

## Time Variation in Phytoplankton Assemblages in a Subtropical Lagoon System after the 1982–1983 “El Niño” Event (1984 to 1986)<sup>1</sup>

ISMAEL GÁRATE-LIZÁRRAGA<sup>2</sup> AND DAVID A. SIQUEIROS BELTRONES<sup>3</sup>

**ABSTRACT:** An analysis of seasonal and geographical distribution and abundance of the total and separate fractions of phytoplankton (nanno- and microphytoplankton) in the Magdalena-Almejas lagoon system was done after the 1982–1983 “El Niño” event. In spite of its being in a subtropical region, the annual variation of phytoplankton abundance in the area was similar to the annual cycle of production of coastal lagoons in temperate regions. There were two peaks of phytoplankton abundance, in spring and in autumn. The upwelling and tidal currents enriching the waters of Bahía Magdalena were responsible for the high concentrations of phytoplankton in the bay. Microphytoplankton was the most important fraction throughout the study period. Nannophytoplankton was somewhat abundant. Using principal component analysis, seasonal variation and frequency were the two factors determining the structure of species assemblages. Lowest values of diversity and dominance were related to circulation patterns and to the phytoplankton blooms that occurred throughout the year in Bahía Magdalena-Almejas. High values of diversity and low dominance were estimated at those areas under the influence of oceanic waters. The 1982–1983 El Niño caused a drastic drop in phytoplankton abundance during 1984. The recuperation process was slow, starting in 1985 and completed by 1986. Recorded increases in phytoplankton abundance surpassed all previous records. “El Niño” caused changes in the structure of the microphytoplankton assemblages. Species richness and specific diversity diminished because of the occurrence of few species.

SEVERAL STUDIES ON THE periodic variation of primary productivity and phytoplankton abundance have been done on coastal ecosystems in temperate regions subject to a marked seasonality (Margalef 1958, Boney 1975, Raymont 1980) and in tropical regions

where species successions are much less pronounced (Guillard and Kilham 1977).

In areas between those two biogeographical regions, such as the southern part of the Baja California peninsula (Dawson 1960), time variations in the structure of marine communities are subject to a complex interaction of oceanographic conditions. These determine a zone with transitional characteristics where tropical and subtropical phytoplanktonic species have been reported (Hernández Becerril 1989).

These conditions also determine the distribution limits of macroalgae and mangrove species in the Bahía Magdalena-Almejas lagoon system (Dawson 1961, Blasco 1984*a,b*, García de la Rosa 1990, Riosmena Rodríguez and Siqueiros Beltrones 1995). There, differential occurrence of well-defined populations and morphotypes of macroalgal

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<sup>2</sup> Laboratorio de Fitoplancton, Departamento de Plancton y Ecología Marina, Centro Interdisciplinario de Ciencias Marinas, A.P. 592, La Paz, B.C.S., México 23000.

<sup>3</sup> Departamento de Biología Marina, Universidad Autónoma de Baja California Sur, A.P. 19-B, La Paz, B.C.S., México 23081.

taxa have been observed (Garza Sánchez 1994, Riosmena Rodríguez and Siqueiros Beltrones 1996).

The Bahía Magdalena-Almejas system is an area of great biological and fisheries significance. It is the main area for sardine catch in the southern Baja California peninsula. There have been few hydrographic studies in the lagoon system (Alvarez-Borrego et al. 1975, Acosta-Ruiz and Lara Lara 1978, Guerrero-Godínez et al. 1988). However, in 1980, the Center for Scientific Marine Research (CICIMAR) in La Paz, México, began continuing studies on plankton dynamics (Funes Rodríguez 1985, Cota-Meza et al. 1992, Palomares-García and Gómez-Gutiérrez 1996) and on the distribution and abundance of ichthyoplankton (Anonymous 1984, 1985, Saldierna Martínez et al. 1987).

Very few studies are available concerning phytoplankton species distribution and abundance in the area. Microphytoplankton structure and abundance (including nanophytoplankton) were determined for an annual cycle (1980–1981) by Nienhuis and Guerrero (1985). Later, they also reported on the distribution of the dominant species, diversity ( $H'$ ) values, and abundance of the two phytoplankton fractions (Nienhuis and Guerrero 1986). Sampling was carried out before and during the 1982–1983 “El Niño” event.

That “El Niño” caused numerous changes in marine populations. A decrease in phytoplankton production along the coasts of Chile and Perú was reported by Cowles et al. (1977), Barber et al. (1983), Guillén et al. (1985), and Avaria and Muñoz (1987). Torres Moya and Alvarez Borrego (1985) and Martínez López (1993) reported similar results for the western coast of the Baja California peninsula. Lara Lara et al. (1984) observed an enrichment in the production and plankton biomass in the Gulf of California. For Bahía Magdalena-Almejas, this event was recorded from the summer of 1982 until the end of 1984 (Saldierna Martínez et al. 1987).

The purpose of this paper is to describe the spatial and seasonal variation of the total phytoplankton abundance (cells  $l^{-1}$ ), abundance by size fractions (nanno- and micro-

phytoplankton), and the structure of microphytoplankton assemblages in Bahía Magdalena-Almejas through two and a half annual cycles (June 1984–October 1986). We also aimed to assess these changes during the last phase and immediate period of relaxation of the 1982–1983 “El Niño” warming event.

### Study Area

The Magdalena-Almejas lagoon system is on the west coast of Baja California Sur, between 24° 15' and 25° 20' N and 111° 30' and 112° 15' W (Figure 1). The lagoon system has been divided into three hydrologic zones: (a) northern (zona de canales), composed mainly of estuaries and channels with an average depth of 3.5 m, an area of 137 km<sup>2</sup>, and surrounded by small but abundant mangrove trees, *Laguncularia racemosa* and *Rhizophora mangle*; (b) central (Bahía Magdalena), connected to the Pacific Ocean by a mouth 40 m deep; (c) southeastern (Bahía Almejas), connected to the ocean by a narrow (0.2 km), shallow (5–7 m) channel (Alvarez Borrego et al. 1975). In the last two zones, *Avicennia germinans* is also present, and there are consolidated mangrove forests (Blasco 1984a,b).

## MATERIALS AND METHODS

### Field Sampling

Twenty-eight stations in the Magdalena-Almejas lagoon system (Figure 1) were sampled monthly from June 1984 to December 1984 and seasonally from January 1985 to October 1986. A total of 187 surface samples (500 to 1000 ml) was collected using oceanographic bottles. To support the taxonomic determinations of species, surface net hauls (223 samples) were made at each station using a phytoplankton net with 54- $\mu$ m mesh. All samples were preserved in buffered 5% formalin. Surface water temperatures were recorded using a Kahlsico thermometer. These values were coupled with temperature measurements taken since 1982 by staff of the Department of Plankton and Marine Ecology of CICIMAR.

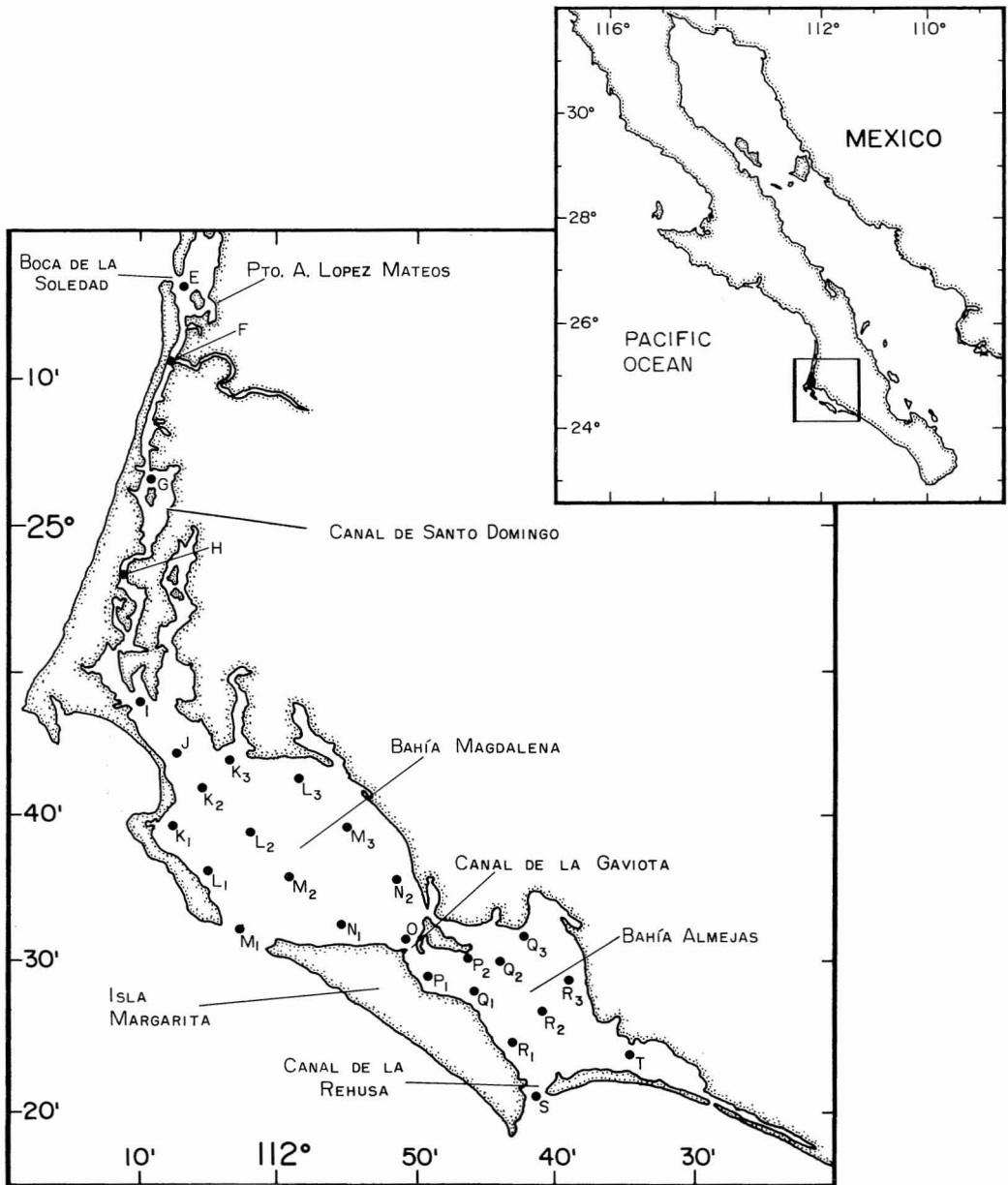


FIGURE 1. Location of Magdalena-Almejas lagoon system, México, and sampling stations.

### Sample Analysis

Phytoplankton bottle samples were sedimented in 5-ml settling chambers and observed using phase-contrast inverted microscopy (Hasle 1978). The total phytoplankton and nanno- (organisms  $<20 \mu\text{m}$ ) and mi-

crophytoplankton (organisms  $>20 \mu\text{m}$ ) abundances (cells  $\text{l}^{-1}$ ) were estimated simultaneously with species composition determinations. Phytoplankton collected by net hauls was analyzed using a phase-contrast microscope (Zeiss STD16). Quantifications were made using a sample size of 250 or-

ganisms, adapted after Margalef and Vives (1972) and Nienhuis and Guerrero (1985).

Taxonomic determinations were made consulting the works of Hustedt (1930, 1959), Schiller (1937), Cupp (1943), Graham and Bronikovsky (1944), Sournia (1967), Ferguson Wood (1968), Saunders and Glenn (1969), Steidinger and Williams (1970), Licea Durán (1974), Taylor (1976), Pesantes (1978), Sournia et al. (1979), Humm and Wicks (1980), Navarro (1981*a,b*, 1982), Murray and Schrader (1983), and Sundström (1986).

To define the structure of the phytoplankton assemblages for each sampling station, species richness ( $S$ ), diversity ( $H'$ ), and dominance ( $D$ ) indices were computed (Peet 1974, Brower and Zar 1979). Abundance data from December 1982 to June 1984 were used to estimate the annual cycle and anomalies of the phytoplankton. The annual variability was examined by plotting monthly mean values, where mean values were calculated as follows:

$$MMV = \sum Xi/N$$

where  $MMV$  = monthly mean value,  $Xi$  = value of the variable in the  $i$ th month for all years, and  $N$  = number of months used in the analysis. Phytoplankton anomalies were calculated by:

$$A_{ij} = \frac{X_{ij}}{Y_i} - 1$$

where  $A_{ij}$  = anomaly of the  $i$ th month in the  $j$ th year,  $X_{ij}$  = value of the variable in the  $i$ th month of the  $j$ th year; and  $Y_i$  = mean value of the  $i$ th month.

Based on the frequency of species occurrence, a principal component analysis was done to explore annual variations in the microphytoplankton assemblages and to detect changes in the species composition. An R matrix was computed using only one transect. This transect included seven sampling stations (I, J, K2, L2, M2, N1, and O) in the middle of Bahía Magdalena. These stations were the only ones sampled regularly (Figure 1).

Following Matta and Marshall (1984),

only those species represented in at least 10% of the samples were used because rare species increase variability without adding any important information. However, during our analysis, rare species were grouped into clusters of taxonomic affinities, species of the same genus, or by life forms: thycoplanktonic species, neritic and oceanic forms, etc. Such species were included in the analysis because of their numerical importance and possible ecological significance.

## RESULTS

Sea surface water temperatures from 1982 to 1986 showed clear seasonal changes during our sampling period. Low values occurred in winter–spring, and high values in summer–autumn (Figure 2). However, during our sampling, the lowest average values for water temperatures were recorded in April 1984 (20.2°C), February 1985 (18.4°C), and April 1985 (19.3°C). The highest values were in September 1984 (28.2°C). In August 1985 (26°C) and October 1986 (23.6°C), values were significantly lower. The temperature increased during 1982–1984 in the lagoon system because of the influence of the 1982–1983 “El Niño” and began to recede during the relaxation period, at the start of our sampling period.

The estimated annual phytoplankton standing crops exhibited two peaks of abundance (Figure 3): a spring peak, with an average of 277,000 cells  $l^{-1}$ , and an autumn peak, with an average of 330,000 cells  $l^{-1}$ . The lowest abundances were during the summer and winter. In general, of the three areas that constitute this lagoon system, lowest abundance was in the Santo Domingo channel, particularly during 1984. The richest area was in Bahía Magdalena, particularly in the April 1985 and October 1986 samples (Figure 4).

The microphytoplankton fraction was the major contributor to phytoplankton abundance (Figure 5). The highest mean values of this fraction were closely related to high total phytoplankton abundances. Nannophytoplankton was abundant only in the

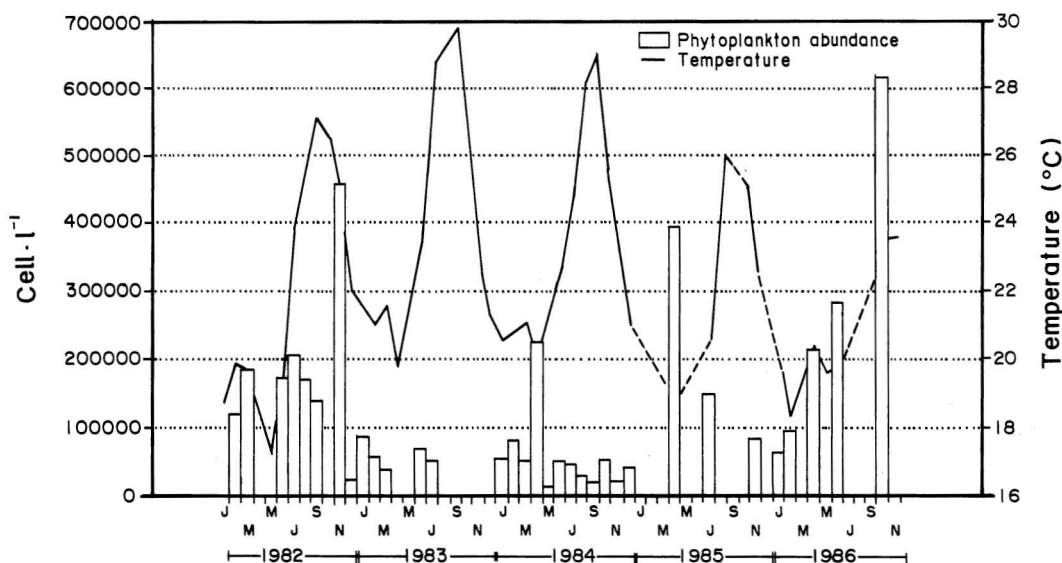


FIGURE 2. Variation of mean temperature and phytoplankton abundance values, 1982 to 1986.

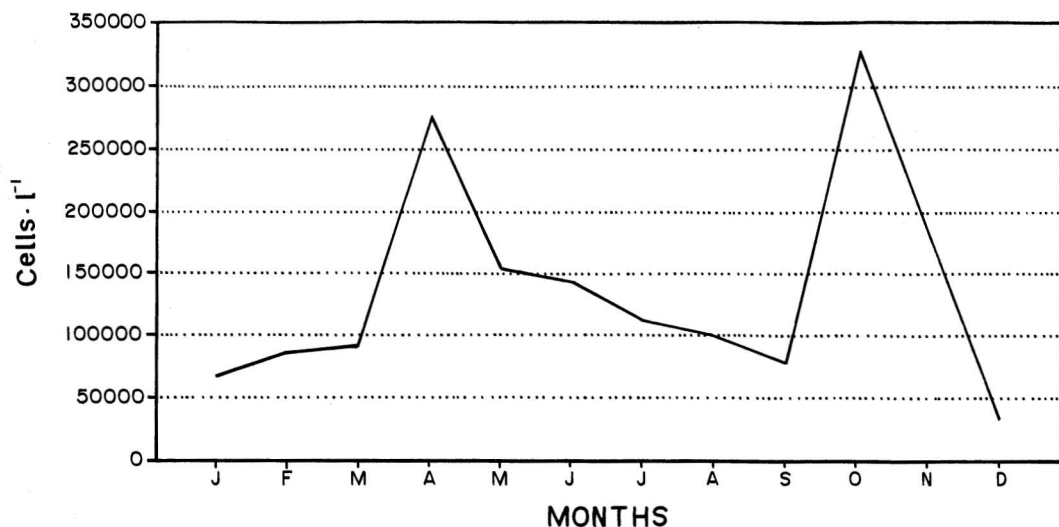


FIGURE 3. Average annual phytoplankton abundance variations in the Magdalena-Almejas lagoon system from 1982 to 1986.

August and September 1984 samples, coinciding with the highest temperatures.

A total of 270 taxa in 87 genera was recorded. Diatoms and dinoflagellates were by far the most diverse and abundant groups in number of taxa determined, with 171 and 84 representatives, respectively. Other groups

recorded were silicoflagellates (five species), cyanobacteria (five), and euglenophytes (one) (Gárate-Lizárraga 1992). The most diverse and abundant groups within the microphytoplankton assemblages were diatoms. The genera with most species represented were *Chaetoceros* (27), *Rhizosolenia* (15), and *Co-*

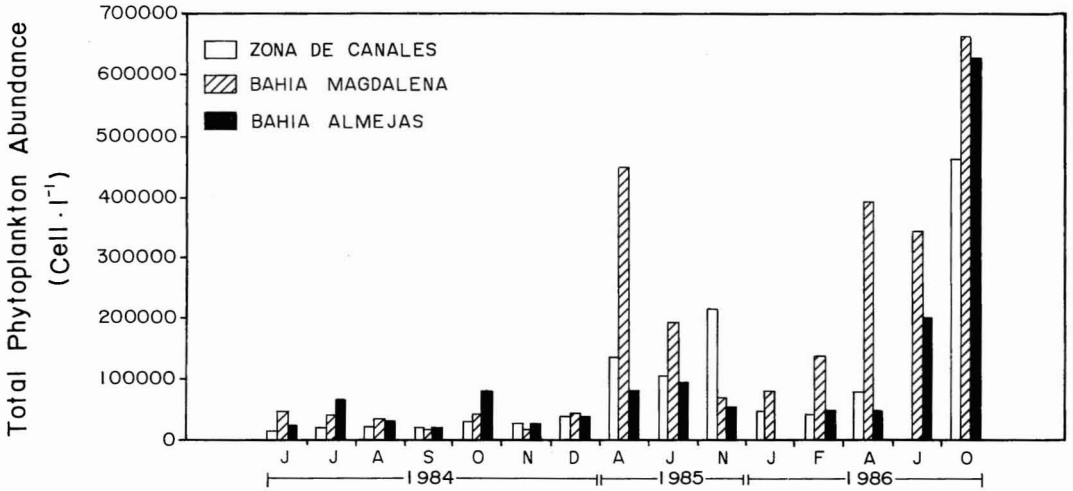


FIGURE 4. Variation of mean phytoplankton abundance values for the three different areas of the Magdalena-Almejas lagoon system, 1984 to 1986.

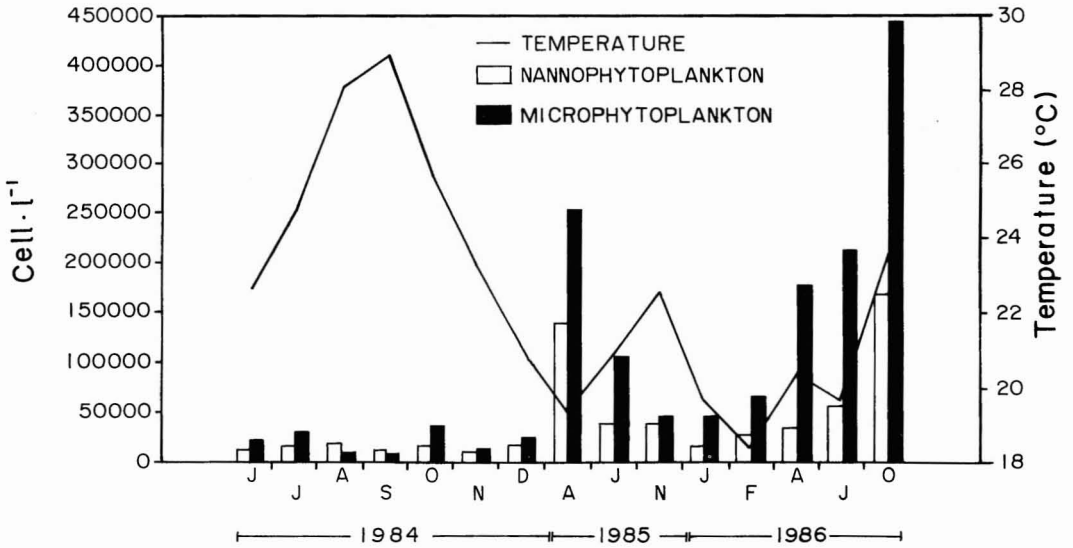


FIGURE 5. Variation of mean of temperature and fractionated phytoplankton abundance values (nanno- and microphytoplankton) in the Magdalena-Almejas lagoon system from 1984 to 1986.

*scinodiscus* (9). Table 1 shows the most abundant microphytoplankton species found in this study.

Among the species that can be considered characteristic of the warm seasons, *P. alata*, *C. asteromphalus*, *P. calcar avis*, *Rh. robusta*, *Ch. coarctatus*, *S. palmeriana*, *H. membra-*

*naceus*, *Rh. hyalina*, and *C. perforatus* were the most frequent taxa. In the cold seasons, *Rh. imbricata*, *G. flaccida*, *Ch. compressus*, *C. pelagica*, *A. glacialis*, *Th. frauenfeldii*, and *Th. nitzschioides* were dominant. *Ch. curvisetus* and *E. zodiacus* were present during both seasons. From the warm season group, an

TABLE 1  
MICROPHYTOPLANKTON IN THE MAGDALENA-ALMEJAS LAGOON SYSTEM, 1984–1986  
(SETS OF DOMINANT SPECIES BY SAMPLING PERIOD ARE SHOWN)

DATE	DOMINANT SPECIES
June 1984	<i>Coscinodiscus radiatus</i> , <i>C. asteromphalus</i> , <i>Ceratium fusus</i> , <i>Chaetoceros curvisetus</i> , <i>Noctiluca scintillans</i>
July 1984*	<i>Proboscia alata</i> , <i>Ch. curvisetus</i>
Aug. 1984*	<i>P. alata</i> , <i>Pseudosolenia calcar avis</i> , <i>C. fusus</i>
Sept. 1984	<i>P. alata</i> , <i>Stephanopyxis palmeriana</i> , <i>C. asteromphalus</i> , <i>Chaetoceros compressus</i> , <i>Oscillatoria erythraeum</i> , <i>Rhizosolenia robusta</i> , <i>C. asteromphalus</i>
Nov. 1984	<i>P. alata</i> , <i>Ditylum brightwellii</i> , <i>P. calcar avis</i> , <i>Rh. imbricata</i>
Dec. 1984	<i>P. alata</i> , <i>P. calcar avis</i> , <i>Bacteriastrum hyalinum</i> var. <i>princeps</i> , <i>Nitzschia pungens</i>
Jan. 1985	<i>Guinardia flaccida</i> , <i>Chaetoceros affinis</i> , <i>Paralia sulcata</i>
Apr. 1985	<i>Eucampia zodiacus</i> , <i>G. flaccida</i> , <i>Cerataulina pelagica</i>
July 1985	<i>P. alata</i> , <i>Ch. curvisetus</i> , <i>P. calcar avis</i>
Nov. 1985	<i>G. flaccida</i> , <i>P. alata</i> , <i>P. calcar avis</i> , <i>Odontella aurita</i>
Jan. 1986	<i>P. calcar avis</i> , <i>G. flaccida</i> , <i>Rhizosolenia stolterfothii</i>
Feb. 1986	<i>Ch. curvisetus</i> , <i>Rhizosolenia imbricata</i> , <i>O. erythraeum</i> , <i>Hemiaulus sinensis</i>
Apr. 1986	<i>Ch. curvisetus</i> , <i>C. pelagica</i> , <i>E. zodiacus</i> , <i>Chaetoceros californiensis</i>
June 1986	<i>Haslea warwickae</i> , <i>Thalassiosira rotula</i> , <i>P. sulcata</i> , <i>E. zodiacus</i> , <i>Rhizosolenia hyalina</i>
Oct. 1986	<i>P. alata</i> , <i>Rh. imbricata</i> , <i>G. flaccida</i>

\*From Martínez López (1987).

association was observed between *Rh. cleveii* var. *communis*, *Rh. acuminata*, *H. sinensis*, *H. membranaceus*, *Ch. compressus*, and the cyanobacteria *Richelia intercellularis*, which occurred as an endophyte, particularly during 1984. Another association was seen between the protozoan *Vorticella oceanica* and the diatoms *Ch. coarctatus* and *C. asteromphalus*. The last species is recorded for the first time in the Mexican Pacific. These types of associations are common in tropical areas. Their increased frequency during 1984 may well be in response to the warming of the western waters of the peninsula caused by El Niño.

Although most dinoflagellate taxa were present throughout the study period, only *N. scintillans*, *C. furca*, *C. fusus*, *P. steinii*, *Diplopsalis* sp., *D. caudata*, *C. dens*, and *G. sanguineum* showed a preference for the warm seasons. From this group, a great number of temperate-tropical species were present: *Amphisolenia bidentata*, *C. macroceros* var. *gallicum*, *C. carriense*, *C. declinatum*, *C. eucarcatum*, *C. falcatum*, *C. gibberum* var. *dispar*, *C. hexacanthum*, *C. massiliense*, *C. pentagonum* var. *robustum*, *C. ranipes*, and *C. vultur*. These all are considered rare within the Magdalena-Almejas system.

The lowest mean values of diversity ( $H' = 0.50$ ) and species richness ( $S = 6$ ) were found in October 1986 (Figure 6). This was caused by a bloom of *P. alata* throughout the lagoon system. In consequence, the highest value of dominance was recorded ( $D = 0.86$ ) in that month. The highest diversity ( $H' = 3.47$ ) and the lowest value of dominance ( $D = 0.017$ ) were in June 1986. The highest species richness was in February. This indicates that a more uniform distribution of organisms from different species occurred in June 1986.

#### Monthly Variation of Temperature and Phytoplanktonic Abundance from 1982 to 1986

The mean values of phytoplankton abundance varied from a minimum of 21,600 cells  $l^{-1}$  in May 1984 to a maximum 610,000 cells  $l^{-1}$  in October 1986. Three peaks of abundance are shown in Figure 2. The first was in November 1982, the second in April 1985, and the third in October 1986. The second and third peaks coincide with the blooms of spring and autumn characteristic of temperate coastal lagoons. In the 1983–1984 annual cycle, the average values of

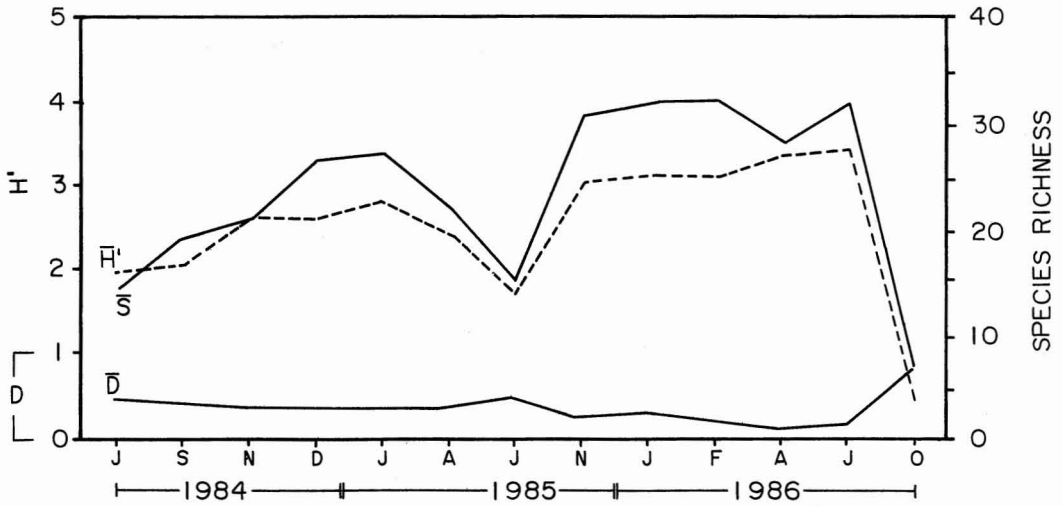


FIGURE 6. Variation of mean values of diversity ( $H'$ ), dominance ( $D$ ), and species richness ( $S$ ) from June 1984 to October 1986.

abundance were lower, exhibiting only a spring peak of low magnitude.

A drastic drop in phytoplankton abundance was seen, with values below 100,000 cells  $l^{-1}$ , from December 1982 until the end of 1984. The reduction in phytoplankton abundance corresponds with the increase of surface water temperature caused by the "El Niño" event, which replaced the nutrient-rich coastal waters off Baja California Sur with warm oligotrophic waters. Phytoplankton concentrations increased during 1985 and 1986 with abundances similar to those recorded in 1982, except for the bloom observed in autumn 1986, which was the highest peak recorded.

By comparing annual cycles (Figure 7a), a thermal anomaly of  $+4^{\circ}C$  can be noted during 1983–1984. The warming confirms the influence of the "El Niño" event along the coast of the Mexican Pacific, particularly in the Magdalena-Almejas lagoon system, and supports our explanation of phytoplankton abundance variations.

An inverse correspondence can be observed for thermal anomalies and phytoplankton abundance anomalies. These were detected at the beginning of 1983 (Figure 7b). Negative anomalies were recorded during 1983 and

1984, which coincided with marked positive thermal anomalies. Since 1985, positive anomalies of phytoplankton abundance have been observed. Although these are lower, they indicate the recuperation of phytoplankton abundance in the lagoon system.

When comparing values from 1984 and 1985, a drastic drop in the surface water temperature is evident for the second year. Negative anomalies were recorded for the first half of the year and positive anomalies for the rest of the year. In addition to the relaxation phase of the El Niño warming, the "normal" temperature variations in the Magdalena-Almejas lagoon system are seen (Figure 7). Correspondingly, negative thermal anomalies during 1986 ( $-2.65^{\circ}C$ ) indicate cooling of the Magdalena-Almejas waters, similar to those recorded during 1981 and 1982 before the onset of the El Niño event. During 1986, the average values of abundance were the highest, yielding positive anomalies of phytoplankton abundance.

#### Principal Component Analysis

Only the first two components derived showed any relation with variations in the microphytoplankton assemblages. The com-



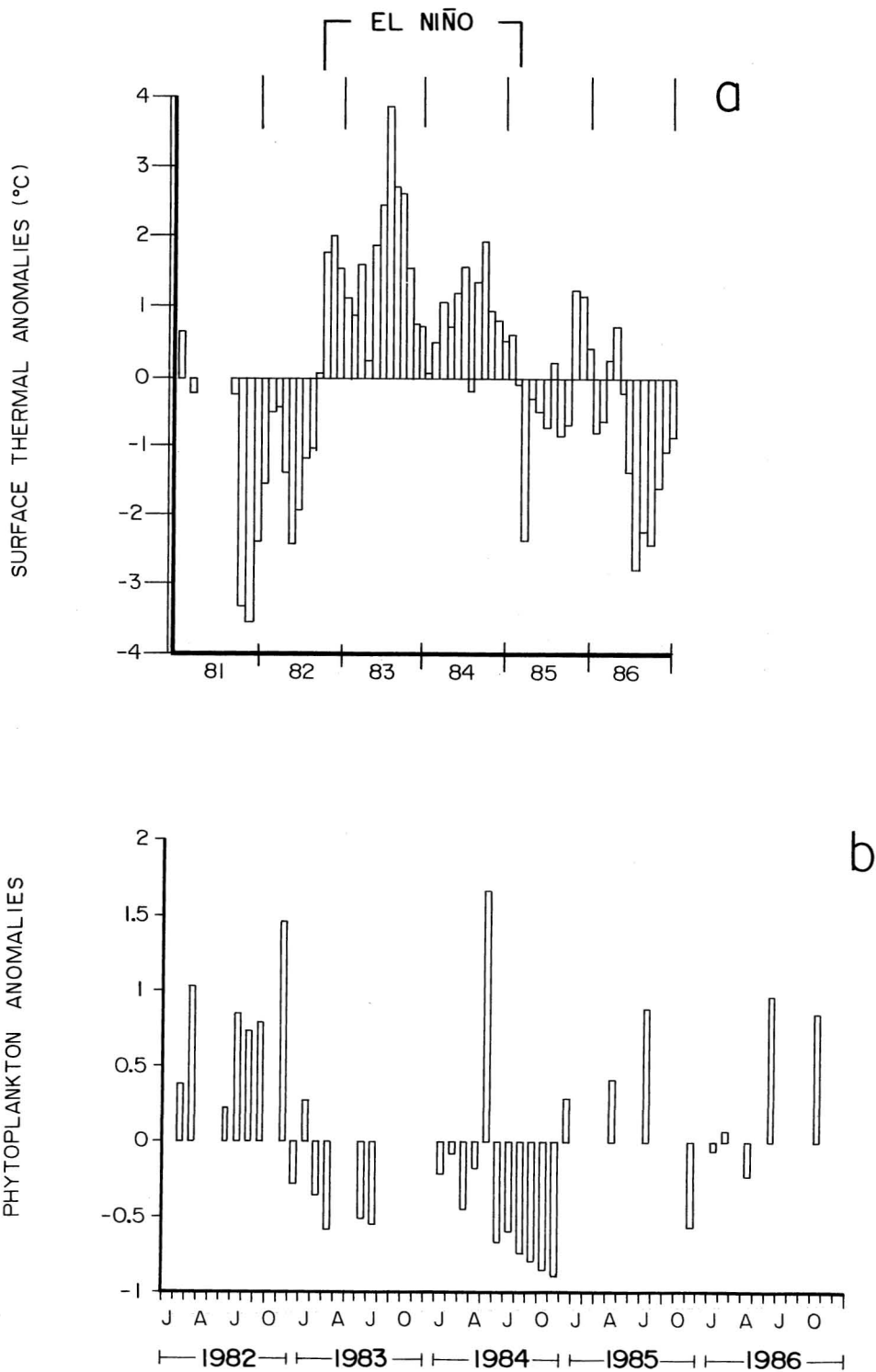


FIGURE 7. Variation of (a) thermal anomalies (from Saldierna Martínez et al. 1987) and (b) anomalies of phytoplankton abundance, 1980 to 1986.

TABLE 2

AMOUNT (%) OF VARIANCE EXPLAINED BY THE FIRST (SEASONAL) AND SECOND (ABUNDANCE) PRINCIPAL COMPONENTS FOR THE MICROPHYTOPLANKTON ASSEMBLAGES SAMPLED AT MAGDALENA-ALMEJAS LAGOON SYSTEM, 1984-1986

COMPONENT	1984		1985		1986	
	VARIANCE	ACCUMULATED	VARIANCE	ACCUMULATED	VARIANCE	ACCUMULATED
First component	14.31	14.31	13.82	13.82	16.68	16.68
Second component	12.60	26.91	11.80	25.62	15.57	32.25

ponents were defined as follows: the first is the seasonal component, which reflects temporal variation of species throughout the year; the second component represents the abundance or frequency of occurrence of the species.

Although the amount of variance explained by the two components was low (Table 2), they were used for further analysis because an acceptable grouping of species was observed. The graphic representation of the components and their association with the microphytoplankton assemblages shows, for the 3 yr of the study, that much variation occurred from one season to another in terms of species abundance, biogeographic affinities, and substrate preferences.

The 1984 cycle (Figure 8) shows four clusters of species and their association with the principal components. Only the spring cluster had a positive correlation with the first component. The summer, autumn, and winter clusters were inversely related to the first component, which means the grouped species occurred in at least two seasons.

The most abundant species in the spring cluster were *A. splendens*, *A. lineolata*, *O. aurita*, *P. sulcata*, *T. favus*, and the subgroup designated as thycoplanktonic (pennate) diatoms, indicating sediment resuspension processes. Temperate species accounted for 48% of the total. The most abundant species (related to the second component) were *Rh. fragilissima* and *C. centralis*. The only warm-water species was *Ch. peruvianus*. The summer group was characterized by a larger number of dinoflagellate species from warm waters (e.g., *C. fusus*, *N. scintillans*, and *P. steinii*). Such tropical influence also defined the affinity of the diatom species. Their

abundances relate the group to the second component.

The autumn cluster was inversely correlated with both components. Four subgroups could be defined by species affinities: ubiquitous (*P. alata*); miscellaneous (thycoplanktonic diatoms and dinoflagellates); temperate and tropical species (*N. pungens* var. *atlantica* and *C. lineatus*; *P. calcar avis* and *C. deflexum*); and warm oceanic species (*Rh. hyalina* and *C. massiliense*). The lack of association with seasonal or abundance patterns shows the marked transitional characteristics of Magdalena-Almejas during that time of year. A mixture of species from different habitats and biogeographical affinities composed the winter group. The species present most frequently were *G. flaccida*, *H. sinensis*, and *R. stolterfothii*. The last, a warm-water representative, shows a remaining tropical influence.

Figure 9 represents the 1985 cycle. The spring and summer clusters showed a positive correlation with both components and were defined mainly by ubiquitous species from coastal lagoons. Only in spring were two warm-water dinoflagellates represented. The high frequency of temperate species (*A. glacialis*, *O. aurita*, and *C. fusus*) is explained by the lower temperatures recorded that year versus 1984. The autumn group was inversely correlated with the first component. This shows that no exclusive autumn species were present; all occurred in more than one season. The group also had a partial positive association with the second component (high abundances), especially those species from the southern part of the central transect in Bahía Magdalena. Species showing a negative association with this component were mainly neri-

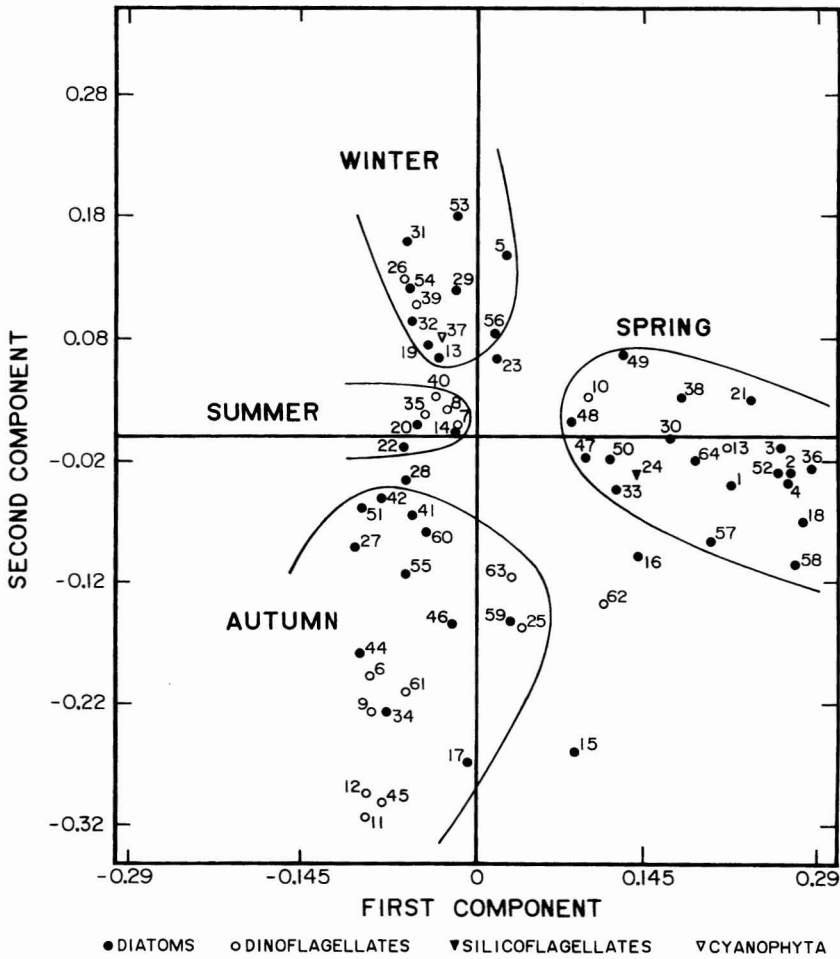


FIGURE 8. Graphic representation of microphytoplankton species using the first two principal components, for 1984. 1, *Actinoptychus splendens*; 2, *Amphora lineolata*; 3, *Bacteriastrium delicatulum*; 4, *B. elongatum*; 5, *Cerataulina pelagica*; 6, *Ceratium deflexum*; 7, *C. furca*; 8, *C. fusus*; 9, *C. lineatus*; 10, *C. macroceros*; 11, *C. massiliense*; 12, *C. trichoceros*; 13, *Chaetoceros compressus*; 14, *Ch. curvisetus*; 15, *Ch. didymus*; 16, *Ch. lorenzianus*; 17, *Ch. messanensis*; 18, *Ch. peruvianus*; 19, *Climacodium frauenfeldianum*; 20, *Coscinodiscus asteromphalus*; 21, *C. centralis*; 22, *C. perforatus*; 23, *C. radiatus*; 24, *Dictyocha messanensis*; 25, *Dinophysis caudata*; 26, *D. hastata*; 27, *Ditylum brightwellii*; 28, *Eucampia zodiacus*; 29, *Guinardia flaccida*; 30, *Hemiaulus hauckii*; 31, *H. sinensis*; 32, *Leptocylindrus danicus*; 33, *Nitzschia delicatissima*; 34, *N. pungens* var. *atlantica*; 35, *Noctiluca scintillans*; 36, *Odontella aurita*; 37, *Oscillatoria erythraeae*; 38, *Paralia sulcata*; 39, *Protoperidinium assymetricum*; 40, *Phyrophacus steinii*; 41, *Pleurosigma formosum*; 42, *Proboscia alata*; 43, *Protoperidinium* sp.; 44, *Pseudosolenia calcar avis*; 45, *Rhizosolenia hyalina*; 46, *Rh. bergonii*; 47, *Rh. cleveii* var. *communis*; 48, *Rh. delicatula*; 49, *Rh. fragillissima*; 50, *Rh. imbricata*; 51, *Rh. robusta*; 52, *Rh. setigera*; 53, *Rh. stolterothii*; 54, *Stephanopyxis turris*; 55, *Thalassionema frauenfeldii*; 56, *Thalassiosira eccentricus*; 57, *Triceratium favus*; 58, "tycoplanktonic diatoms;" 59, "neritic diatoms;" 60, "oceanic diatoms;" 61, "*Ceratium* spp.;" 62, "*Protoperidinium* spp.;" 63, "dinoflagellates;" 64, "*Chaetoceros* spp."

tic forms (*G. flaccida* and *Ch. debilis*) or thycoplanktonic (*A. splendens* and *N. cancellata*), indicating a mixing process in the system.

Figure 10 shows four clusters of species for 1986, all located in different quadrants.

The autumn cluster had a positive correlation with the two principal components. The seasonal component was related to *P. alata* massive blooms that, because of its abundance, showed a positive relation with the

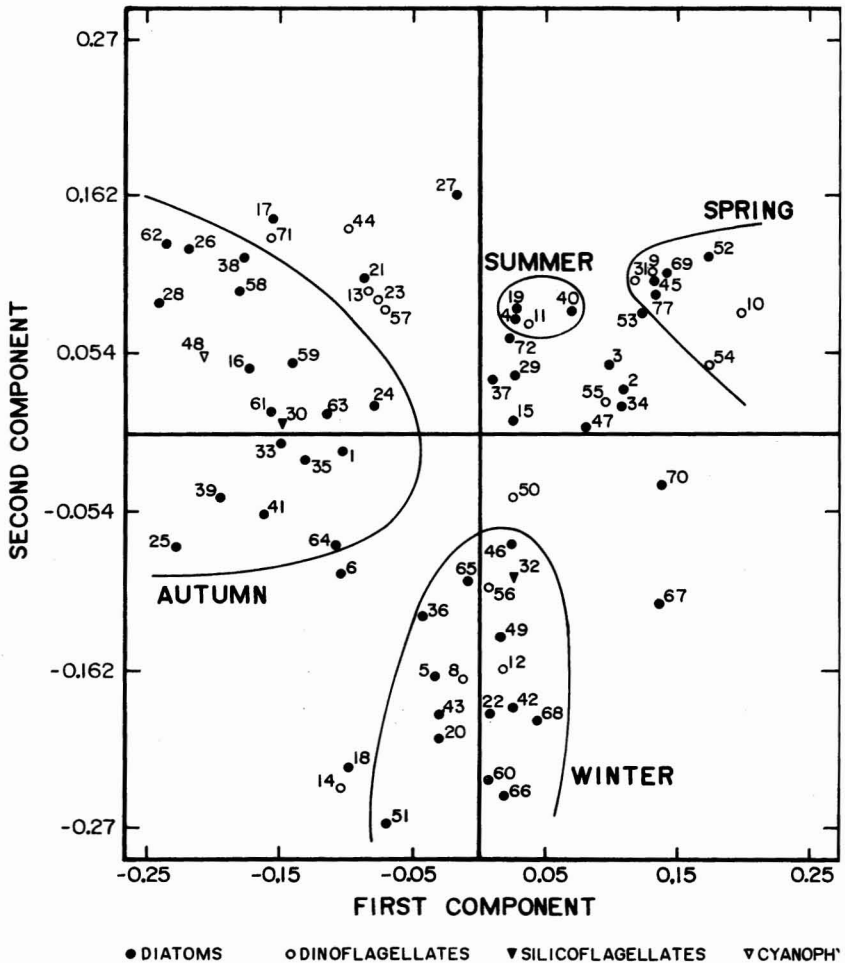


FIGURE 9. Graphic representation of microphytoplankton species using the first two principal components, for 1985. 1, *Actinoptychus splendens*; 2, *Amphora marina*; 3, *Amphora* sp.; 4, *Asterionellopsis glacialis*; 5, *Bacteriastrium comosum*; 6, *Bacteriastrium delicatulum*; 7, *Cerataulina pelagica*; 8, *Ceratium azoricum*; 9, *Ceratium dens*; 10, *C. furca*; 11, *C. fusus*; 12, *C. horridum*; 13, *C. lineatus*; 14, *C. trichoceros*; 15, *Chaetoceros affinis*; 16, *Ch. brevis*; 17, *Ch. coarctatus*; 18, *Ch. compressus*; 19, *Ch. curvisetus*; 20, *Ch. didymus*; 21, *Ch. lorenzianus*; 22, *Ch. messanensis*; 23, *Ch. peruvianus*; 24, *Ch. debilis*; 25, *Climacodium frauenfeldianum*; 26, *Coscinodiscus asteromphalus*; 27, *C. perforatus*; 28, *Cylindrotheca closterium*; 29, *Detonula pumila*; 30, *Dictyocha messanensis*; 31, *Dinophysis forthii*; 32, *Distephanus pulchra*; 33, *Ditylum brightwellii*; 34, *Eucampia zodiacus*; 35, *Guinardia flaccida*; 36, *Hemiaulus hauckii*; 37, *H. membranaceus*; 38, *Lauderia annulata*; 39, *Leptocylindrus danicus*; 40, *Lithodesmium undulatus*; 41, *Navicula cancellata*; 42, *Navicula distans*; 43, *Nitzschia pungens* var. *atlantica*; 44, *Noctiluca scintillans*; 45, *Odontella alternans*; 46, *O. aurita*; 47, *O. mobilensis*; 48, *Oscillatoria erythraea*; 49, *Paralia sulcata*; 50, *Phyrophacus steinii*; 51, *Planktoniella sol*; 52, *Pleurosigma* spp.; 53, *Proboscia alata*; 54, *Protoperidinium claudicans*; 55, *P. conicum*; 56, *P. pellucidum*; 57, *P. pyrum*; 58, *Pseudosolenia calcar avis*; 59, *Rhizosolenia hyalina*; 60, *Rh. bergonii*; 61, *Rh. cleveii* var. *communis*; 62, *Rh. imbricata*; 63, *Rh. setigera*; 64, *Rh. stolterfothii*; 65, *Stephanopyxis palmeriana*; 66, *Streptothecha tamensis*; 67, *Thalassionema frauenfeldii*; 68, *Th. nitzschiioides*; 69, *Thalassiosira rotula*; 70, *Thalassiosira* sp.; 71, *Thalassiothrix heteromorpha* var. *mediterranea*; 72, *Triceratium favus*.

second component. The winter group showed an inverse correlation with both components. It was defined mainly by ubiquitous diatoms typical of coastal environments (*Ch. affinis*,

*Ch. curvisetus*, *H. hauckii*, and *Rh. imbricata*) and by the temperate dinoflagellate *C. lineatus*.

The spring group had an inverse correla-

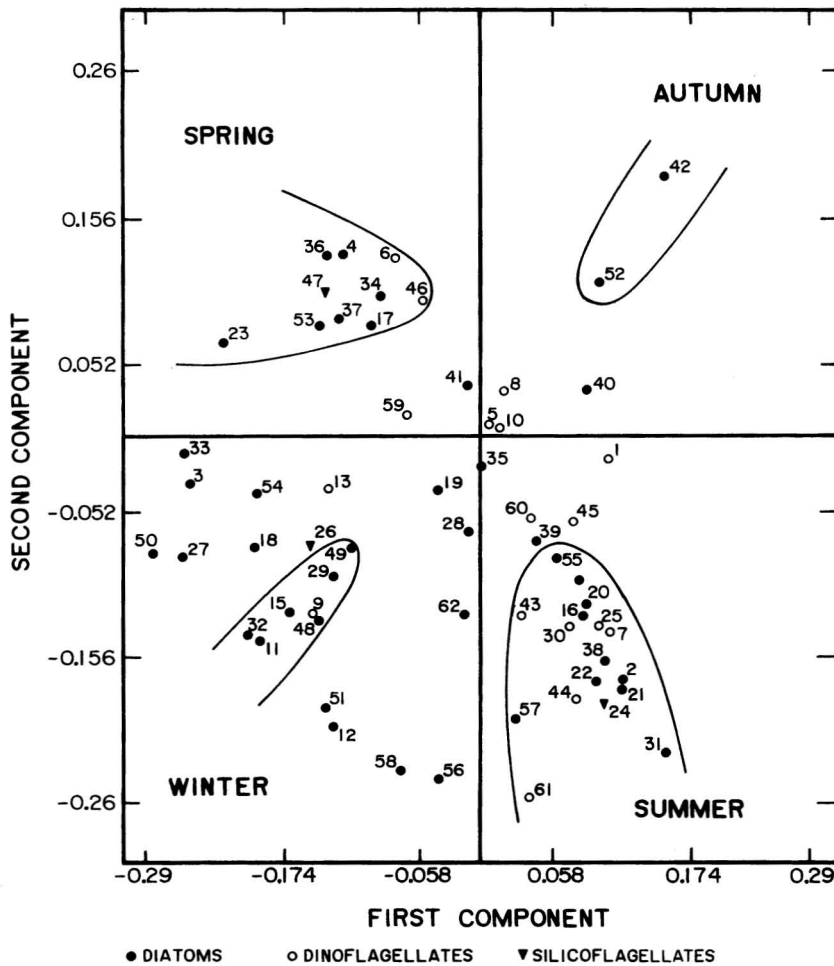


FIGURE 10. Graphic representation of microphytoplankton species using the first two principal components, for 1986. 1, *Actinoptychus splendens*; 2, *A. vulgaris*; 3, *Asterionellopsis glacialis*; 4, *Cerataulina pelagica*; 5, *Ceratium dens*; 6, *C. falcatum*; 7, *C. furca*; 8, *C. fusus*; 9, *C. lineatus*; 10, *C. trichoceros*; 11, *Chaetoceros affinis*; 12, *Ch. brevis*; 13, *Ch. compressus*; 14, *Ch. costatus*; 15, *Ch. curvisetus*; 16, *Ch. danicus*; 17, *Ch. didymus*; 18, *Ch. lorenzianus*; 19, *Ch. criophilum*; 20, *Coscinodiscus perforatus*; 21, *C. radiatus*; 22, *Cylindrotheca closterium*; 23, *Detonula pumila*; 24, *Dityocha messanensis*; 25, *Dissodinium lunula*; 26, *Distephanus pulchra*; 27, *Ditylum brightwelli*; 28, *Eucampia zodiacus*; 29, *Guinardia flaccida*; 30, *Gymnodinium sanguineum*; 31, *Haslea warwickae*; 32, *Hemiaulus hauckii*; 33, *H. sinensis*; 34, *Leptocylindrus danicus*; 35, *L. mediterraneus*; 36, *Nitzschia pacifica*; 37, *N. pseudodelicatissima*; 38, *N. pungens* var. *atlantica*; 39, *Odontella mobiliensis*; 40, *Paralia sulcata*; 41, *Pleurosigma formosum*; 42, *Proboscia alata*; 43, *Prorocentrum micans*; 44, *Protoperdinium claudicans*; 45, *P. conicum*; 46, *P. pellucidum*; 47, *Rhizosolenia hyalina*; 48, *Rh. fragilissima*; 49, *Rh. imbricata*; 50, *Rh. setigera*; 51, *Rh. stolterfothii*; 52, *Stephanopyxis palmeriana*; 53, *Thalassionema frauenfeldii*; 54, *Th. nitzschioides*; 55, *Thalassiosira rotula*; 56, “tycoplanktonic diatoms;” 57, “neritic diatoms;” 58, “oceanic diatoms;” 59, “*Ceratium* spp.,” 60, *Protoperdinium* spp.; 61, “subgroup of dinoflagellates;” 62, “*Chaetoceros* spp.”

tion with the first component and a positive one with the second component. It was defined mostly by ubiquitous species from neritic systems, plus three warm-water species: *Rh. hyalina*, *C. falcatum*, and *P. pelluci-*

*dum*. The summer cluster showed a positive correlation with the first component and a negative one with the second. It consisted of a miscellaneous array of diatoms from different environments and biogeographical affinities.

Ubiquitous diatoms from coastal lagoons were somewhat dominant.

#### DISCUSSION

The seasonal cycle of phytoplankton standing stocks observed in the Magdalena-Almejas lagoon system exhibited the classical patterns described elsewhere for coastal lagoons of temperate regions (Robinson 1970). The temperature pattern was the same as reported by Saldierna-Martínez et al. (1987) from 1981 to 1983, with the warm (summer–autumn) and cold (winter–spring) periods being similar in both studies. Correspondingly, two annual peaks of phytoplankton abundance were recorded, one in spring and another in autumn.

Upwelling events are common off Bahía Magdalena-Almejas. Alvarez-Borrego et al. (1975) determined upwelling conditions during March, June, July, August, and October west of the bay. Upwellings are more intense during March and June (Bakun and Nelson 1977), which explains the more prominent spring peak in April observed in our study. The resulting nutrient enrichment of the surface waters may have supported the phytoplankton abundances that coincided with the low temperatures recorded for the western side of the bay and were detected in our study.

Earlier, Nienhuis and Guerrero (1985, 1986) suggested that the higher phytoplankton biomass in Bahía Magdalena was caused by upwellings. Guerrero-Godínez et al. (1988) determined that high primary production inside the bay depended on tidal currents transporting the rich upwelled water into the bay. This agrees with our high estimates of phytoplankton abundances for the mouth of the bay. Tidal currents also resuspend bottom sediments, explaining the high concentrations of thycoplanktonic diatoms in our samples and the higher overall biomass.

The observed dominance of microphytoplankton over the nanno fraction throughout the period of the study agrees with earlier estimates (Nienhuis and Guerrero 1986). High

phytoplankton production in coastal waters is frequently related to the larger fraction (Varela and Costas 1987). Such correspondence was noted in Magdalena-Almejas, but in some periods high production was due to high concentrations of nannophytoplankton.

Grazing by zooplankton can cause a marked decrease in phytoplankton abundance during summer (Dawes 1991). In agreement with Saldierna-Martínez et al. (1987), in our study zooplankton biomass increased after the phytoplankton spring peak, reaching its peak in July 1982. The autumn blooms in October and November can be related to nutrient availability. Cushing (1975) indicated that these blooms coincide with the decline in zooplankton biomass. Zooplankton grazing may also alter the fraction composition of phytoplankton.

Size fraction in phytoplankton may be quite important in energy transfer in the upper trophic levels (Varela and Costas 1987). When microphytoplankton dominates the scene, the trophic chain is shorter; macrozooplankton is the sole intermediary. This is of utmost importance because microphytoplankton constitutes the major food source for several sardine species (Rojas de Mendiola 1979, Kawasaki and Kumagai 1984, Varela et al. 1988). In Bahía Magdalena, phytoplankton may be as much as 60% of the diet of *Opisthonema libertate* (Romero Ibarra and Esquivel Herrera 1989).

The species composition and relative abundances within the assemblages did not show constant changes or seasonal variations. Throughout the study, a few species determined the structure of the assemblages. This agrees with the reports by Nienhuis and Guerrero (1985, 1986) for the 1980–1981 period. About 22 phytoplankton species were dominant and may be regarded as responsible for the main phytoplankton dynamics in Magdalena-Almejas.

The hydrographic characteristics of Magdalena-Almejas, such as water temperature variation, are determined by its location within a transitional zone. These, combined with the availability of nutrients through periodic upwelling events, determine the diamic nature of the observed phytoplankton

species. Many important species (neritic or benthic) in the lagoon system belong to genera that develop resting spores (*Chaetoceros*, *Coscinodiscus*, *Paralia*, and *Odontella*). This mechanism may be being used to overcome periods of unfavorable conditions.

The species responsible for most blooms in the lagoon system was *P. alata*. It begins to proliferate when water temperature increases, becoming very abundant in the warm season, which in 1984 extended to December. According to our observations and previous reports for *P. alata*, it is a ubiquitous species, quite common along the coasts of California, Baja California, and the Gulf of California (Cupp 1943, Round 1967, Venrick 1971, González-López and Siqueiros Beltrones 1990). It is adapted to proliferate in oligotrophic waters, but frequently thrives under nutrient pulses (Guillard and Kilham 1977). The transitional nature of the study area poses an ideal environment for the behavior of this highly opportunistic species.

The positive thermal anomalies caused by the 1982–1983 “El Niño” lasted throughout 1984 in the California Current (Glynn 1988) and were detected even into 1985 inside the Magdalena-Almejas lagoon system, causing a drastic drop in phytoplankton abundance from 1983 to December 1984. This caused a decrease in egg production for *Sardinops caerulea* and an increase for *Opisithonema libertate*, a species of tropical affinity (Saldierna-Martínez et al. 1987), in spite of the low estimated availability of food.

The phytoplankton recuperation process was slow, developing in 1985 and completed by 1986. This contrasts with observations for the Peruvian coast, where recuperation occurred by the end of the warming event (Barber et al. 1983). This could be because the warm water mass was displaced northward, where it remained, permitting normal upwelling off Perú. This did not happen along the west coast of southern Baja California where the upwelling was warm and poor in nutrients (Fielder 1984).

In both regions, the subsequent increases in phytoplankton biomass surpassed all previous records. During the influence of El Niño in 1982–1983, *P. alata* proliferated

more in the warmer months. In spite of the prevailing conditions, dinoflagellate species were never abundant, developing isolated blooms of *C. furca*, *C. fusus*, and *N. scintillans*, which did not displace the diatoms. Although the presence of several dinoflagellate species characteristic of oligotrophic warm waters could indicate the influence of the El Niño event of 1982–1983, only *C. declinatum* and *C. vultur* have been closely associated with the event in the Gulf of California and these are not considered good indicators (González-López 1994). They more likely represent the Costa Rican Current or gulf water influence during normal oceanic circulation.

During our study, species richness and diversity were much lower in 1984, similar to the 1983–1984 estimates by Nienhuis and Guerrero (1986). This can be attributed to the El Niño warming in Magdalena-Almejas. By 1985 and 1986, species richness and diversity had increased notably. Ocean circulation patterns, which determine the spatial distribution of phytoplankton, are closely related to diversity and dominance in the Magdalena-Almejas assemblages.

The low diversity and high dominance measurements were associated with monospecific blooms occurring all year long (*P. alata*). This is typical of coastal lagoons and is considered characteristic of immature communities (Margalef 1977). The highest diversity values corresponded to those areas with great oceanic influence (e.g., the mouth of Bahía Magdalena). The mixing of different water masses causes an increase in diversity (Margalef 1977). In shallow systems, diversity rises because of mixing with benthic diatom associations.

The species composition analysis using principal components confirms the above. This analysis was a useful tool to permit the identification of associations among the species and to describe their seasonal variation. According to seasonal and abundance components, clusters of species of diverse habitats and biogeographical affinities were defined. These reflected the transitional nature of the study area, showing the influence of the California Current and warm waters.

The discussion above describes the conditions during 1984. The following year the waters were colder, and a typical behavior of the system was expected, except perhaps for the thermal anomaly at the end. But the positive association of the spring clusters remained, corresponding with the abundance peak. The rest of the groups varied more or less erratically.

Finally, the reestablished colder conditions in 1986, similar to those in 1981–1982, precluded the proliferation of warm-water species, although they did appear in summer when a mixture of species with different biogeographical affinities occurred. The influence of benthic forms indicates the importance of mixing processes in a system that depends on tidal periodicity, given the shallow depth of the system.

The particular hydrological conditions of Magdalena-Almejas are the main factors determining variations in the association structure of phytoplankton assemblages. Although the subtropical definition of the region ensures a constant supply of temperate and tropical species and favors the establishment of eurytolerant and diamic species, the transitional nature of the study area somewhat clouded the effects of the 1982–1983 El Niño on the phytoplankton assemblages.

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