Upwelling and phytoplankton in the Bay of Panama

Luis D'Croz, Juan B. Del Rosario and Juan A. Gómez
Centro de Ciencias del Mar y Limnología. Universidad de Panamá, Estafeta Universitaria, Panamá.

Abstract: A four year study documented changes in the seawater of the Bay of Panama due to seasonal upwelling. A warm watermass, with salinity below 30 o/oo, low phosphate concentration (0.5 µg atom/l), low chlorophyll a (0.5 mg/m³) and low density of phytoplankton (20-30 cells/ml) was observed during the rainy season. In contrast, during the dry season, when upwelling occurred, a cold (17-20°C) and saline (32-35 o/oo) watermass with high phosphate concentration (2 µg atom/l), high chlorophyll a (3 mg/m³) and abundance of phytoplankton (100-300 cells/ml) prevailed in the bay. A species succession was observed related to these seasonal changes. *Chaetoceros cinctus* was the dominant rainy season diatom whereas *C. curvisetus* was the main diatom found during the dry season.

Key words: Upwelling, temperature, phosphate, chlorophyll, phytoplankton, species sucession.

Changes in sea temperature and nutrient levels in the Bay of Panama are consequence of seasonal coastal upwelling. This upwelling is induced by the offshore displacement of surface water by northerly winds during the dry season, from January to April (Fleming 1939, Schaefer, Bishop & Landa 1958). The upwelled water fertilizes the euphotic zone, leading to a high phytoplankton productivity (Smayda 1966, Forsbergh 1963, 1969). However, during the rainy season (May to December) a warm, low salinity and nutrient-poor watermass prevails in the bay. Blooms of phytoplankton develop as a response to upwelling, and support the rich fishery of anchovetas (*Cetengraulis mysticetus*) in the Bay of Panama (Smayda 1966, Forsbergh 1969).

Phytoplankton in the bay is affected by these variations in the marine environment (Smayda 1963, 1966). Community changes of phytoplankton have been reported in relation to temperature (Goldman & Mann 1980), light intensity (Ryther 1956) and chemical conditions, mostly enrichment episodes (Sanders et al. 1987). Since phytoplankton species are different in their tolerance to environmental changes, the patterns of seasonal succession may be a consequence of these changes (Guillard & Kilham 1977).

Here we examine the phytoplankton from a fixed station in the Bay of Panama. This study aims to compare changes in the phytoplankton community between the typical tropical warm and nutrient-poor seawater condition observed during non-upwelling season, and the cool and nutrient-rich condition of the upwelled water.

MATERIAL AND METHODS

Seawater samples were collected on a weekly basis, from January 1985 to December 1988, at the Smithsonian Tropical Research Institute's pier at Naos Island (8° 55'N, 79° 32'W) Bay of Panama (Fig. 1). Seawater samples were obtained with a reversible Nansen bottle 5 m below the surface during high tides (mean tidal range: 4 m). Approximately 200 ml of water from each sample were fixed with 5% formaldehyde, and stored in dark bottles. Phytoplankton was counted using a Sedwick-Rafter (SR) Counting Cell (APHA 1985).
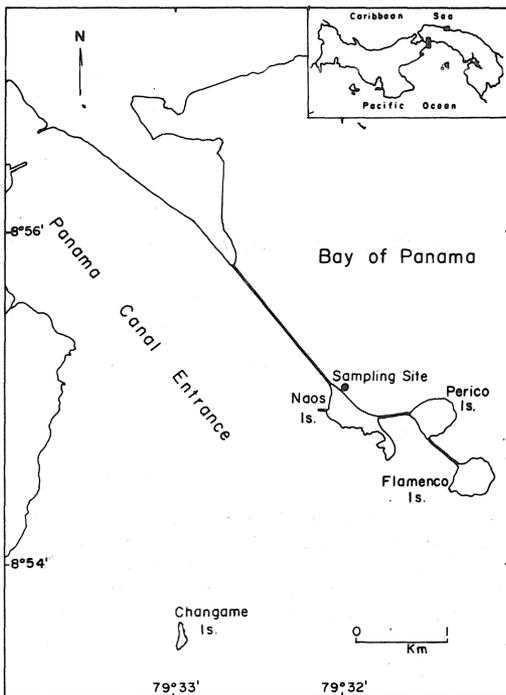
Fig. 1. Location of the sampling station at Naos Island, Bay of Panama.

Samples were homogenized by shaking, and an aliquot of 1 ml was pipetted into the SR Cell. Three aliquots per sample were taken, and the cells counted in 3 strips of the SR Cell; the mean values (n=9) are reported. Species were identified according to Cupp (1943), Hendley (1964), Hasle (1972), and Simonsen (1974).

The concentration of chlorophyll a was determined according to the method of Strickland & Parsons (1972). After sampling, seawater was immediately filtered through membrane filters (0.45 μm). During the rainy season one liter of seawater was filtered, while during the dry season 250 to 500 ml were filtered. Magnesium carbonate was added to the membrane filters to prevent acidification and consequent loss of chlorophyll. Filters retaining the phytoplankton were frozen (-5°C) and stored for a period of less than 30 days before analysis. Chlorophyll a from the phytoplankton cells retained on the filter was extracted with 90% acetone. A Teflon tissue grinder was used to assure complete extraction of the pigment. The absorbance of the extracts were read in a Spectronic 21 spectrophotometer at 630, 645 and 665 nm.

Temperature of the seawater was recorded with a protected type reversible thermometer installed in the Nansen sampler.

Salinity was measured in the laboratory with a Beckman RS7-C electrodeless induction salinometer.

The dissolved phosphate-phosphorus (PO4-P) content was analyzed by the ascorbic acid, potassium antimony-tartrate method of Murphy & Riley (1962). Seawater was filtered through membrane filters (0.45 μm) before analysing. Samples were stored at -5°C in a deep freezer for a period of less than 30 days before analysis.

Chemical, physical and biological data for each year were correlated using the Pearson's correlation coefficient in order to obtain a correlation matrix. Additionally, a cluster analysis with the data of each year was performed based on a data matrix elaborated with the standardized values (Romesburg 1984) of salinity, temperature, phosphate, chlorophyll a and phytoplankton abundance. Euclidean distance and average linkage were used for clustering the samples. Both cluster analysis and the Pearson's correlation matrix were performed with the SYSTAT program.

RESULTS

Temperature during rainy season was generally between 26 and 28°C (Fig. 2), although maximum temperature reached 29.8°C (October, 1988). During the dry season seawater temperature often decreased to near 20°C, or even below, as a consequence of upwelling. Drops below 20°C in seawater temperatures were generally recorded each year, however inter-annual variations may result in "warm" years as occurred in 1987. During this year dry season showed a relatively high temperature and sea temperature decreased only to 21.42°C. The lowest temperature recorded during this study was 16.75°C (April, 1985).

Salinity during the rainy season was generally below 30 o/oo (Fig.2). The lowest records were more frequent from September to November when rainfall is usually more intense and salinity may drop below 25o/oo. During the dry season salinity usually ranged from 32 to 35 o/oo.

The phosphate concentration fluctuated according to the type of prevailing seawater mass

in the bay (Fig. 2). Phosphate concentrations during the dry season were frequently close, or slightly above, 2 μg atom/l. Contrarily, during the rainy season, phosphate concentrations were low, mostly in the vicinity of 0.5 μg atom/l.
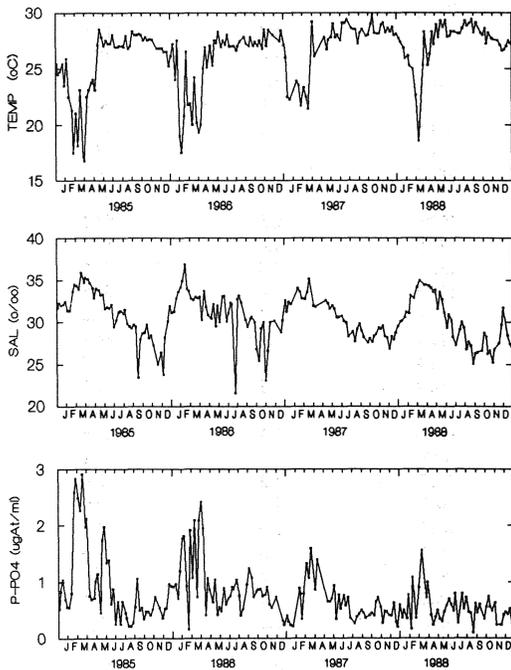

Fig. 2. Time series for seawater temperature, salinity and phosphate concentration.

Phytoplankton density roughly followed the concentration of dissolved nutrients (Fig. 3). Cell densities during the dry seasons of 1985 and 1986 were near 300 cell/ml, while during the rainy season these were mostly between 20 to 30 cells/ml. However, cell peaks during 1987 and 1988 were much lower, near 130 cells/ml.

Chlorophyll a concentration showed a similar seasonal pattern as the phytoplankton trend (Fig. 3). High concentrations of chlorophyll were recorded particularly during the dry season of 1985 and 1987, when the highest values exceeded 3 mg/m³. However, chlorophyll concentrations during 1988 were low and showed narrow differences between the rainy and the dry season. Chlorophyll concentrations during the rainy season were around 0.5 mg/m³.

A Pearson's correlation matrix of all data of this study gave high correlations (p ≤ 0.001) between the seawater temperature and salinity,

dissolved nutrients, phytoplankton density and chlorophyll a concentration (Table 1).
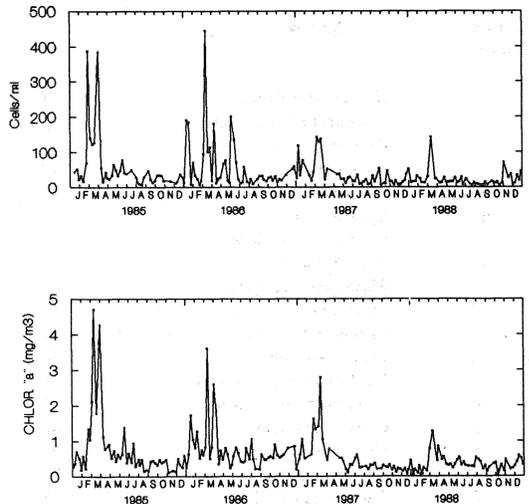

Fig. 3. Time series for phytoplankton abundance and concentration of chlorophyll *a*.

TABLE 1

Matrix of Pearson correlation coeficients for temperature, salinity, phosphate, chlorophyll a *and phytoplankton density*

	Temperature	Salinity	Phosphate	Chlorophyll *a*
Salinity	-0.78***			
Phosphate	-0.98***	0.79***		
Chlorophyll *a*	-0.80***	0.58***	0.76***	
Cell density	-0.86***	0.67***	0.83***	0.79***

*** = P ≤ 0.00

Two hundred and eleven (211) taxa of phytoplankton were recorded during this study, and most of them were diatoms (165). Nine taxa of dinoflagellates, three taxa of ciliates, a blue-green algae, and a silicoflagellate were also found. It was not possible to identify 32 taxa. Table 2 shows the 58 taxa which accounted for nearly 90% of all phytoplankton recorded during this study. The numerically dominant diatoms were *Chaetoceros cinctus* and *C. curvisetus*, which accounted for nearly 20% of the population. Other common taxa were *Cyclotella* sp., *Nitzschia pungens*, *Rhizosolenia stolterfothii* and *C. socialis*. The nine most abundant taxa represented nearly 50% of the population

TABLE 2

Species that accounted for nearly 90% of all phytoplankton collected in the Bay of Panama from January, 1985 to December, 1988

Rank by Number	Species	Fre- quency	Number of cells	% by Number	Cumulative % by Number
1	*Chaetoceros cinctus*	57	757.8	9.7	9.7
2	*Chaetoceros curvisetus*	66	719.3	9.2	18.9
3	*Cyclotella* sp. 2	60	516.5	6.6	25.5
4	*Nitzschia pungens*	78	500.2	6.4	31.9
5	*Rhizosolenia stolterfothii*	67	378.9	4.9	36.8
6	*Cyclotella* sp. 1	74	371.5	4.8	41.6
7	*Chaetoceros socialis*	61	319.7	4.1	45.7
8	*Nitzschia* sp. 1	54	263.4	3.4	49.1
9	*Rhizosolenia setigera*	61	235.3	3.0	52.1
10	*Eucampia zoodiacus*	17	193.9	2.5	54.6
11	*Chaetoceros debilis*	16	185.0	2.4	57.0
12	*Chaetoceros* sp. 6	24	155.4	2.0	59.0
13	*Stephanopyxis palmeriana*	11	137.6	1.8	60.8
14	*Navicula membranacea*	53	128.8	1.7	62.5
15	*Chaetoceros affinis*	40	121.4	1.6	64.1
16	*Rhizosolenia acuminata*	25	118.4	1.5	65.6
17	*Nitzschia* sp. 2	6	116.9	1.5	67.1
18	*Chaetoceros* sp. 2	15	111.0	1.4	68.5
19	*Chaetoceros radican*	26	108.0	1.4	69.9
20	*Skeletonema costatum*	29	99.2	1.3	71.2
21	*Thalassionema nitzschioides*	43	94.7	1.2	72.4
22	*Asterionella kariana*	26	94.7	1.2	73.6
23	*Asterionella glacialis*	14	81.4	1.0	74.6
24	*Pleurosigma* sp. 1	28	79.9	1.0	75.6
25	*Nitzschia longissima*	30	74.0	1.0	76.6
26	*Melosira* sp. 1	15	66.6	0.9	77.5
27	*Chaetoceros didymus*	16	63.6	0.8	78.3
28	*Psammodiscus nitidus*	26	54.8	0.7	79.0
29	*Fragilaria crotonensis*	7	45.9	0.6	79.6
30	*Thalassiosira eccentrica*	17	45.9	0.6	80.2
31	*Detonula confervacea*	7	44.4	0.6	80.8
32	Non identified species 45	6	42.9	0.6	81.4
33	*Coscinodiscus perforatus*	12	38.5	0.5	81.9
34	*Chaetoceros laevis*	2	37.0	0.5	82.4
35	*Coscinodiscus granii*	16	35.5	0.5	82.9
36	*Biddulphia regia*	15	35.5	0.5	83.4
37	*Synedra nana*	14	34.0	0.4	83.8
38	*Bacteriastrum hyalinum*	13	34.0	0.4	84.2
39	Non identified species 26	4	31.1	0.4	84.6
40	*Thalassiosira* sp. 1	14	31.1	0.4	85.0
41	*Guinardia flaccida*	10	29.6	0.4	85.4
42	*Ditylum* sp. 1	13	28.1	0.4	85.8
43	*Ditylum brightwellii*	9	28.1	0.4	86.2
44	*Nitzschia closterium*	13	28.1	0.4	86.6
45	*Chaetoceros diversus*	9	26.6	0.3	86.9
46	*Chaetoceros* sp. 5	11	25.2	0.3	87.2
47	*Melosira granulata*	13	25.2	0.3	87.5
48	*Rhizosolenia alata*	6	25.2	0.3	87.8
49	Non identified species 24	2	23.7	0.3	88.1
50	*Gyrosigma* sp. 1	12	23.7	0.3	88.4
51	*Thalassiotrix frauenfeldii*	7	22.2	0.3	88.7
52	*Leptocilindrus danicus*	11	22.2	0.3	89.0
53	Non identified species 4	9	22.2	0.3	89.3
54	*Goniaulax* sp. 1	6	20.7	0.3	89.6
55	*Chaetoceros pseudocurvisetus*	6	20.7	0.3	89.9
56	*Chaetoceros compressus*	5	19.2	0.3	90.2
57	*Navicula* sp. 5	4	19.2	0.2	90.4
58	*Chaetoceros* sp. 3	6	17.8	0.2	90.6

and their frequency among samples was the highest (Table 2). *N. pungens* was the most frequent taxa among the samples (Table 2). Centric diatoms dominated the community structure throughout the study (Fig. 4). The highest density of centric and pennate forms were usually related to upwelling episodes, however outburst of dinoflagellates often occurred during upwelling or immediately after (Fig. 4).
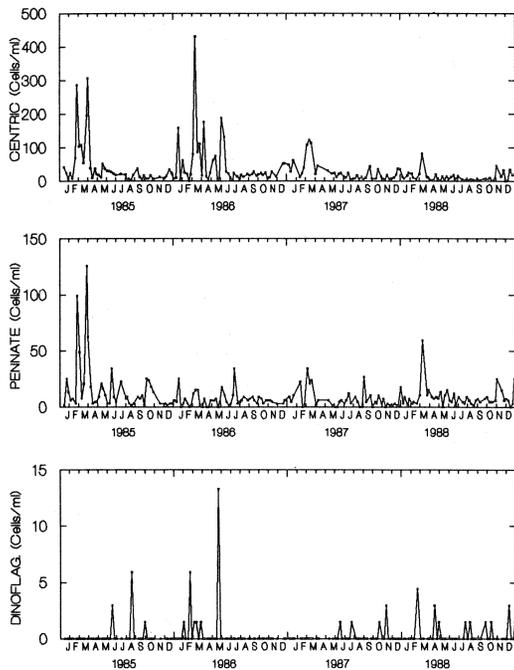

Fig. 4. Time changes in the composition of the collected phytoplankton.

Samples from each year's collection were clustered according to seawater temperature, salinity, dissolved nutrients, chlorophyll a, and phytoplankton density (Fig. 5). These clusters indicate a species succession between the rainy season and the upwelling period. In order to facilitate the description of this succession, clusters of collections were grouped to form "rainy" and "upwelling" assemblages. The rainy season assemblage included clusters of samples collected when seawater temperatures were above 25°C. Upwelling assemblages included samples when seawater temperatures were below 25°C. Upwelling was divided into three phases: Phase I, with seawater temperatures ranging from 23 to 25°C, representing marginal upwelling conditions (beginning and ending of upwelling); Phase II, with seawater temperatures

from 20 to 23°C representing moderate upwelling; and Phase III, with seawater temperatures below 20oC (intense upwelling). *C. cinctus* and *C. socialis* generally resulted as the most important elements in the rainy season assemblages, while *C. curvisetus* was the dominant diatom during the upwelling episodes. The stability of this succession from year to year is summarized in Table 3. Although *C. curvisetus* is also present in rainy season collections, its rank of numerical importance is relatively low. As upwelling conditions prevailed in the bay, the proportion of *C. curvisetus* within the phytoplankton assemblage was increased. The proportion of other species, such as *R. stolterfothii*, also often increased during the upwelling. Despite this successional pattern in chaetocerid species, taxa such as *N. pungens* and *Cyclotella* were abundant either during the rainy season or during the upwelling episodes.
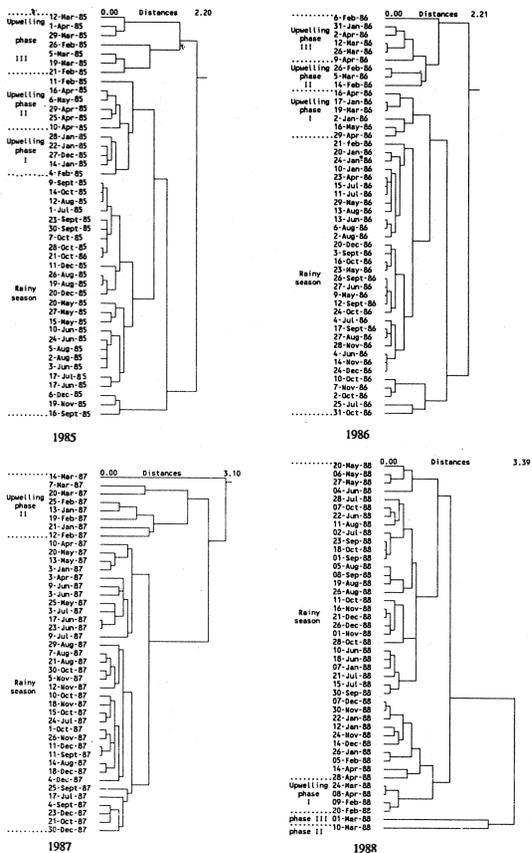

Fig. 5. Cluster analysis of the seawater samples collected from 1985 to 1988. Samples were grouped according to the dendogram to form assemblages corresponding to the rainy season and to the upwelling period. Upwelling has been divided into phases representing the intensity of the event.

Table 3

Dominant taxa (by abundance) representing nearly 70 % of the phytoplankton population from the Bay of Panama (1985-1988)

	Rainy season		Upwelling Phase I		Phase II		Phase III	
	sp.	umulative % by number	sp.	Cumulative % by number	sp.	Cumulative % by number	sp.	Cumulative % by number
1985	N. pungens	9.1	F. crotonensis	17.4	Cyclotella sp. 1	9.6	Ch. curvisetus	9.8
	Ch. cinctus	15.9	Ch. laevis	33.6	Cyclotella sp. 2	35.0	E. zoodiacus	19.4
	Cyclotella sp. 2	21.8	Cyclotella sp. 2	42.6	Melosira sp. 2	45.4	Cyclotella sp. 1	28.9
	Ch. curvisetus	27.0	R. stolterfothii	50.3	Ch. curvisetus	53.6	Cyclotella sp. 2	37.0
	Non identified species	32.0	Chaetoceros sp. 2	53.6	Nitzschia sp. 5	60.8	S. palmeriana	44.1
	N. membranacea	36.9	T. decipiens	56.1	R. setigera	68.0	Nitzschia sp. 2	51.1
	Cyclotella sp. 1	41.5	Ch. curvisetus	58.7	N. membranacea	72.2	Chaetoceros sp. 2	56.8
	R. stolterfothii	45.8	Cyclotella sp. 1	61.3			N. pungens	62.3
	A. kariana	49.6	N. pungens	63.2			Nitzschia sp. 1	65.2
	Ch. socialis	52.6	S. costatum	65.2			A. glacialis	68.0
	Nitzschia sp. 1	55.3	Ch. costatus	67.1			R. setigera	70.6
	S. nana	57.8	S. palmeriana	69.0				
	C. perforatus	60.1	R. setigera	70.3				
	Chaetoceros sp. 5	61.9						
	D. confervacea	63.5						
	N. longissima	65.1						
	A. glacialis	66.7						
	Ch. radican	68.2						
	T. eccentrica	69.4						
	Chaetoceros sp. 6	70.5						
1986	Ch. cinctus	28.0	Ch. cinctus	29.7	Ch. curvisetus	39.8	Ch. curvisetus	18.8
	N. pungens	36.8	R. stolterfothii	40.6	R. stolterfothii	48.4	Ch. debilis	35.1
	Ch. socialis	44.8	Ch. curvisetus	51.1	R. setiger	55.9	Ch. cinctus	51.0
	R. stolterfothii	51.1	Cyclotella sp. 2	55.9	Ch. socialis	61.3	Cyclotella sp. 2	65.1
	R. setigera	55.7	N. pungens	60.5	Cyclotella sp. 2	66.7	Ch. socialis	72.7
	Ch. curvisetus	59.3	R. acuminata	64.7	Cyclotella sp. 1	71.0		
	Cyclotella sp. 1	62.7	Ch. debilis	67.5				
	Cyclotella sp. 2	66.0	Chaetoceros sp. 6	69.9				
	T. nitzschioides	69.0						
	Chaetoceros sp. 6	71.5						
1987	S. costatum	8.86	Ch. curvisetus	14.3				
	Ch. cinctus	17.1	R. stolterfothii	27.4				
	Ch. socialis	24.3	Cyclotella sp. 2	38.2				
	N. pungens	29.8	N. pungens	48.1				
	Cyclotella sp. 2	34.4	Ch. cinctus	58.1				
	R. setigera	38.6	R. acuminata	63.4				
	Ch. curvisetus	42.6	R. setigera	68.2				
	Cyclotella sp. 1	46.4	Ch. socialis	73.0				
	N. membranacea	49.6						
	Nitzschia sp. 1	52.7						
	Pleurosigma sp. 1	55.5						
	B. hyalinum	58.0						
	Ch. didymus	60.3						
	Ch. affinis	62.7						
	Chaetoceros sp. 6	64.6						
	D. brightwellii	66.2						
	Gyrosigma sp. 1	67.9						
	L. borealis	69.4						
	M. granulata	70.9						
1988	N. pungens	14.3	N. pungens	27.7	C. nitidus	33.3	N. pungens	38.1
	Melosira sp.	22.6	C. nitidus	41.5	N. pungens	61.9	Ch. curvisetus	60.8
	Ch. affinis	28.9	Thalassiosira sp. 1	53.9	Ch. curvisetus	81.0	Ch. didymus	69.7
	Pleurosigma sp. 1	35.0	Ch. curvisetus	60.0				
	T. nitzschioides	40.2	S. turris	66.2				
	Ch. curvisetus	43.6	Cyclotella sp. 1	70.8				
	C. granii	47.0						
	N. longissima	50.5						
	R. setigera	53.7						
	N. pungens	56.8						
	G. flaccida	59.9						
	N. closterium	62.5						
	N. membranacea	65.0						
	Ch. pseudocurvisetus	67.3						
	Cyclotella sp. 1	69.6						

DISCUSSION

Pronounced seasonal changes were observed in the marine environment of the Bay of Panama. High temperatures, low salinities and phosphate concentrations during the rainy seasons are typical of the Tropical Eastern Pacific. This nearshore watermass is subjected to high dilution from rainfall and freshwater runoff (Forsbergh 1969). The rainy season conditions were followed by low sea temperatures during the dry season, accompanied by high salinities, high phosphate concentrations, and high biological production as inferred from the chlorophyll a concentrations and the densities of phytoplankton cells (Figs. 2 and 3). Low sea surface temperatures in the Bay of Panama during the dry season are related to upwelled waters (Fleming 1939, Schaefer, Bishop & Landa 1958, Forsbergh 1963) as a result of the northerly winds displacement of the surface watermass. Strong inverse correlations were observed during this study between sea temperature and salinity, phosphate, chlorophyll a and the density of phytoplankton cells (Table 1). This clearly suggests that the hydrological changes of the dry season are a consequence of the seasonal upwelling. Inter-annual differences in sea surface temperature, and linked parameters during the upwelling, might be due to the variation in the intensity of upwelling and the origin of the upwelled water. The intensity of upwelling has long been suggested to be the result of the wind stress over the sea surface of the bay (Forsbergh 1963, 1969). However, the depth of the thermocline at the beginning of the dry season might also influence the nature of the upwelled watermass as inferred from Kwiecinski, Chial & Torres (1988), who suggest that the intensity of upwelling in the bay is related to the regional Eastern Pacific climatology and oceanography. Data from Forsbergh (1969) and Kwiecinski, Jaen & Muschett (1975) indicate that the watermass in the Bay of Panama with temperature ranging from 16 to 20°C is commonly found just below the thermocline, at 50 to 75 meters in depth during the rainy season. These authors suggest that the thermocline rises 30 to 40 meters during the upwelling. Recorded sea surface temperatures during the dry seasons monitored during this study were frequently below 20°C (Fig. 1) and thus may give an idea of the depth of origin of the upwelled watermass in the bay.

Phytoplankton data indicate that the biomass and cell densities increase with the upwelled seawater (Fig. 3). The collected phytoplankton was mostly composed of diatoms as reported in other nearshore and upwelling areas in the Eastern Pacific (Nienhuis & Guerrero 1985). Centric diatoms dominated the community structure during the study (Fig. 4). Although centric diatoms may have a lower growth rate than pennate, the former are usually the dominating phytoplankton in nearshore and upwelling environments (Turpin & Harrinson 1979). This could be due to the larger seed stock of centric diatoms when compared with pennate diatoms, specially in subsurface layers of shallow coastal water (Ishizaka, Takahashi & Ichimura 1983, 1986). Dinoflagellates increased their relative abundance during the dry season or at the beginning of the rainy season, although comparatively the abundance of diatoms was largely higher. These occasional dry season blooms of dinoflagellates could be related to the increased concentration of nutrients resulting from upwelling as suggested by Estrada & Blasco (1979). However, at the beginning of the rainy season, some outburst of dinoflagellates were also observed. This could suggest that these blooms might be a response to marked environmental disturbances related with the shifting from one seasons to another.

Compositions of species of the rainy and upwelling assemblages from 1985 to 1988 (Table 3) suggest that the phytoplankton population of the bay is basically autochthonous since species between both seasons are almost similar. Although the rank of importance of the species might vary from one season to the other, the pool of species is basically the same. For instance, *C. curvisetus* and *R. stolterfothii* are high density species during the upwelling, but they are also found in the rainy season assemblages, although with lower abundance ranks. On the other hand, *C. cinctus* and *N. pungens* are often dominating taxa during the rainy season but, although less abundant, these species are also part of the upwelling assemblages. The observed dominance of *Chaetoceros* and *Rhizosolenia* apparently is common in the Eastern Pacific as inferred from our results and previous work (Nienhuis & Guerrero 1985). Smayda (1963, 1966) reported a very stable species succession of phytoplankton in the Gulf of Panama during a three year study. Our findings coincide with Smayda's work on the stability of

this succession and that the phytoplankton population of the bay is basically autochthonous. However, there are differences in the species involved in the succession between Smayda's work and this paper. Smayda's results reveal a rainy season community dominated by *Skeletonema costatum* f. *tropicum* and *C. compressus* and the intense upwelling community dominated by *Nitzschia delicatissima* in co-dominance with other unpredictable diatoms.

The observed effect of upwelling on phytoplankton in the Bay of Panama is clearly positive, as indicated by Smayda (1966). Nevertheless, some previous considerations have suggested that upwelling may pose some ecological problems to phytoplankton due to the loss of biomass during the offshore displacement of surface water (Smayda, 1966), and also because the low concentration of phytoplankton seed in upwelled water could reduce production (Brown & Field 1986). Our data suggest that the response of phytoplankton to upwelling is almost immediate (Figs. 2 and 3). High abundances of phytoplankton and chlorophyll a were recorded with short lag phase in relation to a decline in sea temperatures and an increase in dissolved nutrients. Probably, the suggested negative impact of upwelling on phytoplankton may be applicable to offshore communities, but not to shallow water phytoplankton where the seed stock is high (Ishizaka, Takahashi & Ichimura 1983), light intensity is sufficient for photosynthesis and nutrients usually are the most important limiting factors.

RESUMEN

Un estudio de cuatro años de duración caracterizó los cambios que ocurren en la Bahía de Panamá por efecto del afloramiento costanero. Durante la temporada lluviosa se observó una masa de agua cálida y con salinidad inferior a 30 o/oo, baja concentración de fosfato (0.5 μg atom/l) y clorofila a (0.5 mg/m³) y de baja densidad de células del fitoplancton (20-30 células/ml). Por el contrario, durante la temporada seca, cuando ocurre el afloramiento, la temperatura del agua es fría (17-20°C) y altos los valores de salinidad (32-35 o/oo), fosfatos (2 μg atom/l), clorofila a (3 mg/m³) y abundancia del fitoplancton (100-300 células/ml). Hay una sucesión en las especies que componen la comunidad del fitoplancton asociada a estos cambios hidrológicos; se caracteriza por la dominancia de *Chaetoceros cinctus* durante la estación lluviosa y *C. curvisetus* durante la estación seca.

ACKNOWLEDGEMENTS

REFERENCES

APHA. 1985. Standard methods for the examination of water and wastewater 16th Edition. Amer. Pub. Health Ass. Inc. N. Y. 1268 p.

Brown, P. C. & J.G. Field. 1986. Factors limiting phytoplankton production in a nearshore upwelling area, J. Plankton Res. 8: 55-68.

Cupp, E. E. 1943. Marine plankton diatoms of the West Coast of North America. Bull. Scripps Instn. Oceanogr. 5: 1-237.

Estrada, M. & D. Blasco. 1979. Two phases of the phytoplankton community in the Baja California upwelling. Limnol. Oceanogr. 24: 1065-1080.

Fleming, R. H. 1939. A contribution to the oceanography of the Central America Region. Proceedings of the 6th Pacific Sci. Congress 3: 167-176.

Forsbergh, E. D. 1963. Some relationships of meteorological, hydrographic, and biological variables in the Gulf of Panama. Bull. Inter-Amer. Trop. Tuna Comm. 7: 1-109.

Forsbergh, E. D. 1969. On the climatology, oceanography and fisheries of the Panama Bight. Bull. Inter-Amer. Trop. Tuna Comm. 14: 49-259.

Guillard, R. R. & P. Kilham. 1977. The ecology of marine planktonic diatoms, p. 372-469 In: D. Werner (ed.). The biology of diatoms. Blackwell, London.

Goldman, J. C. & R. Mann. 1980. Temperature-influenced variations in speciation and chemical composition of marine phytoplankton in outdoor mass culture. J. Exp. Mar. Biol. Ecol. 46: 29-39.

Hasle, G. R. 1972. The distribution of *Nitzschia seriata* Cleve and allied species. Nova Hedwigia, Beih 39: 11-119.

Hendley, N. I. 1964. An introductory account of the smaller algae of British coastal waters. Part V: Bacillarophyceae (diatoms). Min. Agr. Fish. and Food. Fish. Invest. series IV. 315 p.

Ishizaka, J., M. Takahashi & S. Ichimura. 1983. Evaluation of coastal upwelling effects on phytoplankton growth by simulated culture experiments. Mar. Biol. 76: 271-278.

Ishizaka, J., M. Takahashi & S. Ichimura. 1986. Changes in the growth rate of phytoplankton in local upwelling around the Izu Peninsula, Japan. J. Plankton Res. 8: 169-181.

Kwiecinski, B., A. L. Jaen & A. M. Muschett. 1975. Afloramiento en el Golfo de Panamá durante la temporada de 1973. An. Centro Cienc. del Mar y Limnol. Univ. Nal. Autón. México 2: 73-80.

Kwiecinski, B., B. Chial & A. Torres. 1988. El Niño and Post El Niño (1982-1986) in the Gulf of Panama. Tropical Ocean-Atmosphere Newsletter 44: 7-8.

Murphy, J. & J. Riley. 1962. A modified single solution method for determination of phosphate in natural waters. Anal. Chim. Acta 27: 31-36.

Nienhuis, H. & R. Guerrero. 1985. A quantitative analysis of the annual phytoplankton cycle of the Magdalena lagoon complex (Mexico). J. Plankton Res. 7: 427-441.

Romesburg, H. C. 1984. Cluster Analysis for Researcher. Lifetime Learning Publications, Belmont, CA. 334 p.

Ryther, J. H. 1956. Photosynthesis in the ocean as a function of light intensity. Limnol. Oceanogr. 1:61-70.

Sanders, J. G., S. J. Cibik, C. F. D'Elia, & W. R. Boynton. 1987. Nutrient enrichment studies in a coastal plain estuary: changes in phytoplankton species composition. Can. J. Fish. Aquat. Sci. 44:83-90.

Schaefer, M. B., Y. M. Bishop & G. V. Landa. 1958. Some aspects of upwelling in the Gulf of Panama. Bull. Inter-Amer. Trop. Tuna Comm. 3: 77-130.

Simonsen, R. 1974. The diatom plankton of the Indian Ocean Expedition of R.V. Meteor 1964-1965. Meteor Forschungsergb. 19: 1-66.

Smayda, T. J. 1963. A quantitative analysis of the phytoplankton of the Gulf of Panama. I. Results of the regional phytoplankton surveys during July and November, 1957 and March, 1958. Bull. Inter-Amer. Trop. Tuna Comm. 7: 191-253.

Smayda, T. J. 1966. A quantitative analysis of the phytoplankton of the Gulf of Panama. III. General ecological conditions, and the phytoplankton dynamics at 8o 45'N, 79o23'W from November 1954 to May 1957. Bull. Inter-Amer. Trop. Tuna Comm. 11: 353-612.

Strickland, J. and T. Parson. 1972. A manual of sea water analysis. Fish. Res. Bd. Canada, Bull. 167. 310 p.

Turpin, D. H. & P.J. Harrison. 1979. Limiting nutrient patchiness and its role in phytoplankton ecology. J. Exp. Mar. Biol. Ecol. 39: 151-166.