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SINGLE-SPECIES DOMINANCE IN A SUBSURFACE PHYTOPLANKTON CONCENTRATION AT A MEDITERRANEAN SEA FRONT

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A narrow band of high Chl a (23.1 ug liter^{-1}) was observed at a salinity front in the western Mediterranean Sea in late November 1987. The biomass peak was found deep in the photic zone, at 54 m, in a region of low light. A single diatom species, Thalassiosira partheneia Schrader in gelationous colonies, represented 98% of the total phytoplankton biomass in the layer and achieved abundance >9.8 x 10^{4} cells liter^{-1}. Although lack of temporal sampling precludes precise determination of the processes responsible, the high biomass accumulation and dominance by this species was likely due to its preference for low light coupled with turbulence-induced high nutrient levels. Interleaving patterns in the temperature, salinity, and nutrient profiles suggest increased horizontal advection at the front. High shear at the boundaries of the interleavings might confine the biomass to a thin band, as well as generate turbulence to mix nutrients in from surrounding layers. Alternatively, stabilization of the water column following a brief, pulsed upwelling event could have reduced dispersion of the biomass, thereby confining it to the thin layer we observed.

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Single-species dominance in a subsurface phytoplankton concentration at a Mediterranean Sea front

Abstract—A narrow band of high Chl *a* (23.1 μg liter^{-1}) was observed at a salinity front in the western Mediterranean Sea in late November 1987. The biomass peak was found deep in the photic zone, at 54 m, in a region of low light. A single diatom species, *Thalassiosira partheneia* Schrader in gelatinous colonies, represented 98% of the total phytoplankton biomass in the layer and achieved abundances $>9.8 \times 10^6$ cells liter^{-1}. Although lack of temporal sampling precludes precise determination of the processes responsible, the high biomass accumulation and dominance by this species was likely due to its preference for low light coupled with turbulence-induced high nutrient levels. Interleaving patterns in the temperature, salinity, and nutrient profiles suggest increased horizontal advection at the front. High shear at the boundaries of the interleavings might confine the biomass to a thin band, as well as generate turbulence to mix nutrients in from surrounding layers. Alternatively, stabilization of the water column following a brief, pulsed upwelling event could have reduced dispersion of the biomass, thereby confining it to the thin layer we observed.

In an environment where multispecies assemblages are common and the "paradox of the plankton" is the norm (Hutchinson 1961), it is unusual to find an open ocean region dominated by a single species. Although phytoplankton "blooms" are widespread and have been reported in coastal areas, upwellings, enclosed bays, and during spring stratification, a combination of somewhat atypical conditions is required for bloom formation (Paerl 1988). In November 1987, we observed a Chl *a* maximum concentration of 23.1 μg liter^{-1} in a narrow band at 54 m in the Almeria-Oran Front in the western Mediterranean Sea. Subsequent microscopic analysis revealed a gelatinous colony-forming diatom (*Thalassiosira partheneia* Schrader) as the overwhelmingly dominant species with an abundance $>9.8 \times 10^6$ cells liter^{-1}. What factors enabled this single species to attain such a concentration?

Biological, chemical, and physical factors must be examined in any attempt to answer the above question. Although it is likely that several factors were responsible, it is important to assess the relative importance of each. In terms of the biology, species interactions and the affect of competition must be considered, as must grazer control and nutrient concentrations and distributions. The nature of the physical environment with regard to turbulence, water mass interleaving, and convergence/divergence regimes must also be determined to assess their roles in controlling the observed distribution.

This biomass accumulation was unusual for several reasons. First, it was totally dominated by a single species. Second, such high cell numbers are rarely observed in the open ocean—even in a bloom—and have not, to our knowledge, been reported for the Mediterranean away from the coast. Third, the biomass-rich layer was very narrow—only about 6 m thick. Fourth, the bloom was found late in the year (this station was occupied on 29 November) when there was little thermal stratification. Finally, the biomass was concentrated deep in the water column and in very low light, which is discussed later.

A strong salinity gradient stretches nearly from Almeria, Spain, to Oran, Algeria, in the Alboran Sea in the western Mediterranean, creating the Almeria–Oran Front (A–O Front). This front results from less saline Atlantic water flowing in through the Strait of Gibraltar and converging with more sa-

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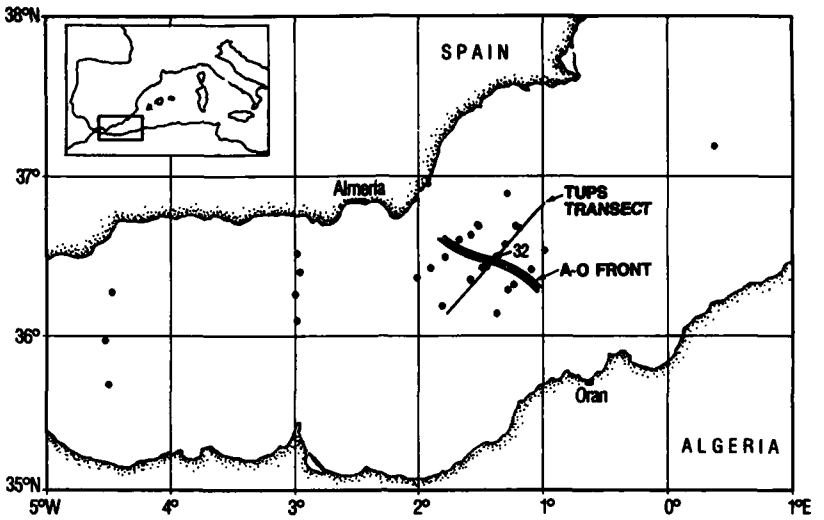

Fig. 1. Station locations in the western Mediterranean during November 1987 in relation to the Almeria–Oran Front. The Chl *a* value of 23.1 μg liter^{-1} was recorded at 54 m at station 32. The position of the front was determined from CTD transects during the cruise.

line Mediterranean water. The Alboran Basin contains twin anticyclonic gyres and the A–O Front is the eastern boundary of the eastern gyre. The front extends to a depth of 200 m, but the upper 60–75 m are unstable and meanders are common. The front is present year-round and surface currents there average 40 cm s^{-1}. The thermal contrast across the front is not large, only 1°–2°C, but the two-salinity-unit change over a distance of 2–15 km creates a sharp density boundary (Arnone et al. 1990). Prevailing winds in the vicinity of the front are generally light but variable in both direction and intensity. Atmospheric fronts move northwest to southeast. The A–O Front does not represent a direct wind response, but the large-scale wind stress of the western Mediterranean probably does affect frontal strength and location (G. Heburn pers. comm.).

Samples were collected in the Alboran Sea from 14 November to 3 December 1987 from the USNS *Lynch*. Station locations are indicated in Fig. 1 relative to the A–O Front, but only station 32 is labeled—the frontal station where the large biomass accumulation was observed. The goal of the study was to assess the biological, chemical, and physical properties in a dynamic frontal region with a high-density sampling strategy. Component investigations included phytoplankton species composition, abundance, biomass, and productivity; activity of the respiratory electron transport system (ETS); bacterial abundance and production; Chl *a* distribution; nutrients; temperature; salinity; oxygen; and optical and meteorological data. Satellite imagery collected at the Naval Ocean Research and Development Activity (NORDA) and telemetered to the *Lynch* provided both real-time data for locating the frontal boundary and a synoptic view of the temperature field in the area. The NORDA towed underwater pumping system (TUPS) was used to exactly locate the front and to map surface features (Rein et al. 1985). A complementary cruise to the same region in May 1986 examined the same properties in spring (Lohrenz et al. 1988*b*).

The TUPS consists of a 2.4-m-long tow body containing a SeaMarTech, Inc., fluorometer and Sea Tech, Inc., beam transmissometer (670-nm operating wavelength, 25-cm pathlength); Sea Bird, Inc., CTD sensors; and Biospherical Instruments upwelling and downwelling irradiance sensors (model QSP 200). The system was towed 2 m below the surface at 400 cm s^{-1} and data

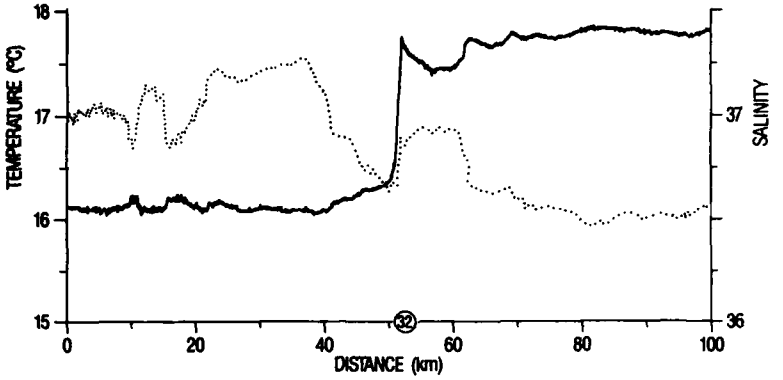

Fig. 2. Temperature (·····) and salinity (——) at 2 m along west-to-east TUPS transect perpendicular to Almeria–Oran Front (transect indicated in Fig. 1). The location of station 32 is noted.

were collected every 12 s, which equated to one measurement about every 50 m horizontally.

The initial protocol for locating and mapping the front was to tow the TUPS for 6–8 h along a straight transect perpendicular to the front. XBTs were launched every 30 min or less along the transect, as well. Then, after plotting temperature, salinity, and fluorescence along the transect, features of interest at the front and on both the Atlantic and Mediterranean sides were selected for immediate, detailed vertical stations. Temperature and salinity data from a TUPS transect through the A–O Front are shown in Fig. 2. The location of station 32 in close proximity to the sharp salinity gradient is noted. After arriving back at a site, there were two CTD casts (Neil Brown Instr., Inc., Mark IIIB CTD)—a deep one (to 500 m) and a shallow one (to 100 m) with a fluorometer (or transmissometer) and submersible pump (Berkeley model 4BM12) attached. A 35-μm-mesh phytoplankton net was attached to the hydrocable during the deep cast for a vertical net tow in the upper 125 m.

The temperature, salinity, and fluorescence profiles for the down-cast of the shallow CTD were examined to select 12 sampling depths for the up-cast. Phytoplankton, bacterial, Chl *a*, and nutrient samples were taken from the pump/hose system. Chl *a* was measured with a Turner fluorometer following slightly modified methods of Smith et al. (1981), as described by Lohrenz et al. (1988*b*). For phytoplankton samples, glutaraldehyde was added to a final concentration of 1% for whole-water samples and 2% for net tows. Samples were kept refrigerated until analysis back in the laboratory at NORDA. The discrete water samples were settled and counted as by Gould and Fryxell (1988) with a Zeiss IM-35 inverted light microscope. In addition, cell sizes and areas were measured for subsequent biovolume and biomass estimates with an attached drawing tube in conjunction with a Summagraphics model MM1201 digitizing tablet and Zenith 248 microcomputer. Phytoplankton biomass was calculated from cell biovolume with the modified Strathmann equations (equations 7 and 8, Smayda 1978).

Incident surface solar flux was measured with an Eppley pyrheliometer and converted from $\mu W\ cm^{-2}$ to $\mu Einst\ m^{-2}\ s^{-1}$ following Parsons et al. (1977). The midday flux on 30 November (the day after station 32) was 65,000 $\mu W\ cm^{-2}$. The light level at 54 m was estimated from $I_z = I_0 \exp(-kz)$, with an attenuation length ($1/k$) of 15 m for Mediterranean water provided by Lohrenz et al. (1988*a*). The mean cell division rate (μF, doublings d^{-1}) of *T. partheneia* was calculated in the 54-m sample from the proportion of dividing cells (Weiler and Chisholm 1976; Rivkin and Voytek 1986):

$$F = \frac{0.5A + B}{0.5A + B + C}$$

where A is the number of single cells recently divided, B the number of paired cells, and

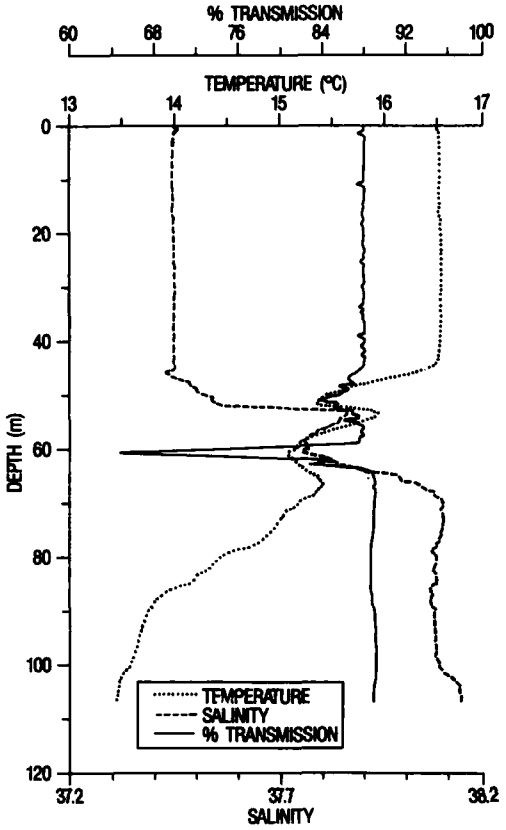

Fig. 3. Temperature, salinity, and percent transmission vs. depth at station 32.

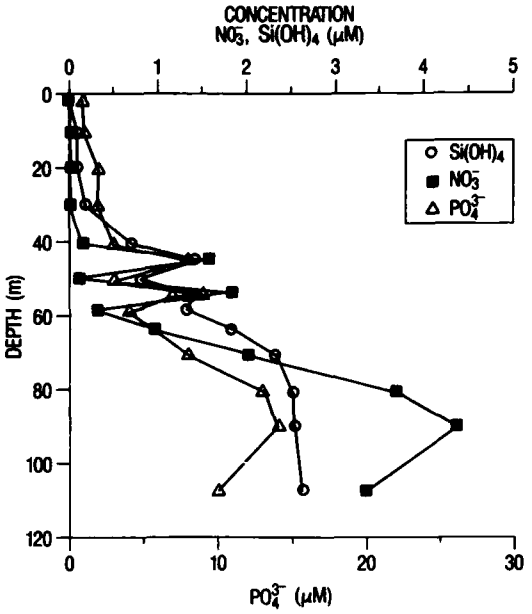

Fig. 4. Silicate, nitrate, and phosphate concentrations vs. depth at station 32.

C the number of single cells that have not recently divided. However, for diatoms this microscopic method cannot distinguish A and C, so the equation reduced to

$$F = \frac{B}{B + D}$$

where D is the total number of single cells, and

$$\mu F = \frac{\ln(1 + F)}{\ln 2 \times t}$$

where t is 1 d.

The estimate provided is very likely an underestimate of the true division rate because several problems and assumptions are involved with the technique. For example, because we did not have a time series of observations, we must assume that our observed F is equal to the maximum daily F and that it is an estimate of all cells undergoing mitosis. Also, paired cells might have dislodged during sample preparation (shaking), and they are difficult to distinguish in valve view. This method cannot detect division rates >1 because there is no way to know if a cell has divided already that day. The estimate must therefore be considered a "minimum division rate."

Temperature, salinity, and percent transmission at station 32 are shown in Fig. 3. The water column is well mixed to 45 m, but interleaving of water masses is apparent from 50 to 65 m. The surface salinity of 37.49 indicates that the station fell just on the Mediterranean side of the front. The temperature minimum at 61 m was coincident with a transmission minimum of 65% and marked the location of the Chl *a* peak. The data plotted are from the down-cast of the CTD; by the time we sampled from the hose during the up-cast, the minimum in percent transmission had shifted to 54 m, probably as a result of internal wave activity or spatial variability associated with ship drift near the frontal boundary. We adjusted our sampling accordingly to sample in and around the Chl *a* peak by using both the in situ transmissometer and a flow-through fluorometer in the lab connected to the pump

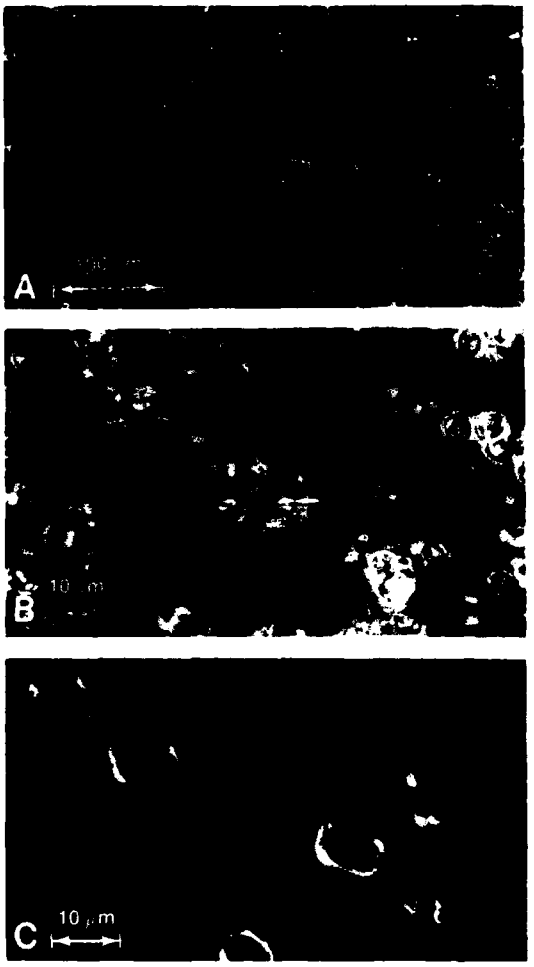

Fig. 5. *Thalassiosira partheneia* colony. A and B. Phase contrast illumination. C. Nomarski differential interference-contrast illumination. A. Orientation view of a colony with several pennate diatoms interspersed on the threads. B. Higher magnification of the colony showing numerous interconnecting threads. C. Detail of cells indicating delicate frustule structure and vacuous nature.

line. This allowed us to place the CTD/pump directly in the very narrow Chl *a* maximum.

Interleaving of water masses in the vicinity of the front is also apparent from the nutrient profiles in Fig. 4. Silicate, nitrate, and phosphate all show a similar "sawtooth" pattern from 40 to 60 m. It is of interest that the Chl *a* maximum at 54 m corresponded to a relative peak in nutrients, suggesting that the biomass there might not have peaked at the time of sampling but was still increasing.

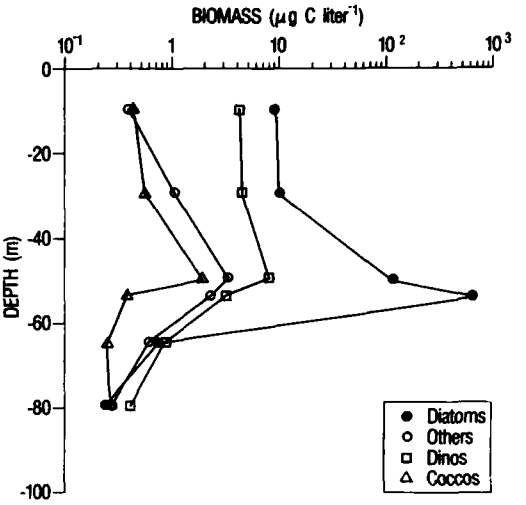

Fig. 6. Phytoplankton biomass vs. depth by group at station 32. Note log scale for biomass.

Vertical phytoplankton net tows were examined from the 32 stations shown in Fig. 1 (several stations sampled on different days were nearly coincident in space). Gelatinous colonies of *T. partheneia* (Fig. 5) were observed at every station, but their abundance varied widely. The colonies were most abundant at stations along the front. Detailed discussion of the distribution of this species and others will be presented elsewhere in conjunction with additional physical and chemical data (Gould et al. in prep). Figure 5A gives an impression of the size of the colonies; they were several millimeters long and clearly visible with the naked eye. Several bicapitate pennate diatoms (*Nitzschia capitata* Heiden and Kolbe?) were interspersed on the threads of the colonies. The numerous interconnecting threads appear as dark lines in Fig. 5B. The high magnification of Fig. 5C shows some of the detail of the cells and their vacuous nature. The diameters were generally 8–10 μm.

The biomass vs. depth profiles for diatoms, dinoflagellates, coccolithophorids, and other algae at station 32 are shown in Fig. 6. There are major differences in species composition between the six sample depths. All four groups exhibited increased biomass around 50–55 m, but particularly the diatoms. The diatom maximum also was about 5 m deeper than the maxima for the other

Table 1. Depth distribution of *Thalassiosira partheneia* abundance (cells liter^{-1}) and biomass (μg C liter^{-1}) at station 32.

Depth (m)	*T. partheneia*		% of total algal	
	Abundance	Biomass	Abundance	Biomass
10	31,000	2.00	11.2	14.2
30	90,700	5.85	37.5	36.6
50	1,690,000	109.12	70.4	85.2
54	9,860,000	635.98	92.1	98.3
65	1,630	0.10	1.3	4.2
80	787	0.05	1.6	4.9

groups and decreased sharply within the next 10 m.

Table 1 provides the depth distribution of *T. partheneia* abundance and biomass at station 32. Note the dramatic increases in those parameters from 30 to 54 m and the even more dramatic decreases below 54 m. That single diatom species represented an increasing proportion of the cell numbers and biomass from the surface to 54 m, where it accounted for 92% of the total phytoplankton cell numbers and 98% of the total biomass. The light level at the maximum was low, about 81 μEinst m^{-2} s^{-1}, 2.7% of the surface flux. Yet, the division rate of *T. partheneia* estimated from the proportion of dividing cells was 0.20 doublings per day. This does not indicate tremendous production, but does indicate, along with the healthy appearance of the colonies and cells, that the population was by no means senescent. Total integrated phytoplankton cell numbers and biomass at station 32 were 1.21×10^{11} cells m^{-2} and 7.03 g C m^{-2} (integrated to 80 m, 0.5% light level).

Total phytoplankton abundance, biomass, and Chl *a* vs. depth followed much the same pattern as *T. partheneia* (Table 2). Chl *a* per unit biovolume, C per unit biovolume and C : Chl *a* ratios are also given. The Chl *a* per unit biovolume values are very similar to the ranges of 2–6 and 1–100 fg Chl *a* μm^{-3} reported by Jimenez et al. (1987) and Nicholis and Dillon (1978), respectively. Although total cell numbers (and subsequently biomass, which was derived from cell numbers and biovolumes) and Chl *a* varied widely over the depth range examined, the Chl *a* μm^{-3} and C μm^{-3} ratios remained remarkably stable in the upper 54 m, but both increased in the deeper two samples (65 and 80 m).

The increased C μm^{-3} ratio reflected a taxonomic shift. The proportion of diatoms in the surface samples was considerably greater than at 65 and 80 m, where small monads dominated (coccoid cyanobacteria and eucaryotes). The larger proportion of nondiatom biomass at depth caused the C μm^{-3} ratio to increase because the modified Strathmann equations estimate less carbon per cell for diatoms compared to other phytoplankton cells of the same size, due to the larger vacuole volume of diatoms. Size-frequency analysis confirmed the shift to smaller cells at depth. In the upper four samples, the percent of the total biovolume that had an equivalent spherical diameter of ≤ 5 μm ranged from 0.3 to 3.0%, while in the 65- and 80-m samples the percentages were 23.4 and 29.9%. The increase in Chl *a* μm^{-3} suggests that the cells might have been exhibiting a photoadaptive response by increasing the amount of Chl *a* in the cell at lower light levels. The C : Chl *a* values above 54 m are close to an empirically derived estimate of 23.4 for another *Thalassiosira* species at a light level of 70 μEinst m^{-2} s^{-1} (from data of Falkowski et al. 1985), suggesting that the Utermöhl settling method could detect most of the biomass in these samples, at least in the upper 54 m.

Although both C and Chl *a* per unit biovolume increased in the 65- and 80-m sam-

Table 2. Total algal abundance (cells liter^{-1}), biomass (μg C liter^{-1}), Chl *a* (μg liter^{-1}), and ratios of Chl *a* and C μm^{-3} of biovolume by depth at station 32.

Depth (m)	Abundance	Biomass	Chl *a*	Chl *a* μm^{-3} (fg)	C μm^{-3} (fg)	C : Chl *a*
10	276,000	14.11	0.60	3.3	76.5	23.5
30	242,000	16.04	0.67	3.9	93.6	23.9
50	2,400,000	128.40	2.78	2.1	95.2	46.1
54	10,700,000	647.02	23.12	3.3	92.9	28.0
65	124,000	2.48	0.22	11.8	133.4	11.3
80	49,400	1.04	0.09	13.3	153.9	11.6

ples, there was a proportionately larger increase in Chl *a*, resulting in lower C : Chl *a* ratios. Alternatively, the lower C : Chl *a* ratios at depth might have been due in part to some "missing biovolume" (and subsequently carbon) associated with the higher proportion of picoplanktonic cells in those samples. Perhaps some of the small cells did not settle in the chambers before counting, were too small to be seen, or were destroyed by preservation, but were retained on the GF/F filters during the Chl *a* determinations. However, even if enough C was added to the 65- and 80-m samples to adjust the C : Chl *a* ratios to 25, the increased biovolume in the samples would decrease the Chl *a* μm^{-3} ratio to just 4.4 fg. This relatively high ratio still suggests that photoadaptation, not loss of small cells, was responsible for the lower C : Chl *a* ratio.

About a dozen species of the diatom genus *Thalassiosira* have been reported to form gelatinous colonies (Fryxell et al. 1984), and such colonies have been reported from a number of locations, including upwelling areas, warm-core rings, near the Antarctic ice edge, and now at a Mediterranean salinity front (Elbrächter and Boje 1978; Fryxell et al. 1984; Youngbluth and Paffenhöfer 1987; Fryxell and Kendrick 1988). Although a variety of environments is represented, all seem to have two factors in common, at least at the time when the colonies were observed: turbulence and high nutrients. In the warm-core rings, which are generally considered oligotrophic, colonies were frequently observed after storms that mixed the water column and brought nutrients into the euphotic zone (Fryxell and Gould 1983). Also, at least for *T. partheneia,* the colonies have been reported to be light inhibited and exhibited greater primary production at the 50% light depth compared to the 100% light depth (Elbrächter and Boje 1978). In warm-core ring 82-E, sampled in August 1982, *T. partheneia* colonies were observed at ring center with maximum cell numbers of about 40,000 cells $liter^{-1}$ at 59 m and decreasing abundances shallower (T. P. Watkins unpubl. obs.). When isolated colonies were placed in a constant-light incubator on board ship, the cells bleached and died within ~2 d (R.W.G. pers. obs.), and culture experiments by Elbrächter and Boje (1978) also showed light inhibition.

The importance of a colony habitat to the diatoms and to the water column trophic structure is not clear. Colony formation evidently occurs with healthy cells, as the photosynthetic activity of single cells is less than colonies, and the colonies disintegrate as they age or if they are light damaged (Elbrächter and Boje 1978). In the Northwest Africa upwelling area, *T. partheneia* colonies represented from 6 to 48% of the primary production at different stations and light depths and from 6 to 33% of the total water-column production (Elbrächter and Boje 1978).

Several hypotheses have been advanced suggesting possible advantages and disadvantages of a colony lifestyle. For example, nutrient availability to individual cells may be increased or decreased, depending on whether flow through the matrix is increased or decreased. If the colonies are an adaptation to increase sinking speed (Smetacek 1985), which according to Smayda (1970) is a means of contacting more nutrient-rich water and enhancing nutrient uptake, increased water column turbulence may be needed to resuspend the colonies. The gelatinous matrix might also act as a chelator to complex toxic substances or trap required trace metals. Grazers fed more readily on single cells of *T. partheneia* than on colonies, so there may be some protection against filter-feeding predation (Schnack 1983). Elbrächter and Boje (1978) observed numerous heterotrophic dinoflagellates, ciliates, and amoebae within healthy colonies, but we did not observe such associations in this study nor were they observed in the warm-core ring colonies (Fryxell et al. 1984). Other than cells of *T. partheneia,* only bicapitate pennate diatoms were observed in the colonies. Bacteria present in the colonies may be using dissolved organic carbon released by the diatoms, or they may be providing remineralized nutrients to the diatoms. Bacteria have been shown to be important colonizers of other types of marine snow and aggregates (Alldredge and Youngbluth 1985). Large colonies also absorb light less efficiently, which may protect against photoinhibition (Kirk 1983). Margalef (1978) views the mucous secretion as

a self-regulating control on nutrient absorbtion to prevent population crashes.

In terms of water-column processes, the colonies act as scavengers that rapidly remove materials through sedimentation, even within a few days (Billett et al. 1983: Lampitt 1985; Youngbluth and Paffenhöfer 1987). As mentioned, the matix may be unpalatable or too large for filter feeders and this may affect abundances and species composition in higher trophic levels. Clearly, much experimental work with cultures is still required to elucidate the advantages of a colony growth habit.

Except for reports of blooms related to river input and manmade effluent near the Mediterranean coast and in semienclosed bays (UNESCO 1988), other studies in the eastern and western Mediterranean during different seasons have reported low Chl *a* values (Furnestin 1973; Dowidar 1984; Estrada 1982, 1985). In fact, Chl *a* values of 23.1 μg liter^{-1} in the open ocean are rare and typically from highly productive coastal upwelling regions such as those off Peru or Africa (Andrews and Hutchings 1980; Estrada and Marrasé 1987; Brown and Hutchings 1987).

With the lack of temporal sampling coverage, it is difficult to determine precisely which factors enabled this single species to attain such a concentration. The biomass accumulation was due to either a hydrodynamic concentration of cells or growth. If growth, the accumulation developed in situ or was advected.

A simple trapping of cells through flow convergence evidently was not the cause because all species would have been equally concentrated, which was not the case. Such a hydrodynamic control cannot be ruled out entirely, however, if the convergence could have somehow selectively concentrated the larger colonies. Microscopic examination and determination of the growth rate of *T. partheneia* indicated that the population was healthy and not just an accumulation of senescent cells.

Advection of a dense population in a narrow layer parallel to the front could account for the observed distribution; high cell numbers near the front at stations to the north and south of station 32 (Gould et al. in prep.), the relatively slow division rate of 0.2 doublings per day, and the interleaving pattern in the temperature, salinity, and nutrient profiles support this possibility. However, the abundance maxima of *T. partheneia* at nearby stations were generally around 40 m (Gould et al. in prep.), suggesting that the biomass accumulation still formed in fairly low light levels, even if it was advected to station 32.

We believe most evidence supports the following scenario. First, the preference of this species for low light levels enabled it to increase in abundance late in the year and at depth in the water column. Second, the growth was probably stimulated by enhanced turbulence and associated nutrient flux from below the thermocline. High shear zones at the boundaries of the interleavings might confine the biomass to a thin band, as well as generate turbulence to mix nutrients in from surrounding layers. Or, stabilization after a brief, pulsed nutrient-injection event could have reduced dispersion of the biomass, thereby confining it to a thin layer, as we observed. The intermittent nature of enhanced production at fronts has been pointed out by others (Pingree et al. 1978; Richardson et al. 1986; Lohrenz et al. 1988*a*) and suggests that some type of pulsed upwelling may indeed be occurring.

At the Almeria–Oran Front the low light, high turbulence, high nutrient regime gave *T. partheneia* a competitive advantage that was exploited to attain very high biomass at depth in an open ocean region. *Thalassiosira* colonies are good indicators of turbulent, nutrient-rich areas. The inferences that can be made from their presence in dynamic, marine environments underscores the importance of microscopic examination of samples in conjunction with pigment analyses.

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