Is the distribution of the toxic dinoflagellate *Alexandrium catenella* expanding along the NW Mediterranean coast?

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ABSTRACT: The toxic dinoflagellate *Alexandrium catenella* is usually known as a cold waters species; however, during the summer of 1996 a bloom was observed in the Barcelona harbour (water temperatures above 20°C). This was the first time that an *A. catenella* bloom occurred in Catalan waters. Recurrent blooms have been observed annually from 1996 to 1999 during the warm season in this harbour. Since its first detection *A. catenella* has been recorded at an increasing number of stations along the coast, suggesting a progressive areal expansion. Two toxic, widespread events of this species occurred in non-confined coastal waters along 100 km of coastline during the summers of 1998 and 1999. We argue that the newly constructed harbours, serving as confined habitats for the development and maintenance of *A. catenella*, have contributed to the expansion of the dinoflagellate on the NW Mediterranean coast.

KEY WORDS: Toxic dinoflagellate · *Alexandrium catenella* · NW Mediterranean Sea · Harmful algal blooms · HAB

INTRODUCTION

The global increase in toxic or harmful algal blooms (HABs) (Anderson et al. 1989, Smayda 1990, Hallegraeff 1993) has also included the NW Mediterranean, where numerous dinoflagellate blooms, especially involving the *Alexandrium* genus (*A. minutum*, *A. tamarense* and the non-toxic *A. taylori*) have been reported (Vila et al. 2001a). The potent neurotoxins (paralytic shellfish poisoning, PSP) produced by some *Alexandrium* species are accumulated by filter-feeding shellfish and other grazers and passed at higher trophic levels to humans, leading to illness, incapacitation, and even death (Anderson 1997). During the last few years, *A. catenella*, a potential PSP-producer, has been detected on the Catalan coast (NW Mediterranean Sea). This species has usually been reported in cold waters in several parts of the world, such as the west coast of

North America from California to Alaska, southern and central Chile, and southern Argentina. It has also been observed in western South Africa, southern Australia (including Tasmania), the Kamchatka peninsula and Japan (Taylor 1984, Taylor et al. 1994, Balech 1995, Steidinger & Tangen 1997). In the Mediterranean Sea, there were only a few references: *A. catenella* was listed as a rare species on a series of cruises across the Balearic basin (NW Mediterranean) (Margalef & Estrada 1987). In 1994, it was detected in the Valencia harbour (NE Spanish coast) (Gomis et al. 1996), and it has also been found in net samples from the Tunis lagoon (S. Fraga pers. comm.). But *A. catenella* had never been observed either at monitoring stations along the Catalan coast from 1991 to 1995 or in the bays of the Ebro delta since 1989 (Delgado et al. 1998, 1999). *A. catenella* is commonly considered a cold-water organism, and so blooms in the Mediterranean Sea were not expected. But in spring 1998, the first widespread PSP toxic event caused by *A. catenella* was detected in the Mediterranean, and the phenome-

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non occurred again, although with less intensity, the next year (Vila et al. 2001b).

The rapid expansion of a toxic dinoflagellate, such as *Alexandrium catenella*, in the Mediterranean may have great environmental and health care consequences, and, thus, efforts directed to understand the mechanisms of such expansion are clearly needed. The aim of this paper is to report the rapid geographical expansion of *A. catenella* along the Catalan coast after its first detection in 1996. Increased distribution and abundance are discussed in relation to the possible causes that might have triggered its expansion, such as the trophic characteristics of the near-shore Catalan waters and the ability of dinoflagellates to colonise, settle and proliferate in confined habitats created or modified by human activity.

METHODS

Spatio-temporal distribution. Data presented in this paper were collected during the Monitoring of Harmful Algal Blooms Programme which operated on the Catalan coast (NW Mediterranean Sea) from July 1995 to December 1999 at 17 fixed stations. Of these stations, 14 were located in harbours, 1 at Cadaqués Bay, and 2 at beaches (Fig. 1A).

The sampling interval was once a week from May to October, and twice monthly from November to April, except for Les Cases harbour which was sampled weekly year-round. Surveillance was increased when potentially harmful phytoplankton was detected at the monitored stations. Additional samples for phytoplankton quantification were then collected from harbours, at beaches and breakwaters at neighbouring localities.

Salinity and temperature have been measured since March 1996. Bucket phytoplankton samples (150 ml) were taken from the surface during the day at selected sites inside the harbours (the most confined areas), bays or beaches, and preserved with formaldehyde (1% final concentration) or Lugol's iodine solution. An aliquot was settled

for 24 h in 50 ml counting chambers, and an appropriate area of the chamber was then scanned (Throndsen 1995) for phytoplankton enumeration at 100 to 400× magnification using a Leica-Leitz DM-IL inverted
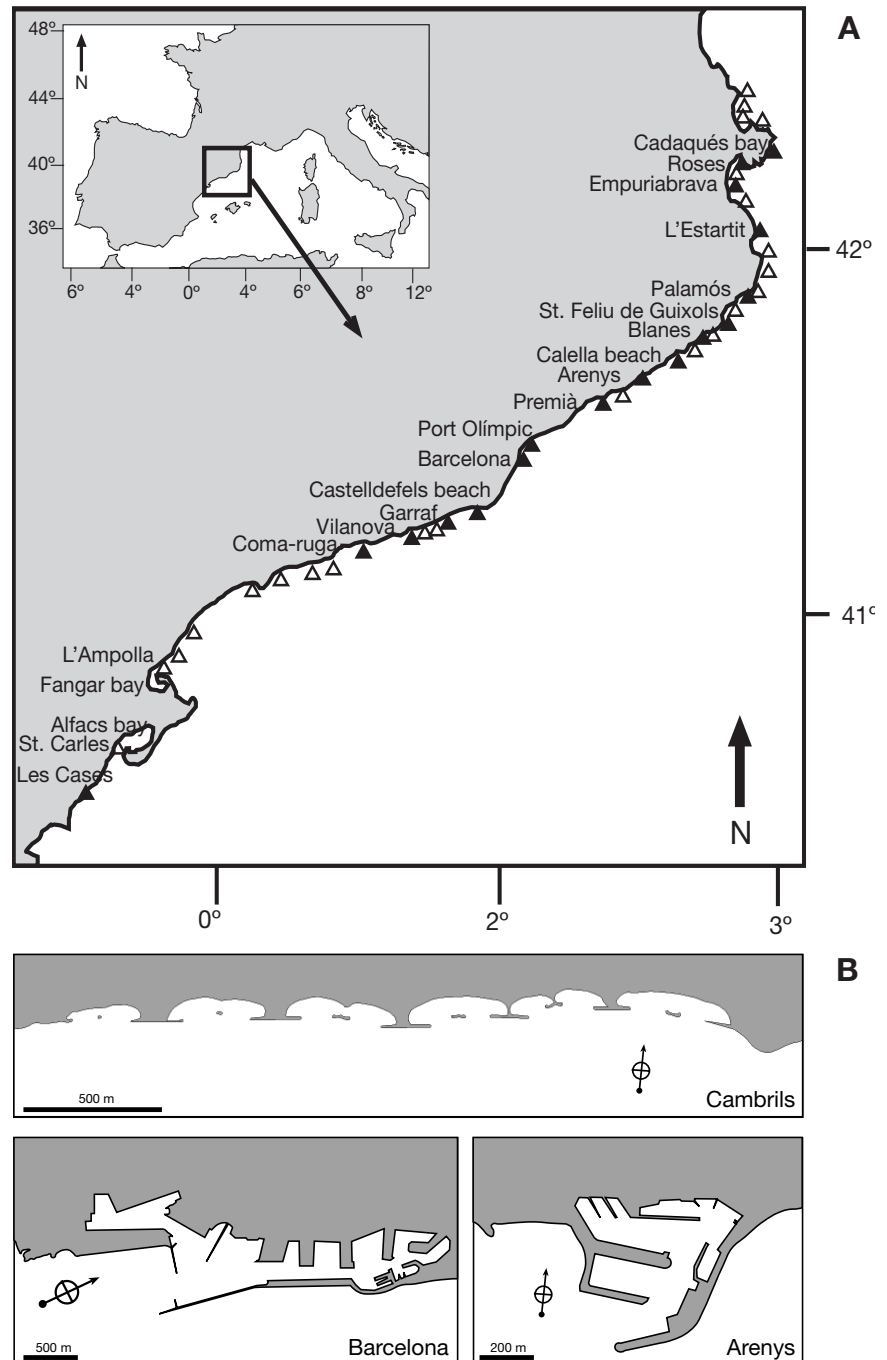

Fig. 1. (A) Study area along the Spanish coast showing the sampled stations (filled triangles) in the Monitoring of Harmful Algal Blooms Programme. Open triangles indicate non-sampled harbour locations. (B) Some examples of man-made confined waters: semi-enclosed beaches in Cambrils and 2 problematic HAB harbours (Barcelona, Arenys)

microscope. About 30 cells were measured (length and width) with an image analysis system (Scion Image V1.62) attached to a Nikon Diaphot TMD microscope.

Small samples of *Alexandrium catenella* blooms were pipetted from the chambers and placed on microscope slides for taxonomical purposes. One drop of sodium hypochlorite was added to separate the thecal plates, and another drop of the fluorescent dye calcofluor white (Fritz & Triemer 1985) was added to dye the plates. The slides were examined under 1000× magnification in the inverted microscope with fluorescent illumination.

Shellfish were collected for toxicity analysis when potentially toxic phytoplankton was detected during monitoring. Toxicity analysis was done following the standard mouse bioassay method (AOAC 1980). The permissible toxicity level in the European Union (EU) is 80 µg saxitoxin-eq. (STX) per 100 g of mussel meat.

Surface water samples for nutrient analysis were collected at approximately 1 m depth and immediately frozen. Nutrients were determined automatically as described in Grasshoff et al. (1983). Nutrient samples come from an extensive environmental monitoring programme that includes 61 beaches and 11 harbours sampled during 3 and 2 annual cycles respectively. However the stations sampled for nutrients were not exactly the same as those sampled for phytoplankton.

Background and study area. Catalonia (NE Spain; 42° 5′ to 40° 5′ N, 0° 2′ to 3° 2′ E) is situated on the NW Mediterranean Sea. Its coast extends along 400 km and is highly populated in some areas. On the central coast the human density is between 500 and 1300 inhabitants km^{-2} and reaches to up to 15 000 inhabitants km^{-2} in the Barcelona area. In addition, total population increases by >50% in some coastal regions during the tourist season. The recreational use of this coast has led to a demand for calm waters (breakwaters, semi-enclosed beaches) and an increase of recreational harbours (40 harbours on 400 km of coast, which, on average, represents 1 harbour for every 10 km of coastline). As a result 1/4 of the Catalan coastline is characterised by man-made structures (Fig. 1B). On a topographic map (scale 1:50 000) we measured 217 km of these man-made structures on a coastal length of 826 km. The proportion of man-made coastal structures increased from 20% in the 1980s to 27% in the 1990s (Institut Cartogàfic de Catalunya).

A phytoplankton monitoring programme has been in effect in the area since 1989, with weekly frequency at the Ebro delta bays, the only shellfish culture site on the Catalan coast; the rest of the coast was sporadically monitored (once every 2 to 3 mo) in non-confined waters from 1991 to 1994. However, since 1995 a new Monitoring of Harmful Algal Blooms Programme has been established; the frequency of sampling and distri-

bution of monitored stations along the coast have been substantially increased and based on a new concept focused on the sampling of confined waters. The unquestionable validity of this strategy in the detection and follow-up of the increase of HABs is discussed in Vila et al. (2001b).

Along the Catalan coast, water circulation is dominated by an along-shore north-southwest flow, associated with a shelf-slope front located approximately above the shelf-break region and characterised by mean velocities on the order of 20 cm s^{-1} (Font et al. 1988). The shelf region is characterised by a weak southward flow, with strong spatial and temporal variability and with the presence of local and intense saline or thermal fronts (Masó & Duarte 1989, Masó & Tintoré 1991). Trophic conditions such as concentrations of inorganic nutrients and their stoichiometric relationships in the near-shore coastal Catalan waters during summer months (June to September) are summarised in Table 1. We divided the area into 3 regions, the northern region, the central area, which is affected by *Alexandrium catenella*, and the southern area. The data indicate that the highest frequency of stoichiometric nutrient limitation is due to silicate limitation, but this is particularly so in the central area, where >50% of the cases are potentially affected by silicate limitation. This central area is characterised by a high human density and consequently higher levels of N-NH_4 and PO_4. If we consider the criteria of probable nutrient limitation (Justic et al. 1995), the frequencies (%) of limitation of the 3 single nutrients decrease (probable silicate limitation being the highest, and similar in the 3 areas, about 25%).

RESULTS

The organism

Given that *Alexandrium catenella* is commonly considered a cold-water species (Balech 1995), we document with microphotographs the organism observed in our study area, for taxonomic comparison (Fig. 2). Cells are small to medium-sized, 22.9 to 32.0 µm long and 25.8 to 32.1 µm wide (mean: 27 µm long; 29 µm wide). Although isolated cells are frequent, this species can form chains (commonly 4 cells per chain, but 2 to 8 have also been observed). Cells are flattened anterior-posteriorly when in chains, although single cells are sometimes isodiametric in shape. When dyed with calcofluor and observed under blue-excitation, plates can be seen (Fig. 2B). The triangular apical plate (Po) shows a connecting pore located near the comma head to its right (Fig. 2C). Plate 1′ is directly connected to Po. The anterior right margin of 1′ is usually concave, but
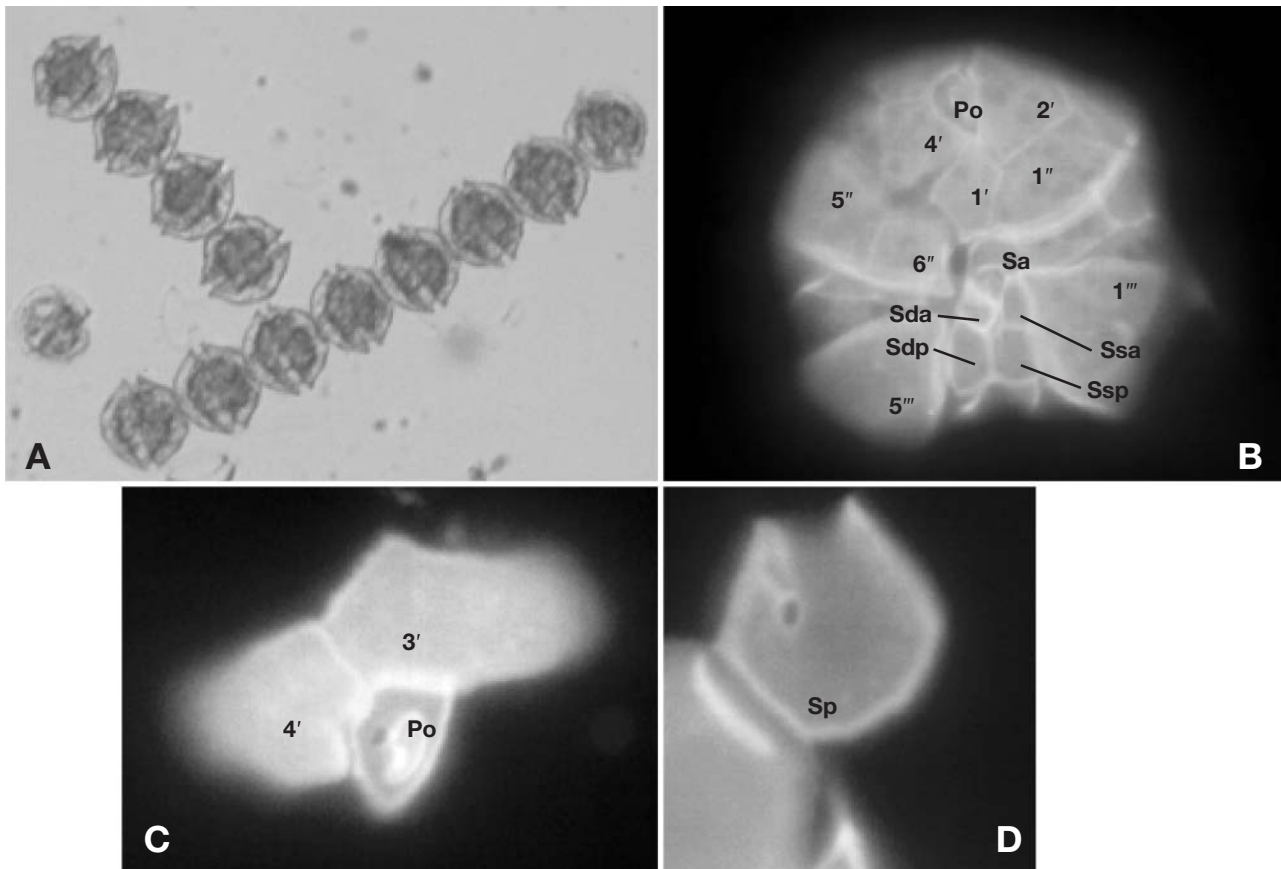
Fig. 2. *Alexandrium catenella*. Light microscope (LM) microphotographs of plankton samples. (A) LM of 4- and 8-celled chain. (B) LM (fluorescence) of cell, ventral view showing the plates. Calcofluor-stained. (C) LM (fluorescence) of details of a triangular apical pore plate (Po) with anterior attachment pore. (D) LM (fluorescence) of details of a posterior sulcal plate (Sp) with posterior attachment pore. The names of thecal plates are indicated by numbers, inverted commas, and letters. S indicates the 'sulcal plates'. Sa: anterior sulcal plate; Sda: right anterior lateral sulcal plate; Sdp: right posterior lateral sulcal plate; Ssp: left posterior lateral sulcal plate

it does not have a ventral pore. Plate 6″ is of medium width. The sulcal plate (Sp, Fig. 2D) is almost as wide as it is long, and presents a connecting pore to the right of the plate. Both pores (in Po and Sp plates) are transitory characteristics associated with chain formation.

Large-scale distribution pattern along Catalan coast over 4 yr

Alexandrium catenella was first detected in the Barcelona harbour in summer 1996. Since then it has increasingly been detected at the routinely monitored stations along the south-central coast, usually in higher concentrations year after year (Fig. 3).

Alexandrium catenella appears simultaneously at several stations every year, i.e. in 1997 at the beginning of July, in 1998 in late May, in 1999 in mid- to late June (Fig. 3). In the Barcelona harbour blooms lasted several months and attained high densities (10^5 to 10^7 cells l^{-1}).

However, at many stations (Garraf, Olímpic, Premià, Arenys and Calella) the population never reached high densities ($<10^4$ cells l^{-1}), and cells were present only during a few sampling occasions, often discontinuously. In the summers of 1998 and 1999, the maximum cell concentration occurred during the same week at several stations. In 1998, the maximum cell concentration was observed at the end of May at the southernmost stations (Coma-ruga, Vilanova) and at the beginning of July in the northern stations. In 1999, maximum cell concentration was observed at the end of June at all stations. Bloom terminations coincided at several stations in mid-September, except in 1999 when some cells were observed in mid-October.

Widespread blooms

In the summers of 1998 and 1999, 2 widespread blooms of *Alexandrium catenella* were also observed in

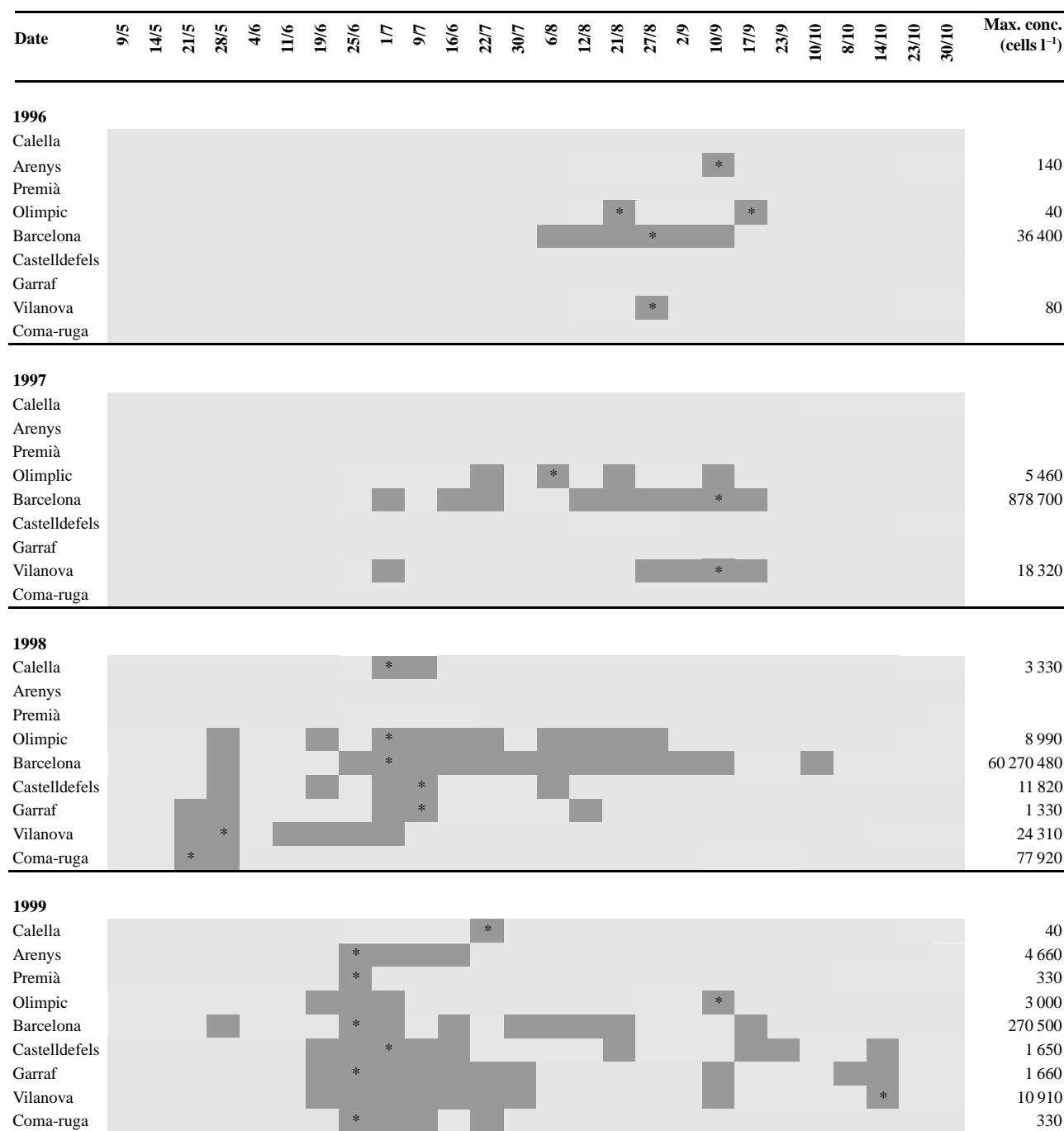| Date	9/5	14/5	21/5	28/5	4/6	11/6	19/6	25/6	1/7	9/7	16/6	22/7	30/7	6/8	12/8	21/8	27/8	2/9	10/9	17/9	23/9	10/10	8/10	14/10	23/10	30/10	Max. conc. (cells l^{-1})
1996																											
Calella																											
Arenys																			140
Premià																											
Olimpic																											40
Barcelona																											36 400
Castelldefels																											
Garraf																											
Vilanova																											80
Coma-ruga																											
1997																											
Calella																											
Arenys																											
Premià																											
Olimplic																											5 460
Barcelona																											878 700
Castelldefels																											
Garraf																											
Vilanova																											18 320
Coma-ruga																											
1998																											
Calella																											3 330
Arenys																											
Premià																											
Olimpic																											8 990
Barcelona																											60 270 480
Castelldefels																											11 820
Garraf																											1 330
Vilanova																											24 310
Coma-ruga																											77 920
1999																											
Calella																											40
Arenys																											4 660
Premià																											330
Olimpic																											3 000
Barcelona																											270 500
Castelldefels																											1 650
Garraf																											1 660
Vilanova																											10 910
Coma-ruga																											330

Fig. 3. Vegetative cell occurrence of *Alexandrium catenella* from 1996 through 1999, based on weekly samples during the warm months (May to October). Only the stations where the organism was present are shown. Note that 1995 is not shown because the species was not observed. Maximum cell concentration detected is given for each station; asterisk indicates the date of maximum concentration

non-confined waters (open beaches) and semi-enclosed beaches such as Cambrils (Fig. 1B). These blooms coincided with sunny days and calm weather, with surface water temperatures of 20 to 25°C. Maximum cell concentrations and the areas affected are summarised in Fig. 4. Maximum cell concentrations in non-confined waters were 10^4 cells l^{-1}. More than 10^6 cells l^{-1} were detected in some harbours in 1998, and >10^5 cells l^{-1} in 1999. In both 1998 and 1999, saxitoxin concentrations exceeded acceptable EU levels (AOAC 1980): up to
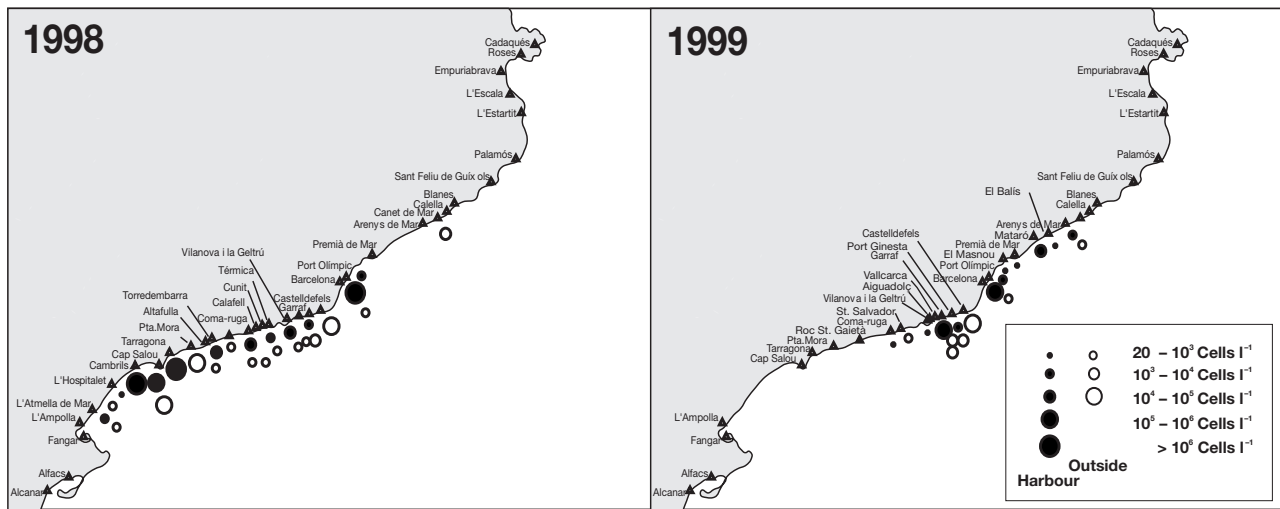
Fig. 4. Maximum coastal extension and concentration of *Alexandrium catenella* during the widespread blooms in summer 1998 and 1999 (closed symbols, cell concentration inside confined areas such as harbours or embayments; open symbols, cell concentration in non-confined waters; triangles, the location of stations monitored)

983 µg STX/100 g in 1998 and 150 µg SXT/100 g in 1999. In 1999, bloom duration was shorter, and the maximum cell concentration and shellfish toxicity were lower than in 1998. However, in both years, *A. catenella* persisted in the confined waters for much longer (e.g. from July to mid-September in the Barcelona harbour) than in non-confined waters. The widespread blooms lasted for 8 wk in 1998 and 4 wk in 1999.

cell densities in September coincided with the decrease in water temperature during this month. No cells were found after October. Temperature and *A. catenella* concentrations are weakly but significantly correlated (n = 36, r = 0.4, Fig. 6) in this harbour. However, no significant correlation exists when we consider all the stations.

Alexandrium catenella in Barcelona harbour

A. catenella was first observed in Barcelona harbour during August through September 1996, reaching cell concentrations of up to 36 400 cells l^{-1}. Since then it has been observed every year in the harbour during the warm months (from May/June to September/October), achieving cell concentrations of up to 60×10^6 cells l^{-1} (Fig. 5). Thus, *A. catenella* shows well-defined seasonality, with its vegetative cells detected only in water temperatures of 22 to 28°C. In general, abundance increases suddenly, coinciding with the increase in water temperature (above 22°C) that occurs in May to June. Maximum cell densities between 10^5 and 10^7 cells l^{-1} were observed during July to August, coinciding with water temperatures above 24°C. The decrease in
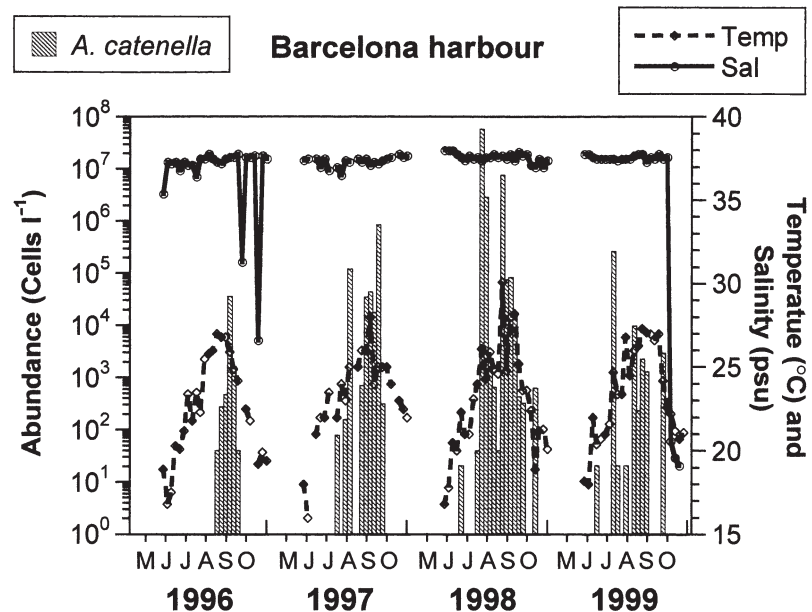

Fig. 5. Summer evolution (May to October) of cell density of *Alexandrium catenella* at the Barcelona harbour based on weekly samples (1996 to 1999) and associated temperature and salinity
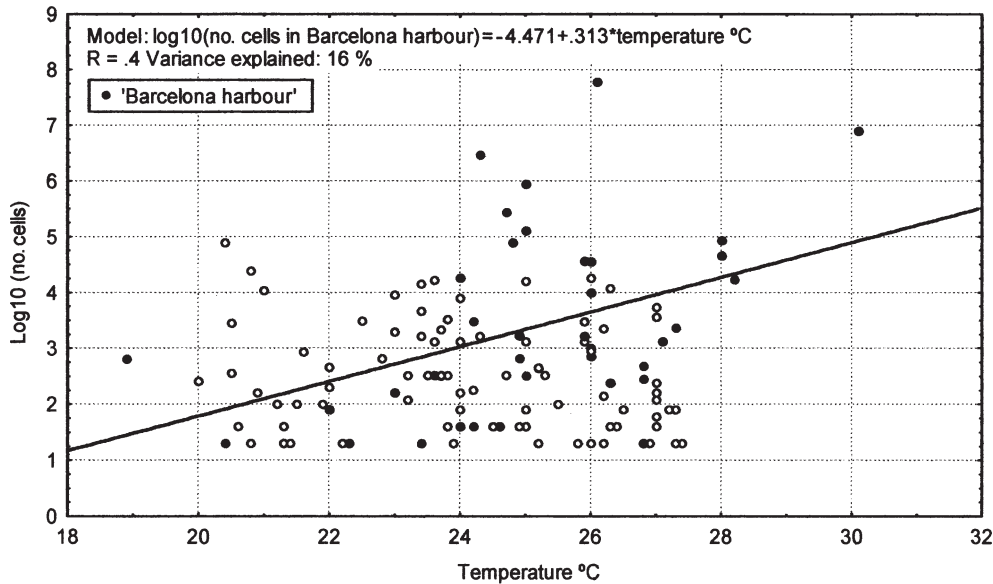
Fig. 6. Relationship between temperature and *Alexandrium catenella* concentrations in all the positive stations (closed symbols, Barcelona harbour data; open symbols data for remaining sites). A weak correlation exists when we consider only the Barcelona harbour data

DISCUSSION

Alexandrium catenella is considered to be a cold-water species that is seldom found at temperatures over 12°C and usually does not reproduce at above 16°C (Balech 1995). However, there are some reports that contradict the above assertions. It bloomed in Japanese waters (Tanaby Bay) during May 1981 and 1984, reaching up to 3.5×10^6 cells l^{-1}, with water temperatures between 19.8°C and 21.5°C (Takeuchi et al. 1990, Takeuchi 1994). Furthermore, Balech (1995) described the species *Alexandrium* sp. II from warm waters of Mexico (in the Pacific Ocean, in the state of Jalisco), which is morphologically similar to *A. catenella* and *A. fundyense*, and forms chains of between 2 and 6 cells. However, the size reported for this organism is larger than that from the Mediterranean organism. Mediterranean *A. catenella* was identified in this study based on cell morphology and the thecal plate pattern. In addition, Avila et al. (1999) claimed that the toxin profile was typical for *A. catenella* and that it cannot be confused with other dinoflagellate PSP producers from the Mediterranean. The blooms reported here extend the range of temperatures in which this organism has been observed to bloom. The well-defined seasonality during the summer months in Catalan waters makes it clear that at water temperatures over 20°C this species not only survives, but also blooms. *A. catenella* is, thus, a cosmopolitan species that can live in a wide range of temperatures from cold to warm waters. It is tempting to suggest that the warm *Alexandrium* sp. II of Balech (1995) may be related to *A. catenella* from Mediterranean and Japanese waters.

The historical absence of *Alexandrium catenella* in the samples taken for monitoring prior to the summer of 1996 (Fig. 3) suggests that during recent years the dinoflagellate is expanding its geographical distribution along the Catalan coast. This is of importance because its toxicity may cause considerable economic damage to aquaculture and the shellfish harvest. Three possible explanations have been suggested for the world-wide increase of HABs: (1) an increase in the research of phytoplankton and resulting gains in knowledge, (2) the stimulation of phytoplankton growth due to anthropogenic effects leading to eutrophication, and (3) an increase in the geographical dispersion due to the transport of resting cysts in ballast water, or due to the movement of mollusc stocks from one area to another.

We do not think that in our study area *Alexandrium catenella* was missed in the past. Despite the long tradition of phytoplankton studies, the species was only observed once in very low concentrations (Margalef & Estrada 1987). Thus, we can conclude that the abundance and distribution along the NW Mediterranean have increased.

The second explanation suggested for the world-wide increase of HABs is stimulation due to the eutrophication effect of anthropogenic activities. Coastal waters all over the world are, in general, sufficiently rich in nutrients, and the coast studied here is no exception. Imbalance in the ratios between nitrogen, phosphorus and silicate has been reported as a cause of changes in phytoplankton communities (Justic et al. 1995). The general shift in nutrient ratios toward silicate limitation, as suggested previously, could favour growth of dinoflagellates over diatoms.

Table 1. Concentrations of major inorganic nutrients (µM) and their average atomic ratios in the near-shore Catalan surface waters in summer (June to September). The area is divided into 3 regions (North; the area affected by *Alexandrium catenella*; South). Frequency of single nutrient limitation (% of occurrence), stoichiometric (Stoich) and probable (Prob), has been calculated as in Justic et al. (1995) (criteria, see footnotes). Range is given from the 25th to 75th quartile. Data come from an extensive environmental monitoring programme (61 beaches and 11 harbours sampled monthly during 3 and 2 annual cycles respectively)

	n	Nutrient concentrations (µM) Mean	Median	Range
NO$_3$				
North	347	9.9	2.4	1 – 4.8
Catenella	353	8.4	2.3	1 – 5.4
South	150	9.9	1.7	1 – 5.7
NO$_2$				
North	345	0.4	0.1	0.1 – 0.2
Catenella	355	0.6	0.2	0.1 – 0.4
South	151	0.2	0.2	0.1 – 0.3
NH$_4$				
North	347	6.4	0.7	0.3 – 1.4
Catenella	352	18.7	1.0	0.4 – 2.8
South	151	1.6	1.0	0.4 – 2.3
PO$_4$				
North	347	0.8	0.3	0.2 – 0.5
Catenella	354	1.4	0.3	0.2 – 0.6
South	151	0.3	0.2	0.1 – 0.4
SiO$_4$				
North	347	4.6	2.7	1.3 – 4.2
Catenella	355	4.6	2.5	1.4 – 4.2
South	151	6.1	2.7	1.5 – 8.8

	Average atomic ratios DIN:P	Si:DIN	Si:P
North	19.9	0.3	5.6
Catenella	20.5	0.2	3.4
South	39.8	0.5	20.9

	Frequency of single nutrient limitation (% occurrence) Stoich	Prob
P limitation[a]		
North	10.1	3.2
Catenella	7.3	4.5
South	27.2	17.9
N limitation[b]		
North	22.5	6.9
Catenella	18.0	6.2
South	15.2	5.3
Si limitation[c]		
North	41.5	24.5
Catenella	55.2	25.9
South	31.8	21.2

[a]Stoich (DIN:P > 22; Si:P > 22);
 Prob (P < 0.1 µM; DIN:P > 22; Si:P > 22)
[b]Stoich (DIN:P < 10; Si:DIN > 1);
 Prob (DIN < 1 µM; DIN:P < 10; Si:DIN > 1)
[c]Stoich (Si:P < 10; Si:DIN < 1);
 Prob (Si < 2 µM; Si:P < 10; Si:DIN < 1)

The third explanation is recent importation of the species to the area. The non-indigenous dispersion of species in marine coastal waters in the ballast water of cargo vessels was first suggested 90 yr ago (Ostenfeld 1908), but reports on the occurrence of dinoflagellate cysts in ballast water also appear much later (Hallegraeff et al. 1990, 1991, Hallegraeff & Bolch 1992). Since then, the number of studies dealing with this topic has increased, with major attention to the dispersion of potentially toxic phytoplankton, because of their economic influence. For some regions evidence has already been presented of the introduction of species through ballast water (Scholin 1996, Hallegraeff 1998). Also, the transfer of mollusc stocks from one area to another has been implicated in the dispersion of dinoflagellates (Laabir & Gentien 1999). *Alexandrium catenella* is one of the species now believed to have been introduced into Australian waters from Japan in the last 10 to 20 yr through ballast water transportation (Scholin & Anderson 1996, Hallegraeff 1998). In Hong Kong waters, there was no record of this species until the 1980s, and its form of introduction is still under discussion; Ho (1998) claimed that oceanic currents introduced it from Japan. In the Mediterranean, hidden flora cannot be disregarded as an inoculum of the blooms because *A. catenella* was previously detected in Mediterranean oceanic waters (Margalef & Estrada 1987). However, the fact that the bloom was first observed in Barcelona harbour, an important commercial harbour in the area, points to ballast water as the source of introduction. A total of 17 251 m^3 of water is ballasted monthly into the Barcelona harbour area (inside the harbour or within 12 nautical miles). Other than Mediterranean waters (60%), a large amount of ballasted water entering the harbour (21%) comes from the South and North Atlantic Ocean (African and European coasts) and the North Pacific Ocean (Asian coast) (Autoritat Portuària de Barcelona 2000). Considering that 85% to 95% of the ballast waters brought into Barcelona harbour have been transported for <30 d, there is a high probability that viable cysts could arrive. The possible origin of Mediterranean *A. catenella* will not be discussed further in this study. Future work will focus on this topic. What we propose here is a fourth possibility to explain the *A. catenella* expansion along the Catalan coast. This aspect has hardly been considered, but may be the most relevant in calm, tideless seas and on heavily populated coasts such as those found on the Mediterranean. Recreational use of the coast generates the construction of harbours or enclosed beaches. This, together with the mild effect of tides in the area, generates semi-enclosed bodies of water. Thus, these confined environments have high water residence times of about 20 d, low turbulence and low advection in comparison with non-confined waters. Since low turbu-

lence (Margalef 1978, Margalef et al. 1979) favours dinoflagellate proliferation and some specific properties of these organisms (pattern swimming, auto-regulated aggregation and toxicity) are known to reduce grazing (Fiedler 1982, Bagøien et al. 1996, Smayda 1997, Teegarden 1999), these organisms having low growth rates may bloom in such confined areas. Thus, *A. catenella*, which has a maximum specific growth rate of 0.47 to 0.55 d^{-1} in culture under nutrient-saturated conditions (Matsuda et al. 1999), can attain high cell densities (up to 10^7 cells l^{-1}) within a few days in those nutrient-rich areas and is also favoured by behavioural strategies (swimming, active vertical migrations and aggregation) (Garcés et al. 2000).

Much evidence points to a connection between the *Alexandrium catenella* blooms and the dynamics of benthic resting cysts: (1) the simultaneous *A. catenella* appearance along the coast, not only in the confined areas where it blooms, but in a much larger area, as exemplified by the widespread summer blooms of 1998 and 1999; (2) the observation of hypnozygotes enveloped in a matrix of mucilage at Castelldefels beach, coinciding with a decline in the planktonic population in July 1999 (data not shown); (3) the yearly reoccurrence of *A. catenella* at an increasing number of fixed stations (harbours) (Fig. 3). This latter fact could be due to cyst deposition in previously unaffected areas which provided the species with widely dispersed inoculum sites for future blooms, as has been suggested for other areas (Anderson & Wall 1978). Harbours are considered to be ideal environments for cysts to settle and remain in seedbeds until environmental conditions induce their germination (Anderson et al. 1987). The active growth rate of a small germinating population amplified by the organism's behaviour, the reduction of grazing and the favourable physical factors noted above could cause the blooms in harbours.

The different confined blooms found in the study area are probably part of 1 single, widespread and amplified bloom within the harbours, due to specific favourable environmental conditions in confined waters, as was proposed for *Alexandrium taylori* (Garcés et al. 1999). Maximum cell concentration at harbour stations during summer 1998 and 1999 were coincident with maximum cell concentration at non-confined and open-water stations (detailed in Vila et al. in press), showing a connection between confined, non-confined and open, near-shore blooms.

The problems associated with *Alexandrium catenella* blooms in Mediterranean coastal waters have increased in the past few years. We do not want to imply that anthropogenic influences along the coastlines have changed in the last 5 yr, coinciding with the bloom of *A. catenella*. However, we argue that the Catalan coast has the right conditions for dinoflagel-

late colonisation and later expansion, as well as for colonisation by new species. So, if a new species arrives, the increased number of confined environments will facilitate colonisation and establishment by the organism. The wide geographical and temporal distribution of *A. catenella* in Catalonia during the last 4 summers indicates that it is currently well established in the region, and is a significant contributor to the summer phytoplankton community in many confined areas and, sometimes, in non-confined waters. Our results suggest that in the future the species might further expand its geographical extension in the Mediterranean Sea. However, this possibility has to be considered with caution. Recently, *A. minutum* was reported to exhibit a cyclic occurrence pattern, i.e. occurrence increased, stabilised and decreased (Ismael & Halim 2000) in the eastern harbour of Alexandria, the type locality of the species. This dinoflagellate had been a recurrent summer phenomenon for 40 yr. However, after 1994 it disappeared, and daily observations in the summer of 1999 showed *A. minutum* to have been replaced by a community of other potentially harmful species. In that sense HABs can be compared to the success and subsequent replacement of invasive plagues in agricultural land.

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