
Microplankton distribution in the Strait of Gibraltar: coupling between organisms and hydrodynamic structures

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Abstract. In this paper we present microplankton distribution patterns in the Strait of Gibraltar obtained during a cruise carried out in September 1997. Chlorophyll, microplankton abundance and biovolume increase from southwest to northeast, a tendency that coincides with a gradual elevation of the interface depth in the same direction. The vertical distribution of biomass at the different stations shows deep maxima associated with the pycnoclines. The generation of internal waves and eventual intrusion of deep water on the sill can be decisive in the enrichment of surface water and plankton dynamics. The taxonomic structure agrees with the expected pattern, with a predominance of diatoms in the richer Mediterranean stations (especially in the north) and a predominance of dinoflagellates and microzooplankton at the Atlantic side. Phytoplankton distribution and salinity values found in the Strait of Gibraltar can be explained by a preliminary model that assumes a coupling between diatom life cycles and hydrodynamic features. Thus, the cells in the surface waters of the eastern side of the Strait would aggregate and sink below the interface, moving westwards and returning to the surface waters coupled with the rising and mixing of deep Mediterranean water at the sill.

Introduction

The Strait of Gibraltar connects the Atlantic Ocean with the Mediterranean Sea. The circulation in the Strait is characterized by the existence of a two-layer system: a surface eastward Atlantic water inflow and a deep westward outflow of saltier Mediterranean water (Lacombe and Richez, 1982). Recent estimates of the mean exchange flow through the Strait give a value of ~ 0.7 Sv (1 Sv = 10^6 m³ s⁻¹) (Bryden *et al.*, 1994). This exchange is strongly influenced by tidal currents (García Lafuente *et al.*, 1990) as well as by currents induced by wind and atmospheric pressure variations (Candela *et al.*, 1989).

Most of the research effort carried out at the Strait of Gibraltar has been focused on the physical oceanography, including hydrodynamics, water balances, tidal effects and other physical phenomena of interest. One of these phenomena is the generation of internal waves near the Camarinal sill (Armi and Farmer, 1988).

Interactions between physical processes and biological features have already been investigated in the adjacent region of the northwest Alborán Sea, where the Atlantic jet entering the Mediterranean generates a frontal region between the northern upwelling area and the anticyclonic gyre in the south (García Lafuente *et al.*, 1998). These studies have shown that the physical forcing affects the abundance and composition of phytoplankton directly, and have revealed

the importance of mesoscale hydrodynamic features in the general plankton distribution of the region (V.Rodríguez *et al.*, 1997; J.Rodríguez *et al.*, 1998).

Nevertheless, the biological studies that have included samples from the Strait of Gibraltar have been scarce (Establier and Margalef, 1964; Delgado, 1990). Moreover, none of these studies had been aimed at describing the connection between the peculiar circulation scheme of the Strait and the resulting distribution of plankton.

Within the framework of the European (MAST III) CANIGO project, a summer cruise was carried out at the Strait of Gibraltar allowing this objective to be accomplished by analysing the coupling between hydrodynamic features near the sill and microplankton biomass distribution.

The hydrodynamic features in the Strait that have interest when studying plankton patterns include intermittent mixing events, due to the effect of internal waves, and changes in the average Atlantic–Mediterranean interface depth, which are related to its oscillation along the tidal cycle. In this paper, we show how these features have a clear effect on the abundance and structure of phytoplankton assemblages.

Method

Samples were taken from eight stations during a cruise on board R/V ‘Thalassa’ on 2–9 September 1997. These stations are arranged in three transects at the Atlantic, Central and Mediterranean sections of the Strait (Figure 1). For each station, the samples were collected at 11 depths with a CTD-rosette sampler fitted out with Niskin bottles.

Samples to estimate total chlorophyll *a* (Chl *a*) were filtered (0.5 l) through a

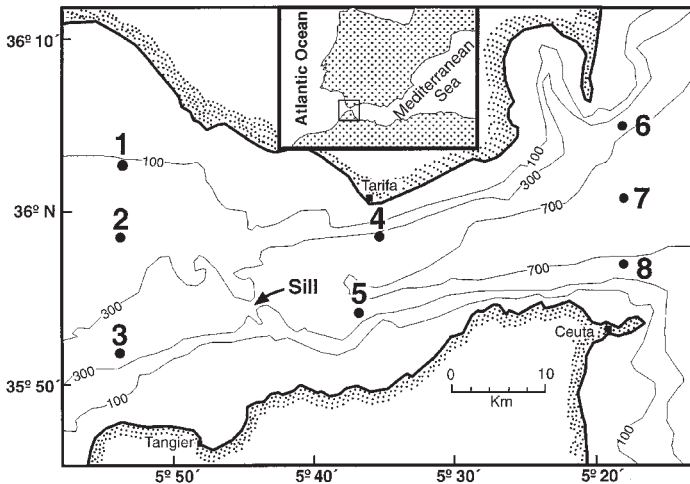


Fig. 1. Bathymetry of the Strait of Gibraltar, showing the position of the sill and the sampling stations. Sampling was carried out spending a day in each station from 2 (station 1) to 9 (station 8) September 1997.

Whatman GF/F filter at low pressure (<100 mmHg). Pigments were then extracted in 90% acetone for 24 h in cold and dark conditions. The Chl *a* concentration was then estimated fluorimetrically using a Turner Designs-10 fluorometer calibrated with pure Chl *a* (Sigma Co.) (UNESCO, 1994). To estimate the concentration of Chl >20 µm, which can be used as a quick estimation of microphytoplankton biomass, 2.5 l of water were filtered through a 20-µm-pore-size mesh. This concentrate was then washed out with filtered sea water and processed in the same manner as described for total Chl *a*.

In order to achieve more detailed analyses of the microplanktonic fraction, we filtered 2 l of sea water through a 5-µm-pore-size mesh. The retained particles were preserved with Lugol's solution. These bottles were kept in a cold dark place until further analysis in the laboratory. Subsamples (10–50 ml) were allowed to settle for 24 h on Utermöhl chambers. Cells or colonies were identified and measured using an inverted microscope (×100 and ×250) connected to a semi-automatic image-analysis system (Analytical Measuring Systems, VIDS V). The biovolume of each individual planktonic organism was calculated by approximation to regular figures (cylinder, ellipsoid, etc.) using length and width measurements. More than 400 cells were counted and measured in each sample in order to keep the counting error within ±10% (Lund *et al.*, 1958). This interactive process allowed the taxonomic identification of the organisms, which were ranked in 10 wide taxonomic categories. Most of the cells within these groups were identified to the level of species, although total biovolume per taxonomic group was calculated only on these 10 classes. A more detailed description of these procedures can be found in previous works (Echevarría and Rodríguez, 1994; García *et al.*, 1994).

Results

Temperature and salinity profiles show a high vertical heterogeneity in the water column, with marked gradients of both variables that generate clear pycnoclines (Figure 2). The halocline is indicative of the interface between the incoming upper Atlantic water and the deep outflowing Mediterranean water. The interface is defined as the isohaline of 37 at the sill region (Bryden *et al.*, 1994) with higher values of the isohaline towards the east (Bray *et al.*, 1995). The position of the interface has a special interest when dealing with biological variables because it represents a limit between deep nutrient-rich waters and the surface nutrient-depleted waters.

The depth of the Atlantic–Mediterranean interface (AMI) defined in this way, as well as that of the shallower thermocline, have been marked in Figure 2 with a continuous and a dashed arrow, respectively. These positions show a clear tendency when the eight stations are examined, with a deepening and a separation of both pycnoclines from northeast to southwest. The thermocline and halocline (AMI) coincide at 65 m depth at station 6, whereas station 3 shows the deepest interface (around 200 m depth) and with a clear separation as it is 100 m deeper than the thermocline.

The total Chl concentration (Figure 2) also increases from southwest towards

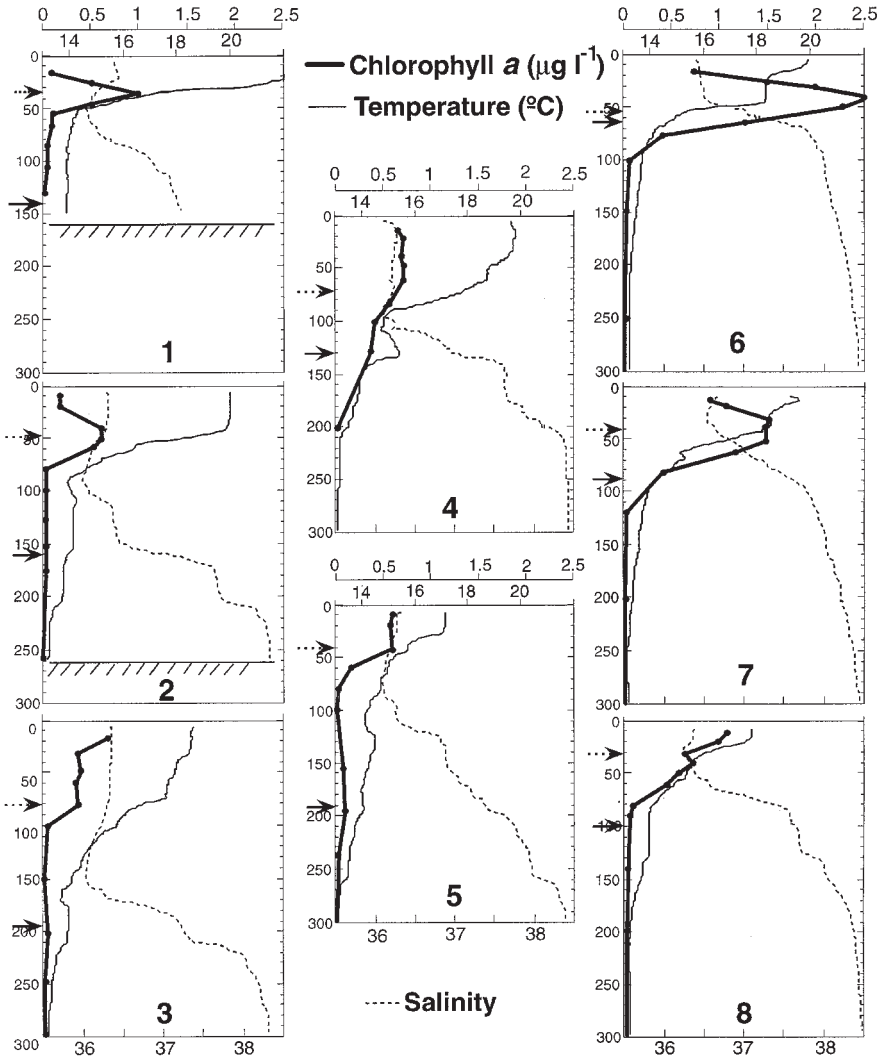


Fig. 2. Profiles of temperature ($^{\circ}\text{C}$) (thin solid line), salinity (dotted) and Chl *a* ($\mu\text{g l}^{-1}$) (thick solid line). Continuous and dashed arrows indicate the interface (AMI) and thermocline depths, respectively.

northeast (stations 6 and 7), where the clear deep Chl maxima (DCM) are associated with the thermocline. The development and importance of the DCM are inversely related to the distance between the AMI and the thermocline, a fact previously reported by Rodríguez *et al.* in a frontal region in the adjacent Alborán Sea (Rodríguez *et al.*, 1998). The contribution of Chl >20 mm to total Chl also differs between Atlantic and Mediterranean waters. Around 40% of total Chl

corresponds to the fraction $>20 \mu\text{m}$ in northeast stations whereas only $<10\%$ of total Chl belongs to cells larger than $20 \mu\text{m}$ in the Atlantic transect (especially at the southern station). Therefore, there is a difference in the predominant sizes and species of phytoplanktonic cells, with larger sized cells in the Mediterranean and Central stations of the Strait.

Vertical profiles of total biovolume at the eight stations (Figure 3) also reveal much higher values in the Mediterranean sector of the Strait. However, central stations have clear microplankton biovolume maxima very close to the surface (Figure 3), a feature which was not registered for total Chl data (Figure 2). This fact could be explained if we take into account that biovolume measurements were made on both heterotrophic and autotrophic organisms and only in the microplankton size range, and a possible photoadaptation effect. Nevertheless, in central northern station 4, a second deeper maximum appears that is still related to high Chl concentration in the column (see also Figure 2).

When total biovolume is split into the main taxonomic groups, significant differences in the composition of microplankton between Atlantic and Mediterranean sections emerge (Figure 3). The diatoms, which are a group representative of nutrient-enriched environments, are clearly predominant in the Mediterranean stations and become gradually less important towards the Atlantic. Biomass in Atlantic stations is dominated, within the studied size range, by dinoflagellates and microzooplankton (mainly ciliates and nauplii), organisms that usually dominate in oligotrophic environments.

This more detailed analysis of the structure of the microplanktonic community also reveals differences along the Strait (Figures 3 and 4). In the Atlantic sector, the percentage of diatoms is much lower, the most frequent genera being *Guinardia* (mainly at station 2) and *Pseudonitzschia* (station 1). Station 3, which is located at the western side of Camarinal sill in the main channel, has the lowest abundance of diatoms. Nevertheless, although less abundant, the diatoms that are present below the interface in station 3 belong to similar taxa to those that predominate in the stations of the Mediterranean side (stations 6 and 7).

There are also relevant differences in community structure between the stations located in the central transect (stations 4 and 5). The northern station 4 is dominated by the genus *Guinardia* (*G.striata* and *G.flaccida*), taxa that were also very abundant at station 2. However, at the southern station 5, we found a phytoplankton community that included several diatoms typical of upwelling areas. Thus, in this station, species of the genus *Chaetoceros* (which reached only a negligible abundance at station 4) become very abundant. Then, the taxonomic composition of samples of station 5 is more similar to that of northern Mediterranean stations.

Chaetoceros spp. have then a remarkable distribution pattern in the Strait (Figure 4). They are highly abundant in Mediterranean stations, where this genus constitutes the bulk of diatom biomass and it forms a maximum in the vicinity of the interface. This fact will lead to the larger proportion of these diatoms being situated in a slower speed layer, and this may affect the time that they spend travelling into the Mediterranean. These diatoms are also important in south central station 5, where they reach a maximum at very shallow depths,

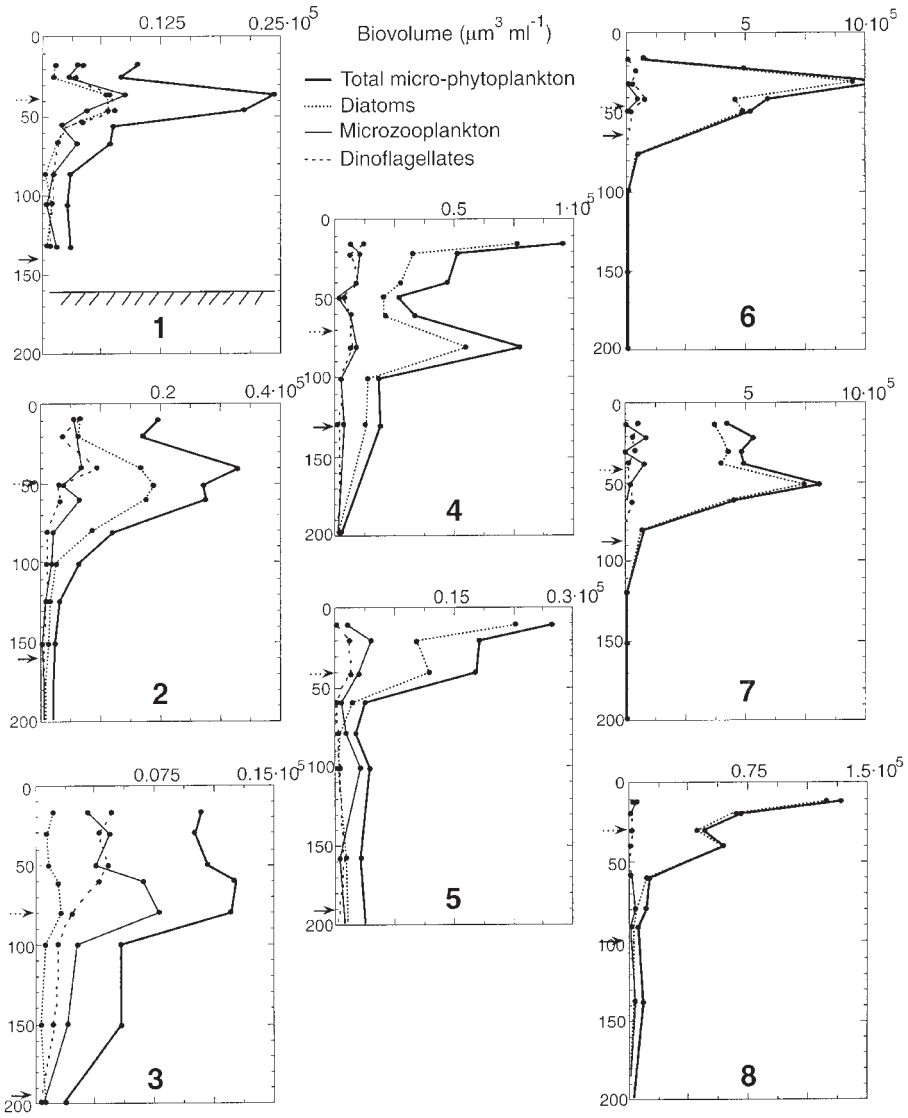


Fig. 3. Distribution according to depth (m) of the main microplankton groups expressed as biovolume ($\mu\text{m}^3 \text{ml}^{-1}$). Total microplankton (thick solid line); ‘cylindrical diatoms group’ (dotted line), which includes mainly *Guinardia*, *Rhizosolenia*, *Leptocylindrus* and *Detonula*; microzooplankton (ciliates + nauplii; thin solid line); dinoflagellates (dashed line). Continuous and dashed arrows indicate the interface (AMI) and thermocline depths, respectively. Note the different scale used at each station.

i.e. in a water layer travelling eastward at high speed. Finally, in the Atlantic side, *Chaetoceros* appears especially in southern station 3 and, although in lower numbers than in Mediterranean stations, it has a noticeable presence at several depths, including very deep waters below the interface, in the outflowing Mediterranean water.

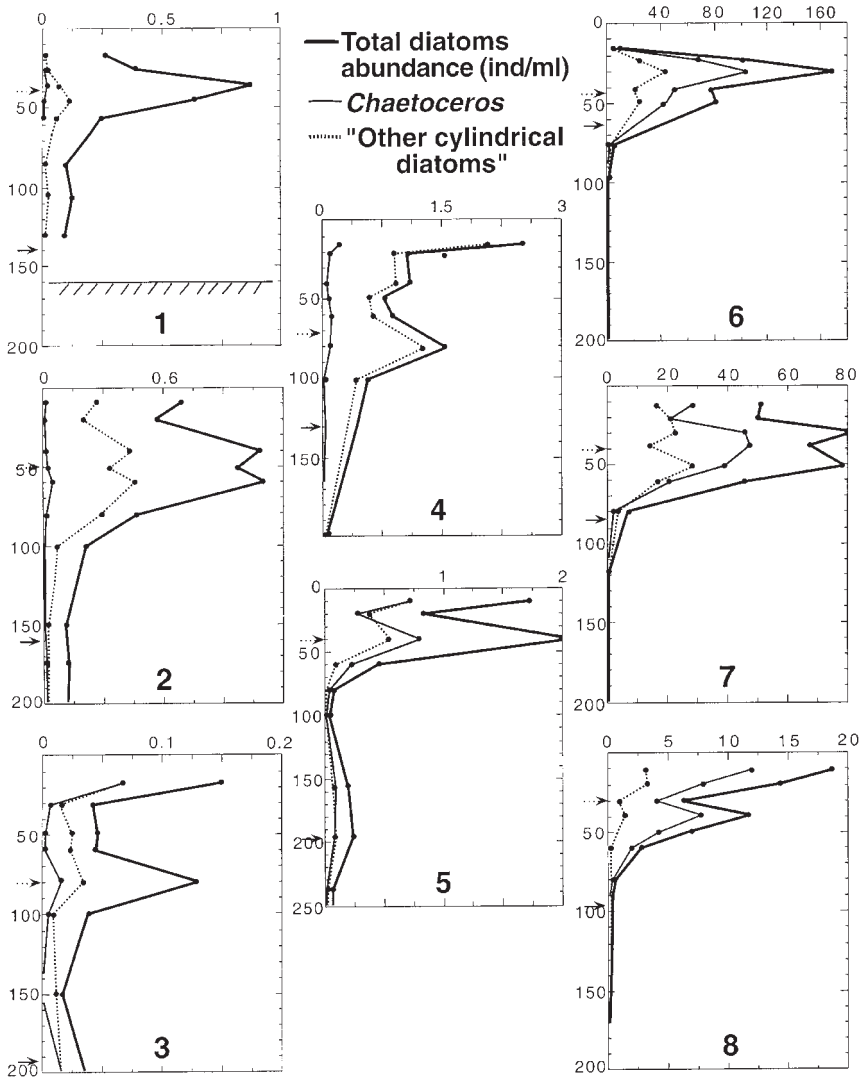


Fig. 4. Distribution according to depth (m) of total diatoms (individuals ml⁻¹; thick solid line), abundance of the genus *Chaetoceros* (thin solid line) and that of 'other cylindrical diatoms' (dotted line). Continuous and dashed arrows indicate the AMI and thermocline depth, respectively. The genus *Chaetoceros* is the most abundant diatom both in Mediterranean stations (6-8) and in station 5, whereas the 'cylindrical diatoms group' predominated in other stations. Note the different scale used at each station.

Discussion

Microplankton distribution and hydrodynamic structures

Microplankton abundance (estimated from Chl, cell number and total biovolume) shows a tendency to increase parallel to a gradual eastward elevation of the AMI in a southwest–northeast direction.

However, one of the main problems in the interpretation of our results is that we have only one estimation of biological variables per station at different moments of the tidal cycle. Therefore, in order to include the effect of tide in the evaluation of our results, we have analysed the average depth of the interface and its range of variation assuming the patterns proposed by Bray *et al.*, which presented an ascent of the interface in the southwest–northeast direction [(Bray *et al.*, 1990); see their Figure 1]. The combination of these average interface depths with the proposed tidal oscillation of the interface at different sectors of the Strait [(Bray *et al.*, 1990); see their Figure 2] leads to the situation depicted in Figure 5, where the depth oscillations of the interface have been estimated by interpolation for the eight stations of our cruise.

The amplitude of the changes in the interface depths oscillates from 50 to 90 m, depending on the station (Figure 5). We can consider on average the 100 m surface layer as the potentially productive euphotic zone. We can also take into account that the deep outflowing waters below the interface are nutrient rich, whereas upper Atlantic waters can be considered as nutrient depleted. These facts can allow our results to be analysed in terms of a coupling between light and nutrients that would lead to an enhancement of primary production. In this context, Atlantic stations present a marked uncoupling between light and nutrients because AMI is very deep. The enriched deep water will rarely arrive at the euphotic zone, even including the periodic oscillation of the interface activated by tides. From this dynamic point of view, the southwest–northeast tendency is again clear: The interface at station 6 is always very shallow (<100 m). The total time that the interface spends in the euphotic zone becomes gradually shorter as we move to the southwest. The dotted area in Figure 5 represents the expected periods in which the interface, probably rich not only in nutrients but also in accumulated materials including viable cells, is in the euphotic zone and a higher primary production can take place. The consideration of thermocline depths (usually shallower and related to microplankton maxima) leads to similar conclusions, as its position follows the same pattern, with deeper thermoclines at the southwest and shallower ones towards the northeast (Figure 2).

Another important hydrodynamic feature must be taken into account when analysing these results. Thus, the generation of internal waves and the eventual intrusion of deep water in the productive zone could enrich the upper illuminated zone east of the sill.

In fact, intermittent mixing events at the sill region are favoured by the special topography of the Strait of Gibraltar, which facilitates the generation of internal bores, an important and perhaps dominant agent of mixing in the Strait (Pettigrew and Needell, 1989). Bottom topography presents highly pronounced slopes in the sill region: in almost 10 km (the distance between stations 7 and 5), depth

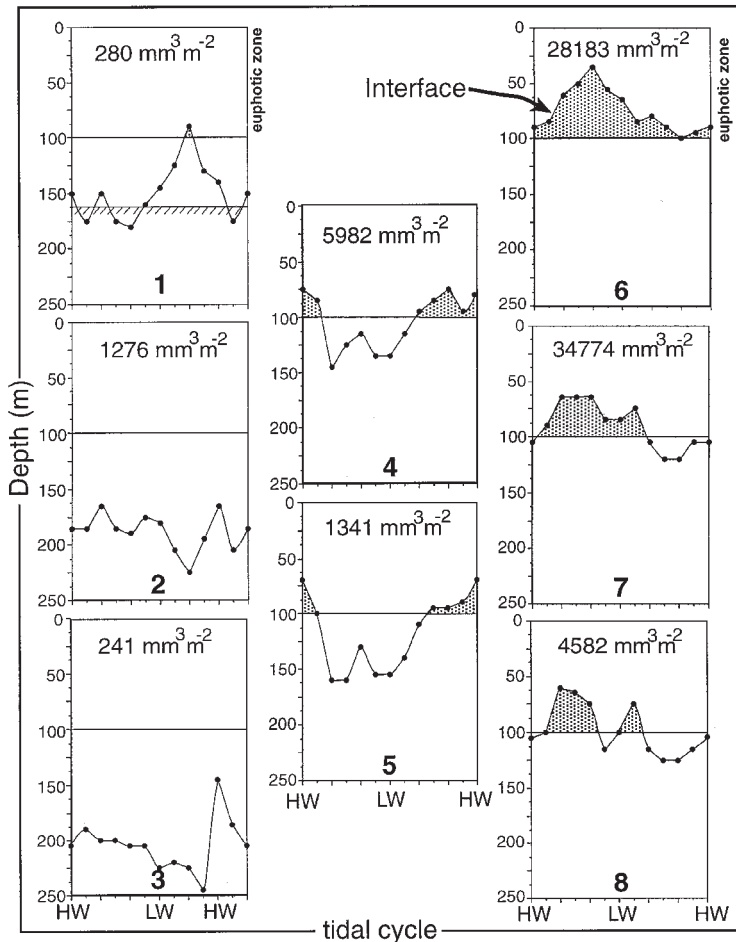


Fig. 5. Interface depth along a semidiurnal tide cycle (HW, high water; LW, low water). The euphotic zone is considered down to 100 m depth. The dotted area indicates the period during which nutrient-rich waters below the interface are illuminated. Microphytoplankton biovolume is expressed as mm³ per m², showing the relationship between the dotted area and microphytoplankton biomass at each station.

changes from 800 to <300 m. Also, the interface depth deepens from 55 m to some 160 m on average (Bray *et al.*, 1990), with important oscillations along the tidal cycle. This slope forces an upwards component in the direction of the Mediterranean outflowing water which approaches the sill.

Camarinal sill is the shallowest sector of the Strait (<300 m depth) and acts as a bottleneck, being the main constriction for the flow in the Strait. The Mediterranean outflow cross-section is reduced because of these bathymetric constraints, thus increasing water velocity and the probability of mixing events (Wesson and Gregg, 1994). Mixing between the two layers is suggested after comparing upper salinity values at both sides of the sill (Atlantic and Central stations of this cruise;

Figure 2). This fact is more evident in station 5, which presents a weaker halocline. Very recent unpublished data from a cruise performed in November 1998 have revealed the presence of singularities just after high water, with high values of vertical velocities (using an Acoustic Doppler Current Profiler) and a high abundance of particulate material (estimated by a transmissometer-CTD) at single moments (Bruno *et al.*, in preparation).

The phenomena described above imply consideration of the Strait as a pulsating upwelling area, in which nutrient-rich deep water upwells in short time single episodes of mixing, as previously suggested by Minas *et al.* (Minas *et al.*, 1991). This should constitute a fertilization mechanism for the westward region of the Strait, and a mechanism that partially explains the high biomass found to the northeast. The background idea is highly related with the Gran effect [e.g. (Mann and Lazier, 1991)] involving enhanced production and blooming of phytoplankton when cells remain packaged in a shallower mixed layer with enough light and nutrients.

Although persistence of phytoplankton patches in a fixed zone depends on transport, turbulence and mean replication time of cells, the problem will become complicated given that the organisms could control their position relative to the interface depth. The region close to the interface will present a near zero horizontal velocity and, given the marked velocity gradients, a dramatic change in mean transport could be caused by a relatively small vertical repositioning relative to interface depth. Moreover, we hypothesize that the high values of Chl can be a general feature of the Mediterranean side near the Strait that can extend farther eastward of the sampled region. In this case, the phenomena on the sill can be considered as the potential agents of these plankton patterns that could then be considered as a permanent feature in the vicinity of the Strait.

The average tendencies discussed above refer to total biomass or Chl data. When the taxonomic structure of phytoplankton is taken into account, some new features are interesting to point out. Microplanktonic community structure is quite different at both sides of the sill, with similarities between Central and Mediterranean stations and a very different community in the Atlantic sector. Also, the diatoms *Chaetoceros* spp., typical of upwelling areas, have been found at stations 6, 7, 5 and 3, covering a transect which crosses the study area from southwest towards northeast (Figure 4). These stations are connected by Strait topography because they are aligned along the main channel (parallel to the 700 m isobath; Figure 1). This alignment follows the main velocity direction of the Mediterranean outflowing water (Sein *et al.*, 1999).

Coupling between hydrodynamics and organisms: a preliminary model

We propose a hypothesis based on the advective connection between the stations through the opposite bilayer currents characteristic of the Strait. Along the main channel, some microplanktonic organisms would travel in a closed cycle using both currents during their life cycle to avoid adverse effects of advection and to maintain themselves in the enriched upwelled water in the vicinity of the Strait.

This conveyor belt drawn by sea water in the circulation scheme could be used by diatoms, which could then be able to adjust their life cycles to this pattern of water movement. In an attempt to explain the empirical data that we have obtained at the different stations analysed, we propose the tentative conceptual model given in Figure 6. This hypothesis takes into account a circulation scheme that includes intrusion to surface waters at the sill region and the return of part of the expected outflow into the Mediterranean sector. The coupling of diatom behaviour and life cycles to this predictable circulation scheme would allow them to stay in the nutrient-rich area of the eastern side of the sill. The proposal of this coupling is based on different mechanisms and adaptations described for diatoms by different authors, together with some direct evidence coming from our own results. A schematic draft of the hypothesis includes four steps.

1. *Sinking and aggregation.* At the northeastern sector (stations 6 and 7), the phytoplankton community is mainly composed by colonies of diatoms with a high abundance ($160 \text{ colonies ml}^{-1}$). This abundance is higher than the critical concentration predicted by models for flocculation (Jackson, 1990). Aggregate abundance and formation are also strongly affected by the occurrence of transparent exopolymeric particles (TEPs) (Kjørboe *et al.*, 1996), and the production of these extracellular mucilages by phytoplankton is greatest under high-light–low-nutrient conditions (Decho, 1990) that are likely when they have been exhausted by algal growth. The presence of spiked protuberances such as setae can further enhance the aggregation of particles when a critical concentration level is achieved (Riebesell, 1991). In this case, the phytoplankton community is dominated by colonies of a genus (*Chaetoceros*) that displays abundant long setae (Figure 4).
2. *Disaggregation and seeding.* There is a separation of colonies into smaller fragments or individual cells in deep waters (Smetacek, 1985). During aggregate sedimentation, microbial exudates and binding material may be sufficiently decomposed by bacteria (Chow and Azam, 1988) to weaken the attraction between attached clusters within the aggregates. Colony disintegration and dispersal of the small individual cells will ensure that the seeds are scattered over a wide depth range in nutrient-rich subsurface waters, thus increasing the chance of transport of some of them back to the surface during further upwelling (Smetacek, 1985). It has also been proposed that diatoms accumulate carbohydrate reserves and increase their sinking velocity after a nutrient depletion (Richardson and Cullen, 1995).
3. *Return to the upper layer.* The possible movement of part of the particulate material, including settled cells, back to the surface waters would be partially related to the topography of the Strait of Gibraltar and the episodic water mixing processes that have been described above for the sill region. Other biological mechanisms such as positive buoyancy described in some diatoms (Villareal *et al.*, 1996) could enhance the return of previously settled cells to the upper layers.
4. *Horizontal advection in the upper layer.* Once in the upper illuminated Atlantic water, the cells coming from the deep outflowing layer could activate their

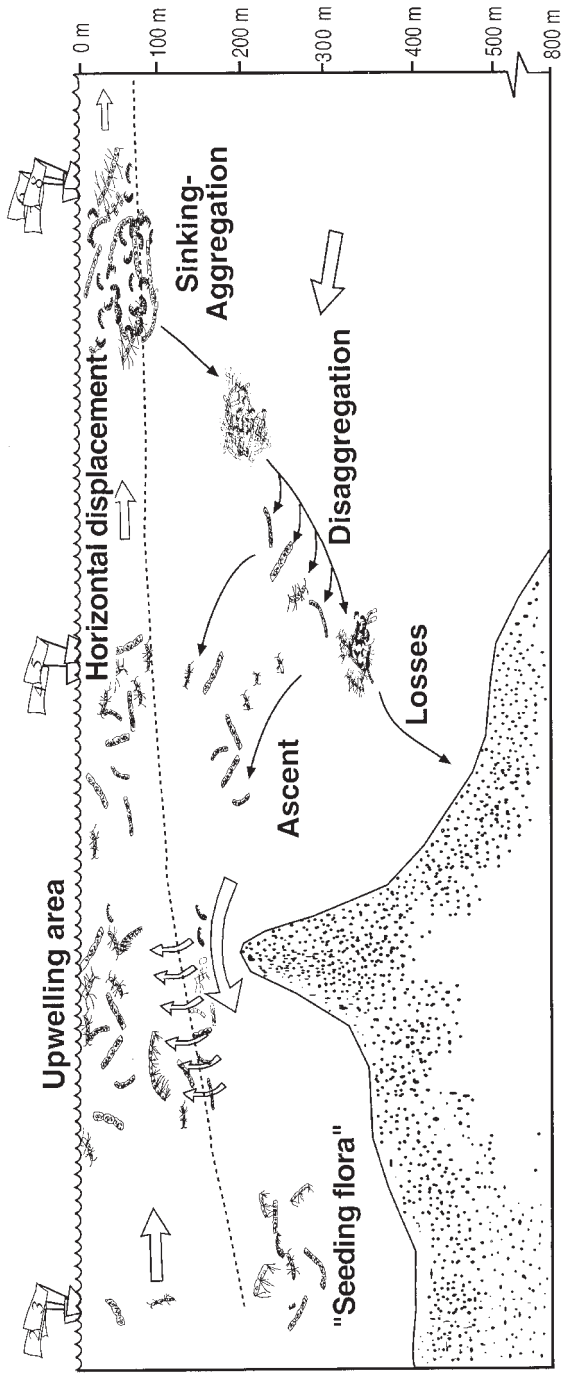


Fig. 6. Scheme of the proposed circulation in the Strait of Gibraltar, and the coupling with some microphytoplankton species. See the text for details.

photosynthetic mechanisms. Diatoms are able to maintain their photosynthetic capacity after a long time in dark conditions (Peters, 1996; Berges and Falkowski, 1998), being able to photosynthesize when they arrive at the euphotic zone. It is likely that the cells arriving from deep waters had incorporated nutrients in their internal reserves (Probyn *et al.*, 1996). The sum of light and nutrients will allow these cells to perform active growth during the transport into the Mediterranean, in the surface current, with several divisions in a day (Malone, 1980). However, an appropriate positioning in the water column is decisive. During the displacement, the cells must accumulate preferentially at the vicinity of the interface where the velocity is lower. Then, the numerical abundance would be higher in this zone (Figures 3 and 4). This is the structure that we have found at the Mediterranean stations (mainly 6 and 7) where aggregation processes would take place, closing the cycle.

Final remarks

In coastal upwelling regions, usually Ekman transport drags the surface waters outwards with a deep current moving towards the coast. Phytoplankton cells settle to deeper layers when reaching poor surface waters far from the coast and are then recycled with the upwelling circulation (Barber and Smith, 1981; Bodungen *et al.*, 1986). Brown and Field conclude that these 'seeding populations' are coupled with the upwelling frequency and have a role in total productivity of the upwelling area that is more important than light or nutrients (Brown and Field, 1986). In these areas, diatoms exploit the opposite bilayer current system to maintain their position in the vicinity of the upwelling (Brown and Field, 1986). These coastal upwelling areas depend mainly on wind, a much more unpredictable phenomenon than tides. A similar feature of coupling is proposed in this paper for the pulsating upwelling in the sill of the Strait of Gibraltar, but in this case the forcing agent of the upwelling is the tide, a much more predictable event. The coupling of life cycles with a more regular physical event would be easier and the fluctuations could be better internalized. Further investigation at a wider spatial and temporal scale and including more accurate estimations in the framework of a quantitative model will be necessary in the zone to confirm this hypothesis.

Acknowledgements

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