Original article

Distribution of chlorophyll *a* and *Gymnodinium catenatum* associated with coastal upwelling plumes off central Portugal

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Abstract

The composition and the distribution patterns of phytoplankton were studied during the early stages of an upwelling event in Lisbon Bay, in September 1999. The distribution of chlorophyll *a* and phytoplankton assemblages was asymmetric about the upwelling centre, with the highest abundance of chlorophyll *a* observed at the inner (coastal) side of the plume. The diatom *Cylindrotheca closterium* dominated in the upwelling core and the chain forming diatom *Proboscia alata* dominated at the outer side of the feature within mature oceanic waters. Chain forming dinoflagellates such as *Alexandrium affine* and the toxin producer *Gymnodinium catenatum* were most numerous at the inshore side of the upwelling front. These patterns were compared with the distribution of *G. catenatum* observed in the same area in 1985 and 1994, under conditions of fully developed upwelling when chlorophyll *a* and *G. catenatum* maxima were observed extending southwards on the inshore side of an upwelling plume. Different hydrodynamic conditions at each side of upwelling plumes associated with pronounced Capes are evoked to explain the asymmetry on the phytoplankton patterns.

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1. Introduction

The west coast of Portugal, located between 37° and 42°N, is at the northern limit of the North Atlantic upwelling system. Here, seasonal upwelling occurs due to steady northerly winds (Fiúza et al., 1982; Wooster et al., 1976). Though, the coastal morphology and the continental shelf/upper slope bathymetry gives rise to different upwelling patterns at different locations along the coast (Fiúza, 1983). On the central part of the west coast, between Nazaré canyon and Cape of Sines, the irregular topography and coastal morphology associated with the Lisbon-Setúbal canyons, the coastal protrusions of the Estremadura headland and the Capes Roca and Espichel (Fig. 1), lead to a complex three-dimensional character of the upwelling system. This area forms the large Lisbon-Setúbal embayment into which the rivers Tejo and Sado drain with an estimated annual run-off of 15.1 km^3 per year, although with a limited influence in the local hydrology (Fiúza, 1984; OSPAR, 2000).

Upwelling intensification may induce a localised centre of colder water near the coast and an offshore elongation of the
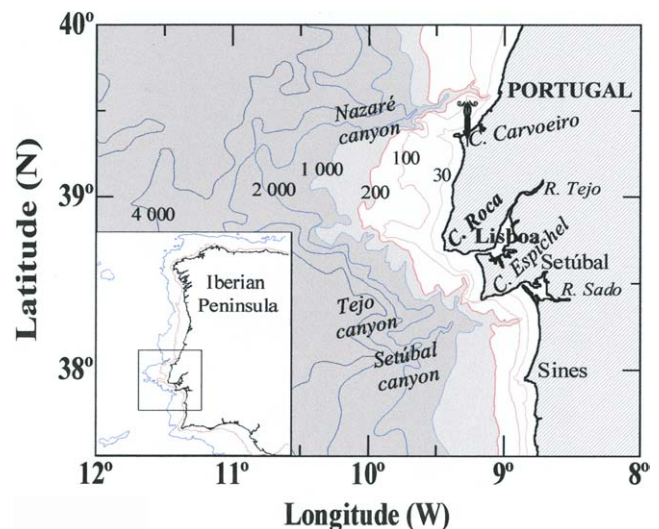

Fig. 1. West coast of Portugal. The symbol ( ) in the map points toward the meteorological station of Cape Carvoeiro.

surface isotherms into a plume structure. Upwelling plumes have been observed frequently in mostly upwelling regions, e.g. (Andrews and Hutchings, 1980; Fiúza, 1983; Jones et al., 1983; Traganza et al., 1983). Off western Portugal, upwelled waters frequently present plume like seaward extensions that

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during summer months show a strong relationship with satellite-derived phytoplankton rich mesoscale structures (Sousa and Fiúza, 1989; Sousa and Bricaud, 1992). Off Lisbon a recurrent filament, the Lisbon plume, can extend southward or westward. This plume seems to be fed by the coastal jet current flowing from north (Sousa and Bricaud, 1992).

The distribution of chlorophyll *a*, indicative of the phytoplankton biomass, often is not symmetric about the elongated temperature axis of plumes (Estrada,1984; Jones et al., 1988). From studies carried out off Point Conception (California), Jones et al. (1988) concluded that in the presence of adequate nutrients and moderate mixed layer depths, the horizontal advection field is the predominant factor determining the asymmetry of chlorophyll distributions in coastal upwelling centres: on the northwestern side of the upwelling centre higher velocities rapidly advect any plankton out of the area; along the southern side, weaker current velocities and more variable directions result in low net advection out of the region. According to those authors, along the equatorward edge of the feature small eddies may form, causing plankton retention.

Phytoplankton from a coastal upwelling region can be described as a series of assemblages, which from the point of view of their species composition can be ordered according to decaying turbulence and nutrient (Estrada and Blasco, 1985; Margalef et al., 1979). Diatoms, in contrast to dinoflagellates, are considerably less sensitive to turbulence and may even be stimulated by motion (Smayda, 1997). Species like chain-forming dinoflagellates have a selective advantage in areas of convergence and downwelling and are able to survive in more turbulent water around upwelling areas (Fraga et al.,1989; Margalef et al., 1979).

The main objective of this paper is to investigate the distribution of phytoplankton biomass and species composition, in particular the presence of the toxic chain-forming dinoflagellate *Gymnodinium catenatum*, a paralytic shellfish poisoning (PSP) producer, in relation to the location of the Cape Roca upwelling plume, based on data from oceanographic cruises and satellites. A schematic conception of the near surface regime and phytoplankton distribution associated with the Cape Roca upwelling plume under different stages of development is proposed.

2. Materials and methods

The Bay of Lisbon (Fig. 1) was sampled on 26–27 August 1985 and 4–6 July 1994 on board the R/V Noruega. Water samples were collected in both cruises with Nansen bottles at the depths of 0, 5, 10, 20, 30, 40, 50 and 75 m. In July 1994, water column temperature and salinity were measured with a SBE19 CTD, while in August 1985, with thermometers coupled to the Nansen bottles and using a salinometer Beckman Mod. RS7C. On 9–10 September 1999, the Bay of Lisbon was sampled on board of the R/V Capricórnio. Physical data and phytoplankton samples were collected using a

combined SBE911 CTD profiler and a rosette sampler. Sampling depths were at 5, 10, 20, 30 and 50 m.

Phytoplankton samples were preserved with hexamethylenetetramine buffered formalin to a final concentration of 2.4%. Subsamples of 100 ml were taken for identification and counting by using the Utermöhl technique and a Zeiss IM35 inverted microscope. Phytoplankton data from August 1985 represents at each station a 100 m depth integrated water column: one composite sample per station was obtained by mixing the water samples from each depth in proportion to the extent of the water column they represent (Venrick, 1978). To evaluate the chlorophyll *a* concentration, 250 ml seawater samples were filtrated and pigments extracted with 90% acetone and determined on a Perkin-Elmer spectrofluorometer (Yentsch and Menzel, 1963).

Upwelling indices, based on the north-south wind component, were calculated according to Bakun (1973) for the 30 d previous to the cruises. Wind data were obtained from the meteorological weather station located at the Cape of Carvoeiro (Instituto Nacional de Meteorologia, Boletim Meteorológico Diário).

Infrared (IR) images for the study region were derived from the Advanced Very High Resolution Radiometer (AVHRR) instrument carried on the NOAA/TIROS-N series of polar orbiting satellites. Satellite data were calibrated and navigated to Earth coordinates and co-registered to an identical coordinate map of the study region. Raw data were acquired at the Dundee Satellite Receiving Station and all post-collection data processing was done at IPIMAR. The brightness temperature from AVHRR channel 4 (11.5–12.5 μm) was used as an estimate of the sea surface temperature (SST) to avoid the noise amplification introduced by atmospheric correction algorithms. The mapping between AVHRR channel 4 brightness temperatures and grey shading was individually selected to enhance the thermal structures of interest.

3. Results

3.1. August 1985

Fig. 2a shows that in August 1985 sampling was carried out after at least 12 d of persistent upwelling favourable winds. These conditions are reflected on the distribution of SST (Fig. 3a) where the presence of colder water centres is visible near the coast and the establishment of several offshorewards filament-like structures in front of Capes Carvoeiro and Roca. In Lisbon Bay, an upwelling plume can be clearly identified off Cape Roca. The core of colder waters extends southward suggesting a strong equatorward flow along the plume axis (Fig. 3b). The presence of relatively warmer waters at the inshore side of the plume suggests the presence of a northward return flow.

Chlorophyll *a* distribution shows a maximum (2.5 mg m^{-3}) off Cape Roca that is positioned over the shelf break (Fig. 4a). The distribution of *G. catenatum* was re-
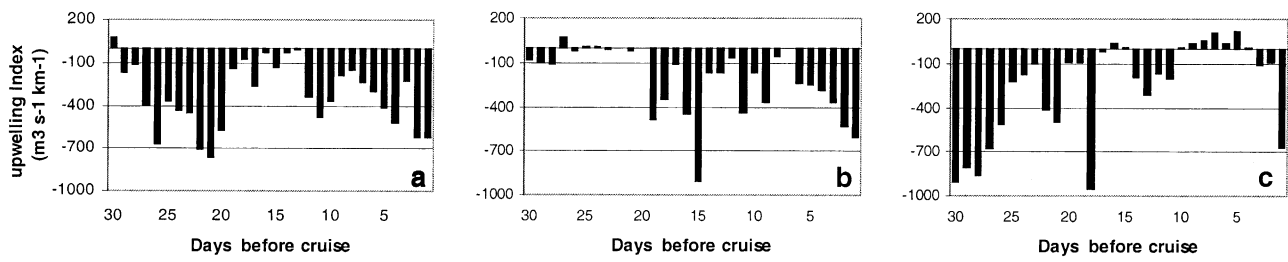
Fig. 2. Upwelling index in the 30 d previous to cruises. Negative values mean upwelling. (a) August 1985; (b) July 1994; (c) September 1999. Data from meteorological station of Cape Carvoeiro.
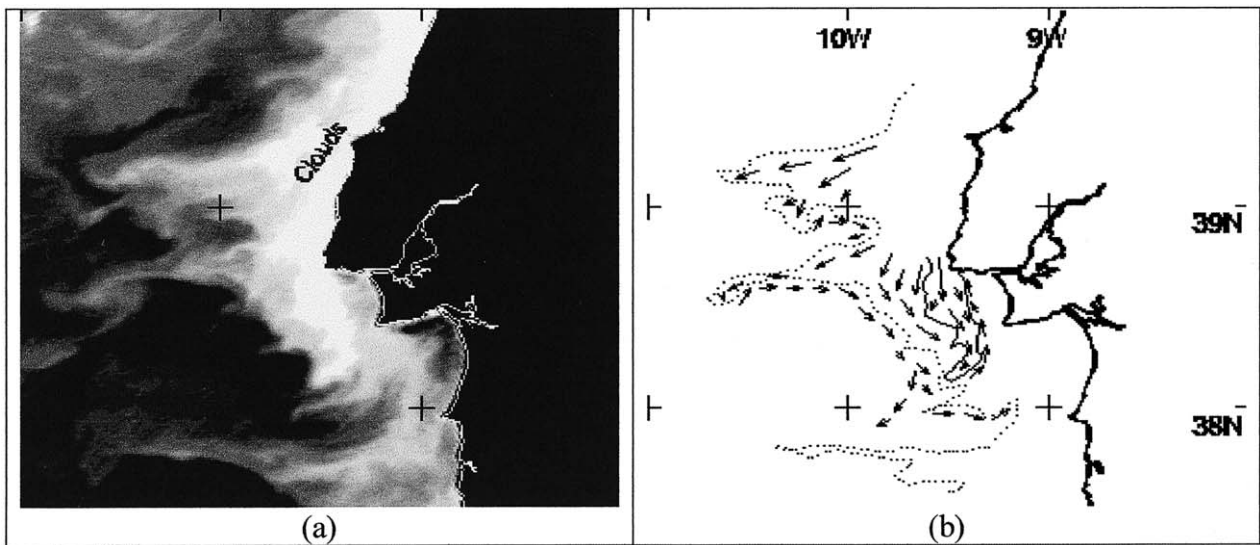

Fig. 3. (a) Satellite IR image from 1 September 1985. Lighter shadings represent cooler waters. (b) Sketch of subjectively determined flow field from comparison with a previous image of August 26. The arrows depict the direction of flow and arrow lengths are representative of the magnitude of the velocities arbitrarily scaled. Lines indicate the boundaries of cold upwelled water, solid line delineates the core of colder water.
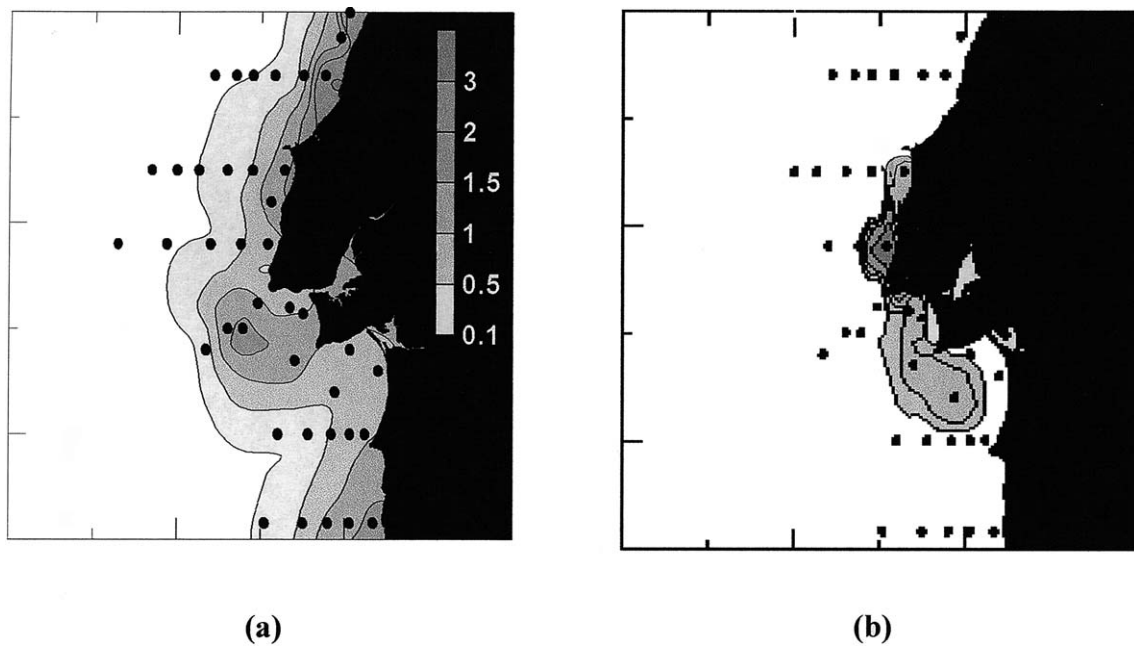

Fig. 4. Distribution of (a) chlorophyll *a* maximum (mg m^{-3}) and of (b) mean values of *G. catenatum* (cells l^{-1}) in the water column, in August 1985.

stricted to the area between Capes Carvoeiro and Sines (Fig. 4b). Higher concentrations were observed south of Cape Carvoeiro plume (6×10^3 cells l^{-1}) and at Lisbon Bay (10^3 cells l^{-1}), at the inshore side of the Cape Roca upwelling plume.

3.2. July 1994

The July 1994 cruise took place during an upwelling event that lasted for 7 d (Fig. 2b). The satellite image shows the presence of a continuous band of cold water along the coast with several offshore protrusions (Fig. 5a). Apart from the smaller extensions of the offshore filaments, the SST pattern off Cape Roca is similar to that of August 1985 (Fig. 3a), with a clearly identifiable upwelling plume extending south of the Cape also revealing an equatorward flow bounded, at the inshore side by a northward return flow (Fig. 5b).

The distribution of *G. catenatum*, with a maximum of 0.5×10^{-3} cells l^{-1} at Lisbon Bay, was similar to the situation of August 1985, with the highest numbers extending equatorwards, on the coastal side of colder upwelling waters (Fig. 6).

3.3. September 1999

The September 1999 cruise occurred after a fortnightly period of upwelling relaxation or even downwelling (Fig. 2c). An upwelling event began to develop on the day preceding sampling. The SST distribution from satellite image and from oceanographic data reveals a core of colder water in the outer area of Lisbon Bay (Figs. 7a and 8a).

Chlorophyll *a* distribution shows the existence of two maxima at each side of the upwelling core: the coastal one reached 2.9 mg m^{-3} while the outer one 1.8 mg m^{-3} (Fig. 8b). These maxima were associated with different phytoplankton assemblages. To illustrate these differences four autotrophic species were selected as indicators. *G. catenatum* and *Alex-*
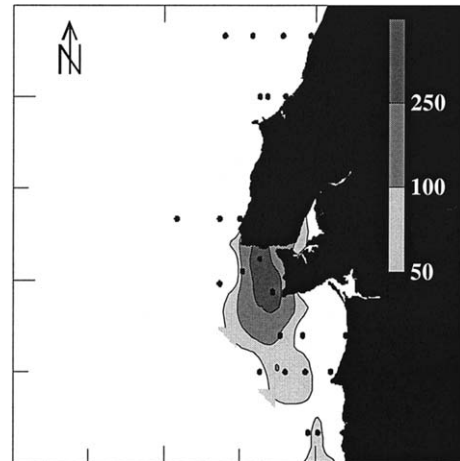

Fig. 6. Distribution of maximum values per station of *G. catenatum* (cells l^{-1}) in July 1994.

andrium affine reached, respectively, 0.5×10^{-3} and 6×10^{-3} cells l^{-1} at surface (0–10 m depth) and species were restricted to the coastal side of the upwelling front coinciding with the inshore chlorophyll *a* maximum (Fig. 9a,b). The highest concentration of *Cylindrotheca closterium* (3×10^{-3} cells l^{-1}), a small diatom with high division rates that reacts strongly to nutrient enrichment (Graneli, 1981; Tanaka, 1984), coincided with the upwelling centre, decreasing afterwards to the coastal side of the core (Fig. 10a). In turn, the large diatom *Proboscia alata* was mainly distributed on the oceanic side of the upwelling front, reaching 3.5×10^{-3} cells l^{-1} in coincidence with the offshore chlorophyll *a* maximum (Figs. 8b and 10b). According to Margalef et al. (1955), this diatom, with relatively high division rates, belongs to the second of three stages of phytoplankton succession related to mixing/stratification cycles that can last 1 or 2 weeks in the Ría de Vigo (NW Spain). This species is often found from mid summer to early autumn in mature stratified waters off
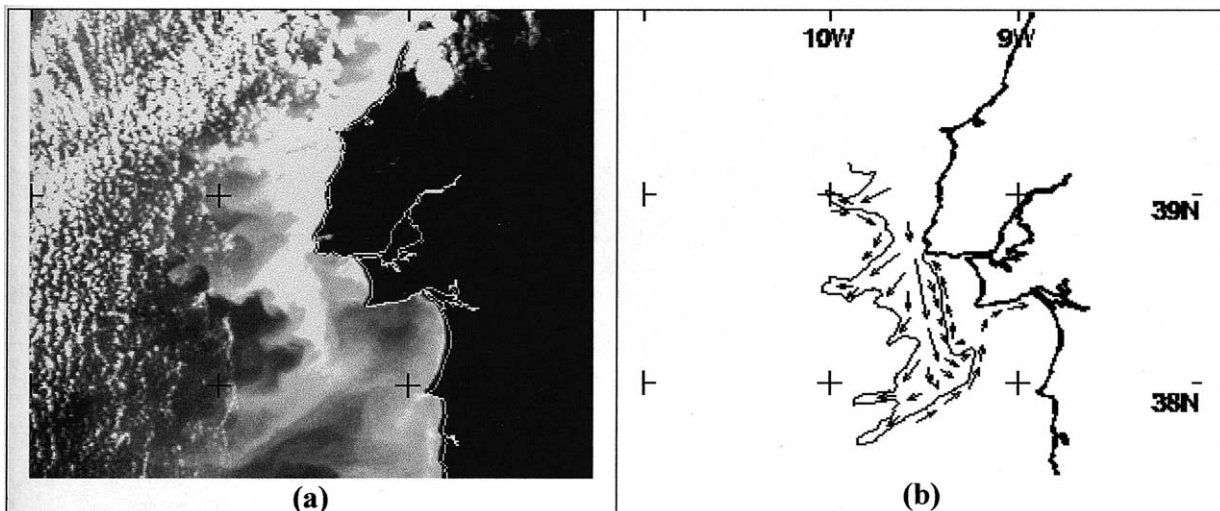

Fig. 5. (a) Satellite IR image from 1 July 1994. Lighter shadings represent cooler waters. (b) Sketch of subjectively determined flow field from previous images of 26 and 28 June. The arrows depict the direction of flow and arrow lengths are representative of the magnitude of the velocities arbitrarily scaled. Continuous line indicates the position of the upwelling front.
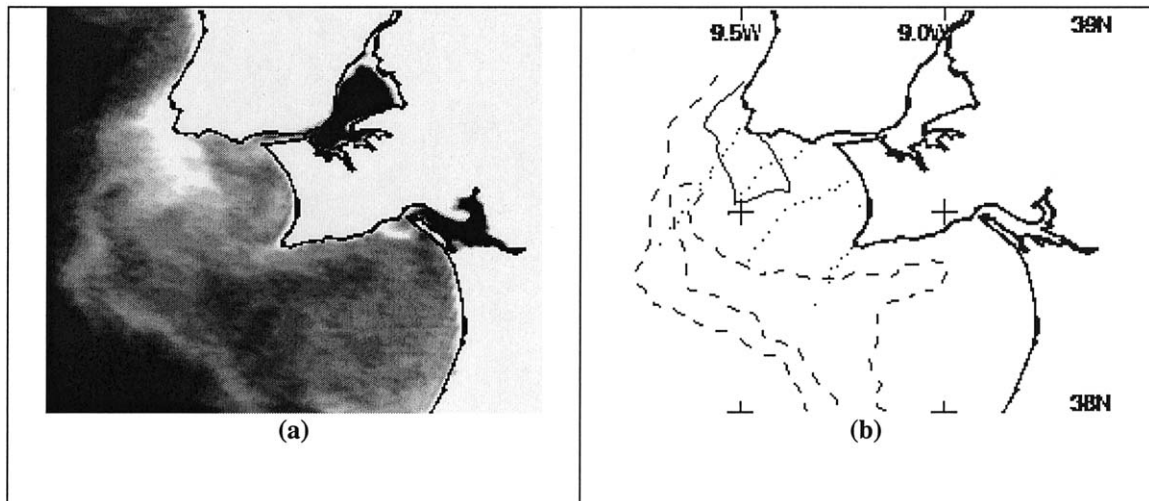
Fig. 7. (a) Satellite IR image from 8 September 1999. Lighter shadings represent cooler waters. (b) Sketch of the boundary of colder waters (dashed line). Solid line delineates the region occupied with the colder core of recently upwelled waters. Dots indicate the position of oceanographic stations.
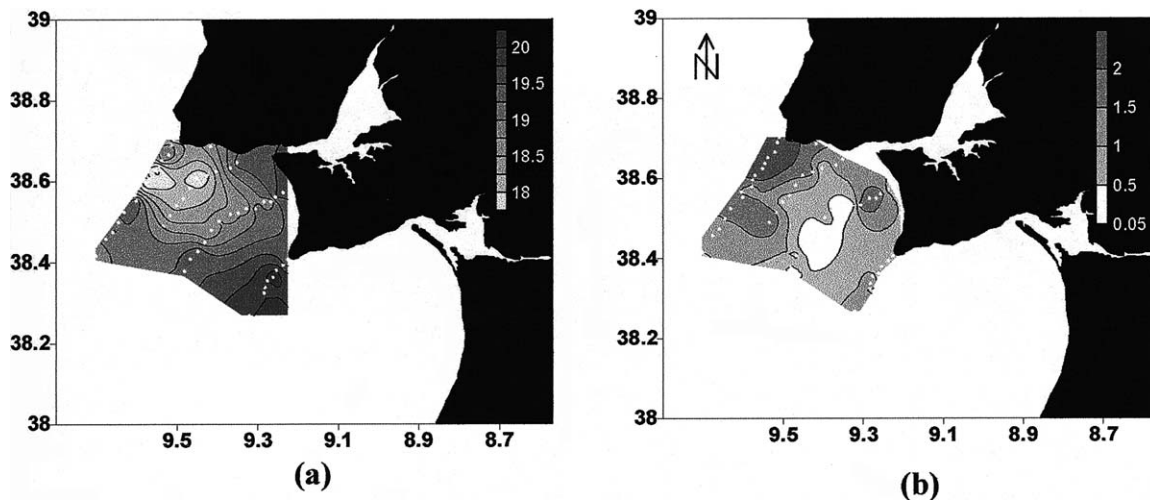

Fig. 8. Distribution of (a) temperature (°C) at 5 m depth and of (b) maximum values per station of chlorophyll *a* (mg m^{-3}), in September 1999.
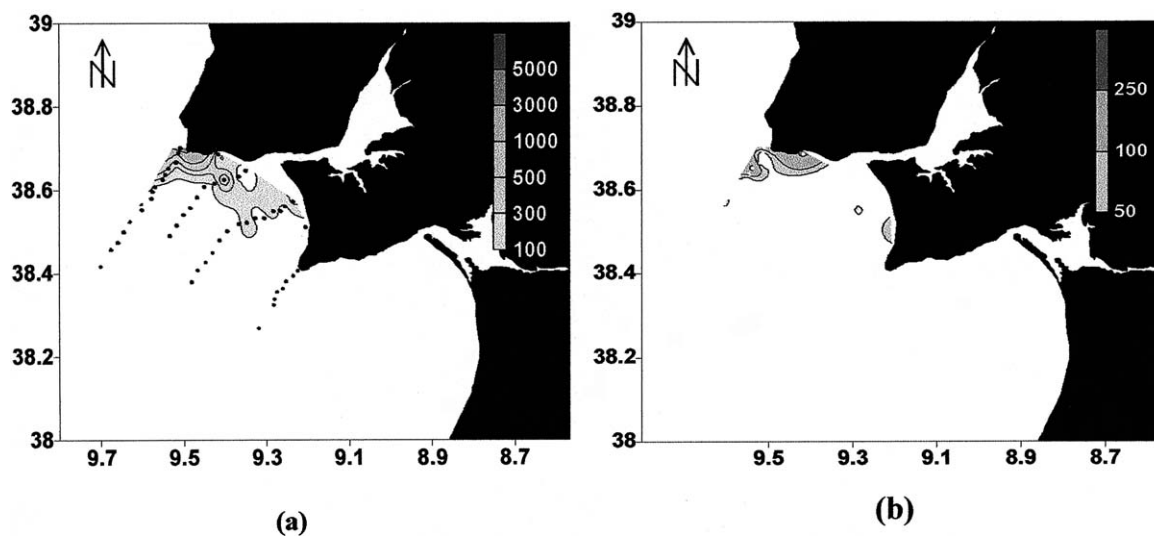

Fig. 9. Distribution of maximum values per station (cells l^{-1}) of (a) *A. affine* and of (b) *G. catenatum* , in September 1999.
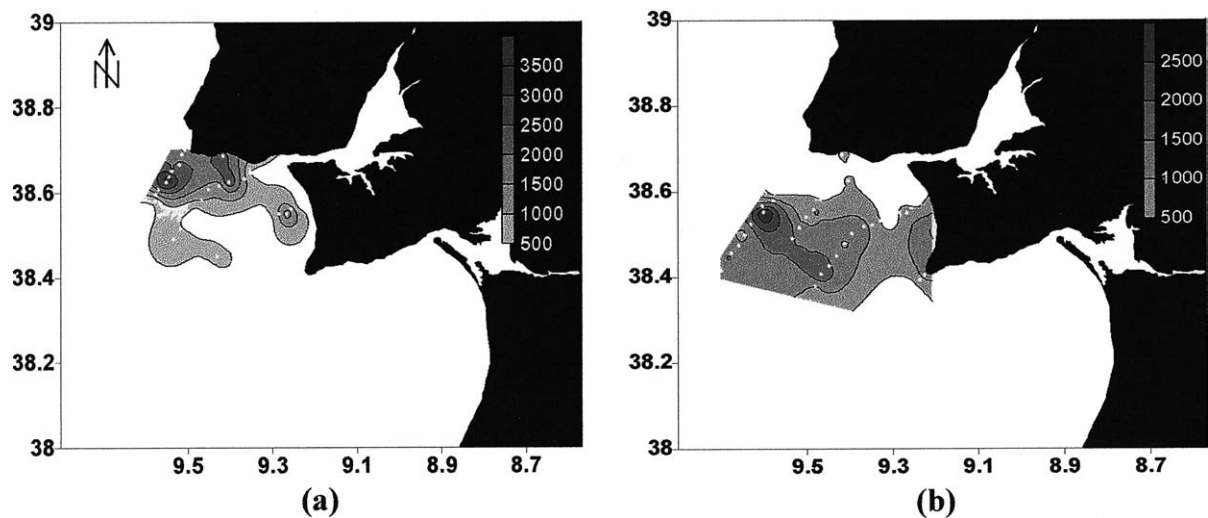
Fig. 10. Distribution of maximum values per station (cells l^{-1}) of (a) *C. closterium* and of (b) *P. alata*, in September 1999.

Iberia, mixed with dinoflagellates (Fernandez and Bode, 1994; Moita, 2001).

4. Discussion

The above results represent two different phases of coastal upwelling along the central part of the West coast of Portugal. In August 1985 and July 1994, the oceanographic cruises were carried out after several days of intensification of northerly winds and the observed distributions of SST, chlorophyll *a* and *G. catenatum* are representative of fully developed upwelling. In September 1999, the survey took place 1 d after the initiation of an event of northerly winds and the results are thus representative of the early stages of an upwelling event. In this cruise, the higher number of closely spaced stations, together with the analysis of a greater number of phytoplankton species, permitted us to investigate in greater detail the asymmetric distribution of chlorophyll *a* and phytoplankton species about the core of upwelling waters off Cape Roca. This combined analysis provided insight into the history of the water mass involved since differences revealed by phytoplankton assemblages amplify the physical variability and reveal subtle changes in the hydrographical parameters (Estrada and Blasco, 1985).

In September 1999, during a typical early stage of an upwelling event, the SST distribution showed the presence of a core of cold water in the outer area of Lisbon Bay. The two sides of the upwelling front showed a different phytoplankton population structure leading to the conclusion that the corresponding water bodies had different life histories. The distribution of indicator species, such as *C. closterium* within the upwelling core and of *P. alata* at the oceanic side of the upwelling front, allow the discrimination between newly upwelled from mature waters inside Lisbon Bay.

During the same cruise, *G. catenatum* and *A. affine*, constrained between the northern side of the upwelling front and the coast, contributed to the highest chlorophyll *a* con-

centrations observed. The higher concentrations found at the northern side of the bay might be related to more stable conditions due to the lower intensity of the northerly winds in that region where the coastline runs in an east-west direction. *A. affine* and *G. catenatum* produced simultaneous and massive blooms along the Portuguese northwestern shelf during autumn 1985 (Moita, 2001). These chain-forming dinoflagellates seem, therefore, to be species with similar environmental demands probably due to their similar vertical swimming capacities, a selective advantage to survive in more turbulent water around upwelling areas or areas of convergence as pointed out by Fraga et al. (1989) and Margalef et al. (1979). In August 1985 and July 1994, the spatial distribution of the equatorward upwelling plumes off Cape Roca, as revealed by satellite imagery, was very similar and the distribution of higher concentrations of *G. catenatum* suggests the species was favoured along the eastward side of the plume within warmer waters. It is hypothesised that the northern side of Lisbon Bay corresponds to an area of slow currents or closed circulation where species like *G. catenatum* are retained. On the other hand, the species maximum observed between the plumes of Capes Carvoeiro and Roca can be explained on the basis of the following model (adapted from Jones et al. (1988) : the shoreward flow in the leeward side of the Cape Carvoeiro plume would create favourable conditions for the species accumulation at the coast, while the high westward velocities in the poleward side of Cape Roca plume would advect and disperse the species. Recent results on the distribution of *G. catenatum* cysts in surface sediments along the Portuguese coast (Amorim, authorised personal communication) have revealed the presence of several maxima at the central region of the western coast off Portugal, which are located south of the major Capes or recurrent plumes. In particular, one of those maxima is located at the northern side of Lisbon Bay. These findings are consistent with our results: the shoreward flow in the leeward side of plumes and the northwards return flow eastward of the equatorward upwelling plumes associated
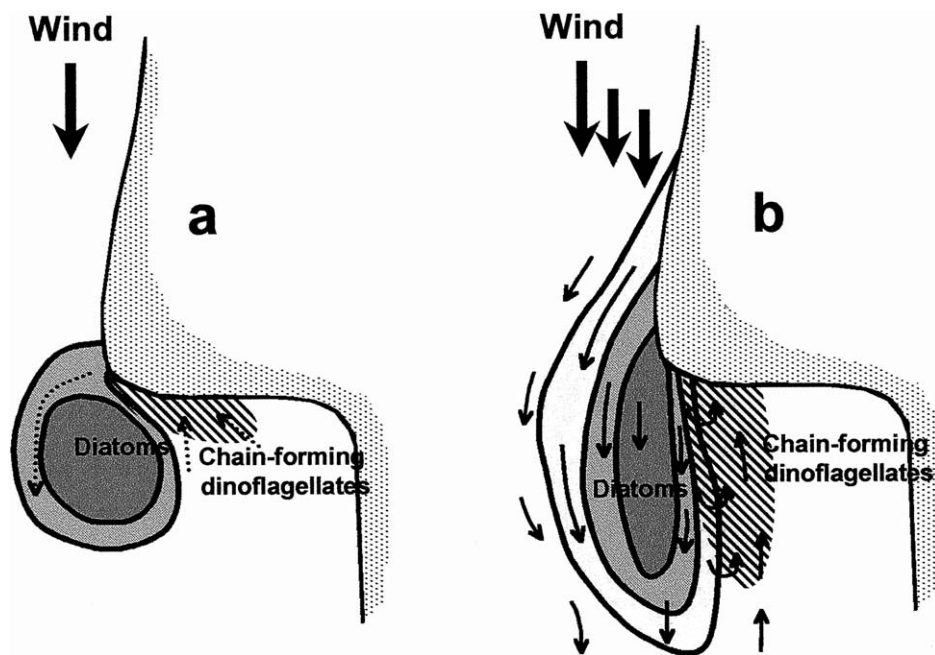
Fig. 11. Conceptual model of the near surface circulation associated with an equatorial trending upwelling plume close to a pronounced Cape and relative position of diatom vs. chain-forming dinoflagellates (stripes). The arrows indicate current direction and relative speed (by length of arrow), inferred from SST and phytoplankton distribution (dotted) and from sequences of satellite images and results from other upwelling areas (solid). Solid lines indicate the shape of isotherms with temperatures increasing away from the upwelling core (darker shading). (a) An early stage of upwelling and (b) a fully developed upwelling.

with pronounced Capes must play an important role on the accumulation (or even growth) of *G. catenatum* as well as on the sedimentation of the species cysts.

Concerning the distribution of chlorophyll *a* observed off Lisbon in August 1985, the pattern also agrees with the model proposed by Jones et al. (1988). These authors stated that "...along the equatorward edge of an upwelling plume there is likely to be a weaker shoreward flow turning equatorward near the coast. The shoreward flow may include some of the recently upwelled water and the slower currents and possible eddies provide a region where phytoplankton populations can develop near the core of the upwelling centre without being advected large distances away". Accordingly, the observed chlorophyll *a* maximum was located close to the core of the upwelling plume within an area where there seems to be a shoreward flow and slower currents. In 1999, the distribution of chlorophyll *a* was asymmetric about the upwelling core, with each of two maxima corresponding to different phytoplankton assemblages. The coastal maximum appears to have resulted not only from the accumulation of phytoplankton at that area but also from the contribution of species with high growth rate that responded to newly upwelled nutrient enriched waters. Instead, the offshore maximum was associated with another mature upwelled water body where an assemblage composed by species characteristic of later stages of succession from previous upwelling cycles seemed to have grown in response to the intensification of the observed upwelling event.

Based on present and published results from other upwelling areas, (e.g. Jones et al., 1988; Rosenfeld et al., 1994;

Strub et al., 1991), a conceptual model for the distribution of diatoms and *G. catenatum* in relation to an equatorial trending upwelling plume close to a pronounced Cape during different phases is proposed (Fig. 11). This scheme closely resembles the one presented by Jones et al. (1988), with the axis of the coastal upwelling plume directed southwards. It can also be seen as an idealisation of the circulation associated with an equatorward trending plume related to the bifurcated flow from an upwelling centre as described by Rosenfeld et al. (1994). In the early stages of upwelling (Fig. 11a), current velocities are low and the first stage of phytoplankton succession is composed of diatoms with a high growth rate and adapted to increasing turbulence in the core of colder water. Phytoplankton populations such as the chain forming dinoflagellates then accumulate in the northern side of the bay. This assemblage, characteristic of late stages of phytoplankton succession (Moita, 2001), would probably be already established close to the Cape due to its sheltering effect from the turbulence induced by previous cycles of northerly winds. With the intensification of upwelling conditions (Fig. 11b), the current velocities increase and trend equatorward close to the core of the cold upwelling plume, decreasing at the inshore direction. These high velocity currents entrain some of the cold upwelled water that contains higher nutrient concentrations but are low in phytoplankton biomass due to advection to unfavourable areas for phytoplankton maintenance. Along the eastward edge of the feature there is likely to be a weaker, possibly northward flow. This flow may include some of the recently upwelled water and the slower currents and possible eddies provide a

region where phytoplankton populations such as chain-forming dinoflagellates can extend and develop along and close to the core of the upwelling plume without being advected away.

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