g^{-1} of sediment, and densities were at this level throughout July (Figure 7). During August, when cell densities increased, there was a simultaneous increase in temporary cysts (10^5–10^6 cysts g^{-1}), with densities remaining at this level until the first week of September when the decrease in vegetative cell density began. The formation of cyst clusters (concentrations $>10^7$ cells l^{-1}) near the sediment was usually observed.

Inshore–offshore transects (general hydrographic structures)

The three cross-sections in Figure 8 show the hydrographic structure of the coast in relation to the different phases of the bloom dynamics (arrows in Figure 5).

Table I. *Alexandrium taylori* cell density at the surface (cells l^{-1}) during summer 1996 at 17 beaches along the Costa Brava from North to South. The asterisk indicates the presence of *A.taylori* (not higher than 10^3 cells l^{-1})

Date	Montgo	Estartit	Gola	Gran Pals	Pals	DelRaco	SaRiera	Fonda	Tamariu	PortBo	Estreta	Castell	La Fosca	Margarida	Palamos	St Pol	Giverola
7 July				0	0	0	200	0	0	0	0	200	100	0	0		0
15 July	0			0	0	200	200	0	0	0	1998	5994	1665	2331	200		200
21 July	0			0	0	0	0	0	0	0	0	0	194 524	0	0		0
28 July	0			0	0	0	200	0	0	0	200	50 960	2331	200	0		0
4 August	0	221 050	574 730	132 630	11 322	26 640	1332	0	0	0	0	0	240 000	0	0		
11 August	0		8842	2345	200	0	0	0	0	0	0	0	378 000	200	0	77 589	0
18 August	1665	1665	36 963	70 929	2100	150	300	200	0	0	200	10 800	2 500 000	200	0	245 752	0
25 August	0			200	200	0	0	0	0	0	1200	200	150 000	0		25 308	0
1 September	0	0	*	100	100	0	*			0	0	*	5994	0	0	162 656	0
8 September	0		0	*	*	0	0	0	0	0	0	0	6993	0	0	0	0
15 September	0	0	0	0	0	0	0	0	0	0	0	0	300	0	0	0	0
22 September	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0

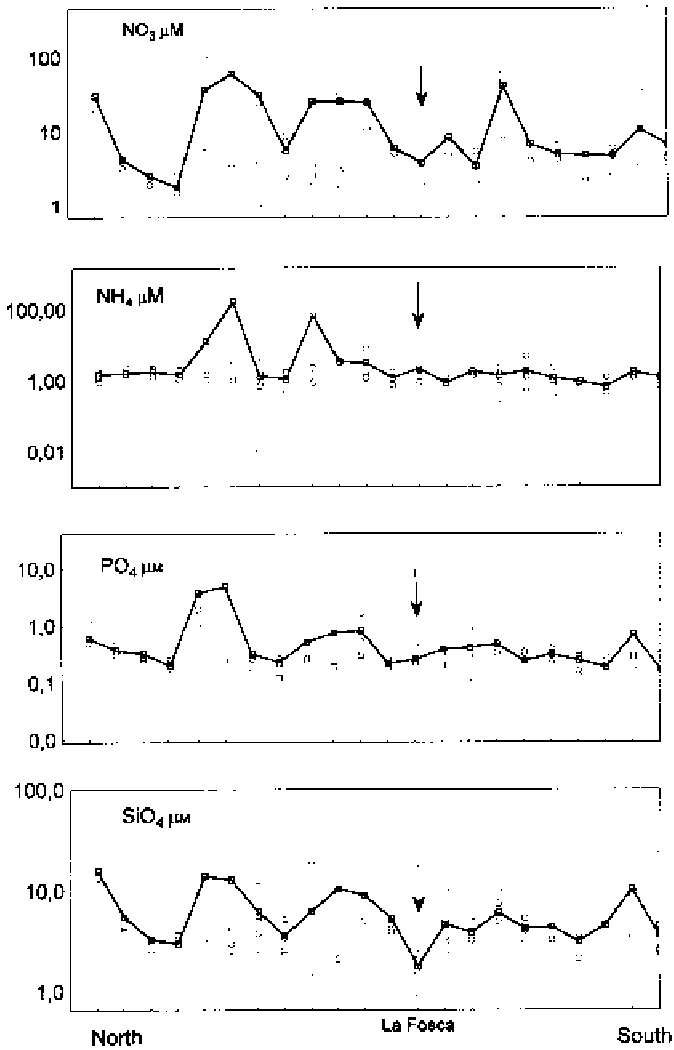

Fig. 4. Nutrient concentration (µM) from north to south along the Costa Brava ($n = 22$ beaches) over 10 months in 1996. Lines are the average values. La Fosca is indicated by an arrow.

Sigma-T and cell densities are shown in Figure 8a, and salinity in Figure 8b. Temperature (not shown) followed the same pattern as sigma-T.

By the beginning of July, the seasonal pycnocline had developed. The surface layer (from 0 to 20 m depth) of the whole area was vertically homogeneous and characterized by a salinity of 37.6 p.s.u. (Figure 8b) and a water temperature of 20°C. *Alexandrium taylori* was present at low concentrations from the station nearest the coastline to 1.5 km from the coast, both at the surface and in the deeper waters near the bottom (Figure 8a). During the first week of July, *A.taylori*

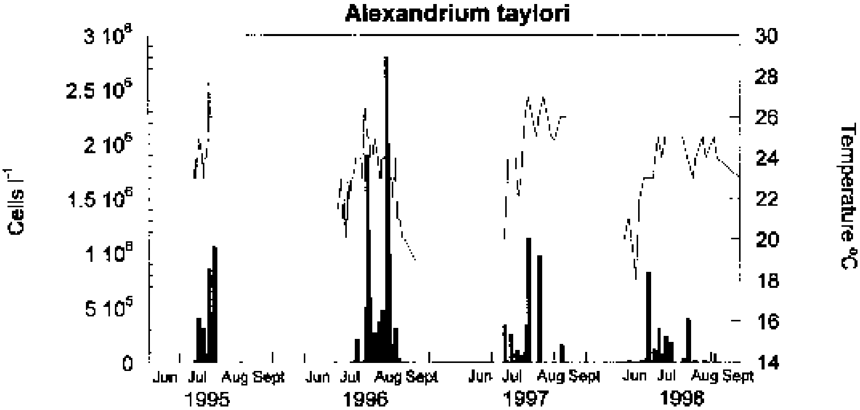

Fig. 5. Water surface temperature and cell density of *A.taylori* at the surface from June to September 1995–96–97–98 at La Fosca (fixed point A).

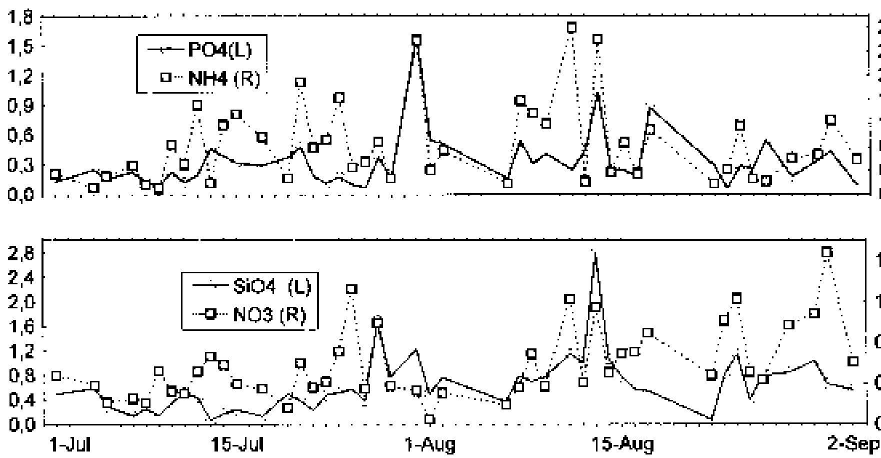

Fig. 6. Surface inorganic nutrient concentrations (NO_3, NH_4, PO_4 and SiO_4 µM) from July to August 1996 at La Fosca on a weekly basis at fixed point A.

was found at the beach (station A) at low cell densities of 10^3 cells l^{-1} (water discoloration was not visible).

In August, there was intense stratification from offshore towards the coast. The surface temperature increased by 3°C relative to July and salinity was uniform in the area with surface values of 37.9 p.s.u. up to a depth of 20 m (Figure 8). *Alexandrium taylori* was only found near the coastline. At the beach, water discoloration was evident with cell densities of 10^6 cells l^{-1}. By September, the surface layers had been mixed, and the surface temperature had decreased and was practically homogeneous from 21.5°C at the surface to 20.8°C at the bottom. The

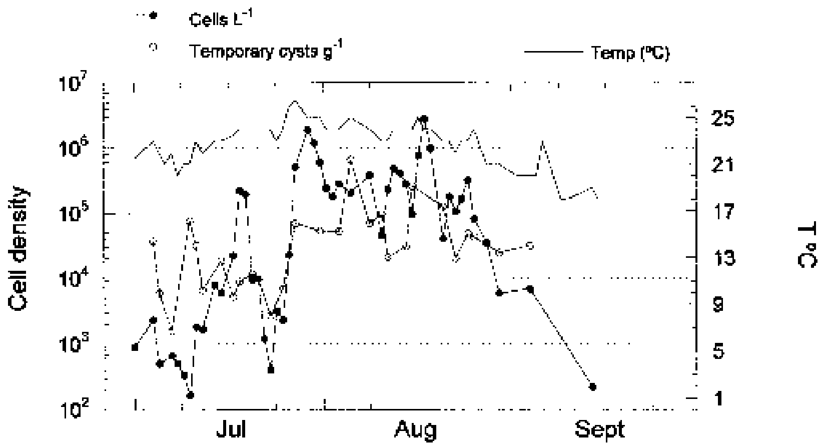

Fig. 7. Densities of *A.taylori* vegetative cells at the surface, temporary cysts in the sediment and water surface temperature on a weekly basis at La Fosca fixed point A during summer of 1996.

temperature sigma-T structure followed the salinity pattern (Figure 8). The area closest to the coast was vertically homogeneous. *Alexandrium taylori* was more widespread and patches of high cell densities (>7000 cells l^{-1}) were found 1–3 km offshore at the level of the pycnocline.

The surface distribution of nutrients during the three cruises is shown in Figure 9. No clear gradient was observed across the shelf. However, seasonal changes in silicate occurred with a marked decrease towards open sea during September. In addition, nitrate increased in September, although the spatial pattern was not defined.

Small-scale distributions in La Fosca

Relationships between surface temperature and cell distributions in three different cruises undertaken in the summers of 1995 and 1996 are presented in Figure 10. At the beginning of July, *A.taylori* was present at all points inshore within the area of La Fosca and Castell down to a depth of 10 m. There was no correlation between *A.taylori* and surface water temperature in this month. By 21 July, the area of La Fosca was characterized by higher water temperatures than its surroundings. There was a clear temperature gradient (1.5°C) and the cell density decreased away from the beach. The correlation between *A.taylori* density and temperature was significant (July, R = 0.88). In August 1996, the surface water temperature pattern and the distribution of *A.taylori* were the same as in mid-July. However, the temperature gradient across the coast was highest (2°C) and the correlation between temperature and *A.taylori* density was stronger (August, R = 0.9). Very low concentrations of surface inorganic nutrients characterized all the area, with occasionally higher values in the inshore area of the beach (results

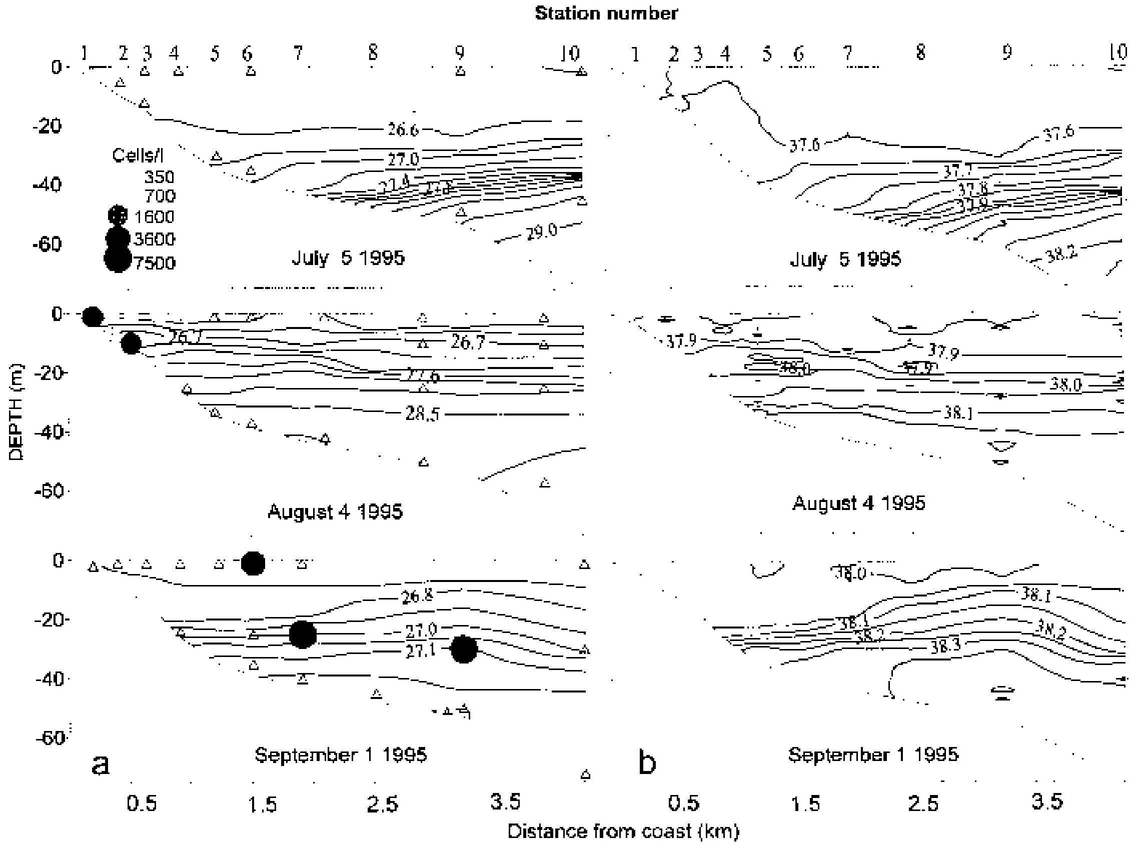

Fig. 8. Across-shelf sections of sigma-T and cell density of *A.taylori* from La Fosca beach to 3.5 km from the coast on 5 July, 4 August and 1 September 1995. △ indicates stations sampled for cell counts. Numbers across the top indicate station number.

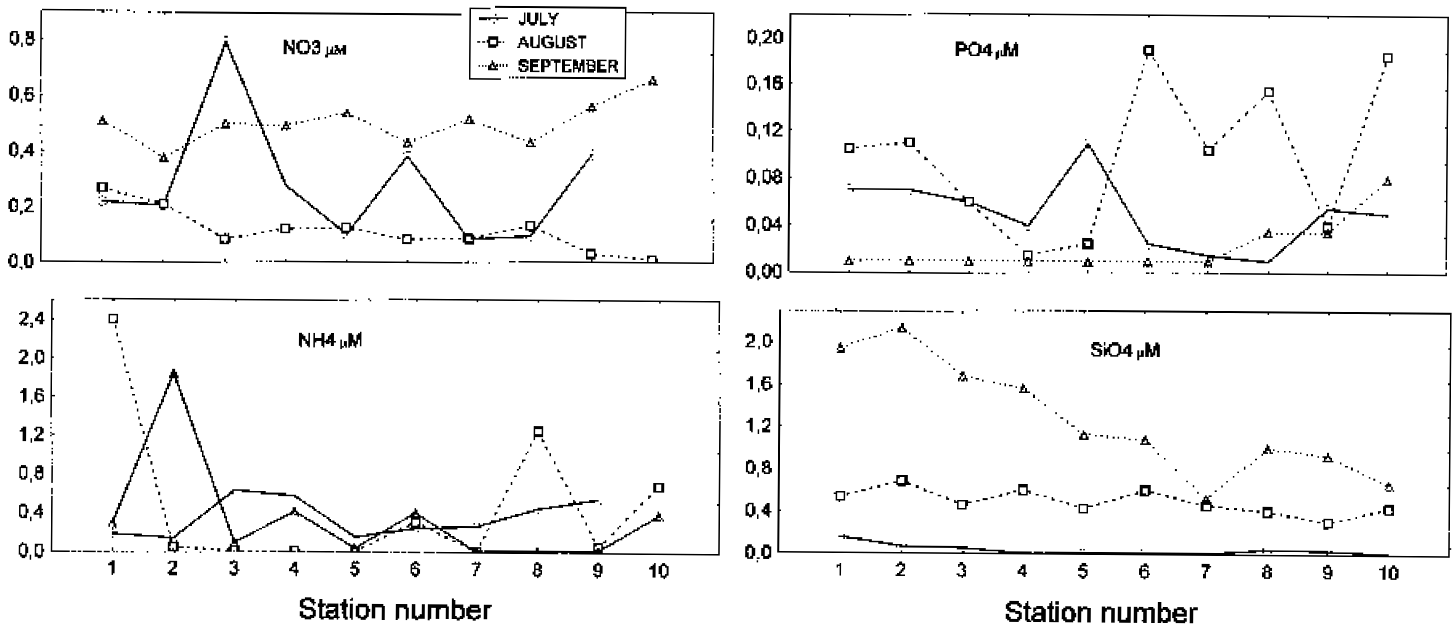

Fig. 9. Inorganic nutrient concentrations (NO_3, NH_4, PO_4 and SiO_4, µM) across shelf sections on 5 July, 4 August and 1 September. Numbers at the bottom indicate station number as in Figure 8.

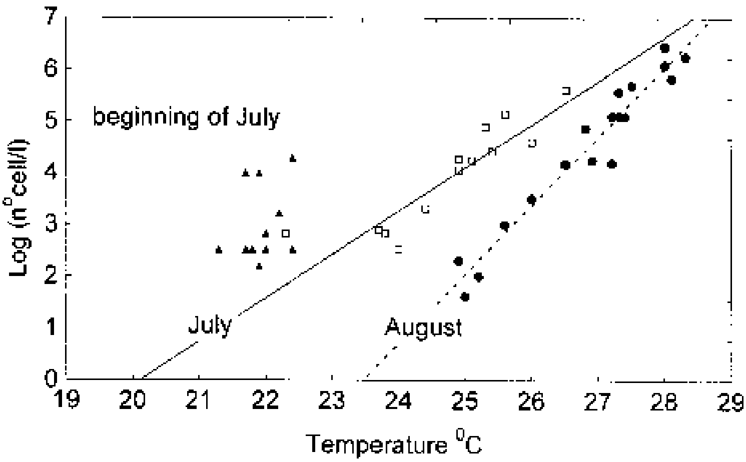

Fig. 10. Scatter plots of surface temperature and *A.taylori* cell concentration (log cells l^{-1}) at La Fosca on 7 July and 21 July of 1995, and 20 August of 1996.

not shown), but no higher than the values that characterize La Fosca beach (Figures 4, 6 and 9).

On the above dates (July and August), floats were left to drift from the furthest projection of the beach (Roca Negra). The floats returned and remained behind station A where temperatures were highest, or they floated approximately halfway along the beach. This area was characterized by the accumulation of objects of a diverse nature (plastic, seaweed, wood) and the highest densities of *A.taylori.*

Discussion

The different phases of the bloom dynamics (Figure 11) are described based on the distribution pattern of *A.taylori* and environmental parameters at the different spatio-temporal scales, together with the previous knowledge of its life cycle (Garcés *et al.*, 1998).

Initiation

The most likely hypothesis of the initiation of the bloom is that the vegetative population arises from resting cysts [described in Garcés *et al.* (1998) and Giacobbe and Yang (1999)]. These are presumably located in sites of preferential deposition, although not on the beach itself, since no resting cysts have been found in beach sediment (monthly sampling–annual cycle) and the vegetative population is sparse near to the coastline in early July, with higher abundance in deep waters. Maintenance of the vegetative population in the water during winter should not be ruled out, although this is highly improbable since *A.taylori* has not been detected in winter months (monthly sampling–annual cycle).

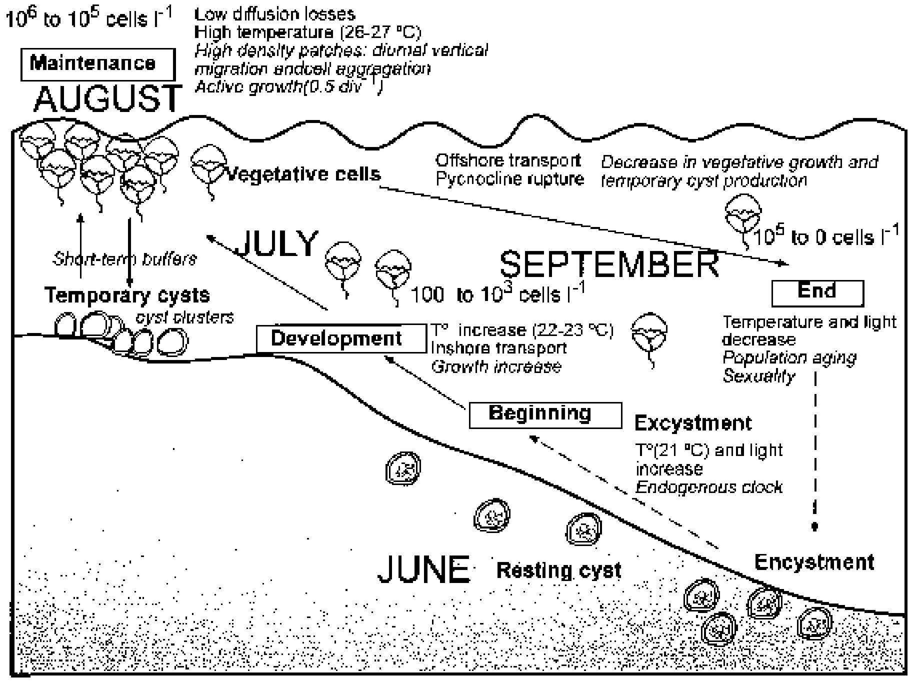

Fig. 11. Hypothetical *A.taylori* bloom dynamics. Phases of the bloom are in the squares. Physical factors and biological processes that take part in the bloom phases are written in plain text and italics, respectively. Dashed arrows are processes not observed in the field.

The appearance of *A.taylori* at different points along the Costa Brava was almost simultaneous at several beaches in July (see Table I). Therefore, the spread of a single focus of proliferation is an unlikely explanation for the observed distribution. Initiation of excystment may be triggered by changes in environmental conditions, the simultaneous increase in temperature and light, and/or an endogenous clock of the organism (Anderson and Keafer, 1987). The date difference between years in the appearance of vegetative cells at La Fosca was 15 days, which could represent the variation in these environmental parameters. Later, the environmental conditions during summer (high temperatures and calm weather) were favourable for maintaining a baseline vegetative population that could grow, and explain the wide distribution in the area.

Development

Only at La Fosca beach did a notable increase in cell densities occur in the following 2 weeks (see Table I). Therefore, the physiological response of the organism (e.g. the vegetative growth favoured by increasing temperatures) and the environmental conditions at La Fosca were critical in this phase. The development phase occurred during July and involved an increase in cell densities from

10^2 to 10^5–10^6 cells l^{-1}, the latter being reached and maintained in August (maintenance phase).

Maintenance

The *A.taylori* population reached and maintained high concentrations in excess of 10^5–10^6 cells l^{-1} for ~6 weeks, a feature rarely detected during *Alexandrium* blooms (Anderson, 1997). *In situ* growth rates obtained during the maintenance phase were 0.5 day^{-1} for vegetative cells and 0.14 day^{-1} for temporary cysts (Garcés *et al.*, 1998). It is obvious that other processes interact to enable high densities to persist if losses are considered. In terms of possible losses from the population, physical losses from diffusion or advection would be a crucial factor in the development and maintenance of the population at La Fosca. The morphological and physical characteristics of La Fosca are critical in this regard. The positive temperature anomaly of La Fosca, with a significant increase at the beginning of summer (high irradiance levels), indicates confinement of water (little renewal). Water becomes warmer because there is little interchange with the surroundings. The relationship between surface water temperature and cell density in the small-scale distribution in La Fosca in July and August (high inshore–offshore temperature gradients) also indicates the low renewal rate. Moreover, an analysis of the average size of the sand at La Fosca at different points along the beach showed areas characterized by finer materials, which indicates preferential deposition. Results from the drifters also support the retention of the water. All these features indicate low advective losses at La Fosca, which favour population growth and persistence according to the cross-sections in August when the cells were only found inshore.

Furthermore, *A.taylori* is quite widespread along the Costa Brava, although high cell densities were only reached and maintained for more than 1 month at La Fosca. It seems improbable that nutrient characteristics are a determining factor of *A.taylori* bloom maintenance in La Fosca beach since analyses of inorganic nutrient concentrations made at several spatial and temporal scales showed that nutrient concentrations at La Fosca and surrounding waters were never higher than those characteristic for the area. Water confinement can be considered to be the differential characteristic of La Fosca beach in a regional framework. Therefore, the interaction between low physical losses (low water renewal rates) and population growth (enhanced at the same time by the high temperatures reached) could be responsible for high long-lasting cell densities in La Fosca.

Temporary cysts could play an essential role in this entire context. Low variability in temporary cyst density in the sediment during the bloom maintenance period (August) was observed. After an environmental disturbance (i.e. a wind event) and a consequent decrease in the vegetative cell population, the population could increase rapidly from the ‘revival’ of the reserve of temporary cysts. The contribution of the temporary cysts remaining in the sediment may be an important factor in sudden population increases after adverse environmental conditions. Moreover, information on the encystment and excystment dynamics of temporary cysts is necessary in order to evaluate these proposed aspects of population growth.

Dense aggregates (>10^7 cells l^{-1}) of cells are found near the sediment. *Alexandrium* species are not known to secrete exopolymers, but cell-to-cell aggregation occurred in this case. Cell aggregation near the bottom may be a way of avoiding advection from the area (Margalef, 1997) and this will prevent losses from the population. Examples of the gregarious encystment of dinoflagellates can be found in the literature (Lombard and Capon, 1971; Horstmann, 1980) in sites of strong dilution, such as tidal areas, rock tide pools and estuaries.

Dissipation

The disappearance of surface blooms is most frequently the result of a meteorological change, from calm, sunny conditions to turbulent water, flushing of the area and general rapid change (Steidinger, 1973). However, biological mechanisms may also participate in a decline in population numbers, such as sexual processes, ageing of the population and cell death. Initiation of encystment may be triggered by physical factors (temperature and irradiance decrease), and by an endogenous clock of the organism (Anderson, 1998). The disappearance of *A.taylori* occurs almost simultaneously along the Costa Brava in early September. That month corresponds to the end of summer conditions in the NW Mediterranean with a significant decrease in temperature and irradiance. Bloom decline in La Fosca is a consequence of the interaction of several factors: an increase in water renewal rates and changes in biological processes modulated by environmental conditions at the end of summer. For example, on the one hand, the September cross-section indicates that the *A.taylori* patch broke up on the beach and that cells were advected in dense patches to the open sea. On the other hand, temperature decreases affect several stages of the life cycle of *A.taylori* (vegetative growth rates and temporary cyst production; Garcés *et al.*, 1998).

We can conclude that the *A.taylori* bloom in La Fosca is a manifestation of a higher scale proliferation that occurs every summer. A narrow window of environmental conditions would be needed to reach and maintain high cell densities, and this seems to occur principally in La Fosca. However, from the beginning of this study, other beaches have been affected. Similar problems at two beaches in the Balearic Islands motivated an extensive study there, and three similar blooms of *A.taylori* were identified recently (Garcés, 1998); moreover, Giacobbe and Yang (1999) described a bloom of *A.taylori* in Sicily. Also, it seems that the magnitude of the event is increasing in some places where before only its presence had been detected (e.g. in the Catalan coast). The assumption that the species has appeared over the last decade and is in a phase of expansion needs to be investigated.

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