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Hydrodynamics and the spatial distribution of plankton and TEP in the Gulf of Cádiz (SW Iberian Peninsula)

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During a summer cruise in the Gulf of Cádiz area (Southern Iberian Peninsula), an upwelling episode off the eastern coast of Cape Santa María was noted. The observed temperature field data suggested an anticyclonic circulation from NW to SE and a velocity of the associated surface currents ranging between 10 and 15 cm s^{-1} *was estimated. Research was carried out on the physical–biological coupling by analysing the influence of these hydrodynamic patterns on the mesoscale distribution of several chemical and biological variables. During the cruise, nitrate concentration, total chlorophyll, chlorophyll (>20 μm), phaeopigments and TEP bulk concentration were measured. The distribution of biological variables appears to be organized by physical forcing. The upwelling area acts as a notable disturbance in the area. A sequence of maxima of different variables classified as bloom phases was observed, arranged in the same direction as dominant currents. A clear frontal structure in radial transects was also apparent. Discussion focusses on the variability of the hydrodynamic patterns observed in the framework of previous observations and the role of physical forcing, moulding the biological distributions and altering their spatial correlations. Special reference is made to TEP, as this variable is scarcely analysed in extensive field studies. The distribution of TEP patches in the area was heterogeneous, which has been discussed in the framework of current theory. Chlorophyll (>20 μm), phaeopigment ratio and TEP concentration maxima had no direct spatial correlation with chlorophyll maxima. The sequence of typical processes in phytoplankton bloom phases and the influence that hydrodynamics has both on environmental suitability for growth and on displacement of patches, could explain the distribution of these biological variables in the area. Subsequent studies on hydrodynamics variability are suggested as a valuable tool for the future understanding of biological processes in the region.*

INTRODUCTION

The Gulf of Cádiz is strategically located connecting the open Atlantic Ocean with the Mediterranean Sea through the Strait of Gibraltar. The Gulf has been scarcely studied, particularly from the viewpoint of physical–biological coupling, which contrasts with the extensive oceanographic literature on the Strait of Gibraltar and the other adjacent basin, the Alborán Sea.

The physical structure and dynamics of the Gulf were first studied by Stevenson (Stevenson, 1977) describing the so-called Huelva front by a combination of Sea Surface Temperature (SST) remote sensing and in situ temperature observations. Fiúza *et al.* (Fiúza *et al.*, 1982) and Fiúza (Fiúza, 1983) provided evidence of upwellings off the Algarve coast in Portugal both at Cape St Vincent and west of Cape Santa María, which were easily detectable in many SST images. Folkard *et al.* (Folkard *et al.*, 1997) also mentioned the existence of this cold sea-surface temperature signature extending from the western Iberian coast around Cape St Vincent and eastward as far as Cape Santa María, which was more evident in summer. The structure of the Huelva front (Stevenson, 1977) suggests an anticyclonic circulation in the Gulf of Cádiz. The mean circulation in the area is also influenced by winds, especially westerlies, at shorter time scales (Folkard *et al.*, 1997). One interesting hydrodynamic feature is the appearance of local upwelling events in the eastern part of Cape Santa María that would be associated with the wind field. During our cruise, upwelling was clearly observed off Cape Santa María.

This paper analyses the possible influence of the physical background observed, during a cruise carried out in June–July 1997, on the distribution of biological variables in the area. This distribution may be interpreted in a manner similar to phytoplankton bloom stages, but segregated in space according to water circulation. Distribution patterns in the biological variables arise, in this case, from the ordered sequence of processes established in the prevailing currents deriving from a focal region, where upwelling occurs. These sequential processes will include the upwelling of cold deep water, nutrient enrichment, phytoplankton production and pigment degradation. To this conceptual scheme may be added the appearance of other biological variables, which are either less studied or which do not bear such a non-direct spatial correspondence with physical forcing and chlorophyll patches, such as local abundance of ichthyoplankton or Transparent Exopolymer Particles (TEP) abundance. This latter variable has a special interest as it is not usually included in the planning of cruises and plays an ecological role in the termination of phytoplankton blooms that has not been widely studied in the field.

TEP are formed from dissolved extracellular polysaccharides mainly exuded by phytoplankton (Alldredge *et al.*, 1993; Kiørboe and Hansen, 1993). TEP concentration is usually higher subsequent to the phytoplankton spring blooms. This has been observed in Kattegat (Mari and Kiørboe, 1996), California (Passow *et al.*, 1994), Antarctic waters (Hong *et al.*, 1997) and Baisfjord (Norway) (Riebesell *et al.*, 1995). Production of TEP is of major importance for the aggregation of diatom blooms, both in the ocean (Passow *et al.*, 1994; Passow and Alldredge, 1994; 1995b; Riebesell *et al.*, 1995; Schuster and Herndl, 1995; Mari and Kiørboe, 1996; Hong *et al.*, 1997) and in fresh waters (Grossart *et al.*, 1997). In spite of these references, TEP concentration data in the field are scarce and they have been obtained both from heterogeneous marine systems, and by using diverse techniques. Field data of TEP, which allow for discussion of structures on a basin scale, and which also attempt to couple their distribution with the observed hydrodynamics, are even scarcer.

The spatial distribution of TEP will depend on several biological and physical processes that affect its production and the persistence of patches in surface water. This will be discussed in the framework of the observed physical dynamics and current theory. The observed situation includes two main features. First, a major input of nutrients related to the pulsing upwelling event, which acts as an initial disturbance that enhances plankton production. Second, a dominant anticyclonic circulation pattern, which will organize spatial distribution, eventually leading to successive patches or maxima of variables, gradually becoming more typical of the final phases of the bloom.

The aim of this work is two-fold. First, to investigate the circulation pattern and hydrological structure in the Gulf of Cádiz area during the cruise, discussing their variability in a more extended temporal context. Second, to discuss the possible influence of this circulation pattern on the spatial distribution of biological variables in the area, including a more detailed discussion of the TEP patterns observed in the sea.

METHOD

The dataset

Samples were taken during IctioAlborán-Cádiz 97 cruise on board O/V Cornide de Saavedra from the Instituto Español de Oceanografía (IEO). The cruise was carried out from June 29th to July 2nd 1997 and included 43 sampling stations. The area covered from Cape Santa María off the Southern Portuguese coast of the Gulf of Cádiz to the northern Alborán Sea immediately adjacent to the Strait of Gibraltar (Figure 1). Sampling was accomplished starting from the west (stations 1, 2, 3...) and sailing to the east (stations 44, 43, 42).

For each station, a temperature and salinity profile was made with a Seabird 25 CTD probe, followed by water sampling using a line of oceanographic Niskin bottles arranged at 5, 25, 50, 75 and 100 m.

Wind data was recorded at the Ceuta and Tarifa coastal stations (see Figure 1) of the Instituto Nacional de Meteorología. Data analysed included wind direction and intensity in four daily observations (0:00, 06:00, 13:00 and 18:00 GMT) taken during June and July 1997.

Satellite images presented correspond to NOAA (USA) AVHRR MCSST Surface Sea Temperature daily composite images of the area, obtained via Internet from ISIS (DLR, Germany) web pages. The 256 grey levels of information on the original bitmap file was treated to enhance contrast in the same manner for all images. The entire original range of temperatures (0–31.75°C) contained in the extended histogram was reduced to a range of between 15°C (darker) to 23.5°C (lighter grey).

Nutrient analyses

Samples to measure dissolved inorganic nutrient con-centration were taken from the oceanographic bottles. Samples were kept in hermetic polyethylene vials and immediately stored frozen (–20°C). Further analysis in the laboratory was made by using a Technicon AAII

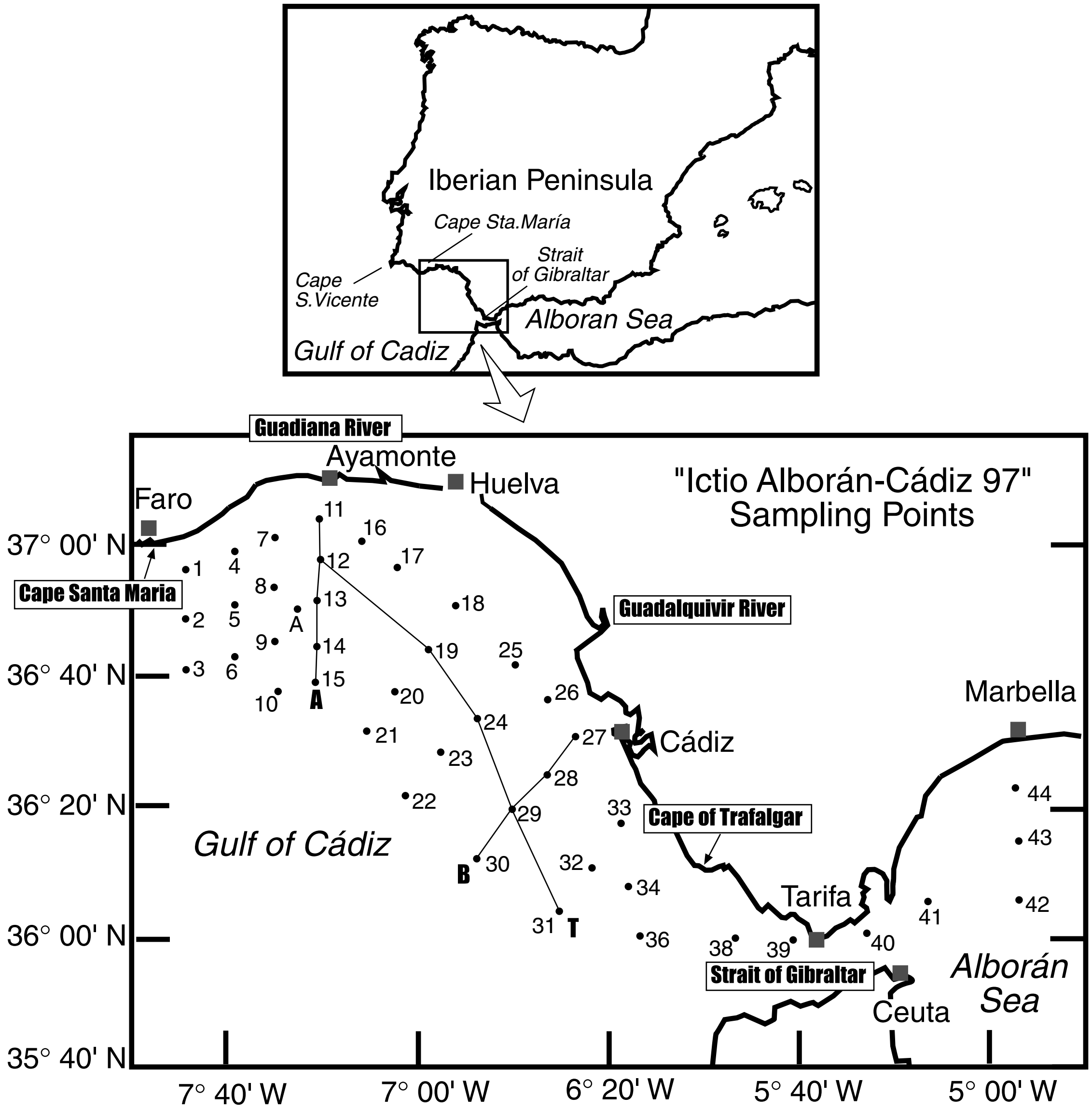

Fig. 1. Sampling points for IctioAlborán-Cádiz 97 cruise, showing geographical points of reference mentioned in the text as well as a scheme of transects that have been analysed in detail (transects A, B and T).

autoanalyser following Tréguer and Le Corre (Tréguer and Le Corre, 1975).

Pigment analyses

Samples to estimate total chlorophyll *a* (500 ml) were filtered on board through Whatman GF/F (~0.7 μm) filters. To obtain the percentage of total chlorophyll corresponding to larger cells (>20 μm) we filtered 2–3 l of water through a 20 μm mesh and collected the fraction with a sprayer. This concentrated fraction was then filtered through Whatman GF/F in the same manner as described for total chlorophyll. The extraction of these pigments retained by the filters was carried out in acetone (24 h, dark, cold storage). Measurements of chlorophyll a and phaeopigments followed the method proposed in JGOFS (1994) protocols based in Holm-Hansen and Riemann (Holm-Hansen and Riemann, 1978). Results have been expressed as integrated values. The integrated values, which use data from different samples through the vertical profile in the water column, give synthetic information about phytoplankton biomass levels and potential production. It was considered recommendable, however, to extend the integration only to a moderate depth to obtain a graph that allows a better comparison between shallow and deep stations. This surface part of the column is also the best illuminated. This is the reason why values extracted from the three more superficial samples (down to 50 m) were used wherever possible (the shallowest coastal stations only down to 25 m).

Transparent Exopolymer Particles abundance

Samples to measure the abundance of TEP were filtered on board (50–100 ml) through a polycarbonate Poretics membrane (0.4 μm) using a constant filtration pressure (~95 mm Hg). The samples were immediately stained with alcian blue and the membranes stored frozen in capsules to be analysed later in the laboratory. The concentration of TEP was estimated following the spectrophotometric method of Passow and Alldredge (Passow and Alldredge, 1995a) by using a very recent standard curve built on the same used reagent. Results are expressed as gum xanthan equivalents (GXeq), as this was the reagent used to build the standard curve. In this case, the sensitivity of this method was estimated at 25 μg GXeq l^{-1}. This concentration marks the lower isopleths value shown. Lower values were considered as undetectable.

Ichthyoplankton

A Bongo-40 net, equipped with two independent flowmeters 'General Oceanics 2030' and one depth-meter gauge, was employed to carry out double-oblique trawls from the surface to 100 m depth. The subsample collected on the 350 μm mesh size net was used for taxonomic identification of the ichthyoplankton. Age was estimated according to Regner (1985) from the individual development stage and temperature, in the case of anchovy eggs, and according to the Palomera (1989) model for larvae.

RESULTS

Horizontal patterns in the area

The physical framework

The general conditions in the area during the cruise are well described by the SST image of Figure 2A and by the maps in Figure 3. The prevailing wind was westerly from 26th June (3 days before the start of the cruise) until 5th July (3 days after the cruise end). The area east of Cape Santa María was flooded with cold waters denoting a local upwelling. Cold upwelled waters seem to merge later with those turning counter clockwise from Cape St Vincent, as previously reported by Fiúza (Fiúza, 1983).

In situ temperature at 5 m depth (Figure 3B) matches well with the SST AVHRR image of Figure 2A. The pool of cold surface waters extends from Cape Santa María towards the Southeast. Isotherms run along a NW–SE bearing, roughly following the bottom. The very low surface temperature (<15°C) just east of the Cape, coinciding with the more intense signature of cold waters in the satellite image of Figure 2A, strongly suggests that this area is the source of the cold tongue.

Temperature distribution at 50 m and 100 m depth (data not shown) shows a pattern very similar to that of the surface, with isotherms following isobaths and warmer water offshore. Density field is dominated by temperature because of the homogeneity of the salinity distribution in the upper layers of the Gulf. Consequently, the picture depicted above suggests an anticyclonic circulation in this area, in accordance with the previous general description.

To obtain a rough estimation of surface currents, we have computed the dynamic topography using both the 100 db and 200 db reference level. In each case, only stations where the probe was lowered to 100 db and 200 db (respectively) were used. Figure 3A shows the good correspondence between the dynamic topography and the isotherm map in Figure 3B. Since the no-motion reference level was not known, the geostrophic velocities computed are only indicative. For instance, using stations 13, 14 and 15 from transect A (see Figure 1), the estimated alongshore current is 12 cm s^{-1} referred to 100 db and 14 cm s^{-1} if we use the 200 db level as reference. Surface velocity increases at 2 cm s^{-1}, indicating that the 100 m thick layer from 100 to 200 m moves very slowly if it is not at rest. It may be concluded that, as the temperature field suggests, surface currents flow clockwise from NW to SE with a typical velocity ranging between 10 and 15 cm s^{-1}. Similar results have been obtained using stations of transect B. Offshore thermal surface gradients in the stations close to shore are generally stronger than at the outer stations (see Figure 3B and Figure 4A). If, as suggested by the similitude of dynamic topography and surface temperature maps, horizontal temperature gradients were indicative of current strength, higher velocities would be expected to exist near the shore.

Distribution of biological variables

Patterns of total chlorophyll integrated down to 50 m include maxima associated with stations close to the upwelling surface cold waters (Figure 3E), although slightly displaced offshore. In the northern Gulf of Cádiz region, the highest values generally occur in a coastal northwestern band, gradually decreasing towards SE. Nevertheless, there is a clear maximum at station 36, off Cape Trafalgar and surrounding areas that has also been observed in previous cruises. The higher percentages of large cells, when expressed as a percentage of total chlorophyll, usually present maxima in the coastal stations of the

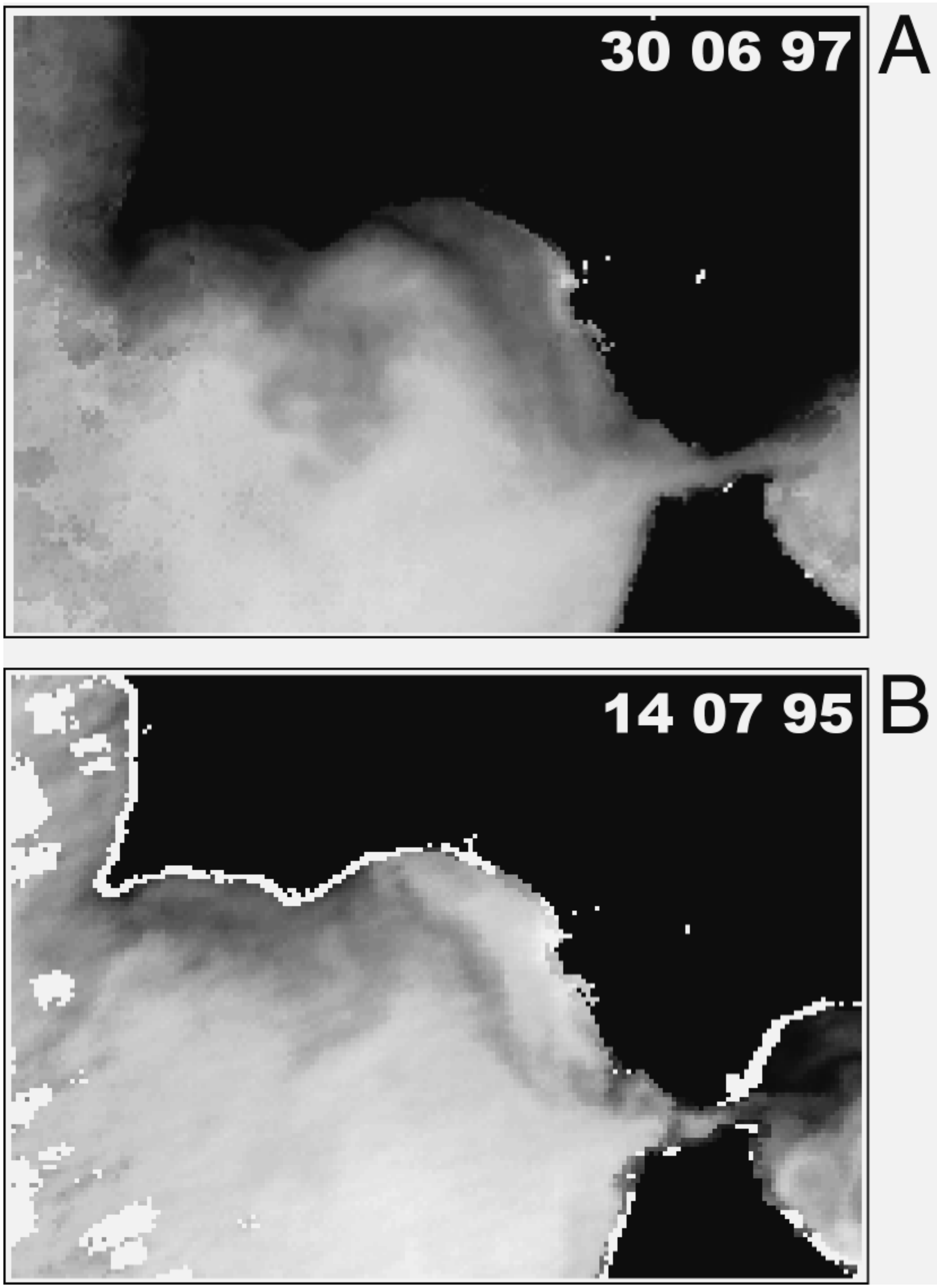

Fig. 2. Daily SST satellite composite graphics (NOAA AVHRR MCSST) corresponding to (**A**) 1997 cruise and (**B**) a previous cruise carried out in 1995. The range of temperatures that is shown extends from 15°C (darker) to 23.5°C (lighter).

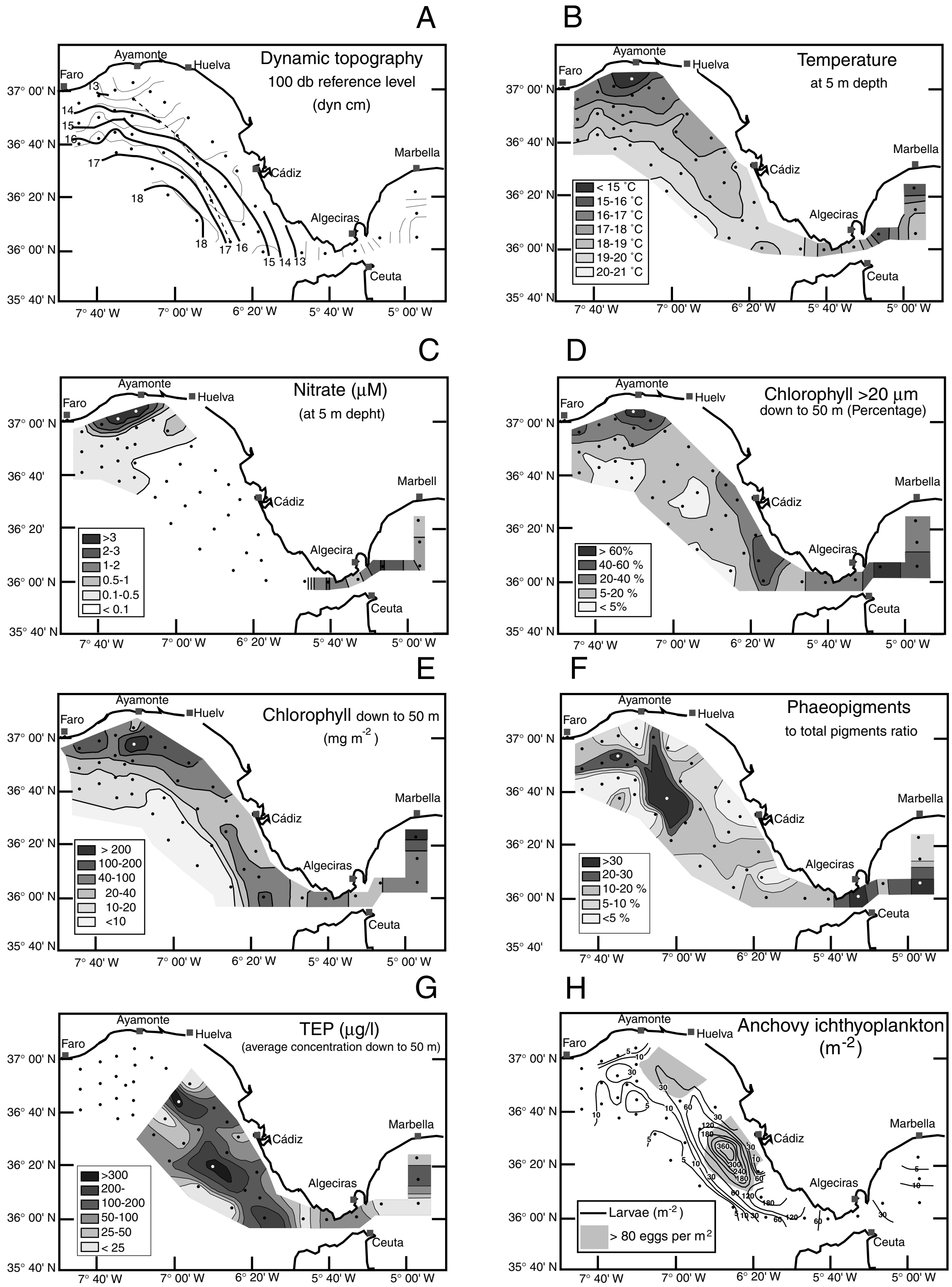

Fig. 3. Results obtained for several variables during IctioAlborán-Cádiz 97 cruise for the Gulf of Cádiz, also including some data on Gibraltar and Alborán Sea. (**A**) Dynamic topography calculated using 100 db reference level. This graph also includes the outline of temperature distribution (solid thin lines) and the position of transect T (dotted line). (**B**) Temperature at 5 m depth derived from CTD measurements. (**C**) Nitrate concentration at 5 m depth. (**D**) Percentage of total chlorophyll contained in cells >20 µm, calculated on the integrated values of chlorophyll down to 50 m depth. (**E**) Chlorophyll concentration per area estimated for the water column from surface to 50 m depth. (**F**) Phaeopigments to total pigments ratio expressed as a percentage and calculated down to 50 m depth. (**G**) Average concentration of TEP for the first 50 m in the water column. (**H**) Abundance of anchovy (*E. encrasicolus*) larvae expressed per square metre (lines). Shadowed areas represent zones with >80 anchovy eggs per square metre.

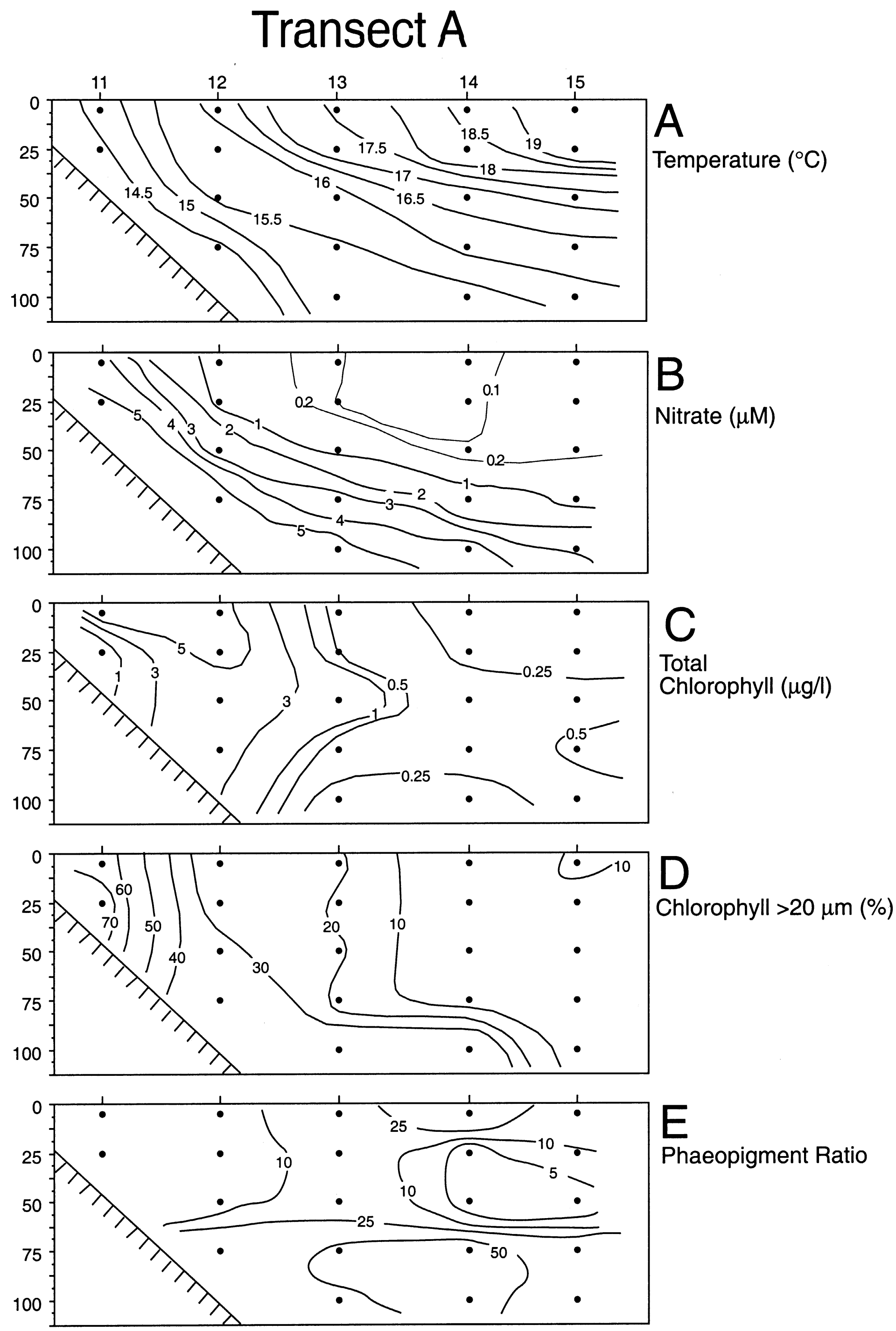

Fig. 4. Results observed in transect A described in the text for (**A**) water temperature, (**B**) nitrate concentration, (**C**) total chlorophyll *a* concentration, (**D**) percentage of chlorophyll contained in cells >20 µm, and (**E**) percentage of phaeopigments in relation to total pigments.

Gulf of Cádiz (Figure 3D). The highest percentage occurs in the station of minimum surface temperature in the Huelva Bay. There is also a high percentage nearer the coast in the rich Trafalgar area cited, as well as in a station just to the east of the Strait of Gibraltar with a high ratio of large autotrophic cells (>60%).

Phaeopigment data has been presented as a ratio of their concentration versus the total measured pigments

(Figure 3F). The abundance of these, for the most part, degradation products also follows the chlorophyll patterns, although a further displacement towards peripheral zones offshore and eastward of the chlorophyll maxima occurs. This agrees with previous observations in the area (Prieto *et al.*, 1999). Coastal stations with cold surface waters and a high concentration of chlorophyll in larger cells (e.g. stations 11, 12 and 34; Figure 3D) present minimum values of the ratio, indicating a predominance of active pigments.

TEP concentration in the water could be measured only from stations 18–44, including the eastern side of the sampled area. To express TEP abundance we have used data of averaged concentration (μg l^{-1}) to obtain values more suitable for comparison with the values presented in the literature. There are higher values of TEP concentration (Figure 3G) in a band placed, on average, around 25 nautical miles offshore, which does not coincide with maxima of chlorophyll nor phaeopigments, except in the Trafalgar area.

Although there are no data on herbivorous mesozooplankton, some data on ichthyoplankton distribution in the Gulf may be shown, this being a further step in the chain, with a more unclear relationship with hydrological patterns. Anchovy (*Engraulis encrasicolus*) is the dominant ichthyoplankton among other neritic fish species. This species accounts for 36% of total larvae and 52% of total eggs. Both eggs and larvae distributions present maxima of abundance at stations with 50–100 m depth, especially off Huelva and Cádiz (Figure 3H). Their distributions are clearly restricted to coastal areas with a marked absence (eggs) or shortage (larvae) in more oceanic waters, a fact already observed in previous cruises in the zone (Rubín *et al.*, 1997a; 1999).

Vertical distribution patterns

Some transects (see Figure 1) have been selected to investigate vertical distributions. Transects A and B follow a coast–offshore direction, approximately normal to the contours of dynamic topography. Transect T runs parallel to the coast, roughly following the contour of 200 (~150–250 m) depth. This last transect was selected to illustrate downstream variations of the different distributions. However, as Figure 3A shows, the transect does not follow the geostrophic streamlines and, therefore, the different distributions in this transect would reflect not only a likely downstream advection but also some cross-stream features.

Radial transects (A and B)

Radial transect A intersects the upwelling area of Cape Santa María (Figure 4). Isotherms show a very steep profile near the coast with strong offshore horizontal gradients of temperature, in agreement with the maps in Figure 3 and with the SST images. This is the signature of the thermal front associated with the upwelling. Moreover, the closer to the shore, the greater thermal gradient, which suggests enhanced alongshore currents towards the shore. Nitrate concentration and temperature distributions are well correlated. Areas with $T < 15.5°C$ and with nitrate concentration >3 μM are almost the same. Total chlorophyll concentration also matches the upwelling structure, with a tendency to deepen and decrease concentration offshore (Figure 4C). The percentage of chlorophyll from larger cells (Figure 4D) is very high at upwelling station 11, always being higher than 60% of total chlorophyll. Phaeopigment ratio, which expresses the degree of senescence of the phytoplankton assemblage due to decay and grazing, is higher at depth (Figure 4E). Station 13 has the highest ratio, which may be related to the very low nutrient concentration and moderate and decreasing values of total chlorophyll.

Radial transect B in the poorer area near the Bay of Cádiz (Figure 5) does not exhibit upwelling signature so clearly. Nevertheless, the presence of thermal front is suggested by the warm pool of surface water that floods the outermost station of the transect. The correlation between water of $T < 15.5°C$ and nitrate >3 μM still stands. Surface nitrate concentration (Figure 5B) is lower than in transect A, and it is undetectable (<0.04 μM) in the upper water column. The pattern of total chlorophyll concentration (Figure 5C) clearly depicts a gradual deepening and decrease moving offshore, following isothermal surfaces. Unlike the previous transect A, the maximum percentage of chlorophyll contained in particles larger than 20 μm reach only values slightly higher than 20%. A subsurface maximum of this percentage is found at station 29 (Figure 5D, see next section for comments). There are high values of TEP concentration at localized depths, from surface at coastal stations (27, 28) towards intermediate depths at station 29. TEP distribution has a structure that is visually connected to that of chlorophyll. Thus, TEP reached maxima approximately on the surface margin of the chlorophyll maxima and were undetectable by the method used in the outer waters (station 30), although station 29 maintained subsurface maxima in a low chlorophyll environment.

Transect parallel to the shelf edge (T)

Water temperature in the uppermost layer increases as we move toward the Southeast (Figure 6A). Part of this warming could be explained by surface mixing as the upwelled water moves downstream. However, the fact that the transect is not parallel to the geostrophic streamlines suggests that the temperature distribution in the transect is more related to the water mass distribution than to the

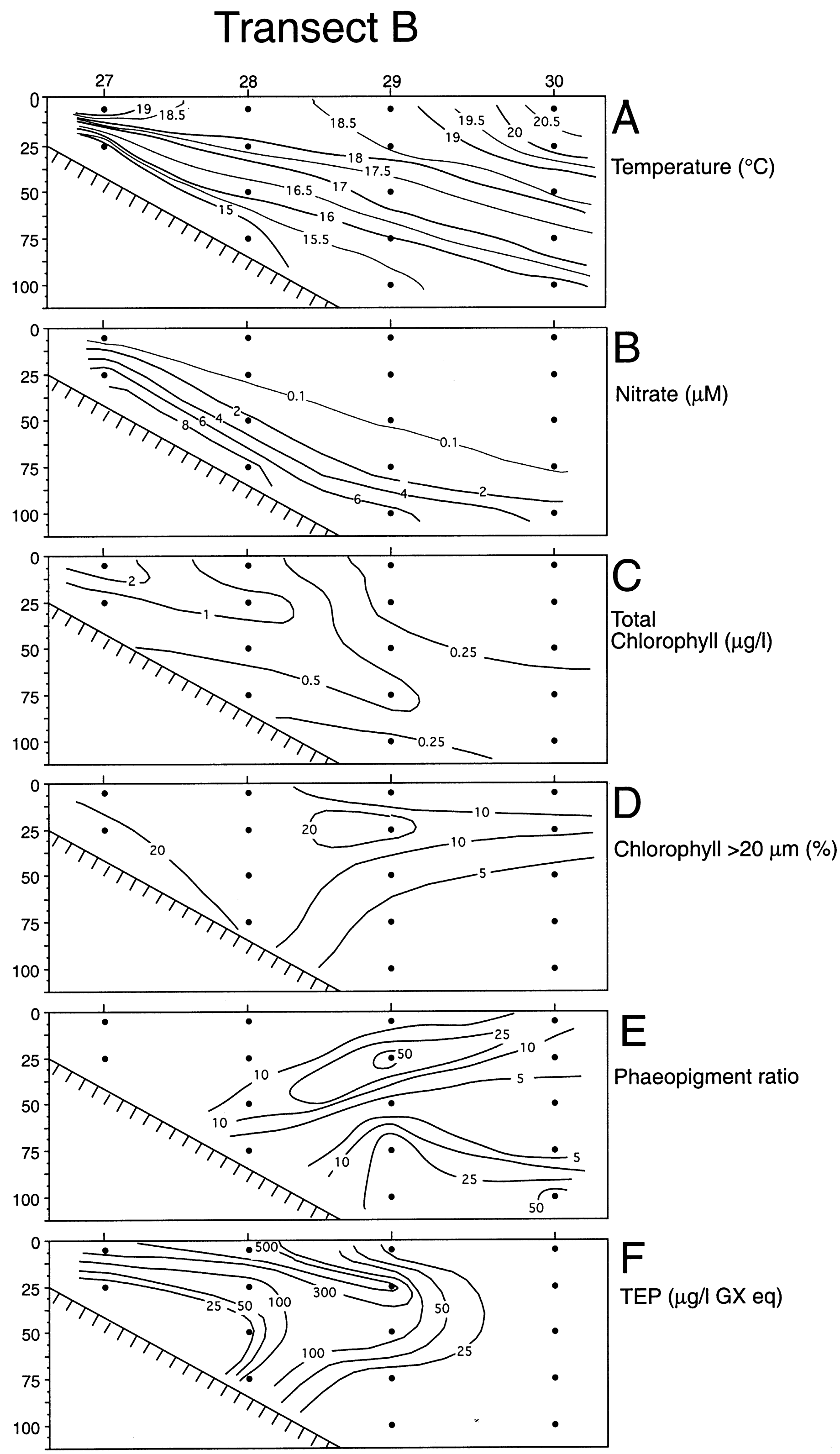

Fig. 5. Results observed in transect B described in the text for (**A**) water temperature, (**B**) nitrate concentration, (**C**) total chlorophyll *a* concentration, (**D**) percentage of chlorophyll contained in cells >20 μm, (**E**) percentage of phaeopigments in relation to total pigments, and (**F**) TEP concentration expressed as Gum Xanthan equivalents.

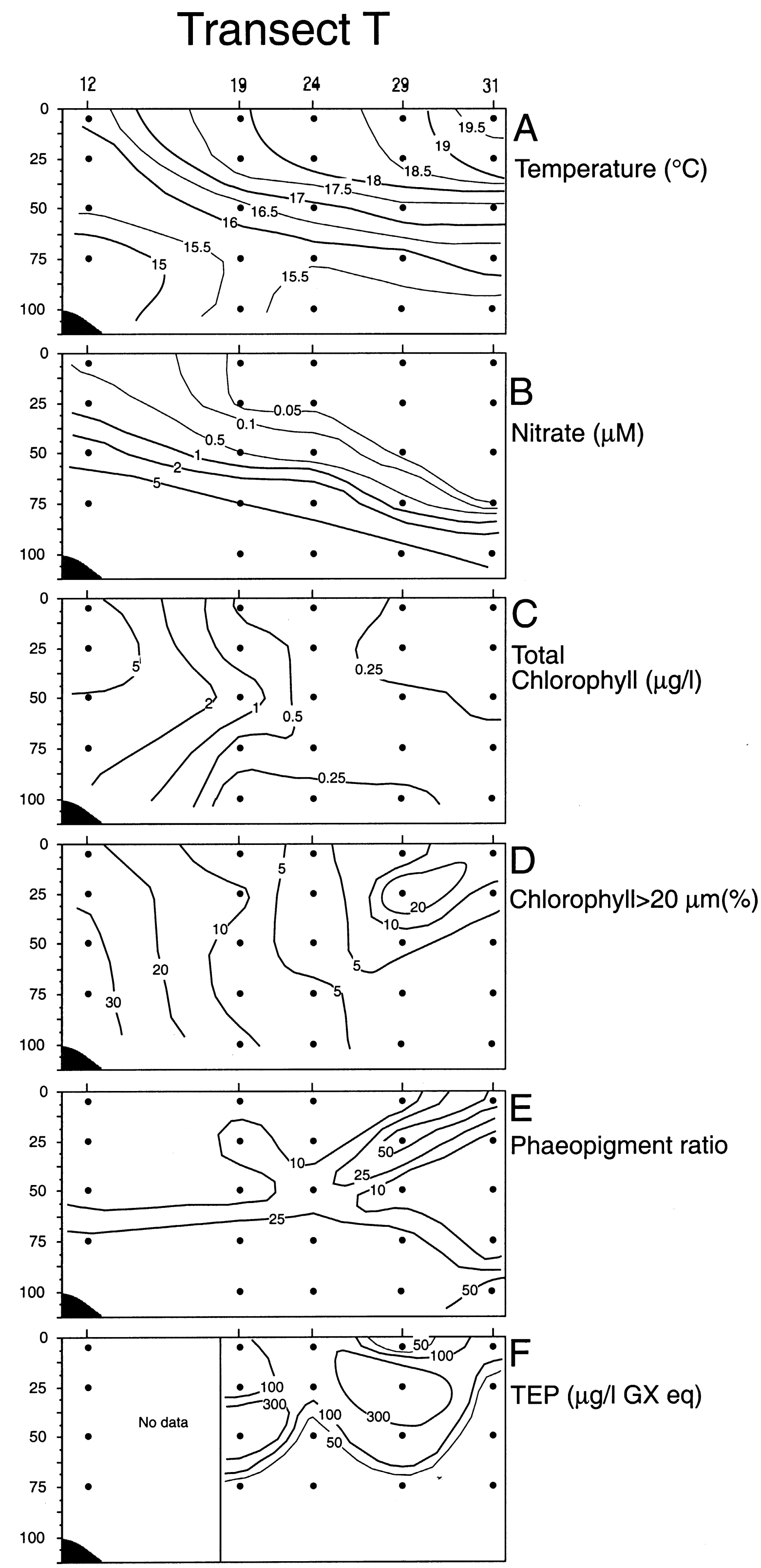

Fig. 6. Results observed in transect T described in the text for (**A**) water temperature, (**B**) nitrate concentration, (**C**) total chlorophyll *a* concentration, (**D**) percentage of chlorophyll contained in cells >20 µm, (**E**) percentage of phaeopigments in relation to total pigments, and (**F**) TEP concentration expressed as Gum Xanthan equivalents.

mixing processes in the area. The final figure shows, therefore, a gradient from rich to poor areas, which combines both distance to the upwelling region and the crossing of the front.

Nutrient concentration (Figure 6B) matches well with the temperature distribution (Figure 6A) and shows a strong decrease toward the warmer side of the front. Total chlorophyll (>0.7 μm) (Figure 6C) reaches values >5 $\mu g\ l^{-1}$ in the surface layers of station 12, placed in the upwelling zone, and then a gradual decrease and slight deepening of maximum values occurs towards the Southeast. Total chlorophyll concentration east of the area is very low, always <0.2 $\mu g\ l^{-1}$ in surface layers. The percentage of chlorophyll contained in particles >20 μm has a gradual decrease from the upwelling zone to the Southeast, with the exception of station 29, where a subsurface maximum is observed. This unexpected maximum, which coincided with very low chlorophyll content (0.05 $\mu g\ l^{-1}$), seems to be non-active as phaeopigment ratio is very high (Figure 6E), so could correspond largely to organic detritus or decaying aggregates.

TEP concentration is low in general throughout the lower part of the water column. There are two maxima placed in different environments. One of them, placed in moderately nutrient-rich water (station 19) is associated with the lower edge of a moderate chlorophyll maximum. Another is placed at the mentioned sample (station 29) with low chlorophyll, very low nutrient concentration, presumably higher size of particles and higher phaeopigment ratio.

DISCUSSION

Water circulation, upwelling and hydrodynamics variability

Temperature distribution and dynamic topography indicate the existence of an anticyclonic circulation following bottom contours running from NW to SE. This circulation pattern would agree with the literature (Stevenson, 1977; Fiúza, 1983; Folkard *et al.*, 1997) and with the surface circulation from regional models of the Canary–Azores basin in the North Atlantic Ocean (Johnson and Stevens, 2000).

The AVHRR SST patterns for the Ictio Alborán-Cádiz 97 cruise (Figure 2A) show a general agreement with the patterns previously proposed in the literature. The SST image presented in Figure 2B shows the surface temperatures recorded during a previous cruise carried out in 1995 (Rubín *et al.*, 1999; Prieto *et al.*, 1999). A comparison of both images reflects variability. The situation corresponding to 30 June 1997 depicts a wide front of cold waters that fills the shelf area between Cape Santa María and the Guadalquivir River. The image corresponding to 1995 also shows a cold tongue of water parallel to the coast, but a warmer inner region appears on the shelf. SST images corresponding to July 1997 some days after the image of Figure 2A show this warmer region as well, which probably indicates a typical summer situation. Stevenson (Stevenson, 1977) had already proposed the existence of a warmer coastal signature originating on the Iberian shelf between the Cape of Santa María and Cádiz, a fact also reported by Folkard *et al.* (Folkard *et al.*, 1997). This coastal warm band was registered *in situ* during our previous cruise (1995) in the zone (Prieto *et al.*, 1999; Rubín *et al.*, 1999), and was especially clear surrounding Cádiz and the Guadalquivir River mouth. The presence of a surface counter current close to the coast in a SE–NW direction relating to this latter situation was suggested by Stevenson (Stevenson, 1977). It has also been proposed by Fiúza (Fiúza, 1983) for the whole Gulf as a situation that would appear during the upwelling spin-down periods. In the same paper, Fiúza reported that these warm waters even reach Cape St Vincent turning clockwise, although a tongue of upwelled waters still remains offshore. In fact, in previous reports (Rubín *et al.*, 1997a; 1999), surface waters did not present such clear signatures of either upwelling or anticyclonic circulation. Intermediate layers, however, had the same behaviour as observed in the 1997 cruise, the topography of 15°C isotherms suggesting anticyclonic circulation near the continental slope edge (Rubín *et al.*, 1997a; 1999). This coincidence of the subsurface circulation with the edge of the continental slope would corroborate the notion that anticyclonic circulation in this area seems to be a permanent feature in summer time.

Data obtained during this cruise also supports an anticyclonic circulation scheme, but some questions about short term or seasonal variability of circulation patterns are still open. Álvarez *et al.* (Álvarez *et al.*, 1999) analysed a one year time series of surface currents taken at a permanent monitoring station near station 24 of our survey (see Figure 1) under the Puertos del Estado Project RAYO (Red de Alerta Y Observación). They present statistical results showing a clearly prevailing southeastwardly current at this site, in agreement with the previous descriptions of an anticyclonic circulation. Nevertheless, a seasonal analysis showed that currents flow in the opposite direction during the period December–February, which could indicate an inversion of the surface circulation pattern during winter.

At shorter time scales, winds have influence on the mean circulation. Folkard *et al.* (Folkard *et al.*, 1997), using SST images and a statistical analysis, point out a coupling between the surface thermal pattern and the wind field. This has been observed especially during the summer, when thermal contrast facilitates the use of this technique to identify surface structures. Westerlies will cause upwelling along the Iberian coast, enhancing the cold surface signature near Cape St Vincent. This situation would probably produce the new upwelling area in the coast east of Cape Santa María, whose orientation makes its downwind area particularly suitable for upwelling. Figure 2A illustrates this phenomenon. Westerlies were blowing the week before 30 June 1997 and were still blowing at the time of the image. A strong upwelling signature east of the Cape and a cold filament extending southeast, whose source seems to be this area, are quite visible. Some days later (graphics not shown) the cold signature was still visible, but became weaker and a warmer coastal area appeared, perhaps due to a change in wind pattern, leading to a situation similar to that observed in the previous 1995 cruise (Figure 2B); (Prieto *et al.*, 1999). During the 1995 cruise, a westerly was also the dominant wind in the area, but an analysis of the differences in persistence and intensity of the wind is needed. Vargas (personal communication), studying seven years of weekly composite SST images of the area by means of empirical orthogonal functions analysis, found a good correlation between this upwelling and the wind field. The upwelling event in Santa María could not be a permanent summer situation in the area, but may be largely dependent on short-scale wind patterns. Therefore, the discussed variability in hydrodynamics patterns in the area leads to the need to interpret our results as only one of the possible states. The need to study the physical phenomena in the Gulf in variable seasonal and meteorological situations must also be emphasized.

Regardless of the time variability of the local upwelling events and circulation pattern near Cape Santa María, the upwelling and circulation situation at the time of the cruise seems to organize the spatial distribution of the biological variables. During our 1997 cruise the situation seemed to be an upwelling pulse followed by an enhanced transport along the shelf edge in the upper surface layer. We will use this conceptual model of a conveyor structure where biological processes will then be spatially organized by a NW–SE flow.

Biological response to hydrodynamics

The biogeochemical variables analysed in this work appear to distribute according to the proposed hydrodynamic model. There is a response from the biological community, firstly by an accumulation of indicators of production, and then by indicators of senescence and degradation following the main direction of the flow.

The more potentially important area of surface water enrichment in the sector observed in the Gulf could be that which is closer to the eastern side of Cape Santa María. Nevertheless, some other coastal enrichment episodes can also be expected. We can consider, however, some indicators of upwelling to enhance the importance of the Santa María upwelling event explaining the general surface physical structure during the cruise. Geostrophic theory does not allow us to calculate vertical velocities. The grid of stations is not appropriate for applying the higher order formulation of quasi-geostrophic theory and vector Q formulation. Nevertheless, other results can be useful in analysing this point. Figure 3C shows high nutrient concentration east of the Cape, coinciding with higher percentages of large phytoplankton cells (Figure 3D), which usually reflects the greater importance of vertical velocities or mixing. The surface nitrate concentrations, which are high near Cape Santa María, are only moderate offshore and become depleted towards SE reaching very low values (<0.05 μM) in the majority of the surface water east of Huelva. This pattern enhances the importance of this upwelling area as the possible main local source of surface nutrients with presumably higher supply rates than other potential coastal sources.

The areas near Cape Trafalgar and the eastern sector in the Strait of Gibraltar also show a high percentage of large cells (Figure 3D) which is related to a high concentration of nitrate in this latter case. These observations agree with conceptual models that indicate enhanced local mixing processes (Vargas *et al.*, 1999; Echevarría *et al.*, 2002). Nevertheless, its influence on the general scheme presented for the duration of the cruise is more difficult to establish, especially in the case of Gibraltar. This is due to a lack of evidence of a suitable surface circulation pattern acting as a link during the cruise, so these zones should be considered as situated downstream.

Phytoplankton biomass analysed through the maxima of total chlorophyll concentration was higher in the same wide general regions where the higher percentages of larger phytoplankters appear. Total chlorophyll, however, reaches its maximum slightly displaced offshore (and southeast), in a direction roughly similar to the main surface currents. This lag can indicate a growth response time of the phytoplankters initially present, closely associated with depletion of surface nutrient concentrations (Figure 3C,E). The smaller size groups gradually come to dominate the phytoplankton assemblage while mixing and nutrient concentration decrease (Figure 3D).

The surface velocity of the upper layer (~0–25 m) is ~12–14 cm s^{-1} (~11 km day^{-1}) at the outer stations of the region (stations 13–15). It is likely that the current speed near the shore is higher, as already mentioned, and might reasonably range from 15 to 20 cm s^{-1}. This gives daily displacements of 13–17 km for the shallower layers (<10 m). We attempt to explain our observations using this estimation as a reference. The phenomena occurring in the upwelling area (stations 11–12) could then influence the surface patterns in station 19, some 40 km away to the

Southeast, with a delay of ~2–4 days. Growth rate of microphytoplankton and larger nanoplankton species are usually of the order 0.5–1.5 day^{-1} under favourable conditions [(see compilation in (Jørgensen *et al.*, 1991)]. This would lead to a potential increase of phytoplankton biomass by a factor ranging from e^1 to e^6 while moving this distance (for ideal, non-limited conditions not usual in the field). Even if we argue that the upwelling event could consist of variable or intermittent pulsing episodes, the cruise (performed only during 2.5 days in the Gulf area and proceeding from NW to SE) can be considered as functionally synoptic. The observed distributions of variables would then be more easily linked, by assuming a steady conveyor belt structure, and a similar upwelling situation immediately before and during the time of the cruise.

The very apparent steep gradient of surface nitrate concentration in the upwelling area near Ayamonte and Faro (Figure 3B) seems to be related to a very rapid response of phytoplankton to the local enrichment. We can assume an enhancement of primary production in this local area that will decrease gradually as nitrate concentration becomes low for surface layers. In fact, observed integrated chlorophyll values decrease gradually seawards and following the direction of the flow from NW to SE. This fact is parallel to the distribution of surface temperature and will include dilution and losses of initial biomass due to several processes (grazing, settling, etc).

The next process in the sequence is the degradation of chlorophyll, which can be explained mainly by phytoplankton decay and grazing activity. The estimation of phaeopigments in the surface layers (down to 50 m) agrees well with the pattern observed for total chlorophyll concentration, but its maxima are, again, slightly displaced offshore and southeast. Although the response by zooplankton populations can be rapid, the highest accumulated amount of phaeopigments would be expected to occur not directly on chlorophyll maxima, but rather slightly displaced downstream. This effect is more apparent if we represent the ratio of phaeopigments to total pigments. The 'older' water masses, where surface nitrate has just been depleted, have higher percentages of the non-active degraded fraction of chlorophyll. This effect is found not only in a coast–open sea direction, but it is also clear following the main direction of the current. Thus, the percentage of these degraded fractions of chlorophyll remains moderately high following the main current direction, but there is a much sharper gradient relative to coastal stations placed off Faro and Huelva (Figure 3F). This sharp gradient is also true for chlorophyll and absolute phaeopigment concentrations. This could indicate a clear preferential transport of organisms and derived material southeastwardly and the existence of an organization of sequential processes in the same direction. As part of this point of view, the area with a higher relative amount of degraded pigments placed off Faro, may include a contribution of degraded pigments from still further west.

Neritic ichthyoplankton distribution is also closely related to the hydrodynamic structure on the continental shelf. The presence of some neritic larvae or eggs is considered as a good tracer of offshore movements of upwelled waters (Rodríguez *et al.*, 1999). Water temperature and wind have been found to be the environmental factors most associated with its spatial distribution (Laprise and Pepin, 1995). In fact, previous reports in the Alborán Sea and Strait of Gibraltar show clear preferential sites for the presence of eggs and larvae of several neritic and oceanic species. These sites are strongly related to surface and intermediate water temperature differences in summer (Rubín *et al.*, 1997b).

Quantitatively, the most important ichthyoplankton neritic species in the area at the time of the summer 1997 cruise was anchovy (*E. encrasicolus*). The shoreward side of the front with intermediate surface temperatures (16.5–19°C) was the site where anchovy egg and larvae abundance were maximal. Some indications of a southeastwardly drift of eggs and larvae have been reported, as well as an increase in the average age of eggs offshore. This has been interpreted as a passive displacement of surface water from their inshore spawning areas (Rubín *et al.*, 1999). The usual range of ages observed in the Gulf is ~10–90 h (eggs) and 2.5–16 days (larvae). The peak spawning period of anchovy in this area occurs from June to August (Millán, 1999), coinciding with the dates of all the July cruises cited. Furthermore, 87% of the total annual catches of anchovy in the Gulf occur from March to July, mainly between Guadiana and Guadalquivir rivers and from 50 to 150 m depth (Millán, 1992). This area (which coincides roughly with that where phaeopigment ratio is higher in our scheme, Figure 3F), is slightly displaced offshore and SE relative to maxima of both total chlorophyll and, hypothetically, smaller zooplankton (Rubín *et al.*, 1999).

Transparent exopolymeric particles

Abundance of TEP has been expressed frequently as the number of particles or total area per volume of water in a defined size range, using image analysis (Passow *et al.*, 1994; Passow and Alldredge, 1995a; Schuster and Herndl, 1995; Long and Azam, 1996; Mari and Kiørboe, 1996; Grossart *et al.*, 1997; Mari and Burd, 1998). This procedure is the clear choice when size structure dynamics is to be investigated. Nevertheless, the comparison in abundance of TEP among different studies is highly dependent on the size range of the TEP studied. As the colorimetric-based method is standardized by calibration of the stained solution and targets whole particles >0.4 μm, this may be considered as a reasonable way of comparing different sample sets in standard cruises. In any case, there is only a little data showing TEP abundance distribution in the field, and data obtained as spectrophotometrically measured total amounts is even scarcer. If we compare our results with this data, the average concentration of TEP is of the same order (~100 μg GXeq l^{-1}) as most of them. These other studies include field data from coastal areas of California (Passow and Alldredge, 1995a), a temperate fjord (East Sound) (Kiørboe *et al.*, 1996), a sub artic fjord (Baisfjord) (Riebesell *et al.*, 1995) and Antarctic waters (Passow *et al.*, 1995). The maximum values in this study (600 μg GXeq l^{-1}) are in the upper range of the literature for field data. This indicates a marked accumulation of particles localized in nutrient-depleted stations with moderate to low chlorophyll values (Figure 3). Hong *et al.* (Hong *et al.*, 1997) measured higher TEP concentration during a bloom dominated by *Phaeocystis antarctica* in the Ross Sea (Antarctica), reaching surface values up to 2800 μg GXeq l^{-1} (308 μg GXeq l^{-1} on average). Their high amounts of TEP could be partially due to the dominant presence of Phaeocystis and the disintegration of its large mucous colonies (Hong *et al.*, 1997).

The ultimate source of TEP is dissolved organic matter (DOM), and hence, we could expect its field distribution to be mainly affected by biomass and production processes. TEP production has been related to the presence and activity of several types of organisms, mainly diatoms (Passow *et al.*, 1994; 1995; Passow and Alldredge, 1995a, Logan *et al.*, 1995; Kiørboe *et al.*, 1996; Mari and Kiørboe, 1996). This is probably the reason why, in the literature, TEP and chlorophyll concentrations are usually positively correlated (Passow and Alldredge, 1995a,b; Hong *et al.*, 1997). This appears to be logical as TEP production can be conceptually linked, in a first step, to the abundance of organisms. Nevertheless, the absence of a direct correlation between TEP and chlorophyll has been found in some systems. This is the case of the Adriatic Sea in oligo- and eutrophic conditions (Schuster and Herndl, 1995) and of Antarctic waters during a bloom dominated by cryptomonads (Passow *et al.*, 1995). In fact, if we take into account the influence of hydrodynamics, we can suppose some displacement of patches closely related to its origin (e.g. phytoplankton) which, in this way, will experience a gradual change of environmental conditions.

The amount of TEP depends not only on phytoplankton abundance. It also depends on nutrient availability, that can influence the rate of production (Obernosterer and Herndl, 1995; Penna *et al.*, 1999) and on turbulence levels (Schuster and Herndl, 1995) that can enhance the aggregation dynamics, decreasing residence times in surface water. Other factors that, *a priori*, could influence the persistence of TEP patches are bacterial degradation and grazing, although their quantitative contribution has not been established so clearly. We will discuss some relevant aspects about these factors to aid the interpretation of results.

Nutrient availability is a factor with a double effect. On the one side, the larger the initial source of nutrients, the larger the carrying capacity of the medium and, hence, the amount of TEP-producing phytoplankton biomass. On the other side, a decrease in growth rates and a higher TEP production per unit cell occurs when nutrients in the surface water become depleted (Corzo *et al.*, 2000). The absolute amount of TEP would be higher for decaying phases of blooms, especially when there is a high nitrate concentration in the initial point, which could be the case for a strong upwelling episode.

Turbulence levels and all the factors that act on aggregation dynamics will determine the residence times of particles in surface water. We may assume a sequence of processes, with a time delay between the appearance of the chlorophyll maxima and those of TEP, and we may associate a gradual change in size structure of TEP. Time of residence and half lives of the increasingly larger TEP will depend on several flocculation steps that will eventually lead to a critical point where settling is very rapid. TEP concentration presumably starts to increase before large amounts of aggregated cells occur. Once the aggregates appear, their residence times could be short as the increase in size is very rapid (Logan *et al.*, 1995) leading to massive sedimentation events.

Therefore, interpretation of the field distribution of TEP should take into account the state of flocculation, even when data on size structure are not available. We can speculate about this state by analysing both percentages of chlorophyll >20 μm and phaeopigment ratio as rough indicators of later phases. Higher simultaneous values of these indexes and TEP concentration could be an indication of older, more aggregated TEP patches.

On this point, we can compare the case of station 29 with the coastal 27 and 28 (Figure 5). Station 29 had subsurface maxima of TEP associated to relatively higher phaeopigment ratio and percentage of larger chlorophyll containing particles. It should be noted that surface coastal maxima, situated in regions of moderate chlorophyll concentration (stations 27 and 28) were related neither to larger sizes nor to more degraded samples. We can speculate that this could be an indication of a different senescence and flocculation phase in the TEP accumulation process, which will be more advanced offshore. On this basis, early phases will be associated to a higher total chlorophyll content, and presumably to smaller sizes of particles. In these latter cases, the rapid massive export to deep waters would not yet have occurred, and total amounts of TEP would then tend to be slightly higher near the surface. Other samples could correspond to late phases, with some aggregates present and decreasing amounts of TEP. This could lead to slightly higher percentages of chlorophyll >20 μm and to a deeper maximum of TEP.

Degradation rate of TEP patches by bacteria is another factor to discuss as it could also affect the persistence of patches. In fact, Mari and Burd (Mari and Burd, 1998) found deviations between data on observed TEP abundance and the predictions of their model. They concluded that the involvement of TEP in processes not taken into account in their simulation such as bacterial degradation and grazing could be the cause of these deviations.

Nevertheless, the role of degradation on the actual abundance of TEP in nutrient depleted surface waters is not so clear. Fajon *et al.* (Fajon *et al.*, 1999) show that massive accumulation of DOM and carbohydrates in the water can be a consequence of a previous enrichment in nutrients that are usually limiting (N, P), followed by a shortage that inhibits bacterial degradation.

Passow *et al.* (Passow *et al.*, 2001) show a positive relationship between bacteria and TEP (although in richer water), excluding degradation of TEP by bacteria as a dominating process in the surface. These authors hypothesize that bacteria can contribute more on production and stabilization of TEP patches than on degradation. Although the action of bacteria could tend to a higher degradation of TEP, the rate of degradation will depend on the (usually high) C/N ratio of TEP and the presence of sufficient inorganic N or alternative N sources. Although the microenvironment of large aggregates could be comparatively enriched in nutrients, it is likely that the persistence and dynamics of these TEP patches in nutrient-depleted surface waters could be mainly controlled by aggregation and sedimentation processes.

Further to grazing, once again it is not so clear exactly what its quantitative contribution is as an agent of TEP disappearance. It has been shown, from field observations, that zooplankters are associated with marine snow in the euphotic zone (Kiørboe, 2000), and that large aggregates could be sites of enhanced regeneration processes. Nevertheless, Prieto *et al.* (Prieto *et al.*, 2001) suggest, from laboratory experiments, that planktonic copepods do not use TEP as an energy source and its effect could be more likely related to changes in the size structure by microscale shear. Analysed together, these observations point towards the need for more studies on the nature of the role of copepods and other invertebrates on the fate of TEP in a microscale framework.

As regards vertical distribution, the maxima of TEP concentration during the cruise usually appeared near the surface. This occurs not only for the shown transects (Figures 4, 5 and 6) but also for all the observed data during the cruise. More precisely, all the maxima appeared above 50 m. Furthermore, most samples with undetectable concentration were from the deeper bottle at 75 m (we did not analyse data from 100 m during the cruise). Hong *et al.* (Hong *et al.*, 1997) found a similar pattern with shallow highest maxima. It would be reasonable to expect larger amounts of TEP in the mixed layer. However, the ratio TEP/Chl can be higher in deeper waters (Hong *et al.*, 1997), often reflecting a lack of chlorophyll. Our results show that the vertical distribution of TEP maxima compared with those of chlorophyll does not follow a direct correlation. The apparent pattern could be expressed as main TEP maxima placed just in downstream positions of the chlorophyll rich areas (Figures 5 and 6), coinciding with moderate chlorophyll concentration (~1 μg l^{-1}). This could be an indication of the final phase of blooms and suggests a faster sinking of cells leaving a transient slight excess of TEP in surface water, as TEP sink slower than cells (Alldredge *et al.*, 1993; Passow and Alldredge, 1995b). Differential settling is a factor that can lead to mismatching the maxima of chlorophyll and TEP in the vertical.

Residence times of TEP in the water column would depend on degradation, possible ingestion, and especially sinking, which is highly enhanced by aggregation. In fact, mass flocculation and sedimentation of diatom blooms seem to be mainly controlled by TEP concentration (Logan *et al.*, 1995; Mari and Burd, 1998). Therefore, massive TEP accumulation in the mixed layer should only be a transient surface phenomenon, since time of residence is not long. However, successive pulses of production in a preferential area of enrichment could lead to a more or less continuous presence of large amounts of TEP downstream with a resulting pattern strongly linked to hydrodynamics.

The horizontal map distribution shows TEP maxima off Cádiz, in offshore stations near Cape Trafalgar and at the margin of the higher chlorophyll and phaeopigment patches in the westernmost part of the analysed region. These zones would act as a sink for intensive biomass supply from the richer areas. The main sources, if we assume no changes in the previous hydrodynamics situation, can consist of upwelling pulses from Cape Santa María. If we think of these upwelling processes in Cape Santa María as a major source, the patches of TEP would occur displaced in the direction of the main current direction, i.e. offshore and towards the Southeast in terms of the upwelling zone. This area combines the existence of a recent event of production upstream and a poor environment downstream that will lead to large amounts of senescent, nutrient-limited cells. These cells eventually favour massive TEP production, and its own disappearance, mainly by flocculation and sedimentation. We cannot discard as alternative or complementary sources of phytoplankton production the nearby shallow Cape Trafalgar area, which is a rich shallow point with nutrient supply mechanisms (Vargas *et al.*, 1999). There is also a usually rich coastal band near the Guadalquivir mouth and Cádiz coastline. Nevertheless, the Trafalgar area was placed downstream and the coastal rich zone near River Guadalquivir and Cádiz was not apparently connected during our survey.

There is a considerable distance between the possible focus near Santa María and station 29 where the maximum concentration of TEP occurs. Taking the assumptions about current velocity mentioned in a previous section, this distance would imply a hypothetical response time between 5 and 9 days from the initial disturbance. This time will be shorter (some 2–4 days response time) between stations 12 and 19 as they are separated by a shorter distance. The next question would be to examine response time or temporal separation between chlorophyll and TEP maxima in the literature. Usually the highest TEP concentration occurs following a phytoplankton abundance maximum. In the Kattegat (Mari and Kiørboe, 1996) and in Baisfjord (Riebesell *et al.*, 1995) time lags of ~20 days were reported. However, in these cases, only one or no samples were collected in between. Passow *et al.* (Passow *et al.*, 1994) in the Santa Barbara Channel observed a TEP concentration maximum 5 days after that of chlorophyll, using higher-resolution-time sampling. During a several months study in the fresh water system of Lake Constance, highest chlorophyll concentrations appeared ~4–8 days before the TEP maximum (Grossart *et al.*, 1997). Therefore, time resolution of sampling could misrepresent the real lag between both maxima. Laboratory studies show lags of ~1–3 days (Passow and Alldredge, 1995a; Corzo *et al.*, 2000; Prieto, 2000). Therefore, we can accept lags of the order of a few days (1–5 days) making it easy to obtain a positive correlation between TEP and chlorophyll where circulation is not active or in a larger spatial scale. Nevertheless, even that shorter time can lead to the disappearance of a direct spatial correlation between both maxima (TEP and chlorophyll) in the field in mesoscale studies. This would be especially true given a clear current-driven pattern, as is the case for the Northern Gulf of Cádiz.

In the event that different hydrodynamic conditions prevailed in the Gulf, it should not be discarded that the TEP maxima could be related to alternative sources, such as the shallow littoral zone near Guadalquivir or Trafalgar. Whatever the source, a more detailed knowledge of the hydrodynamics in the Gulf will lead to a greater understanding of the coupling between physical and biological processes in the basin. These new schemes would have a potential value for local predictions or regionalization. Therefore, the analysis of hydrodynamic variability can be a recommendable objective for future cruises in the area.

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