ISSN: 0074-0195

Phytoplankton, bacterioplankton and nitrate reductase activity distribution in relation to physical structure in the northern Alborán Sea and Gulf of Cadiz (southern Iberian Peninsula)

L. Prieto, C. M. García, A. Corzo, J. Ruiz Segura and F. Echevarría

Departamento de Biología Animal, Vegetal y Ecología. Facultad de Ciencias del Mar. Universidad de Cádiz. Apdo. 40. 11510 Puerto Real (Cádiz), Spain

Received October 1997. Accepted February 1998.

ABSTRACT

The IctioAlborán-Cadiz 95 cruise (July 1995) covered the northwest sector of the Alborán Sea, the Straits of Gibraltar and the Gulf of Cadiz. We present and discuss the distribution of phyto- and bacterioplankton abundance, nitrate concentration and nitrate reductase (NR) activity according to circulation patterns described previously in the literature. The water-column integrated values of chlorophyll-*a* in the Alborán Sea were higher and more variable (12 to 318 mg m^{-2}) than in the Gulf of Cadiz (3 to 49 mg m^{-2}). This reflects the higher dynamism of the Alborán sector, related to the existence of characteristic mesoscale physical structures. The plankton (2-80 μm equivalent spherical diameter) in the upwelling region of the Alborán Sea had a biovolume 30 times higher than in the nutrient-poorer water of the Gulf of Cadiz. Large organisms were abundant and dominated the size spectrum of one coastal station in the Alborán zone, whereas the slope of the size spectrum became more negative at the Gulf of Cadiz station, as a consequence of the dominance of small cells. Bacterial abundance maxima ($> 3 \times 10^6$ bact ml^{-1}) also occurred in the upwelling region. We found relatively high nitrate and chlorophyll *a* concentrations in Cape Trafalgar's cold surface waters, probably due to the interaction between topography and strong tidal currents. The spatial pattern of the NR activity is discussed according to chlorophyll *a*, nitrate and bacteria distributions. The existence of high NR activity but low chlorophyll *a* and bacterial abundance suggests that this could be related with dissimilatory activity in large-sized particles.

Key words: Phytoplankton, bacterioplankton, nitrate reductase activity, Straits of Gibraltar, Alborán Sea, Gulf of Cadiz.

RESUMEN

Distribución de fitoplancton, bacterioplancton y actividad nitrato reductasa en relación con la estructura física en la zona norte del mar de Alborán y golfo de Cádiz (sur de la península Ibérica)

La campaña IctioAlborán-Cádiz 95 (julio de 1995) cubrió el sector noroeste del mar de Alborán, estrecho de Gibraltar y golfo de Cádiz. En este trabajo se presentan y discuten las distribuciones de abundancia de fitoplancton y bacterioplancton, concentración de nitrato y actividad nitrato reductasa (NR) de acuerdo con los patrones de circulación descritos en la bibliografía.

Los valores de clorofila a *integrados en la columna de agua en Alborán fueron mayores y más variables (12 a 318 mg/m^2) que en el golfo de Cádiz (3 a 49 mg/m^2). Esto refleja el mayor dinamismo de la zona de Alborán, relacionado con la existencia de estructuras físicas características a mesoescala. El análisis de la comunidad nano-microplanctónica (2-80 μm, diametro esférico equivalente) de la región de afloramiento del* *mar de Alborán mostró un biovolumen 30 veces mayor que el de aguas más pobres en nutrientes del golfo de Cádiz. Por otro lado, el espectro de tamaños en una estación costera de Alborán está dominado por organismos planctónicos grandes, mientras que la pendiente del espectro de tamaño se hace más negativa en una estación del golfo de Cádiz, como consecuencia de la mayor abundancia de plancton de pequeño tamaño. En la región de afloramiento se dieron también máximos de abundancia bacteriana (> 3×10^6 bact ml^{-1}). Se han encontrado valores relativamente altos de nitrato y clorofila* a *en las frías aguas superficiales cercanas al cabo de Trafalgar, lo que se debe, probablemente, a la interacción entre topografía y fuertes corrientes mareales. Se discute el patrón espacial de la actividad NR en relación con las distribuciones de clorofila* a*, nitrato y bacterias. En muestras con valores elevados de actividad NR pero bajos de clorofila y abundancia de bacterias, se sugiere que esta actividad se relaciona con actividad disimilatoria en agregados de gran tamaño.*

Palabras clave: *Fitoplancton, bacterioplancton, actividad nitrato reductasa, estrecho de Gibraltar, mar de Alborán, golfo de Cádiz.*

INTRODUCTION

The exchange between Mediterranean and Atlantic waters in the region of the Straits of Gibraltar determines the formation of several characteristic mesoscale physical structures in the water. Therefore, this region has aroused a high level of interest among investigators exploring the connections between hydrodynamic and biological processes (Gil, 1985; Kinder and Parrilla, 1987; Gil and Gomis, 1994; Bormans, Garret and Thompson, 1986; Minas *et al.*, 1991).

The physical oceanographic features of the Alborán Sea have been described by Lacombe (1971), Lanoix (1974), and Kinder and Parrilla (1987), among others. The northwestern Alborán sector is characterised by the existence of a well defined spatial organisation, from coastal upwelling areas near Estepona and Marbella to oligotrophic waters southward, as the permanent anticyclonic gyre is approached (Minas, Coste and Minas, 1987). The upwelling episodes are enhanced in the zone coinciding with the incidence of westerly winds. This region has a narrow continental shelf. In contrast, the Gulf of Cadiz area has a wider shelf, and there are no coastal upwelling bands connected to the Straits' circulation, as in the Alborán case. However, the characteristics of this Atlantic sector remain largely unknown, especially their biological variables. A survey of the literature shows few studies of the hydrology and currents on the shelf in the Gulf of Cadiz (Stevenson, 1977; Bernal, 1987; Villar, 1996). These studies mention a general southeasterly current near the coast, over which a tidal current flows in the same direction during the ebb-tide and in an opposite direction (i.e. northwest) during the flood-tide.

Physical processes related to biological variables have been studied more intensely in the Alborán zone, where a marked gradient from rich coastal upwelling areas on the Estepona and Marbella coast to oligotrophic waters in the southwest gyre has constituted the framework for a number of studies (Rodríguez, García and Rodríguez, 1982; Cabanas, Cortés and García, 1984; Cortés, Gil and García, 1984; Lohrenz *et al.,* 1988; Packard *et al.*, 1988; Delgado, 1990; Morel and André, 1991; Rubín *et al.*, 1992; Rodríguez *et al.*, in press). The Gulf of Cadiz area, however, has been scarcely studied and the relationship between the physical framework and the distribution of biological variables is not well known. Indeed, our general aim was to examine the patterns of phytoplankton biomass and plankton composition in relation to the general hydrography of the Gulf of Cadiz and the Alborán Sea, mainly related to wind-induced upwelling. Another objective was the measurement of nitrate-reductase (NR) activity as an indicator of plankton metabolism in the different zones. Nitrate concentration plays a major role in the relationship between physical and biological variables in the ocean. The methods presently used to estimate nitrate incorporation by phytoplankton are largely based on incubation techniques with labelled nitrogen, which have some associated problems that have been addressed by Berges and Harrison (1995a,b). One alternative technique is the estimation of enzymatic activities. Although the study of NR activity had previously been used in oceanography by employing *in vitro* assays (e.g. Eppley and Coastworth, 1968; Eppley, Coastworth and Solorzano, 1969; Blasco *et al.,* 1984), the present paper is one of the few marine field studies which has involved an *in situ* assay of NR activity

(Corzo and Niell, 1991). The term *in situ* refers to the fact that the enzymatic activity is being assayed at its cellular site.

MATERIALS AND METHODS

Spatio-temporal setting

The 'IctioAlborán-Cadiz 95' oceanographic cruise was carried out in July 1995 aboard the R/V *Francisco de Paula Navarro*. The sampling area covered the northwestern sector of the Alborán Sea, the Straits of Gibraltar and the Gulf of Cadiz, with 58 sampling stations (figure 1). The study started on 5 July in the eastern part of the region (Station 5) and ended in the western part on 17 July (Station 55).

Wind data

Data on wind speed and frequency the zone during the cruise were obtained from local meteorological centres on the coast from Ayamonte to Algarrobo (figure 2). These centres continually record 10 measurements per hour. Wind data were processed and collated in graphs built on each sector from data recorded up to 6 days before the ship entered to sample in the sector, thus taking into account recent past records of the wind.

Physical, chemical and biological variables sampling and analyses

Vertical profiles of conductivity and temperature down to a depth of 300 m at each sample station were made by using an InterOceans Systems S4 CTD. Water samples were collected at each station with Niskin bottles at five discrete depths (10, 25, 50, 75 and 100 m). Nitrate concentrations were determined following the Trèguer and Le Corre (1975) technique (using an autoanalyser). Chlorophyll-*a* concentrations, as well as NR activities, were measured using particulate material (> 0.7 µm) retained in Whatman GF/F filters. Chlorophyll-*a* was measured by fluorometrical method on 90 % acetone extracts (Holm-Hansen *et al.,* 1965).

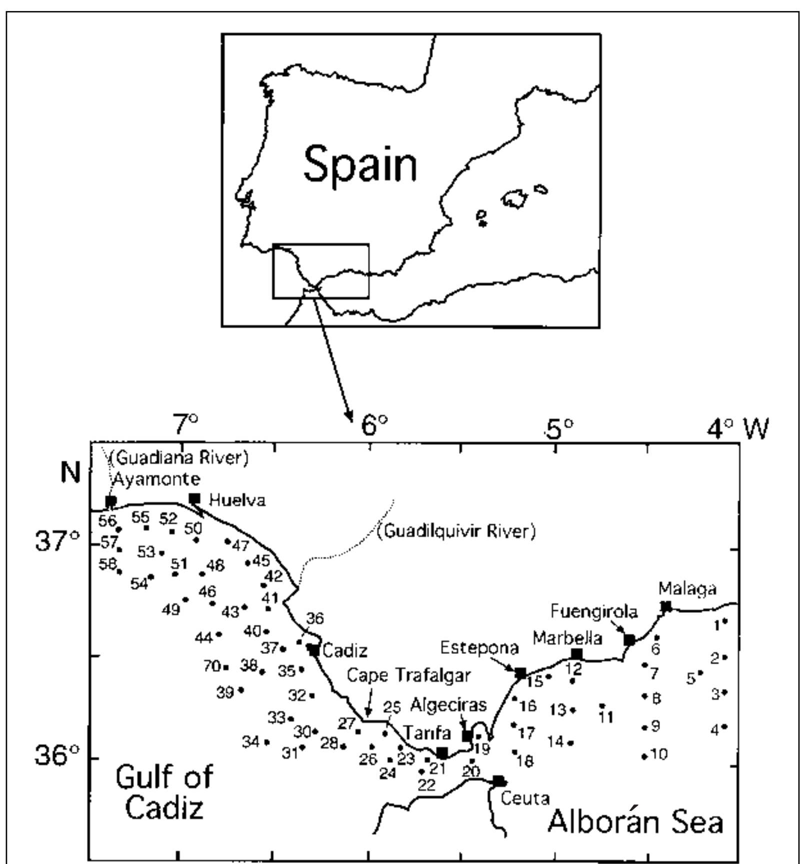

Figure 1. Location of the sampling area and distribution of stations

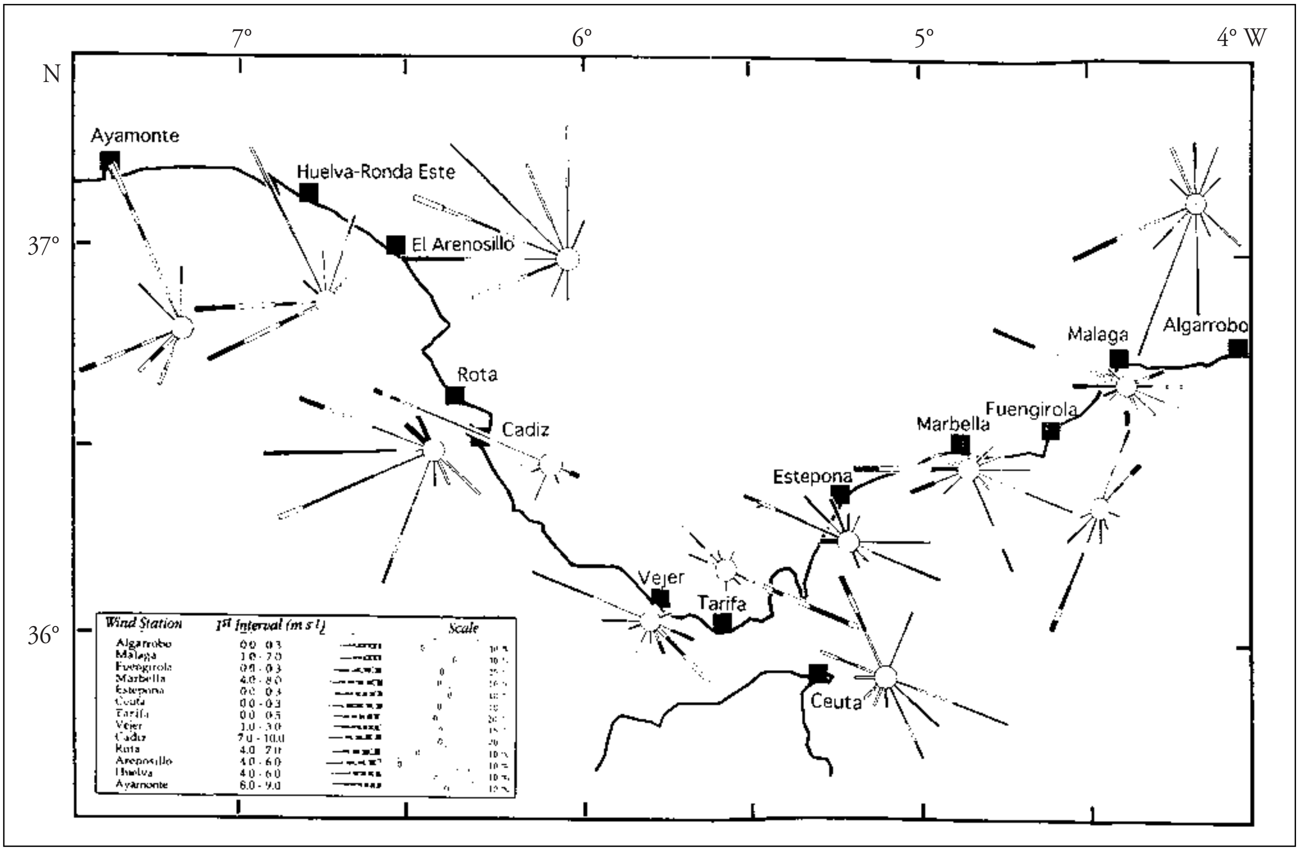

Figure 2. Wind speed (m s^{-1}) and direction obtained from coastal meteorological stations, whose names and positions are marked on the coast. Each graph contains data from the last 6 days before the ship entered and sampled the sector nearest to each meteorological station

NR-activity samples were determined by an *in situ* assay (Corzo and Niell, 1991) adapted to phytoplanktonic communities (Gordillo, 1994). Samples were introduced into vials and brought to the laboratory in liquid nitrogen. Once in the laboratory, the vials were thawed by immersion in a water bath (2 min, 30 °C) and immediately the filters were introduced into test tubes containing 6 ml of the assay medium (30 mM KNO_3, 5 % propanol, 0.5 mM Na-EDTA, 1.5 mM NADH, 0.1 mol phosphate buffer, pH 8), previously flushed with N_2 for 2 min. As soon as the filters were introduced, the test tubes were flushed with N_2 for an additional 2 min and then were immediately closed and incubated in the dark for 30 min (30 °C). At the end of that time, 1 ml of assay medium was taken from the tubes. NADH was removed from samples by adding 0.5 ml of an activated charcoal suspension (0.83 % w/v). After strong stirring, the samples were centrifuged (4 500 rpm, 15 min), and 1 ml of the supernatant was taken and assayed for NO_2^- (Snell and Snell, 1949).

The abundance of pico-, nano- and microplankton was estimated by inverted and epifluorescence microscopy. Bacterial abundance was estimated by epifluorescence analyses on 1-5 ml of a previously preserved (formaline 4 %) sample that was stained with DAPI (Porter and Feig, 1980) and filtered through 0.2 Nuclepore filters. Filters were then examined at ×1 000 by vertical illumination fluorescence microscopy using a Leica 103-12V-100W epifluorescence system (100 W HBO lamp) and Leica A (BP340-380 excitation filter, RKP400 beam splitter and LP430 barrier filter) and Leica I3 (BP450-490 excitation filter, RKP510 beam splitter and LP520 barrier filter) filter sets. Nano- and microplankton abundance was assessed by inverted microscopy, on previously preserved (Lugol) samples that were allowed to settle in chambers (3 h per cm height) and then analysed following the Utermöhl method (1958). Cells were counted and measured at ×10, ×25, ×40 and ×100 (oil immersion) on an inverted microscope assisted by a VIDS V (Analytical Measuring Systems) video-interactive image analyser. Biovolume for each individual organism was estimated as a revolution volume according to a ellipsoidal or cylindrical shape (Rodríguez *et al.*, 1987; García *et al.*, 1994). Colonial organisms were considered and measured as single particles or biomass units (Lewis, 1976). Using this technique, we studied the phytoplankton ranging in size from 2 to 80 µm of equivalent spherical diameter (ESD). The present paper reports the biomass spectrum at a depth of 25 m for two stations representative of the main areas studied.

RESULTS

Hydrography and nutrients

The distribution of surface temperatures (depth: 5 m) generally showed higher values in the Gulf of Cadiz than in the Alborán Sea (figure 3). Surface temperatures show their maxima near Cadiz (> 22 °C), whereas the lowest surface temperatures (17 °C) were found at Alborán coastal stations. Surface temperatures in the northwest Alborán show a clear gradient from these minima at the coastal stations (Marbella and Malaga) to offshore waters, where temperature at a depth of 5 m increased to approximately 20 °C at stations 9, 10 and 14 (figure 3).

The prevailing southwesterly wind recorded during the sampling period near Cadiz could partially explain the accumulation of warm surface waters on the coast of the Gulf of Cadiz, whereas the westerly winds' dominance in the northwest Alborán region facilitates the upwelling pattern related to the inflow of Atlantic water into the Mediterranean,

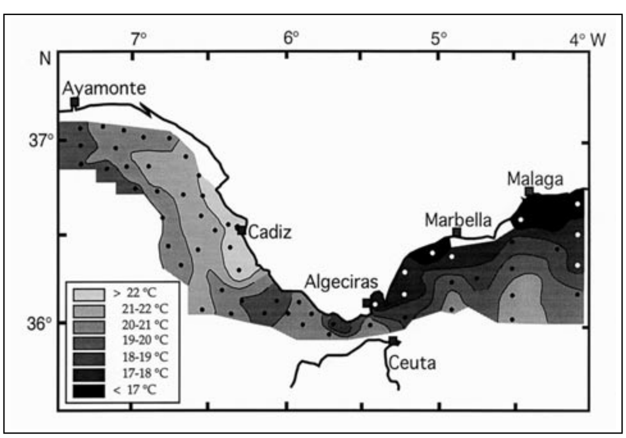

Figure 3. Water temperature (°C) at depth of 5 m

and which is indicated by the lower surface temperature values on the west coast (figures 2 and 3).

The existence of that upwelling area is also apparent when the distribution of nitrate concentration at the surface layer (average in the first 25 m) is examined (figure 4). Thus, in the north Alborán Sea, nitrate concentrations were 2-3 µM NO_3^-, and the values become especially low at the farthest stations (< 0.1 µM NO_3^-), which then presented values more clearly related to the southwest oligotrophic gyre region. Nitrate concentrations in the Gulf of Cadiz were lower than in the Alborán Sea. Nitrate values were higher at coastal stations (0.1-0.5 µM NO_3^-) that at offshore stations (< 0.1 µM NO_3^-). Some local maxima appeared near the Guadiana River discharge zone near Ayamonte, in front of Cape Trafalgar and near Tarifa, with nitrate values higher than 1 µM NO_3^- (figure 4).

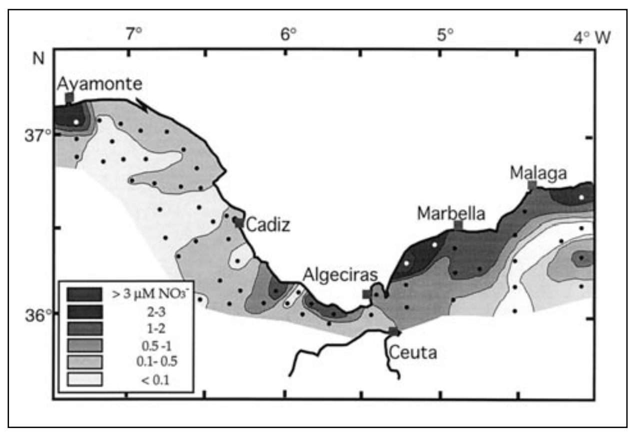

Figure 4. Average concentration of nitrate (µM NO_3^-) between 10 and 25 m

Chlorophyll, phytoplankton and bacterioplankton

The phytoplankton biomass, expressed as chlorophyll-*a* concentration, was higher in the Alborán than in the Gulf of Cadiz sector, with a distribution that is also related to the upwelling structure in the northwest Alborán sector (figures 5a and 5b). Chlorophyll integrated down to 100 m showed high values in this nutrient-rich area (> 100 mg m^{-2}), the maximum (318 mg m^{-2}) appearing at station 12 (figure 5a). Chlorophyll-*a* concentrations were lower (10-40 mg m^{-2}) in the Gulf of Cadiz, where its distribution did not, however, show a clear relationship with that of nitrate, especially when the value at the depth of its maximum is examined.

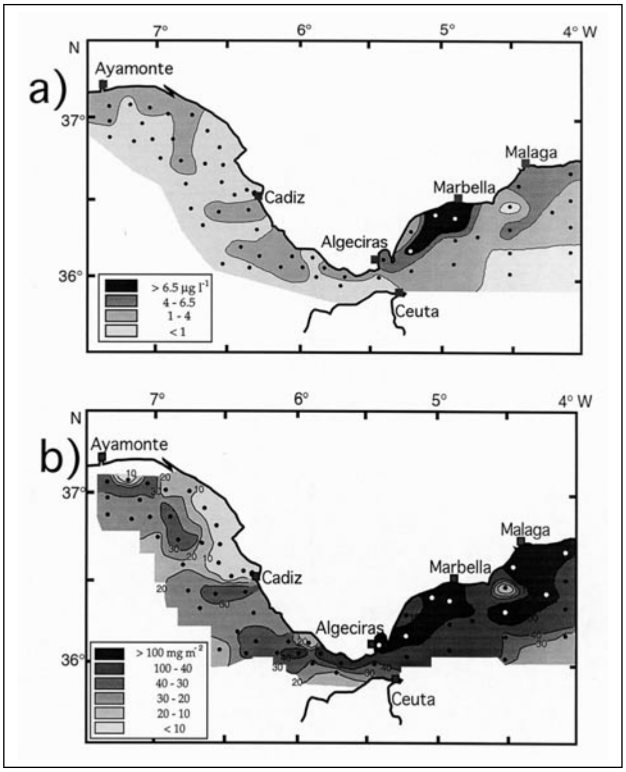

Figure 5. (a): Concentration of chlorophyll (µg l^{-1}) at the depth where its maximum occurs; (b): Chlorophyll concentrations (mg m^{-2}) integrated in the water column to a maximum depth of 100 m, bathymetry permitting

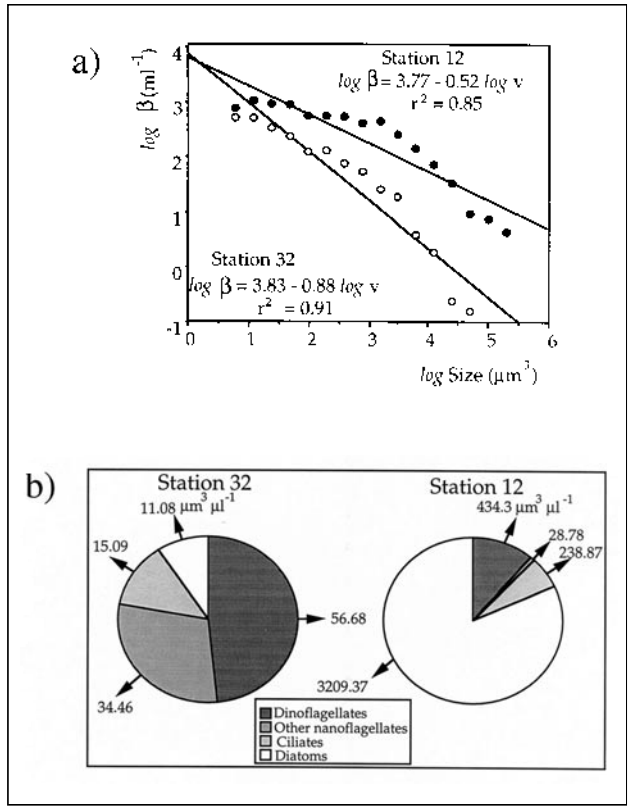

Figure 6. (a): Size-biomass spectrum from station 12 (Alborán Sea) and station 32 (Gulf of Cadiz); ß: normalised biomass; v: individual volume. (b): Biovolume concentration (µm³ µl^{-1}) of the main taxa at both stations (12 and 32)

Differences between the coasts of both sectors, Gulf of Cadiz and northwest Alborán Sea, are also apparent when the planktonic communities (2-80 µm ESD) of representative stations at a depth of 25 m are analysed. Whereas the nutrient-rich station of the Alborán Sea has a size spectrum which indicates that large organisms dominate the community, a characteristic spectrum from the Gulf of Cadiz station has a more negative slope, indicating a lower concentration of large organisms (figure 6a). These differences in the community's size structure are also reflected in both total biomass (expressed as biovolume) and in the taxonomic composition (figure 6b). The planktonic biomass in a station of the upwelling area from northwest Alborán was about 30 times higher than that found in the station of the Gulf of Cadiz.

All of the main taxonomic groups have higher biomasses at the station from the Alborán coast area than at the one from the Gulf of Cadiz; their relative importance changes between both zones, as well. Large centric diatoms (mainly *Rhizosolenia, Chaetoceros, Nitzschia, Hemiaulus, Leptocylindrus, Thalassiosira* and *Bacteriastrum*) clearly dominated the community biomass in the Alborán coast area (3 209.37 µm³ µl^{-1}), whereas dinoflagellates (especially small *Gyrodinium* cells), other small flagellates and ciliates dominated the Gulf of Cadiz community.

Bacterial abundance at the depth nearest to the chlorophyll-*a* subsurface maxima (figure 7) was significantly correlated with chlorophyll concentration ($n = 40$, $r = 0.41$, $p < 0.05$). However, the maximum ($> 3 \times 10^6$ cells ml^{-1}) also appeared on the coastal zone of northwest Alborán, and in general the average bacterial abundance was slightly higher (about $1.5\text{-}1 \times 10^6$ cells ml^{-1}) in the Gulf of Cadiz than in the Alborán Sea (about $0.5\text{-}1 \times 10^6$ cells ml^{-1}). This is due to low bacterial abundance in most of the Alborán sector, especially offshore.

Nitrate reductase activity

The overall NR activities (integrated down to 100 m of the water column or at the depth of the chlorophyll maximum) in the Alborán Sea were

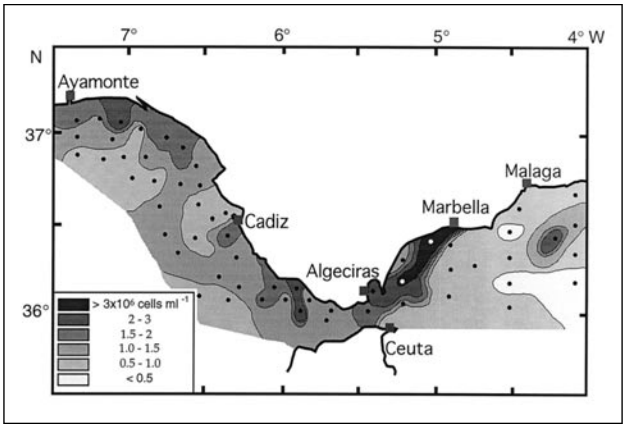

Figure 7. Bacterial abundances ($\times 10^6$ cells ml^{-1}) at the chlorophyll-*a* maximum depth

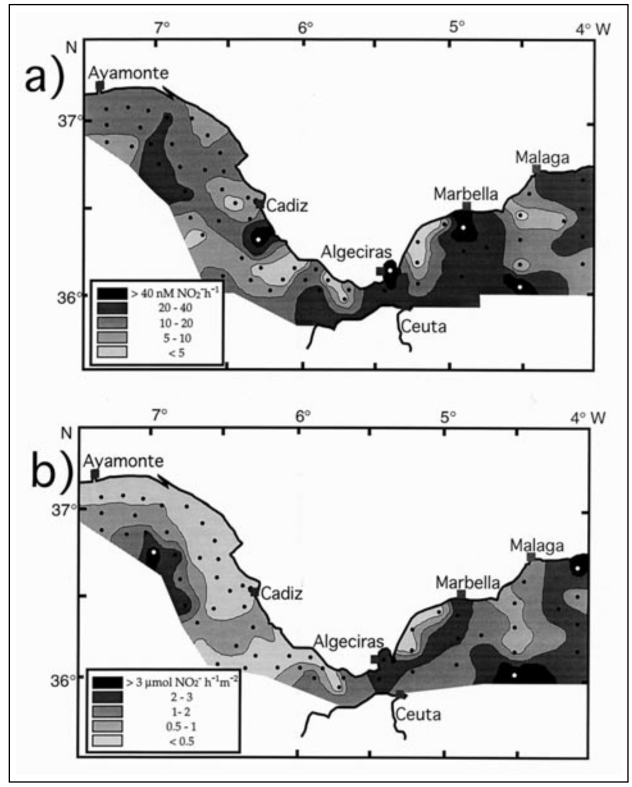

Figure 8. (a): NR activity (µM $NO_2^-h^{-1}$) at the chlorophyll-*a* maximum depth; (b): Integration of the NR activity (µM $NO_2^-h^{-1}m^{-2}$) in the water column to a maximum depth of 100 m, bathymetry permitting

higher than in the Gulf of Cadiz (figure 8a,b). The average range of integrated NR activity values in the Gulf of Cadiz was 0.5-1.0 µmol $NO_2^-h^{-1}m^{-2}$, whereas in the Alborán Sea it was 1-2 µmol $NO_2^-h^{-1}m^{-2}$.

Both distributions of NR activity (water-column integrated or at the chlorophyll maximum) show visible differences when compared with chlorophyll distribution (figure 5). However, the pattern of NR activity integrated down to 100 m presented a significant but weak correlation with integrated chlorophyll ($n = 58$, $r = 0.36$, $p < 0.05$), and was also better correlated with integrated nitrate ($n = 58$, $r = 0.56$, $p < 0.05$). The main differences occur at some stations, especially in offshore waters, where nitrate, chlorophyll and even bacteria abundance remains low, but there is high NR activity (e.g. station 10, figures 8a and 8b).

DISCUSSION

Coupling between biological variables and physical structures

The existence of meso- and macroscale eddies (Tintoré *et al.*, 1991; Gil and Gomis, 1994) and fronts associated with the contact of different water masses in the Alborán Sea, determines both the circulation and the distribution of ecological variables (biomass, productivity and composition of the planktonic community) in the sector.

The distribution of surface temperatures in the Alborán Sea showed a pattern similar to that found during previous cruises carried out in the same month (Rubín *et al.,* 1992; Gil, 1994; Cano *et al.,* 1995; Rubín *et al.,* 1997). The main feature of these patterns is the presence of lower surface temperatures in the northern area of the Alborán Sea. Nevertheless, although the position of the coastal upwelling areas of northern Alborán almost coincides with that found in July of 1991 and 1994, these episodes were localised at a greater distance from the Spanish coast in July of 1992 and 1993. The difference of surface temperatures between the upwelling zone and the anticyclonic gyre region remain, however, within the same range (4-5 °C). Previous data for the Gulf of Cadiz region were only obtained for the July 1994 cruise. During that cruise, the surface temperatures in the Gulf of Cadiz (Rubín *et al.,* 1997) were very similar to those recorded during IctioAlborán-Cadiz 95. Higher temperatures in the zone near the Bay of Cadiz were also reported during the 1994 cruise. These high temperatures have been related to the heating of the surface waters in that zone due to solar irradiation and to a low water turnover rate. In fact, this area is not very much affected by the shelf's prevailing southeastern current. We found low temperatures (< 19 °C) in the area of Cape Trafalgar, also present in July 1994, and probably due to the topography of the coast (lower depths) and its interaction with strong tidal currents, which facilitates vertical mixing episodes (Vargas *et al.*, 1997). These episodes could also be related to the relatively high nitrate concentration values of the shallower layers (> 1.0 µmol l^{-1} on average in the first 25 m) in the Cape Trafalgar area, which is also one of the zones showing a high level of chlorophyll concentration in the Gulf of Cadiz.

According to the circulation pattern in the Gulf of Cadiz described by Stevenson (1977), there are two currents that follow a southeasterly direction, one near the coast and another on the continental slope (at the limit of our sampling area), and between them there is a counter-current aimed to the northwest. Assuming the existence of such a general circulation pattern during the time of sampling, which would have generated a frontal area, the so-called Huelva Front, we could have expected the presence of waters where nutrient enrichment (and hence higher chlorophyll concentration values) would have been facilitated by the hydrologic structure. This point has not been confirmed by the present results, due to the front's spatial-temporal variability and to the low resolution of the sampling grid. Future cruises aimed at studying this area throughout the seasonal cycle could provide better data on the subject by using a higher resolution grid and recording hydrodynamic measurements.

In the Alborán Sea, our findings regarding the pattern of distribution of nitrate concentrations are consistent with those reported in the literature, with high values in the north of the basin (Rubín *et al.,* 1992; Rodríguez *et al.,* 1994; Cano *et al.,* 1995; Rubín *et al.,* 1997). Nitrate values in July 1995 were similar to those presented in other studies (Rubín *et al.,* 1992; Rodríguez *et al.,* 1994), but higher compared with those of the two previous years (July 1993 and 1994). Although the wind data framework was not presented for previous years, the differences among cruises, as far as nitrate concentrations and other features in the northern area of the Alborán Sea are concerned, could be related to an enhancement of the upwelling event due to the wind effect. In fact, the wind characteristics in 1995 were favourable for such enhancement.

Likewise, the distribution of chlorophyll found in the northwest Alborán Sea sector during IctioAlborán-Cadiz 95 is similar to those reported in the literature, but with higher values compared to other references, either from summer samplings (Cortés, Gil and García, 1984; Rubín *et al.,* 1992; Rodríguez *et al.,* 1994; Rodríguez *et al.,* 1997) or from other seasons (Cabanas, Cortés and Gracía, 1984; García, Rubín and Rodríguez, 1988; Delgado, 1990; Minas *et al.,* 1991; Morel and André, 1991). A possible explanation of the higher chlorophyll values could be the one mentioned above, i.e. a wind pattern that favours upwelling. One of the sampling sites near the Fuengirola coast, station 7, presented very low values for all biological descriptors (chlorophyll, bacterial abundance, NR activity) compared with adjacent areas (see figures 5, 7 and 8). Since station 7 was near the upwelling area and completely surrounded by waters with high chlorophyll values, we expected to find high values of both photosynthetic pigment concentrations and NR activity, but this was not the case. Nevertheless, the nitrate concentration at this station was high (figure 4), especially at 50 m, the depth of the chlorophyll maximum (Prieto, 1997). The explanation for this singularity is not clear, since the hydrologic data did not show any special characteristic associated with this anomaly. It is, however, possible that the high levels of nitrate could be due to the fact that this nutrient had not yet been consumed. Then, it could be associated with a rapid input of nitrate related to hydrologic phenomena on a lesser scale, which are frequent in the area (Tintoré *et al.*, 1991; Gil and Gomis, 1994), but whose presence could not be assessed adequately due to the low resolution of the sampling.

There are few references in the literature to chlorophyll distribution in the Gulf of Cadiz, and they refer only to restricted local areas, such as Cadiz Bay (Establier, 1966, 1969, 1970a,b, 1975; Establier and Lubián, 1983; Establier, Lubián and Blasco, 1986; Establier, Blasco and Lubian, 1987), the Huelva estuary (Cortés and Varela, 1992) and the Huelva coast (López, 1993). Our results show that chlorophyll distribution does not follow a clear pattern, although a high phytoplanktonic biomass (> 1.5 µg l^{-1}) found in the area of Cape Trafalgar is probably related to the vertical mixing and nutrient-enrichment mentioned above.

The analysis of the size structure and taxonomic composition of the planktonic community at the selected stations also shows a considerable difference between the nutrient-rich one, typical of the northern coast of the Alborán Sea, and the predominantly oligotrophic station of the Gulf of Cadiz. When the differences in nutrient content and water turbulence are not very marked, we cannot automatically expect a predominance of larger phytoplankters, but an even more negative slope of the size-abundance spectrum (Ruiz, García and Rodríguez, 1996). In this case, when we compare an upwelling station, e.g. at northern Alborán, with an oligotrophic station, the classical paradigm proposed by Malone (1980) of large organisms predominating in turbulent and nutrient rich areas prevails. The taxonomic composition of the northern Alborán sample corresponds to an assemblage typical of coastal upwelling areas, with a dominance of large diatoms.

NR-activity distribution

The results obtained are not as tightly related to chlorophyll abundance as expected, probably due to the dual assimilatory and dissimilatory role of NR activity in the sea and the influence of the presence of aggregates with low chlorophyll content but which presumably support intense nitrate consumption processes.

The general distribution of photosynthetic pigment concentrations and NR activities (figures 5 and 8) always showed a higher biomass and NR activity in Alborán than in the Gulf of Cadiz. In the upwelling influence area of the Alborán Sea, the NR activity values were high, denoting an increase in the relative importance of new production, which is related with nitrate incorporation by the phytoplankton (Dugdale and Goering, 1967) into the total production. In the Gulf of Cadiz, however, the zones with higher NR activity roughly coincide with those of lower nitrate concentration and lower chlorophyll. This could suggest a predominant or at least considerable dissimilatory role in this area, associated with detrital particles, which can have anaerobic sites (Goldman, 1984; Alldredge and Cohen, 1987). If this were the case, it would indicate a serious handicap to using this variable alone as an indicator of new production in the ocean.

In addition, in some cases we found very high absolute values of NR activity when both chlorophyll-*a* values and bacteria abundance were low. A possible hypothesis to explain these high NR activities would be an important protagonism of relatively large-sized detrital particles with low content of chlorophyll-*a* but with a possible high bacterial activity. In fact, bacteria is another fraction to which the NR activity could be attributed (Kirchman, Keil and Wheeler, 1990; Cochlan, Harrison and Denman, 1991, Dickson and Wheeler, 1995). On the other hand, Jones (1979) showed, using differential filtration, how NR activity was associated with large-sized particles. A preliminary study has been conducted on abundance and size of particulate material, in samples with low chlorophyll-*a* and bacterial abundance but high NR activity, compared with samples having a low content of chlorophyll-*a* and bacterial abundance but also low NR activity (Prieto, 1997). This analysis supported our hypothesis, because samples from both the Alborán Sea and the Gulf of Cadiz had either lower number of particles or an average lower individual volume of aggregates when NR activity was low. On the contrary, the samples that exhibited low bacterial abundance and chlorophyll values but a high NR activity showed either a much higher number of particles (Alborán) or a much higher individual particle volume (Gulf of Cadiz). This finding suggests a switch from a predominant assimilatory role of NR in rich waters to a predominant dissimilatory role in the poor marginal waters (e.g. near the anticyclonic gyre). Further studies, however, ought to be carried out to confirm this hypothesis.

ACKNOWLEDGMENTS

Our thanks to Juan Pérez de Rubín from the Instituto Español de Oceanografía (IEO), who invited the authors to participate in the IctioAlborán-Cadiz 95 oceanographic cruise, which was made possible by a co-operative agreement between the University of Cadiz and the IEO. J. Escánez and J. C. Alonso (IEO) performed the nitrate concentration analyses. This research has been supported by the CICYT (CYTMAR) project MAR95-1950-CO2-02 and the MAST European Project MAS3-CT96-0060.

REFERENCES

Alldredge, A. L. and Y. Cohen. 1987. Can microscale patches persist in the sea? Microelectrode study of marine snow, fecal pellets. *Science* 235: 689-691.

Berges, J. A. and P. J. Harrison. 1995a. Nitrate reductase activity quantitatively predicts the rate of nitrate incorporation under steady state light limitation: A revised assay and characterization of the enzyme in three species of marine phytoplankton. *Limnol. Oceanogr.* 40 (1): 82-93.

Berges, J. A. and P. J. Harrison. 1995b. Relationships between nitrate reductase activity and rates of growth and nitrate incorporation under steady-state light or nitrate limitation in the marine diatom *Thalassiosira pseudonana* (Bacillariophyceae). *J. Phycol.* 31: 85-95.

Bernal, E. 1987. Teledetección de las estructuras de turbidez en el golfo de Cádiz y el mar de Alborán. In: *III Seminario de Química Marina.* (January 28-29, 1986. Cadiz, Spain). Servicio de Publicaciones, Universidad de Cádiz: 137-148. Cadiz.

Blasco, D., J. J. MacIsaac, T. T. Packard and R. C. Dugdale. 1984. Relationship between nitrate reductase and nitrate uptake of phytoplankton in the Peru upwelling region. *Limnol. Oceanogr.* 29 (2): 275-286.

Bormans, M., C. Garret and K. R. Thompson. 1986. Seasonal variability of the surface inflow through the Strait of Gibraltar. *Oceanol. Acta* 9 (4): 403-414.

Cabanas J. M., D. Cortés and C. García. 1984. First results of the oceanographic cruise ¿Dónde Vá? in the Alborán Sea: nutrients and chlorophylls. *Informes Técnicos del Instituto Español de Oceanografía* 24: 214-226.

Cano, N., J. García Lafuente, A. Hernández-Guerra, J. M. Blanco and J. Escánez. 1995. Hidrología del mar de Alborán durante la campaña de julio de 1993. *Publicaciones Especiales. Instituto Español de Oceanografía* 23: 11-35.

Cochlan, W. P., P. J. Harrison and K. L. Denman. 1991. Diel periodicity of nitrogen uptake by marine phytoplankton in nitrate-rich environments. *Limnol. Oceanogr.* 36: 1689-1700.

Cortés, D., J. Gil and A. García. 1984. General distribution of chlorophyll, temperature and salinity in the Northwestern sector of the Alborán Sea (August, 1982). *Communication from the XXIX Congre-Assemblee pleniere CIESM*: 11-19. Lucerne.

Cortés, M. D. and M. Varela. 1992. Variación espacio-temporal de parámetros físico-químicos y biológicos en la ría de Huelva y área e influencia, en el periodo 1987-1991. *Informes Técnicos. Instituto Español de Oceanografía* 138: 1-103.

Corzo, A. and F. X. Niell. 1991. Determination of nitrate reductase activity in *Ulva rigida* (C. Agardh) by the *in situ* method. *J. Exp. Mar. Biol. Ecol.* 146: 181-191.

Delgado, M. 1990. Phytoplankton distribution along the Spanish coast of the Alborán Sea. *Sci. Mar.* 54 (2): 169-178.

Dickson, M. L. and P. A. Wheeler. 1995. Nitrate uptake rates in a coastal upwelling regime: a comparison of PN-specific, absolute, and Chl a-specific rates. *Limnol. Oceanogr.* 40 (3): 533-543.

Dugdale, R. C. and J. J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol. Oceanogr.* 12: 196-206.

Eppley, R. W. and J. L. Coastworth. 1968. Nitrate and nitrite uptake by *Ditylum brightwelli*: kinetics and mechanisms. *J. Phycol.* 4: 151-156.

Eppley, R. W., J. L. Coastworth and L. Solorzano. 1969. Studies of nitrate reductase in marine phytoplankton. *Limnol. Oceanogr.* 14: 194-205.

Establier, R. 1966. Variación estacional de la composición química del ostión, *Crassostrea angulata*, Lmk. y su relación con las variables hidrológicas y del fitoplancton. *Inv. Pesq.* 30: 501-528.

Establier, R. 1969. Fitoplancton e hidrografía de la Bahía de Cádiz de abril de 1965 a diciembre de 1967. *Inv. Pesq.* 33 (1): 97-118.

Establier, R. 1970a. Fitoplancton e hidrografía de la Bahía de Cádiz en el año 1967. *Inv. Pesq.* 34 (2): 215-228.

Establier, R. 1970b. Fitoplancton e hidrografía de la Bahía de Cádiz en el año 1968. *Inv. Pesq.* 34 (2): 515-528.

Establier, R. 1975. Fitoplancton e hidrografía de la Bahía de Cádiz de enero de 1970 a diciembre de 1973. *Inv. Pesq.* 39 (1): 225-247.

Establier, R., J. Blasco and L. M. Lubián. 1987. Fitoplancton e hidrografía de la Bahía de Cádiz. Enero de 1984 a diciembre de 1985. *Inv. Pesq.* 51 (4): 501-515.

Establier, R. and L. M. Lubián. 1983. Fitoplancton e hidrografía de la Bahía de Cádiz de enero de 1974 a octubre de 1979. *Inv. Pesq.* 47 (1): 39-59.

Establier, R., L.M. Lubián and J. Blasco. 1986. Fitoplancton e hidrografía de la Bahía de Cádiz (SO España) de marzo de 1980 a diciembre de 1983. *Inv. Pesq.* 50 (1): 69-81.

García, C. M., F. Jiménez-Gómez and J. Rodríguez, (Rapporteurs). B. Bautista, M. Estrada, J. García Braun, J. M. Gasol, F. Gómez Figueiras, F. Guerrero, F. Jiménez Montes, W. K. Li, J. M. López Díaz, G. Santiago and M. Varela. 1994. The size structure and functional composition of ultraplankton and nanoplancton at a frontal station in the Alborán Sea. Working Groups 2 and 3 Report. *Sci. Mar.* 58 (1-2): 43-52.

García, A., J. P. Rubín and J. M. Rodríguez. 1988. La distribución de las áreas de puesta y cría de sardina (*Sardina pilchardus*) en el sector noroccidental costero del mar de Alborán, en marzo de 1982. Complementado con información adicional de parámetros biológicos y físico-químicos. *Informes Técnicos del Instituto Español de Oceanografía* 59: 1-24.

Gil, J. 1985. Consideraciones acerca de un fenómeno de afloramiento de la zona noroccidental del mar de Alborán. *Informes Técnicos del Instituto Español de Oceanografía* 35: 1-11.

Gil, J. 1994. Circulación geostrófica e hidrografía del mar de Alborán en la campaña 'Ictio.Alborán 0792'. *Informes Técnicos. Instituto Español de Oceanografía* 146 (VI): 9-27.

Gil, J. and D. Gomis. 1994. Circulación geostrófica, dinámica de mesoescala y fertilización de los niveles superficiales en el sector norte del Mar de Alborán. Julio 1991. *Boletín. Instituto Español de Oceanografía* 10 (1): 95- 117.

Goldman, J. C. 1984. Oceanic nutrient cycles. In: *Flows of Energy and Materials in Marine Ecosystems.* M. J. R. Fasham (ed.): 137-170. Plenum Press, New York.

Gordillo, F. J. L. 1994. *Relaciones de la actividad nitrato reductasa in situ con la concentración de sustrato en comunidades acuáticas epicontinentales.* Undergraduate thesis. University of Malaga: 102 pp.

Holm-Hanssen, O., C. J. Lorenzen, R. W. Homes and J. D. H. Strickland. 1965. Fluorometric determination of chlorophyll. *J. Cons. perm. int. Explor. Mer.* 187: 9-18.

Jones, G. J. 1979. Microbial nitrate reduction in freshwater sediments. *J. Gen. Microbiol.* 115: 27-35.

Kinder, T. H. and G. Parrilla. 1987. Yes, some of the Mediterranean outflow does come from great depth. *J. Geophys. Res.* 92 (C3): 2901-2906.

Kirchman, D. L., R. G. Keil and P. A. Wheeler. 1990. Carbon limitation of ammonium uptake by heterotrophic bacteria in the subartic Pacific. *Limnol. Oceanogr.* 35: 1258-1266.

Lacombe, H. 1971. Le Dètroit de Gibraltar; Oceanographique Physique. In: *Mèmorie explicatif de la carte gèotechnique de Tanger au 1/25000*: 222: 111-146. Notes et Mém. Serv. Gèologique. Marroc.

Lanoix, F. 1974. Project ALBORÁN. Ètude hydrologique et dynamique de la mer d'Alborán. *Rapport Technique OTAN* 66: 1-40.

Lewis, W. M. 1976. Surface/volume ratio: implications for phytoplankton morphology. *Science* 192: 885-887.

Lohrenz, S. E., D. A. Wiesenburg, I. P. Depalma, K. S. Johnson and D. E. Gustafson Jr. 1988. Interrelationships among primary production, chlorophyll, and environmental conditions in frontal regions of the western Mediterranean Sea. *Deep-Sea Res.* 35 (5): 793-810.

López, I. 1993. *Recursos marinos del golfo de Cádiz. Litoral de Huelva.* Consejería de Agricultura y Pesca, Junta de Andalucía: 145 pp. Sevilla.

Malone, T. C. 1980. Algal size. In: *The Physiological Ecology of Phytoplankton.* I. Morris (ed.): 433-463. Blackwell Scientific Publications, Oxford.

Minas, H. J., B. Coste, P. Le Corre, M. Minas and P. Raimbault. 1991. Biological and geochemical signatures associated with the water circulation through the Straits of Gibraltar and in the western Alborán Sea. *J. Geophys. Res.* 96 (C5): 8755-8771.

Minas, H. J., B. Coste and M. Minas. 1987. The vicinity of the Strait of Gibraltar: a source of a permanent high productivity. *IFREMER Act. Coll.* 5: 41-42.

Morel, A. and J. -M. André. 1991. Pigment distribution and primary production in the Western Mediterranean as derived and modeled from Coastal Zone Color Scanner Observations. *J. Geophys. Res.* 96 (C7): 12685-12698.

Packard, T. T., H. J. Minas, B. Coste, R. Martínez, M. C. Bonin, J. Gostan, P. Garfield, J. Christensen, Q. Dortch, M. Minas, G. Copin-Montegut and C. Copin-Montegut. 1988. Formation of the Alborán oxygen minimum zone. *Deep Sea Research* 35 (7): 1111-1118.

Porter, K. G. and Y. S. Feig. 1980. The use of DAPI for identifying and counting aquatic microflora. *Limnol. Oceanogr.* 25 (5): 943-948.

Prieto, L. 1997. *Estructura hidrólogica, bacterioplancton y fitoplancton en el mar de Alborán y golfo de Cádiz en condiciones de estratificación térmica.* Undergraduate thesis. University of Cadiz: 98 pp.

Rodríguez, J., J. M. Blanco, F. Jiménez-Gómez, F. Echevarría, J. Gil, V. Rodríguez, J. Ruiz, B. Bautista and F. Guerrero. In press. Patterns in the size structure of the phytoplankton community in the deep fluorescence maximum of the Alborán Sea (SW Mediterranean). *Deep-Sea Res.*

Rodríguez, V., J. M. Blanco, F. Jiménez-Gómez, J. Rodríguez, F. Echevarría and F. Guerrero. 1997. Distribución espacial de algunos estimadores de biomasa fitoplanctónica y material orgánico particulado en el mar de Alborán, en condiciones de estratificación térmica (julio de 1993). *Publicaciones Especiales. Instituto Español de Oceanografía* 24: 53-64.

Rodríguez, V., F. Echevarría, J. Rodríguez, F. Jiménez-Gómez and B. Bautista. 1994. Nutrientes, fitoplancton, bacterias y material particulado del mar de Alborán, en julio de 1992. *Informes Técnicos. Instituto Español de Oceanografía* 146 (VI): 53-79.

Rodríguez, J., A. García and V. Rodríguez. 1982. Zooplanktonic communities of the divergence zone in the Northwestern Alborán Sea. P.S. Z.N.I. *Mar. Ecol.* 3 (2): 133-142.

Rodríguez, J., F. Jiménez, B. Bautista and V. Rodríguez. 1987. Planktonic biomass spectra dynamics during a winter production pulse in Mediterranean coastal waters. *J. Plankton Res.* 9: 1183-1194.

Rubín, J. P., N. Cano, P. Arrate, J. García Lafuente, J. Escánez, M. Vargas and F. Hernández. 1997. El ictioplancton, el mesozooplancton y la hidrología en el Golfo de Cádiz, estrecho de Gibraltar y sector noroeste del mar de Alborán, en julio de 1994. *Informes Técnicos. Instituto Español de Oceanografía* 167: 1-44.

Rubín, J. P., J. Gil, J. Ruiz, M. D. Cortés, F. Jiménez-Gómez, M. Parada and J. Rodríguez. 1992. La distribución ictioplanctónica y su relación con parámetros físicos, químicos y biológicos en el sector norte del mar de Alborán, en julio de 1991. (Resultados de la Campaña 'Ictio.Alborán 0791'). *Informes Técnicos. Instituto Español de Oceanografía.* 139: 1-49.

Ruiz, J., C. M. García and J. Rodríguez. 1996. Vertical patterns of phytoplankton size distribution in the Cantabric and Balearic Seas. *Journal of Marine Systems* 9: 269-282.

Snell, F. D. and C. T. Snell. 1949. *Colorimetric methods of analysis* (3rd ed.). Van Nostrand, Princeton (New Jersey): 804 pp.

Stevenson, R. E. 1977. Huelva front and Malaga, Spain, Eddy Chain as defined by Satellite and Oceanographic Data. *Deutsche Hydrographische Zeitshr.* JT 30 (2): 51-53.

Tintoré, J., D. Gomis, S. Alonso and G. Parrilla. 1991. Mesoscale dynamics and vertical motion in the Alborán Sea. *J. Phys. Oceanogr.* 21: 811-823.

Trèguer, P. and P. Le Corre. 1975. *Manuel d'analyse des sels nutrififs dans l'eau de mer (utilisation de l'autoanalyzer 'Technicon AAII').* University of Bretagne Occidentale: 110 pp.

Utermöhl, H. 1958. Zur vervollkommnung der quantitativen phytoplankton-methodik. Vereinigung fuer theoretische und angewandte. *Limnologie* 9: 1-38.

Vargas, M., T. Sarhan Viola, J. García Lafuente and N. Cano. 1997. Un modelo numérico de advección-difusión para explicar anomalías térmicas superficiales en el cabo Trafalgar. In: *Abstract Volume. 2nd Symposium on the Atlantic Iberian Continental Margin* (September 17-20, 1997. Cadiz, Spain). J. Hernández-Molina *et al.* (eds.): 105-107. Universidad de Cádiz. Cadiz.

Villar, O. 1996. *Consecuencias del giro de la corriente del Golfo de Cádiz, por efecto del banco del Hoyo. Su relación con el embolsamiento y penetración pasiva de ictiofauna en estado larvario y postlarvario en el caño de Sancti Petri y marismas gaditanas.* Instituto Hidrográfico de la Marina, Cádiz: 120 pp.