ELSEVIER

Journal of Marine Systems 9 (1996) 269–282

JOURNAL OF MARINE SYSTEMS

Vertical patterns of phytoplankton size distribution in the Cantabric and Balearic Seas

Javier Ruiz [a,*], Carlos M. García [a], Jaime Rodríguez [b]

[a] *Departamento de Biología y Ecología, Facultad de Ciencias del Mar, Universidad de Cádiz, Apartado, núm. 40, 11510 Puerto Real (Cádiz), Spain*

[b] *Departamento de Geología y Ecología, Facultad de Ciencias, Universidad de Málaga, Campus Teatinos, 29071 Málaga, Spain*

Received 24 November 1995; accepted 3 May 1996

Abstract

In this paper we analyze plankton size distribution (2–100 μm of equivalent spherical diameter) under different hydrographic structures, such as the seasonal thermocline of the Cantabric and Balearic seas and the oceanographic front present in the Balearic Sea. Nannoplanktonic fraction (2–20 μm) tends to present biomass maxima at shallower depths than the chlorophyll maximum in stratified waters, as well as in the more productive waters near a front. The slope of the normalized size-biomass spectrum was more negative in these zones of phytoplankton biomass maxima indicating a higher proportion of smaller cells. The main hypotheses to explain chlorophyll and biomass maxima as well as phytoplankton accumulation in productive areas are reviewed. According to the observed results, the most suitable mechanism to explain subsurface biomass maxima is the active net growth of the smaller phytoplanktonic cells. The importance of the methodology employed for analyzing the size distribution of plankton communities and its relationship with hydrographic variability are also discussed.

Keywords: vertical structure of plankton; size distribution; biomass spectra; subsurface maxima; oceanic fronts; Balearic Sea; Cantabric Sea

1. Introduction

Parsons (1969) and Sheldon et al. (1972) characterized the pelagic communities through size structure for their analysis. These authors as well as Witek and Krajewska-Soltys (1989) provided the first analyses on the variability of particle size structure in the horizontal dimension of the ocean. The analyses showed regularities in the size spectra in the sense that they tend to become irregular and unstable as latitude increased (Witek and Krajewska-Soltys, 1989). Conversely, results on vertical changes of the size structure of plankton turn out to be rather contradictory. Rodríguez and Mullin (1986) provided the first study of vertical variability of the size-spectrum for microplankton of Pacific waters down to 120 m, finding an increase in the relative importance of larger microplankters with depth. Quiñones (1992) made an analysis of the variability of these spectra in the vertical dimension at the norwestern Atlantic, from surface to 400 m, but included the nannoplankton fraction. Quiñones divided the water column into four layers (surface, thermocline and two layers below the thermocline) and, in this case, did not find

* Corresponding author. Tel.: 34-56-470836. Fax: 34-56-470811. E-mail: javier.ruiz@uca.es.

PII S0924-7963(96)00045-0

among them any significant variation in the plankton size structure. Delgado et al. (1992) also found no tendency with depth in the size distribution of phytoplankton communities in the western Mediterranean. In the Adriatic sea, Revelante and Gilmartin (1995) described the presence of a higher relative proportion of larger phytoplankters in the subsurface chlorophyll maximum. On the contrary, results of this study in the waters of Cantabric and Balearic seas (Spain) shows how both in the horizontal plane and in the vertical axis the phytoplankton communities of productive waters have a greater proportion of small cells when compared to less productive waters. This feature is discussed in relation with the main hypotheses to explain chlorophyll and biomass subsurface maxima. The role played by the methodology used to obtain plankton size distributions in the observed discrepancies of their vertical variability is also discussed.

2. Materials and methods

The data presented in this paper are the result of three different oceanographic cruises in the coasts of Spain, two of them in the Balearic Sea (FRONTS-89 and FRONTS-91) and another one in the Cantabric Sea (ASFLOR-I). In these cruises different stations were sampled. In the case of the Balearic Sea these stations formed a transect across the Catalan front (Saiz et al., 1992) whereas in the Cantabric Sea they covered the central zone of this Sea (Fig. 1). At each station, samples from different depths were taken for the determination of pigments and nutrient concentrations, and also for the microscope analysis of the size distribution of the plankton community. Some minor differences in the methodology for the sampling and analysis of chlorophyll-a and nutrient concentrations exists between cruises. This is the result of the analysis being made by different research teams and the methods used in each cruise are described below. The methodology used for the microscope analysis of the size distribution of plankton is the same for all the cruises.

2.1. Cantabric Sea

Samples were taken during the oceanographic cruise "ASFLOR-I" in August of 1989 (Fig. 1). At each station, a profile of scalar irradiance was obtained with a LI-COR radiometer with a spherical sensor. This profile was used to sample at 100, 60, 30, 15, 5 and 1% of the incident light by means of Van Dorn (30 l) oceanographic bottles. A subsample of 125 ml (from Van Dorn bottles) was then preserved with acetic Lugol for microscope analysis. Samples for chlorophyll-a, phaeopigments and nitrate concentration were obtained from Niskin bottle casts. A subsample of 100 ml (from Niskin bottles) was filtered on Whatman GF/C filters for chlorophyll-a analysis. The filter was then transferred to acetone (90%) and homogenized. Chlorophyll-a and phaeopigment concentrations were estimated on the filtered acetone extracts following the fluorometric method of Yentsch and Menzel (1963). Nitrate concentrations were determined by the method described in Grasshoff et al. (1983).

2.2. Balearic Sea

The study in the Balearic Sea was made during cruises FRONTS-89 (May-1989) and FRONTS-91 (February-1991). Samples were taken at four stations located along a transect between Barcelona and the channel between Mallorca and Menorca islands (Fig. 1); thus, crossing the Catalan front (Saiz et al., 1992). Samples were taken with Van Dorn bottles at six depths: 0, 20, 40, 50, 60 and 80 m in the FRONTS-89 cruise and at the 100, 60, 30, 15, 5 and 1% of the incident light in the FRONTS-91 cruise (close to 10, 20, 40, 50, 70 and 100 m depths, respectively). At each depth, 125 ml were taken and preserved with acetic lugol for microscopic analysis.

Temperature, as well as nitrate and chlorophyll-a concentration data have been taken from "Informe FRONTS" (Varela et al., 1991) where the following methodology was used. Samples for nutrients and chlorophyll-a concentrations were collected at every 10 m depth with Niskin bottles with reversible thermometers. Chlorophyll-a was measured with the fluorometric method of Yentsch and Menzel (1963) after filtering 50 or 100 ml through Whatman GF/F filters and extracting in acetone (90%) as described above. Nutrient concentrations were measured immediately after sampling with a Skalar autoanalyzer and following the method described by Whitledge (1981). Nutrient concentration data available for the

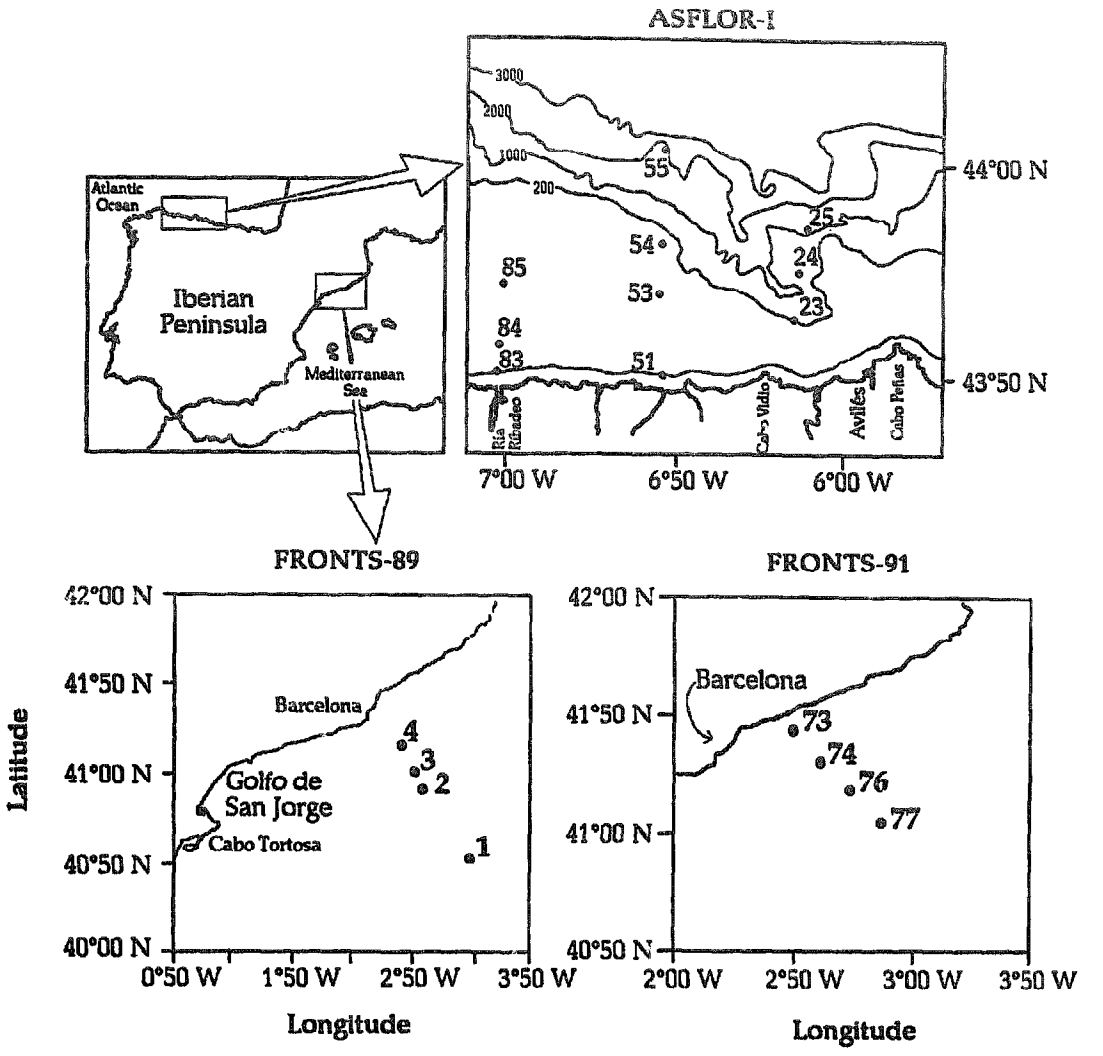

Fig. 1. Location of the studied stations.

FRONTS-89 cruise are nitrate concentrations, whereas for the FRONTS-91 cruise the data are nitrate + nitrite.

2.3. Image analysis

For the analysis of the plankton size structure, 100 ml aliquots were allowed to settle in chambers 10 cm high (3 h per cm height) and then analyzed following the inverted microscope method of Utermöhl (1958). Cells were counted and measured at 100, 400 and 1000 (oil immersion) magnifications on a Nikon TM2 inverted microscope assisted by a VIDS-IV (Analytical Measuring Systems) video-interactive image analyzer. Biovolume for each individual organism was estimated by assigning a certain geometric shape to the individual. The different geometric shapes ranged from a simple sphere for some flagellates to the complex shapes of some species of the genus *Ceratium* that required its decomposition into three cones, a cone frustum and a trapezoid with upper and lower faces of different size (Ruiz, 1993). By using this technique we were able to study phytoplankton in a size range from 2 to 100 μm of equivalent spherical diameter.

2.4. Size spectra

The size data resulting from the microscopic analysis of plankton are usually arranged in octave size

classes (Platt and Denman, 1977, 1978; Rodríguez and Li, 1994) each with a concentration of biomass. Following the techniques of Platt and Denman (1977, 1978) a linear function has been fitted to the log-transformed normalized biomass. The slope of the normalized size-biomass spectrum (b) can be used to assess the size characteristics of the plankton community (see Blanco et al., 1994 for a detailed discussion on this parameter). Thus, in a community with a great proportion of biomass in individuals of small size the value of b will be more negative than another community in which small individuals are not so abundant. Much of the discussion in this paper is based on the value of parameter b which summarizes information on the size distribution of plankton in a single number. Therefore, it simplifies the study of the spatial variability of plankton size distribution and its comparison with other variables such as chlorophyll-a, nutrient or biomass concentrations.

3. Results

The results presented below are divided into two sections that correspond to the different zones studied (Cantabric and Balearic seas). The section dedicated to the Balearic Sea is also divided into three subsections corresponding to the analysis of the response of plankton size distribution to the different hydrographic structures observed in the zone. Thus, during the FRONTS-89 cruise the Balearic Sea was in the period of seasonal stratification characteristic of temperate seas and the presence of an oceanographic front in the zone was also evident. The response of plankton size distribution to these hydrographic features is studied respectively under the sections "The stratification period" and "The case of a front". During the FRONTS-91 cruise the Balearic Sea was in the seasonal mixing period of temperate seas and the response of plankton size distribution to this oceanographic feature is studied under the section "The mixing period".

3.1. Cantabric Sea

The vertical profiles of the different physical, chemical and biological variables display a similar pattern for all the sampled stations. They have a 20 m deep mixed layer and a thermocline of 20– 40 m depth (Fig. 2 A). Nitrate concentration is very low in the first 30 m with a sharp increase in deeper layers (Fig. 2 B). Taking into account this sharp gradient and the high concentrations of nitrogen below 30 m it is sensible to expect that this is the depth from which nutrients do not limit phytoplankton growth. Due to the homogeneity among stations, chlorophyll-a data from different stations were joined together; the selected depth intervals were 0, 5, 5–15, 15–25, 25–35, 35–45, 45–55, 55–65 m and data from > 65 m. The chlorophyll-a profile of the pooled data (Fig. 2C show a clear presence of a subsurface maximum at 40 m depth.

Phytoplankton biomass data, as well as its size spectra, were also pooled for the same depth intervals as chlorophyll-a. Prior to pooling the size spectra data by depths, a test of multiple comparison among slopes (Zar, 1984) was made on the spectra belonging to the same depth interval but from different stations. Thus, we were able to check that the same linear model fitted spectra from the same depth but from different stations (it would have been meaningless to pool spectra which do not fit to the same linear model). Then an unique size spectrum was obtained for each depth interval by joining the data of the different stations that were in that interval. The differences obtained in the value of b for pooled data but for different depth intervals were significant when analyzed by a test of multiple comparisons among slopes ($\alpha = 0.10$; Zar, 1984). A Kruskal-Wallis test was used to assess on significance of spatial heterogeneity of the biomass data. This test, rather than a one-factor ANOVA, is recommended when both the number of data and the variance are very heterogeneous among different groups (Zar, 1984).

Vertical profiles of total biomass (nanno + microplankton) and microplankton (Fig. 3A,C) do not show clear tendencies with depth, except a decrease at > 50 m. No significant differences among depths were detected by means of a Kruskal-Wallis test ($\alpha = 0.10$). Nannoplankton biomass (Fig. 3B), however, has a subsurface maximum at 30 m depth. Although the vertical profile of nannoplankton biomass shows significant differences among the different depths (Kruskal-Wallis; $\alpha = 0.10$), the overlapping bars for the standard error of nannoplankton biomass indicate that variance within each

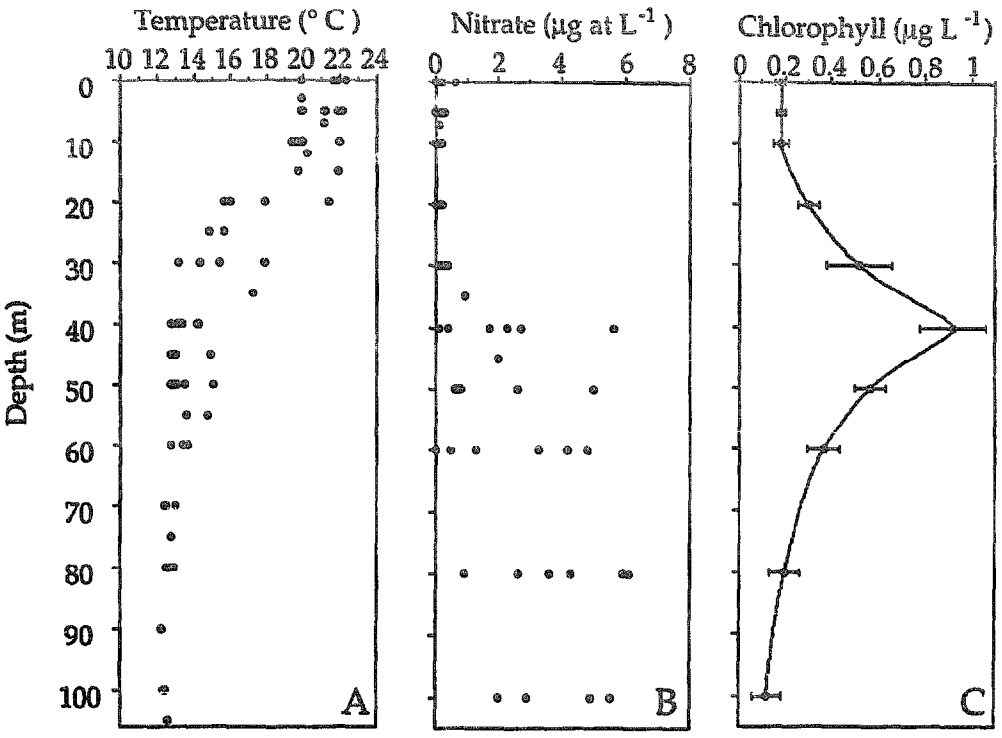

Fig. 2. Vertical profiles obtained for the stations in the Cantabric Sea during ASFLOR-I cruise. A. Set of data from different stations for temperature. B. Set of data from different stations for nitrate concentration. C. Mean values among stations of chlorophyll concentrations; bars represent standard error.

depth is also large. Nevertheless, this nannoplankton biomass maximum appears associated to a more apparent minimum in the slope (b) of the normalized size-biomass spectrum (Fig. 3D) that express a predominance of smaller (nanno) phytoplankters.

If we assume the convention that the compensa-

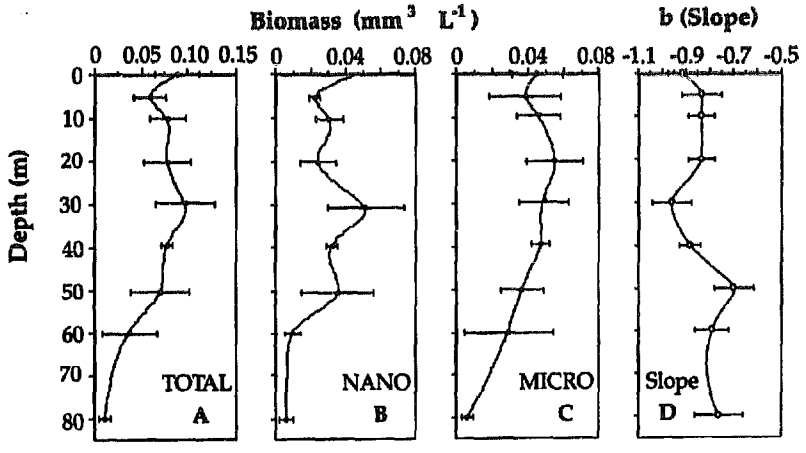

Fig. 3. Vertical profiles of mean biomass among stations in the Cantabric Sea obtained during ASFLOR-I cruise. A. Total assemblage of plankton. B. Nannoplankton. C. Microplankton. Bars represent standard errors. Also in (D) the slope of the normalized size-biomass spectrum and its confidence interval (90%) is displayed.

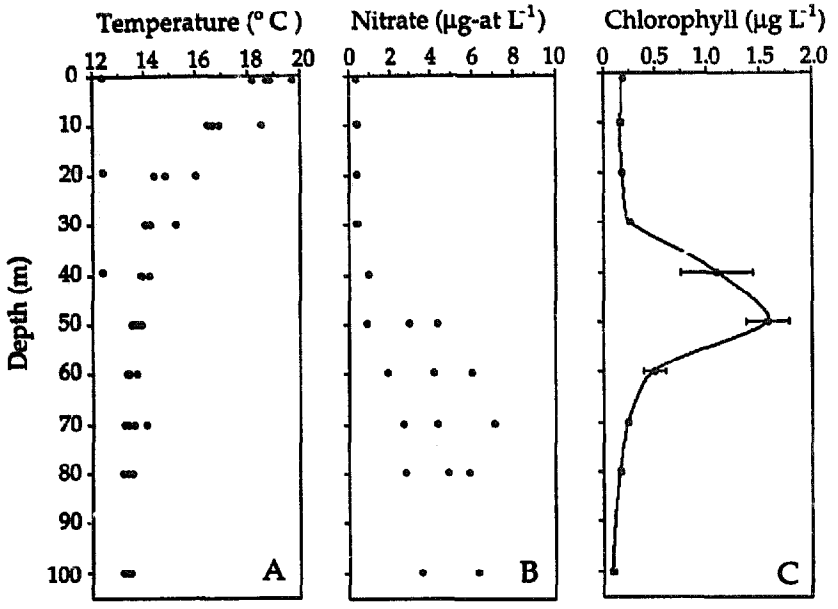

Fig. 4. Profile of temperature (A), nitrate concentrations (B) and mean and standard error of chlorophyll concentrations (C) for the stations in the Balearic Sea during FRONTS-89 cruise.

tion depth is near 1% of incident light (Parsons et al., 1984; Valiela, 1984), it occurs between 40 and 90 m (Biodatos Básicos, 1991). Thus, in layers deeper than 30 m nitrate is not limiting (Fig. 2B) whereas light becomes limiting only for layers deeper than 40 m. Hence, the subsurface maximum of nannoplankton and the minimum value of *b* are associated with a zone where neither nutrients nor light are limiting phytoplankton growth.

3.2. Balearic Sea

3.2.1. The stratification period (FRONTS-89)

The temperature profile for the four biological stations of the FRONTS-89 cruise shows a thermocline that extends from surface to 50 m (Fig. 4A). Nitrate concentrations are very low at the surface and there is a sharp increase from 40 m depth. The high gradient and concentrations of nitrogen make it

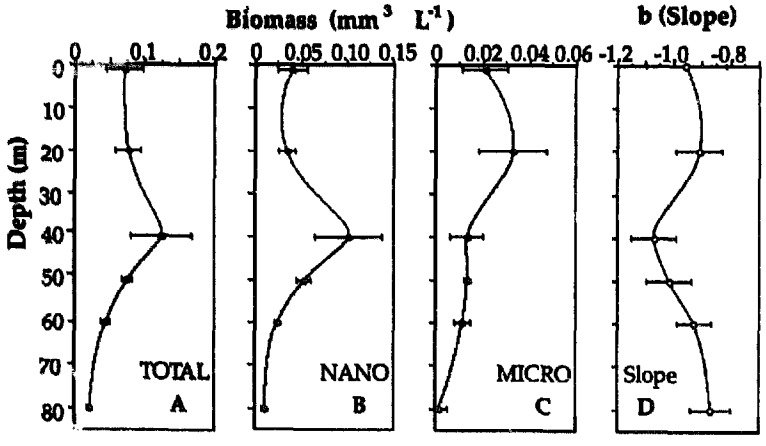

Fig. 5. Vertical profiles of mean biomass among stations in the Balearic Sea during FRONTS-89 cruise. A. Total assemblage of plankton. B. Nannoplankton. C. Microplankton. Bars represent standard errors. Also in (D) the slope of the normalized size-biomass spectrum and its confidence interval (90%) is displayed.

sensible to expect that at depths deeper than 40 m nutrients do not limit phytoplankton growth. Chlorophyll-a profile (Fig. 4C) has a subsurface maximum which coincides with the bottom of the thermocline (50 m). The compensation depth for the zone (Latasa et al., 1992) is between 40 and 60 m.

The size structure of phytoplankton responds to this vertical structure with an even more well-defined pattern than in the case of the Cantabric Sea. Microplankton biomass (Fig. 5C) shows a slight maximum in the upper layers, and then a tendency to decrease with depth, specially at the bottom of the thermocline. Nannoplankton biomass (Fig. 5B) has, however, a maximum at 40 m depth, 10 m shallower than the chlorophyll-a maximum. The tendencies for the total assemblage are similar to that of nannoplankton (Fig. 5A). In the three cases (microplankton, nannoplankton and total biomass), a comparison of biomass values among different depths by means of a Kruskal-Wallis test displayed the existence of significant differences ($\alpha = 0.05$).

The value of b has a minimum at 40 m depth (Fig. 5D). Spectra from different stations but from the same depth were pooled, as in the study of the Cantabric Sea, checking that the same linear model fitted data from the same depth. Nevertheless, the comparison of slopes among different depths displayed the existence of significant differences ($\alpha = 0.05$). Hence, these data also show the presence of subsurface minima of b shallower than the chlorophyll-a maximum and coincident with nannoplankton maximum.

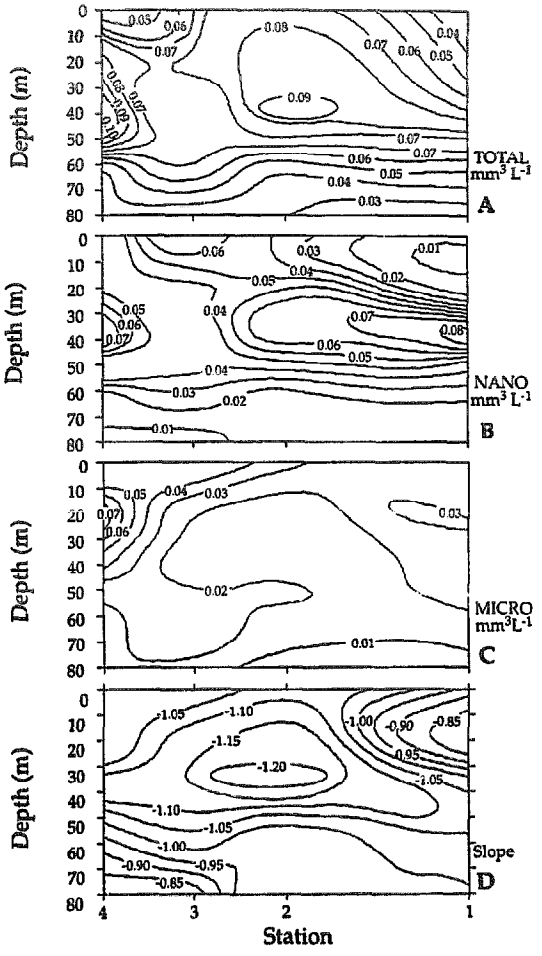

Fig. 6. Contour map of biomass (mm^3/l) for the stations in the Balearic Sea during FRONTS-89 cruise. A. Total biomass (nanno + microplankton). B. Nannoplankton. C. Microplankton. Also in (D) the contour map of the slope of the normalized size-biomass spectrum is displayed.

3.2.2. *The case of a front*

The presence of a frontal system is another important feature of the zone studied during the FRONTS-89 cruise. Station 3 is the closest to this frontal system as it is in the zone of maximum salinity gradient (see description in Saiz et al., 1992). At this station there is a slight increase of nannoplankton biomass between 20 and 50 m depth without a well defined maximum (Fig. 6B). Stations 1, 2 and 4 fit to the vertical biomass pattern described before. Total biomass isolines (Fig. 6A) display a pattern similar to those of nannoplankton. Microplankton biomass (Fig. 6C) has a decreasing tendency with depth, with a maximum at 20 m in station 4. Isolines of b (Fig. 6D) display a subsurface minimum in all the studied zone. This minimum is placed around 40 m depth for stations 2, 3 and 4, but it sinks to 50 m for station 1. Other characteristics of the distribution of b are: at the stations near the front (2, 3 and 4) the stratification of b (in the first 50 m) is not as sharp as at station 1; moreover, at these stations the subsurface minimum of b is more negative than at station 1. That indicates that in the proximity of the front (where the biological productivity is increased; Mann and Lazier, 1991) the size structure of phytoplankton communities changes towards an increase in the proportion of small cells.

3.2.3. The mixing period (FRONTS-91)

The heterogeneity in the physical and chemical variables of different stations is such that it is not possible to pool data from the four biological stations of the cruise FRONTS-91. Fig. 7A shows the presence of a weak thermocline in the sampled stations with small vertical gradients, especially in the stations 73 and 74. This temperature distribution is associated with a gradient in nutrient concentrations (Fig. 7B). Chlorophyll-a (Fig. 7C) has a maximum in the station 73 at 20 m depth and another in station 77 at 40 m depth.

Total biomass isolines (Fig. 8A), as temperature and nutrients, have smaller vertical gradients in the stations closer to the coast; thus evidencing how the stratification in offshore stations bears the vertical structure of phytoplankton community. Spatial distribution of nannoplankton biomass in stratified condi-

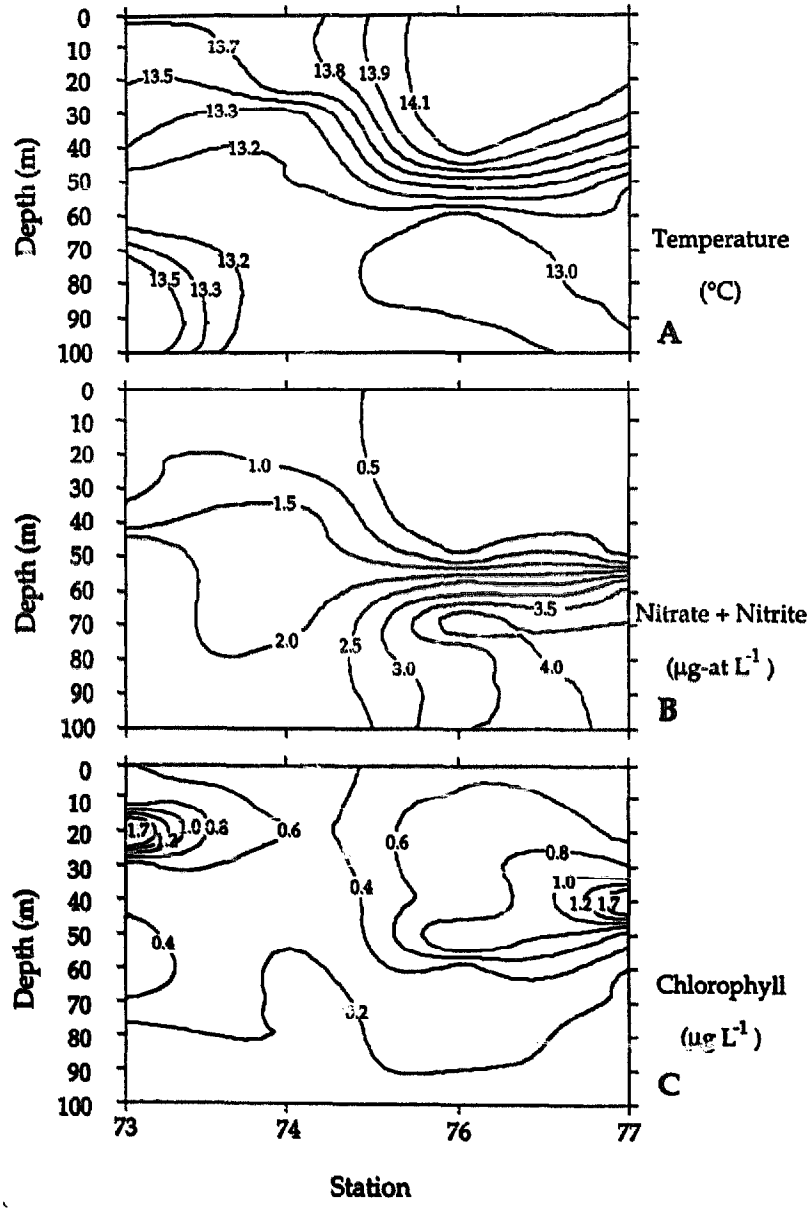

Fig. 7. Contour map of temperature (A), nitrate + nitrite (µg at/l) (B) and chlorophyll (µg at/l) (C) for the stations in the Balearic Sea during FRONTS-91 cruise.

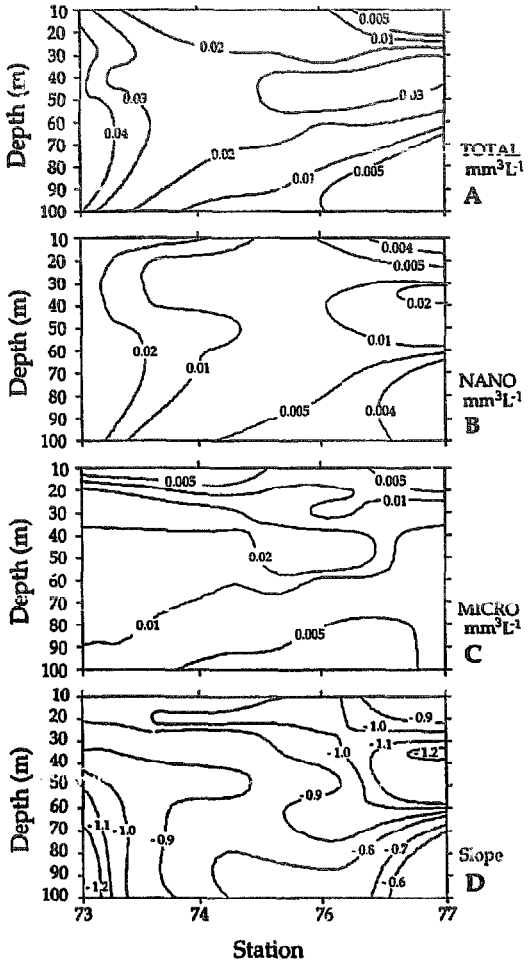

Fig. 8. Contour map of biomass (mm^3/l) for the stations in the Balearic Sea during FRONTS-91 cruise. A. Total biomass (nanno + microplankton). B. Nannoplankton. C. Microplankton. Also in (D) the contour map of the slope of the normalized size-biomass spectrum is displayed.

tions (station 77 in Fig. 8B) exhibits the tendency to accumulate in a slightly shallower depth than the subsurface chlorophyll-a maximum; thus, showing in station 77 (the only one with an association of subsurface chlorophyll-a maximum with the thermocline) a maximum near but shallower than the chlorophyll-a maximum. The remaining stations show no evidence of stratification but rather the presence of a horizontal gradient. Microplankton (Fig. 8C) has a spatial distribution different from nannoplankton with low surface values, an increase between 20–60 m and then a decline down to 80 m. At station 73, the microplankton biomass maximum is slightly deeper than the chlorophyll-a maximum. Microplankton isolines display how neither the stratification in station 77 nor the coastal–open ocean gradient markedly change the described pattern of microplankton distribution.

Isolines of b (Fig. 8D) are similar to those for nannoplankton biomass (Fig. 8B) with two basic characteristics: (1) there is a coastal–open ocean gradient with a tendency to a gradual horizontality in isolines; (2) there is a change in the size structure of the phytoplankton community in station 77 where there is a subsurface minimum at 35 m depth, 5 m above the subsurface chlorophyll-a maximum and coincident with the nannoplankton maximum.

4. Discussion

The presence of subsurface chlorophyll maxima (SCM) in stratified waters is usually related (Longhurst and Harrison, 1989) with nutrients diffusion through the pycnocline towards a zone where light intensity allows a positive net photosynthesis. Chlorophyll and biomass maxima are expected to coincide when maxima develop in waters with a seasonal stratification (Longhurst and Harrison, 1989). The vertical structure of temperature, nitrate and chlorophyll that has been recorded for the Cantabric and Balearic (FRONTS-89) seas is characteristic of the oligotrophic phase of temperate seas (Mann and Lazier, 1991). However, our data clearly display how, even in the case of a seasonal stratification, chlorophyll-a and biomass maxima can be located at different depths. Despite the fact that the vertical resolution of our study is not detailed enough to ensure that the biomass maximum has been sampled by an oceanographic bottle, we can at least affirm that the subsurface chlorophyll-a maximum did not coincide with the nannoplankton biomass maximum at the ten meters resolution with which we have sampled. Moreover, the presence of photoadaptation is clear by the poor correlation between biomass and chlorophyll, both in the Cantabric ($r^2 = 0.10$) and Balearic Sea ($r^2 = 0.07$). This poor correlation could also be originated by a high proportion of chlorophyll-a located at sizes smaller than 2 μm. We cannot discard this possibility as we have no estimates of biomass in size fractions smaller than 2 μm. Nevertheless, the presence of photoadaptation

in the Balearic Sea was also evident when using high pressure liquid chromatography (Latasa et al., 1992) during the FRONTS-89 cruise.

Nannoplankton biomass maxima appear more diffuse in the presence of a frontal system (Fig. 6). They are located, both in the Cantabric and Balearic seas, at a depth shallower than the chlorophyll-a maximum and in a zone where the ambient light and nutrient concentration are favorable for phytoplankton growth. Nannoplankton accumulates in a zone which is favorable for its growth and this increase in the growth rate is likely to be the main mechanism producing this accumulation. There are two other mechanisms that have been proposed in the literature to explain the accumulation of phytoplankton cells in the seasonal pycnocline: sedimentation and motility of phytoplankton cells. The size structure analysis of pelagic communities can be used to check the validity of these different explanations.

Growth rates for small phytoplankters might be higher than those for larger ones in the subsurface maxima either because of the existence of an allometric relationship between growth and size (Peters, 1983) or because the increased light absorption efficiency of smaller cells of phytoplankton at low levels of light due to a lower package effect (Kirk, 1994). If phytoplankton growth rate is size dependent, then nannoplankton would selectively concentrate in the favorable part of the thermocline. If this is the case, a more negative slope should be expected for the size spectrum in the zone of the thermocline where neither nutrients nor light are limiting, which is just what we find in our study.

Our results reflect how in zones of high productivity the size structure of the plankton community changes towards a higher proportion of small phytoplankton. This is true not only in the vertical but also in the horizontal scale as evident from Fig. 6 where the more negative values for b are found in the stations close to the front. These results are, at a first sight, not consistent with both the hypothesis of Malone (1980) (on the importance of phytoplankton of different sizes in relation to the kinetic of nutrient assimilation) and the compilation of results presented by Chisholm (1992) (on the proportion of chlorophyll contained in cells of small size as a function of chlorophyll concentration). According to the hypothesis of Malone (1980), large cells are selected in conditions where nutrients are not limiting. The advantage of large cells being due to differences in the kinetics of nutrient incorporation among cells of different size. The fact that our results are apparently in contradiction with Malone's hypothesis may be related to the influence that low levels of light can exert on the size structure of the phytoplankton community. Thus, it is clear that small phytoplankton has a better capacity to make use of low levels of light because they have higher initial slopes in the curves of photosynthesis versus light (Kirk, 1994; Platt et al., 1983). This fact can lead to a selective increase of smaller phytoplankters at these depths. Therefore, the discrepancy of our results with the expected according to Malone hypothesis can be explained because the size structure of the phytoplankton community in the subsurface biomass maximum (SBM) is governed more by the control that light limitation exerts on photosynthesis than by the kinetics of nutrient incorporation. This explanation recall other studies on the size structure of phytoplankton and its relation with the subsurface chlorophyll maximum (SCM). These studies showed that a very high percentage of the autotrophic cells at the SCM depth have a size smaller than 3 μm (Bienfang and Szyper, 1981 for North Pacific; Li and Wood, 1988 for North Atlantic) supporting the idea of a better light efficiency of smaller cells at this depth. A point that must be taken into account is that the maximum chlorophyll-a concentration that we have found in our samples is always lower than 2 $\mu g\ l^{-1}$. For that reason, our results do not contradict the conclusions obtained by Chisholm (1992) on the relationship between chlorophyll concentration and the proportion of that chlorophyll that is contained in phytoplankton of small size. After compiling the results of several authors, Chisholm concludes that small phytoplankton are associated to zones with low concentrations of chlorophyll whereas large phytoplankton are associated to zones with high concentrations of chlorophyll. However, for chlorophyll concentrations lower than 2 $\mu g\ l^{-1}$, the results compiled by Chisholm have a high scatter and it is possible to find that small phytoplankton can represent both either a high or a low proportion of the total chlorophyll.

As explained above, there are other possible mechanisms, like sedimentation or motility, to ex-

plain the formation of SBM. The different mechanisms do not exclude each other but the vertical distribution of b shows the preponderance of the increase in the growth rate since, as we will discuss below, the vertical pattern of b is not consistent with the formation of the SBM due to motility or sedimentation of cells.

Thus, if sedimentation were the mechanism for the formation of SBM, it should be expected that the proportion of large phytoplankton cells were greater in the zone of the maximum than in shallower waters. The reason for this expectation is that shallower waters would be under a constant loss of their larger cells (due to their high sedimentation velocity), and these cells would become part of the SBM. Consequently, if the accumulation of plankton in the SBM were the result of such a sedimentation from shallower layers, it should be expected a less negative value of b at this depth. Nevertheless, we have found just the opposite in this study (Figs. 3 and 5), a more negative value of b at this depth, indicating a higher proportion of smaller cells in the SBM. Sedimentation could have, however, some influence on the vertical size structure of the communities below the maximum of biomass where the sedimentation of large cells from this favorable zone could also explain the increasing tendency observed in b below this depth.

Motility of flagellates could lead them to advance towards zones where physical and chemical conditions are favorable (Holligan, 1981). Nevertheless, if this were the main accumulation mechanism, the velocity to which flagellate cells must swim should be higher than the vertical velocity due to turbulence in the pycnocline. This velocity can be obtained under dimensional grounds from the vertical eddy diffusivity (Kv) and a characteristic spatial scale (L) of the pycnocline. The values of Kv cited in the literature range from 10^{-6} m^2/s to 0.05 m^2/s (Okubo, 1980), a common intermediate value is 3×10^{-5} m^2/s (Lewis et al., 1986). A sensible value for L, regarding the length scales reported by Brainerd and Gregg (1993) for stratified surface waters, is of the order of 1 m. To these values of Kv and L correspond vertical velocities, due to turbulence, between 1 μm/s and 5 cm/s. On the other hand, the velocity with which a flagellate is able to swim range between 1 and 10 times its body diameter per second (Purcell, 1977, 1978). Thus, the size range of flagellates which are able to control their vertical position in the thermocline can be obtained from the combination of vertical velocity due to turbulence and swimming velocity (Fig. 9). Fig. 9 displays how under low turbulence levels most flagellates are able to control their position in the thermocline so that they can move towards favorable conditions. The opposite situation occurs when turbulence is high since no flagellate is able to control its position in the thermocline. With an intermediate turbulence value (Kv $= 3 \times 10^{-5}$ m^2/s), nannoplankton is in the limit of those cells which are able to control their position in the thermocline so that the formation of the SBM could, in principle, be also explained by cell motility. Nevertheless, if the subsurface nannoplankton accumulation were due to plankton motility, b should be less negative in the maximum since as a rule, large cells will have usually a better capacity to advance towards favorable zones. This generalization, i.e., large phytoplankters more motile than smaller ones, is likely to be this case since in stratified conditions the smaller cells turned out to be mainly non motile *Synechococcus* and larger cells consisted mainly of flagellates as *Gyrodinium* and *Gymnodinium* as well as some *Nitzschia* (Delgado et al., 1992). We have found, however, that b becomes more negative in the part of the thermocline where neither nutrients nor light

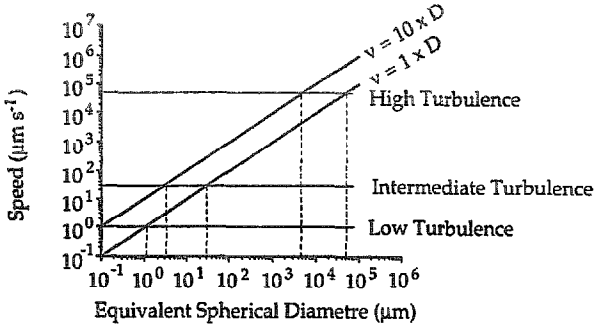

Fig. 9. Swimming velocity of flagellates versus size. Horizontal lines mark different vertical turbulent velocities in the thermocline, according to the values reported by Okubo (19) and Lewis et al. (1986). We can consider, for example, the case of high turbulent conditions in which vertical turbulent velocities can reach 5 cm/s. Under these conditions, for a flagellate swimming at ten times its size per second to control its position in the thermocline, it should has a size of, at least, 5000 μm.

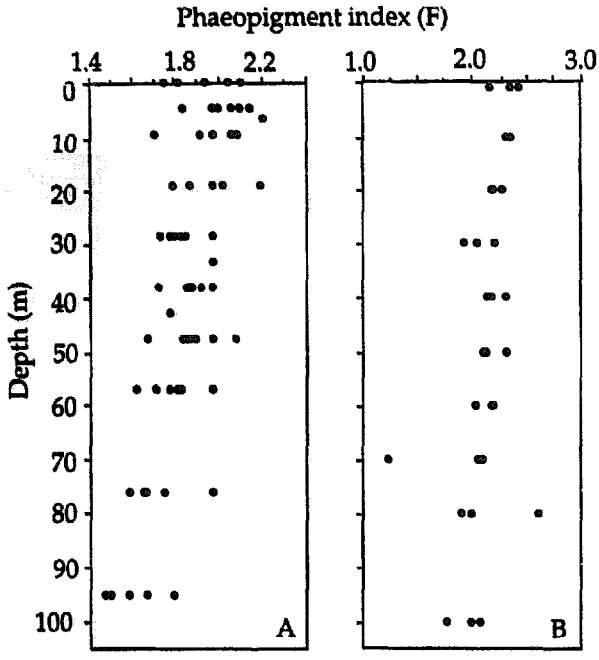

Fig. 10. Profile of the phaeopigments index (phaeopigment concentration/chlorophyll concentration) for (A) the Cantabric and (B) Balearic (FRONTS-89) seas.

are limiting and the biomass maximum develops. This result supports the idea of preferential accumulation of smaller, less motile cells in the SBM due to increased growth rate.

It could be argued against all the above arguments that the more negative value of b in the subsurface maximum could be due to selective grazing pressure on large cells (Hargrave and Geen, 1970; Runge, 1980) at this maximum; thus, decreasing the abundance of large cells with less impact on the small ones. However, the profile of phaeopigments (Fig. 10) does not show any maximum which may indicate the presence of high grazing pressure on a certain depth (Lorenzen, 1967; Vernet and Lorenzen, 1987).

Another important point that must be taken into account when trying to compare results and conclusions of different studies of plankton size structure is the methodology used in these studies. An example of this feature is the fact that our results and conclusions do not coincide with those obtained by Delgado et al. (1992) for the same area. These authors analyze the variability in the vertical distribution of phytoplankton size structure in the same zone (FRONTS-89 cruise) that we have analyzed. Delgado et al. did not find any clear pattern of variation of the size structure of phytoplankton along the water column. This contradiction between our results and those of Delgado et al. is only apparent and arises from the different methodology used. Thus, our methodology is valid to study the size range 2–100 μm whereas that of Delgado et al. is reliable in the 1–10 μm size range. These differences in the explored size range make that what we see as an increase in the proportion of small cells, for Delgado et al. is an increase in all the size classes that they were able to analyze by using their technique.

Our results also disagree with those of Revelante and Gilmartin (1995). These authors found an increase in the relative contribution of microplankton to the plankton biomass in the subsurface maxima of the Adriatic sea. This discrepancy cannot be attributable to the methodology, as the methods used in this study are similar to that of Revelante and Gilmartin. The differences obtained in the size data for the biomass subsurface maxima in the Adriatic and the northwestern Mediterranean seas must then be due to the different structures of the pelagic ecosystem in both zones. Thus, the maxima described by Revelante and Gilmartin are deeper and much closer (less than 30 m) to the bottom than in this study (all stations were deeper than 200 m). The chlorophyll and biomass maxima in the Adriatic are at the same depth and situated below the thermocline. In spite of these environmental differences, we cannot give a clear explanation to the nature of these differences in the vertical structure of size distribution. The difficulty to clearly explain the vertical patterns of plankton size structure is also related to the scarcity of these type of studies and to the methodological differences among these studies. This stresses the need for a standardization of the techniques to obtain plankton size spectra.

Acknowledgements

This work was supported by CICYT projects PPA86/0401 and MAR90/0339 as well as one from Plan Andaluz de Investigación no. 9/88. We wish to thank to Drs. Marta Estrada and Ricardo

Anadón as chief scientists of the cruises ASFLOR and FRONTS for the facilities provided during those cruises and for the suggestions and comments to the ideas developed in this paper. We acknowledge also the suggestions of anonymous referees that improved the final version of the manuscript.

References

Bienfang, P.K. and Szyper, J.P., 1981. Phytoplankton dynamics in the subtropical Pacific Ocean of Hawaii. Deep-Sea Res., 28: 981–1000.

Biodatos Básicos, 1991. Rev. Biol. Univ. Oviedo., 5 (suppl.).

Blanco, J.M., Echevarría, F. and García, C.M., 1994. Dealing with size-spectra: Some conceptual and mathematical problems. Sci. Mar., 58(1–2): 17–29.

Brainerd, K.E. and Gregg, M.C., 1993. Diurnal restratification and turbulence in the oceanic surface mixed layer. 1. Observations. J. Geophys. Res., 98: 22,645–22,656.

Chisholm, S.W., 1992. Phytoplankton size. In: P.G. Falkowski and A.D. Woodhead (Editors), Primary Productivity and Biogeochemical Cycles in the Sea. Plenum Press, London, pp. 213–237.

Delgado, M., Latasa, M. and Estrada, M., 1992. Variability in the size-fractionated distribution of the phytoplankton across the Catalan front of the north-west Mediterranean. J. Plankton Res., 14: 753–771.

Grasshoff, K., Ehrhardt, M. and Kremling, K., 1983. Methods of Seawater Analysis. Chemie, Weinheim.

Hargrave, B.T. and Geen, G.H., 1970. Effects of copepods grazing on two natural phytoplankton populations (A. Tonsa). J. Fish. Res. Board Can., 27: 1395–1403.

Holligan, P.M., 1981. Biological implication of fronts on the northwest European continental shelf. Philos. Trans. R. Soc., 302: 547–562.

Kirk, J.T.O., 1994. Light and photosynthesis in aquatic ecosystems. Cambridge Univ. Press.

Latasa, M., Estrada, M. and Delgado, M., 1992. Plankton–pigment relationships in the northwestern Mediterranean. Mar. Ecol. Progr. Ser., 88: 61–73.

Lewis, M.R., Harrison, W.G., Oakey, N.S., Hebert, N.S. and Platt, T., 1986. Vertical nitrate fluxes in the oligotrophic ocean. Science, 234: 870–873.

Li, W.K.W. and Wood, A.M., 1988. The vertical distribution of North Atlantic ultraplankton, analysis by flow cytometry and epifluorescence microscopy. Deep-Sea Res., 35: 1615–1638.

Longhurst, A.R. and Harrison, W.G., 1989. The biological pump: Profiles of plankton production and consumption in the upper ocean. Progr. Oceanogr., 22: 47–123.

Lorenzen, C.J., 1967. Vertical distribution of chlorophyll and phaeopigments: Baja California. Deep-Sea Res., 14: 735–746.

Malone, T.C., 1980. Algal size. In: I. Morris (Editor), The Physiological Ecology of Phytoplankton. Univ. Calif. Press, Berkeley.

Mann, K.H. and Lazier, J.R.N., 1991. Dynamics of Marine Ecosystems. Blackwell, Oxford.

Okubo, A., 1980. Diffusion and Ecological Problems: Mathematical Models. Springer, Berlin.

Parsons, T.R., 1969. The use of particle size spectra in determining the structure of a plankton community. J. Oceanogr. Soc. Jap., 25: 172–181

Parsons, T.R., Takahashi, M. and Hargrave, B., 1984. Biological Oceanographic Processes. Pergamon, Oxford, 330 pp.

Peters, R.H., 1983. The Ecological Implications of Body Size. Cambridge Univ. Press.

Platt, T. and Denman, K., 1977. Organization in the pelagic ecosystem. Helgol. Wiss. Meeresunters., 30: 575–581.

Platt, T. and Denman, K., 1978. The structure of pelagic marine ecosystem. Rapp. P. Réun. Comm. Int. Expl. Mer., 173: 60–65.

Platt, T., Subba-Rao, D.V. and Irwin, B., 1983. Photosynthesis of picoplankton in the oligotrophic ocean. Nature, 300: 702–704.

Purcell, E.M., 1977. Life at low Reynolds number. Am. J. Phys., 45: 3–11.

Purcell, E.M., 1978. The effect of fluid motion on the absortion of molecules by suspended particles. J. Fluid Mech., 84: 551–559.

Quiñones, R.A., 1992. Size-distribution of planktonic biomass and metabolic activity in the pelagic system. Thesis. Dalhousie Univ.

Revelante, N. and Gilmartin, M., 1995. The relative increase of larger phytoplankton in a subsurface chlorophyll maximum of the northern Adriatic Sea. J. Plankton Res., 17: 1535–1562.

Rodríguez, J. and Mullin, M.M., 1986. Relation between biomass and body weight of plankton in a steady state oceanic ecosystem. Limnol. Oceanogr., 31: 361–370.

Rodríguez, J. and Li, W.K.W., 1994. The size structure and metabolism of the pelagic ecosystem. Sci. Mar., 58(1–2): 1–167.

Ruiz, J., 1993. Patrones espaciales y temporales en la estructura de tamaños del material particulado pelagico marino. Thesis. Malaga Univ.

Runge, J.A., 1980. Effects of hunger on the feeding behaviour of *Calanus pacificus*. Limnol. Oceanogr., 25: 134–135.

Saiz, E., Rodríguez, V. and Alcaraz, M., 1992. Spatial distribution and feeding rates of *Centropages typicus* in relation to frontal structures in the Catalan Sea (Western Mediterranean). Mar. Biol., 112: 49–56.

Sheldon, R.W., Prakash, A. and Sutcliffe, W.H., 1972. The size distribution of particles in the ocean. Limnol. Oceanogr., 17: 327–340.

Utermöhl, H., 1958. Zur vervollkommung der quantitativen Phytoplankton Methodik. Mitt. Int. Ver. Limnol., 9: 1–38.

Valiela, I., 1984. Marine Ecological Processes. Springer, New York, 525 pp.

Varela, R. and Grupo FRONTS, 1991. Informe FRONTS: Datos oceanográficos básicos de las campañas FRONTS 89, FRONTS 90 y FRONTS 91 en el Mar Catalán. Inst. Cienc. Mar Barcelona.

Vernet, M. and Lorenzen, C.J., 1987. The presence of chlorophyll b and the estimation of phaeopigments in marine phytoplankton. J. Plankton Res., 9: 255–265.

Whitledge, T.C., 1981. Automated nutrient analysis in seawater. Brookhaven Natl. Lab. Nat. Tech. Inf. Serv., Springfield.

Witek, Z. and Krajewska-Soltys, A., 1989. Some examples of the epipelagic plankton size-structure in high latitude oceans. J. Plankton Res., 11: 1143–1155.

Yentsch, C.S. and Menzel, D.W., 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Res., 10: 221–231.

Zar, J.H., 1984. Biostatistical Analysis. Prentice-Hall, New Jersey.