

THE SHORT TERM EFFECT OF PHYSICAL PROCESSES UPON NUTRIENTS, PRIMARY PRODUCTION AND SEDIMENTATION IN GUARAPINA LAGOON (RJ), BRAZIL

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RESUMO - EFEITO DA VARIAÇÃO TEMPORAL DE PROCESSOS FÍSICOS SOBRE OS NUTRIENTES, PRODUÇÃO PRIMÁRIA E SEDIMENTAÇÃO NA LAGOA DE GUARAPINA (RJ), BRASIL.

O efeito da variação temporal dos processos vento e maré sobre o comportamento de nutrientes, produção primária e sedimentação, foi estudado durante um período de 19 dias no inverno de 1985 na área jusante da Lagoa de Guarapina, Brasil. Períodos de intensidade baixa de vento e maré resultaram em estagnação de água e acumulação de nutrientes no fundo da coluna de água estratificada. A entrada posterior de água marinha no fundo, promoveu o transporte vertical de sal e nutrientes em direção à haloclina. Concomitantemente, ventos fortes causaram a homogenização vertical da camada superficial e erosão da haloclina, tendo como resultado um transporte parcial de sal e nutrientes no sentido haloclina-superfície. A alta variação temporal dos processos físicos suprimiu a produção primária, mesmo quando os fatores luz e nutrientes se apresentavam razoáveis a produção. A população fitoplanctônica demonstrou estado de "stress"

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devido à intensa turbulência. Foi elaborado um balanço de massa para a camada superficial a partir dos parâmetros estudados.

ABSTRACT - THE SHORT TERM EFFECT OF PHYSICAL PROCESSES UPON NUTRIENTS, PRIMARY PRODUCTION AND SEDIMENTATION IN GUARAPINA LAGOON (RJ), BRAZIL.

The short-term effect of wind and tidal forcing upon the behavior of nutrients, primary production, phytoplankton and sedimentation, was studied during a 19-day period in austral winter of 1985 within the highly stratified lower region of the subtropical lagoon of Guarapina, southern Brazil. Low meteorological and tidal forcing enhanced stagnation of bottom water and nutrient accumulation therein. The onset of tidal intrusion resulted in the vertical transport of nutrients from the bottom water towards the halocline. Concomitantly, erosion of the halocline by wind induced mixing resulted in the entrainment of salt and nutrients from the halocline into the surface mixed layer. The high temporal variation in physical forcing suppressed primary production, in spite of favorable light and nutrient conditions. The phytoplankton population seemed to be stressed by high turbulence. The properties studied were quantified with respect to their increment and loss in the surface mixed layer.

INTRODUCTION

Subtropical and temperate lagoons are in general subject to high spatial and temporal variations in the behaviour of physical, chemical and biological properties (MEE, 1978; SUBBA RAO, 1981). This is particularly accentuated at the entrance and the lower reaches of the lagoon where

marine water inflow and lagoon water outflow occurs. If the tidal inlet is small and of low mean depth, the exchange between marine and lagoon water usually results in saline fronts with strong shear mixing close to the entrance and stratification of the watercolumn in the lower and deeper reaches of the lagoon (MEE, 1978; NICHOLS and ALLEN, 1982; KNOPPERS et al., 1984). The behaviour of chemical and biological properties turns to be highly dynamic and depends upon the time-scale and magnitude of tidal and meteorological forcing and also the variations in morphological configuration, which are characteristic for the lower reaches of lagoons. High frequency wind and tide induced mixing are usually associated with a conservative behaviour of chemical and biological properties and low frequency physical forcing, with stratification and non-conservative property behaviour (BURTON and LISS, 1976). Temporal variations in primary production and phytoplankton biomass have been directly related to short term changes in density stratification in shallow water systems (SINCLAIR et al., 1981).

The present study assessed the effect of short temporal variations of physical processes upon the behaviour of dissolved inorganic nutrients, primary production and sedimentation of particulate organic matter, in a post-frontal and highly stratified lower region of the subtropical lagoon of Guarapina, southern Brazil. The study formed part of an assessment on the seasonal variation of water properties in the lagoon.

STUDY AREA

Guarapina Lagoon (Lat. 22 75'S and Long. 42 41'E) is situated along the coast of the State of Rio de Janeiro, southern Brazil (Fig. 1). It forms part of the larger lagoonal system of Marica, which lies parallel to the coastline. The lagoon exhibits a surface area of 6.38 Km², a volume of

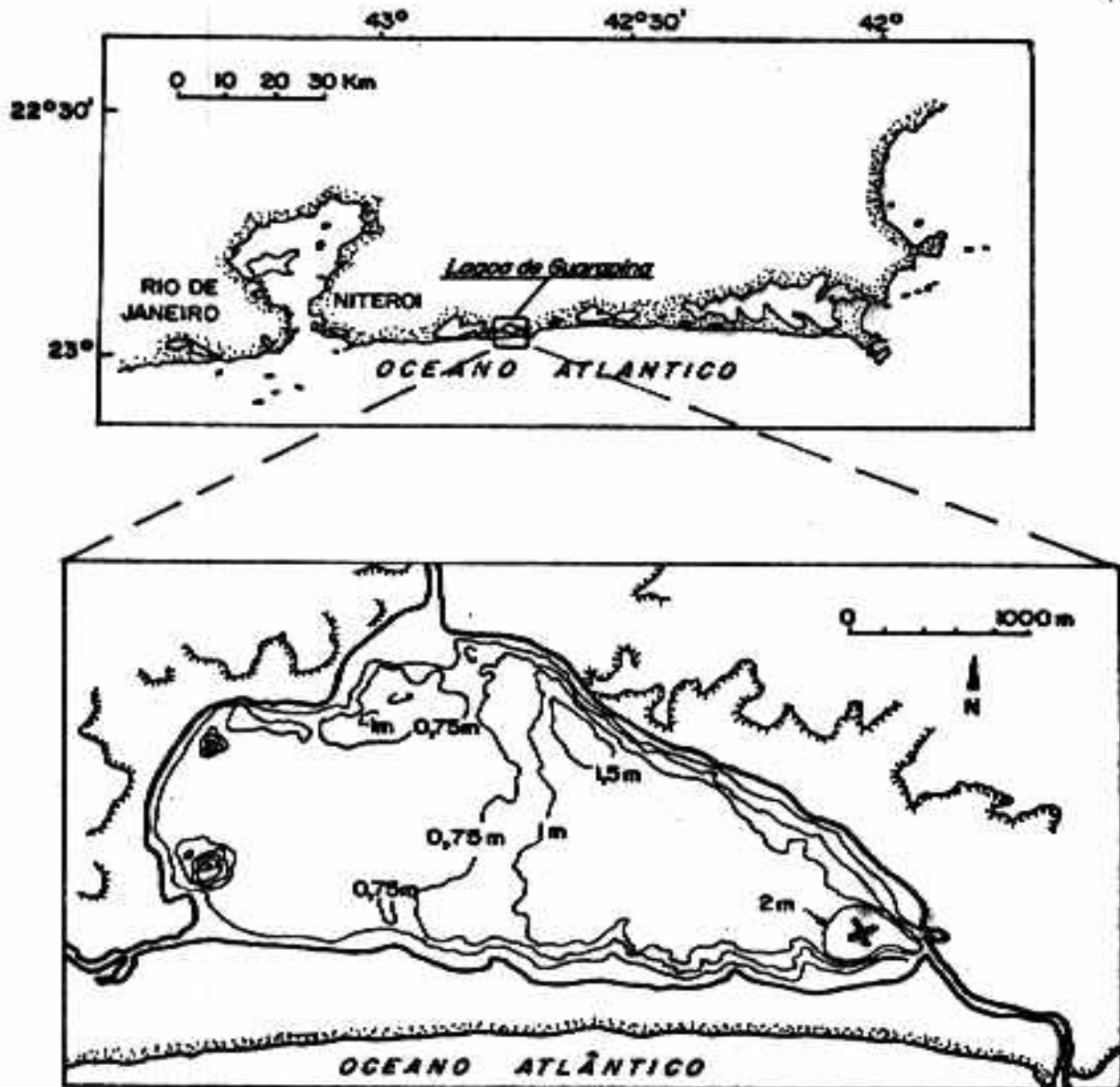


Figure 1. Localization, bathymetry and sampling site (X) of the study area.

5.4 * 10**6 m³ and a mean depth of 0.85m at MLWL. The lagoon has access to the open sea via a tidal channel with a length of 1.5 Km, a crosssectional area of 20 m² and a mean depth of 0.5m. The lower reaches of the lagoon, close to the inner entrance of the tidal inlet, has a maximum depth of 3.5m and represents the site of the present study. The tide outside the lagoon is characterized by diurnal inequality

and ranges between 0.3 and 1.3 m. Low tidal amplitudes are paired with constant outflow conditions of the lagoons water and high tidal amplitude, particularly in conjunction with strong SE-winds, with marine water inflow up to 2% of the lagoons volume per tidal cycle (KNOPPERS & TURQ, 1985). Annual precipitation is in turn of 1300 mm (BARBIERI, 1986).

MATERIAL AND METHODS

Sampling and Instrumentation - The study was conducted during austral winter from 05.08. to 24.08.1985 at a fixed station in the lower stratified reaches of the lagoon (Fig. 1). Water properties were monitored at 1 to 2 day intervals, and on some occasions twice a day. Vertical profiles of temperature, salinity and light were obtained at a resolution of 0.2 to 0.5 m and water samples were collected with a Van Dorn type bottle at 0 m, 1 m and 2.5 m depths.

Temperature and salinity were measured with a T/S - Sensor (Type MC 5, Electronic Switchgear, London), incident radiation and light profiles with Li-Cor PAR sensors, pH with an electrode (WTW-Weilheim) and dissolved oxygen and nutrients (nitrate, nitrite, ammonia, orthophosphate and silicate) according to STRICKLAND and PARSONS (1972).

Samples of particulate were filtered over Whatman GF/C filters and stored at -18°C prior to analysis. Seston dry weight (DW) was determined as in LENZ (1971) and pigments as described by STRICKLAND and PARSONS (1972). Measurements of primary production were carried out with the C-14 method of STEEMANN-NIELSEN (1952). After the addition of 1 ml of radioactive bicarbonate ($2\mu\text{Ci}$) 100 ml samples were incubated in situ for three hours (0 m, 1 m and 2,5 m depths) and thereafter filtered over Millipore filters (0.47 mm, porosity $0.45\ \mu\text{m}$) and acidified with 2 ml of 0.1 N HCl. Filter readings were conducted with a Geiger-Mueller Counter INAPM, Brazilian Navy. Alkalinity and carbon dioxide were evaluated

through the acid titration method (STRICKLAND and PARSONS, 1972).

Phytoplankton samples were fixed with 1% buffered formalin and analysed for species composition and biomass. Counts were conducted with an inverted microscope (NIKON-Diaphot) according to UTERMÖHL (1958). Phytoplankton biomass was evaluated from plasma or cell volume (STRATHMANN, 1967; SMETACEK, 1975) according to the recommendations of the Baltic Marine Biologists WG-9 (EDLER, 1979, Ed). Phytoplankton carbon (PPC) was calculated by multiplying $0.11 \times \text{plasma volume}$ for diatoms, cyanophytes and flagellates and $0.13 \times \text{cell volume}$ for dinoflagellates.

Sedimentation of suspended matter was measured with cylindrical traps which exhibited a length to diameter ratio of 5:1. They were suspended at 1m and 2.5m depths and collected at two-day intervals. Chloroform was used as a preservative.

RESULTS AND DISCUSSION

DESCRIPTION OF PROCESSES

The study may be subdivided according to the occurrence of the physical, chemical and biological events into four phases:

Phase I - The first five days of the study were characterized by relatively stable physical conditions. Incident radiation fluctuated at $40 \text{ Em}^{-2} \text{ d}^{-1}$ (Fig. 2), and NE-winds with speeds up to 3 ms^{-1} (Fig. 3) and a stable strongly stratified water column predominated (Fig. 4a). The water column exhibited a surface mesohaline mixed layer up to 1m depth, a marked halocline ($S = 10\%$), which oscillated between 1 and 1.5m depth, and a polyhaline bottom layer. As low wind forcing coincided with low tidal amplitudes ($A = 0.3\text{-}0.6\text{m}$) outside the lagoon the surface mixed layer

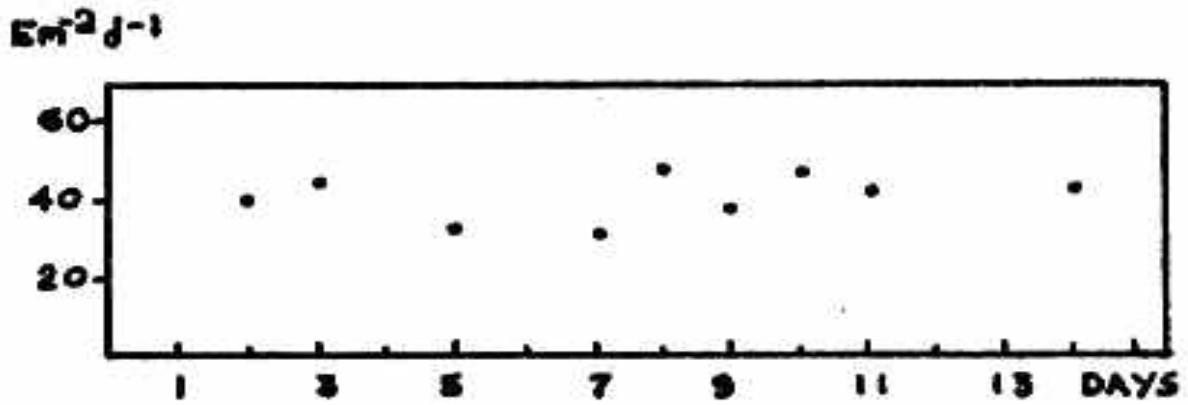


Figure 2. Incident radiation in $\text{Em}^{-2}\text{d}^{-1}$.

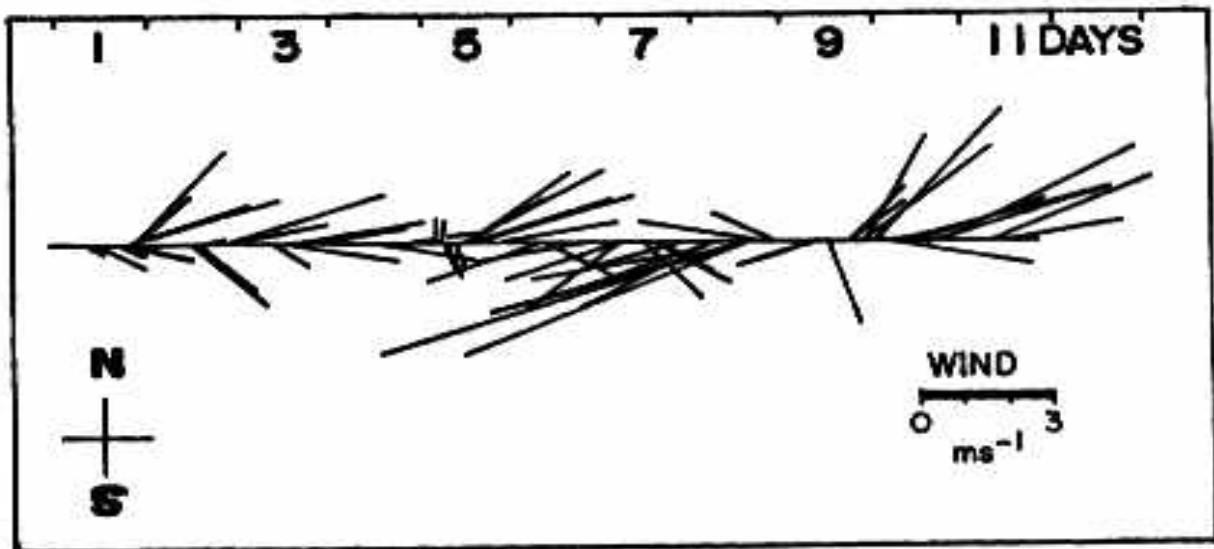


Figure 3. Wind vectors for speed and direction close to the sampling site.

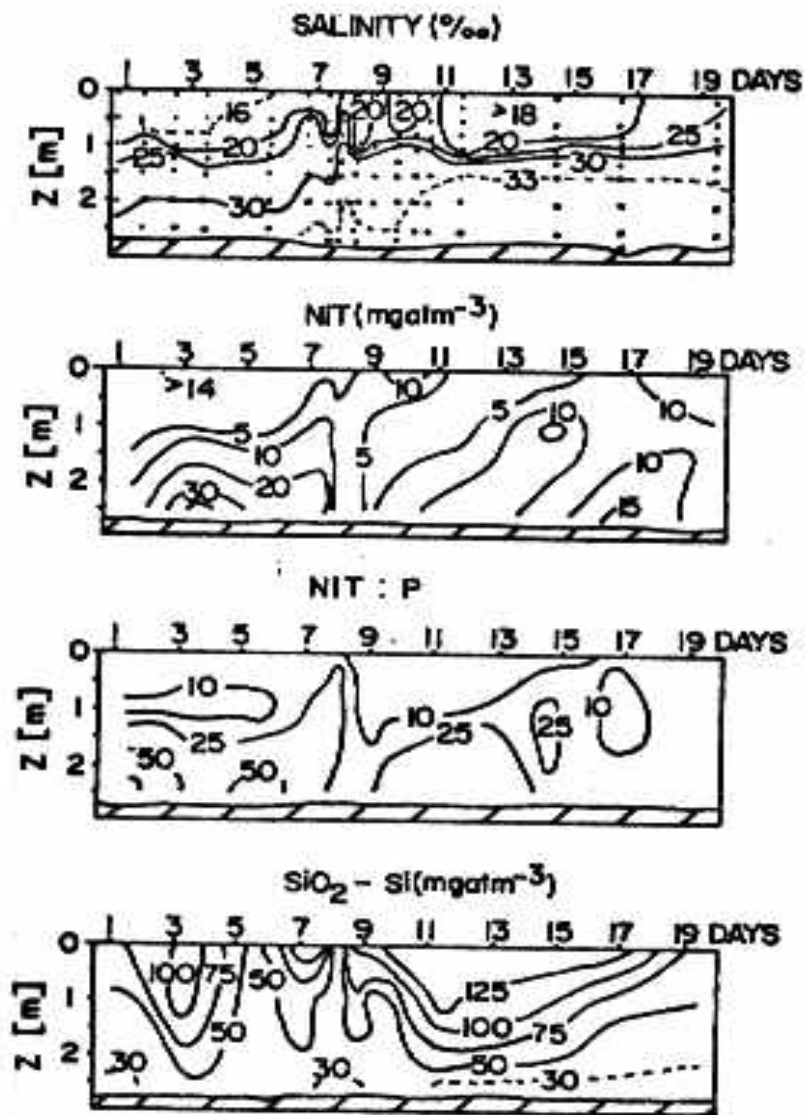


Figure 4a-d. Time-depth plots for salinity, inorganic nitrogen (TIN), the ratio inorganic nitrogen to phosphate (TIN:P) and silicate resp.

exhibited constant outflow towards the tidal channel and the bottom layer stagnated conditions with the development of anoxia close to the sediment surface. This was paired with an accumulation in total dissolved inorganic nitrogen (TIN, Fig. 4b) which was high in comparison to orthophosphate as shown by the high atomic TIN:P ratios (35-70:1, Fig. 4c), encountered. Silicate values in the bottom layer were by a factor of three lower than at the surface and were inversely related to salinity. Intrusion of marine water poor in silicate (10 mg atm^{-3}) prior to the study, was thus responsible for the low concentrations at the bottom, waters.

The surface mixed layer had TIN concentrations below 2 mg atm^{-3} , an N:P range between 10 and 20:1 and high silicate concentrations around 75 to 100 mg atm^{-3} . Primary production was limited to the surface mixed layer with rates between 30 and $40 \text{ mg Cm}^{-3}\text{hr}^{-1}$ at the surface and $10 \text{ mg Cm}^{-3}\text{hr}^{-1}$ at the halocline (Fig. 5a). Light intensities around 100 and $150 \mu\text{Em}^{-2}\text{s}^{-1}$ prevailed at the halocline; this represented approximately the 10% light-depth level. In contrast, chlorophyll a with concentrations around 25 mg m^{-3} was homogeneously distributed in the mixed layer, bottom water concentrations were by a factor of two lower than at the surface (Fig. 5b). These values were not corrected for phaeopigment content. The distribution of phaeopigments in Figure 5c shows that the Chl. a values at the bottom were in part attributed to phaeopigment content. This indicates that the bottom water was the site of Chl. a accumulation and subsequent degradation. Seston DW had a similar distribution as Chl. a, but showed stronger temporal variations (Fig. 5d).

Phase II - The second phase of the study extended from day 6 to 11 and was characterized by unstable physical conditions. The increase in tidal amplitudes outside the lagoon ($A = 0.9$ to 1.3 m) caused sporadic intrusions of oxygen saturated marine water and the passage of a cold weather front brought about SE-winds with speeds up to

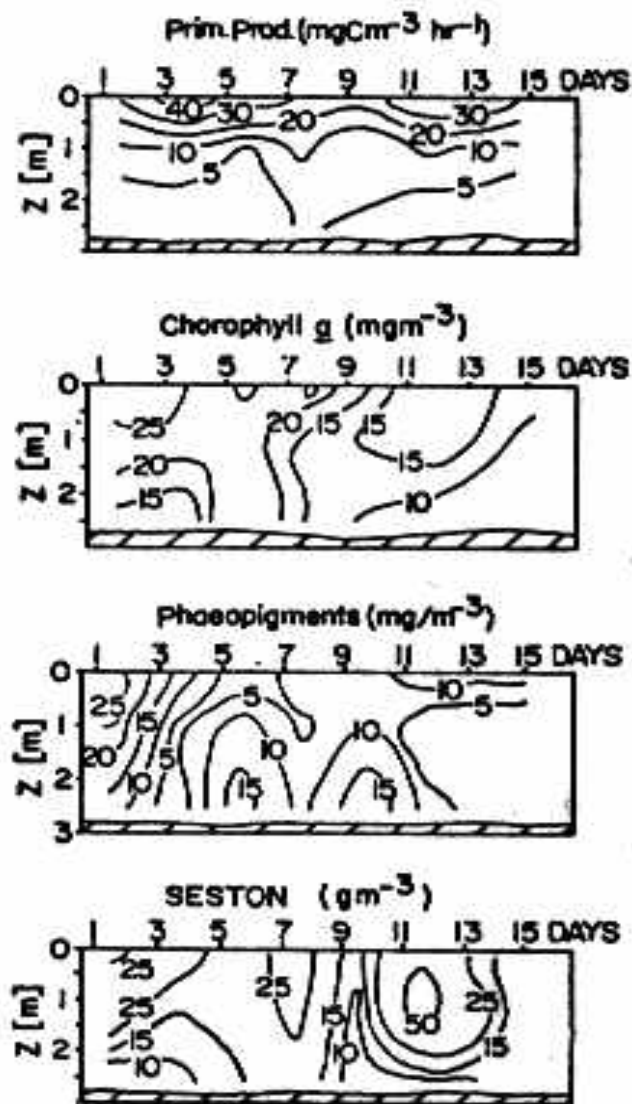


Figure 5a-d. Time-depth plots for primary production (Prim. Prod.), Chlorophyll *a*, phaeopigments and Seston dry weight respectively.

8 ms⁻¹. Thereafter, a rapid shift to NE-winds with speeds up to 3.5 ms⁻¹ occurred. The tidal intrusion caused vertical transport of stagnated bottom water (Fig. 5a) and associated nutrients (Fig. 4b), mainly in the form of ammonia (Fig. 4c, TIN:P ratio) towards the halocline via the process of density displacement (SMETACEK et al., 1976) and also mixing. This caused an uplift of the halocline from 1m to 0.5m depth on day 6, and day 7 strong wind induced mixing resulted in the erosion of the halocline with the effect of salt water entrainment and associated nutrient input into the mixed layer. This was evidenced by the surface increase in salinity (Fig. 4a; / S = 40/00) and TIN (Fig. 4b) and also the marked short temporal oscillations of the halocline. Salt water entrainment was paired with a dilution of surface silicate concentrations. In spite of the inoculation of nutrients to the surface layer, primary production was by a factor of 1.5 lower than in phase I. Light intensities dropped to 25 uEm^{-2s}-1.

Phase III - This phase lasted between day 12 and 16 and was characterized by relatively calm weather, high incident radiati. (I = 50 uEm^{-2s}-1) and permanent outflow conditions of the surface mixed layer. This was paired with lower TIN and higher silicate concentrations (Figs. 4b and 4c resp.) and an increase in primary production (Fig. 5a) and Seston DW (Fig. 5d). The decrease in surface salinity (Fig. 4a) and silicate increase indicated the passage of outflowing water masses originating from the lagoon itself. However, salinity values were still higher than during phase I which suggested that the marine water introduced during phase II proliferated towards the upper reaches of the lagoon at the bottom and was subsequently mixed in the area. KNOPPERS et al (1986) have shown that this process is important to water renewal of the upper reaches of the lagoon.

Phase IV - Conditions during the last phase of the study were similar to phase II. A second phase of tidal

intrusion and SE-wind forcing prevailed, nutrients were transported from the bottom to the surface and a near to complete dissolution of the halocline by wind forcing became evident. Unfortunately, the parameters wind, primary production and Seston DW were not determined.

TEMPORAL VARIATIONS

The behaviour of the properties studied revealed that the lower reaches of Guarapina Lagoon were subject to marked temporal variations in its functioning. Transient meteorological conditions, typical for the austral winter period in the region (BARBIERI, 1986), interacted with the tides on more or less the same time-scales. Low meteorological forcing, here defined as periods of maximum wind speeds up to 3ms^{-1} , coincided with low tidal amplitudes outside the lagoon and surface water outflow, and high meteorological forcing (wind speeds between 4 and 8ms^{-1}) with high tidal amplitudes and marine water intrusion. These extremes conditions in physical forcing alternated with each other at five to six day intervals and governed the overall picture of chemical and biological property behaviour. A second higher frequency temporal scale was given by the periods of rapid shifts in wind speed and direction and the variable duration and intensity of tidal intrusions which lasted between about two and six hours. The former had an obvious impact on surface flow characteristics (evaluated on a qualitative basis) and the latter short term changes in bottom salinity and nutrient concentrations (days five to seven). The most striking effect was the strong oscillation of the halocline during the initial impact of tidal intrusion and SE-wind forcing. Vertical movements of the halocline ranged about 0.5 m various times during a day. The assessment of a time scale dependent quantitative relationship between the parameters was difficult to conduct because sampling frequency of the

physical parameters was higher than for the remaining parameters. Measurements of all parameters was only congruent at two day intervals. This interval reflects the upper most time scale limit for the detection of algal physiological responses to high frequency physical forcing and the lowest limit for the observation of ecological response of phytoplankton populations to the changing environment (HARRIS, 1980).

With this in mind, an attempt is made to assess the combined effect of the physical processes upon the behaviour of the chemical and biological properties by quantifying the increment and loss of matter at two-day intervals for the upper 1m of the watercolumn. This delimitation coincides more or less with the surface mixed layer with the exception during the onset of phase II of the study. Figures 6a to d represent the increment and loss of the parameters salt, TIN, phosphate and silicate respectively, and Figures 7a to d for primary production, Chlorophyll a, Seston DW and also, Seston DW and chlorophyll a sedimentation rates at 1m depth, i.e. the lower premises of the surface mixed layer.

In general, the increment and loss of salt was more or less only proportional to TIN. An inverse relationship existed between salt and silicate, primary production, Chl. a and Seston DW. The former thus substantiates the process of TIN injection by wind induced halocline erosion from sub-halocline layers into the surface. With respect to the behaviour of the remaining parameters the quantitative relation with salt merely suggested that, the properties decreased in concentrations due to dilution by salt entrainment. Conservative behaviour thus became evident for most of the properties although some discrepancies existed.

Particularly during phase III a tendency towards non-conservative behaviour became eminent due to physical stabilization of the watercolumn. The slight quantitative discrepancies between salt increment and loss and the other

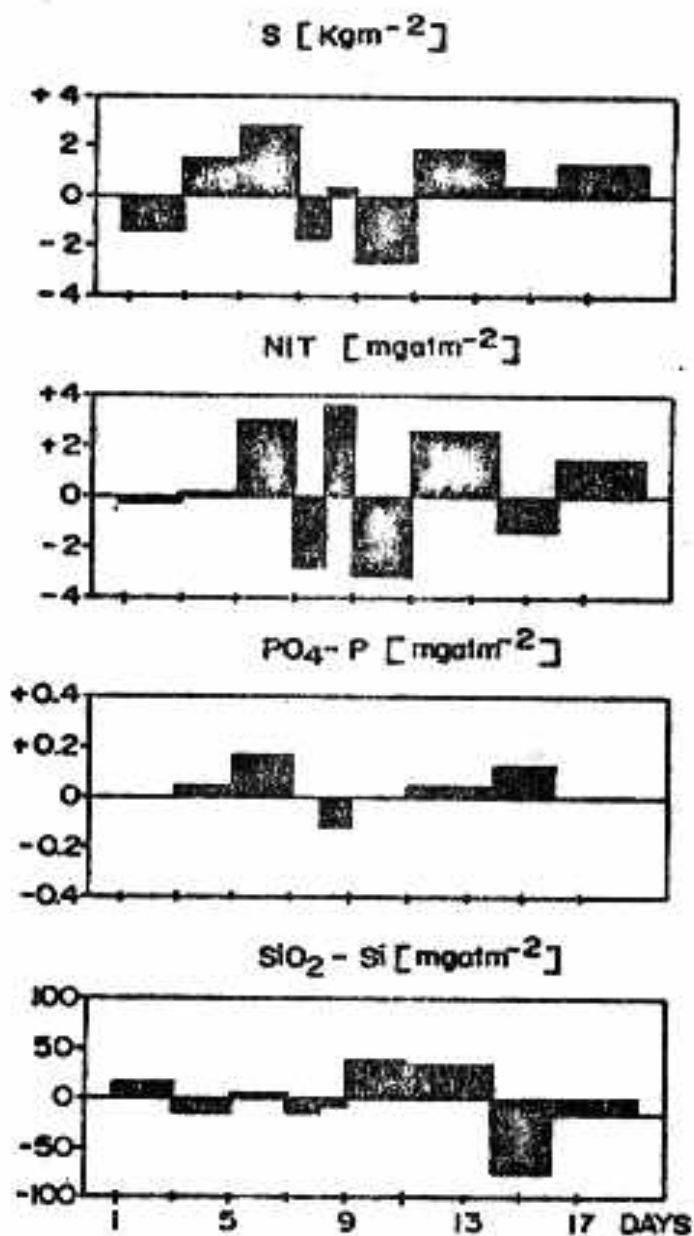


Figure 6a-d. Increment and loss of salinity (S), inorganic nitrogen (TIN), orthophosphate (PO₄-P) and silicate (SiO₂-Si) respectively for the surface mixed layer.

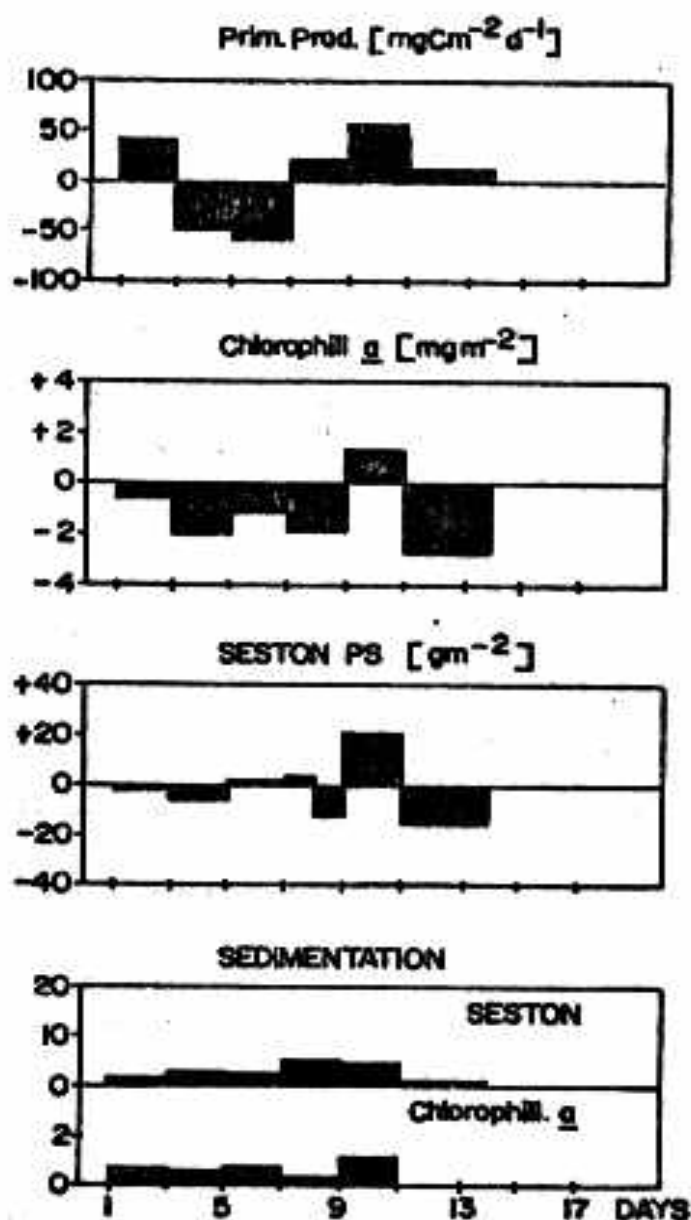


Figure 7a-d. Increment and loss of primary production (Prim. Prod.), chlorophyll a, seston dry weight and also sedimentation of Seston dry weight and chlorophyll a, respectively, for the surface mixed layer.

parameters during phases I, II and III were caused by the changing conditions in lateral advection which also interacted with the processes of vertical water transport.

The increment or loss of the properties studied was summarized for the 14-day and 19-day periods of the study in Table 1.

Table I - Surface mixed layer ($z = 1$ m) increment or loss of measured properties for the time periods of 14 days and 19 days.

Parameter		Time	
		14 days	19 days
Salinity	(Kgm ⁻²)	3.93	8.23
TIN	(mgatm ⁻²)	7.70	9.55
Phosphate	(mgatm ⁻²)	0.29	0.49
Silicate	(mgatm ⁻²)	193.7	-1.30
Prim. Prod.	(mgCm ⁻² d ⁻¹)	8.5	-
Chl. <u>a</u>	(mgm ⁻²)	-15.7	-
Seston DW	(gm ⁻²)	-21.0	-
Sedimentation			
Chl. <u>a</u>	(mgm ⁻²)	7.5	-
Seston DW	(gm ⁻²)	39.9	-

The 14-day period represents two phases of surface water outflow and one phase of tidal intrusion and strong wind mixing. The 19-day period included an additional phase of tidal intrusion and wind mixing. The high increment in silicate during the first period in comparison to the second period thus shows that lateral advection of surface water from the lagoon proper surpassed the influence of the processes that governed vertical transport within the water

column. For TIN this is not so eminent because during phase IV (included in the 19-day period) less nitrogen in relation to salt was transported vertically. This was due to the prevalence of lower TIN accumulation during phase III than during phase I. Due to the marked short temporal variation of the physical regime primary production increment was extremely low, increment and loss nearly equaled each other out.

Sedimentation of Chl. a was by a factor of two lower than calculated from the Chl. a from the water column. In contrast, sedimentation rates of Seston DW were by a factor of two higher than the water column loss. Furthermore, sedimentation rates recorded by sediment traps below the halocline at 2.5m depth, were during phase II of the study by a factor of three higher than in 1m depth. Peripheral wave action (PWA) and wind induced mixing caused resuspension of matter in the shallow areas close to the study site (PORTELA and TURCO, this volume) and advection and subsequent sedimentation probably transported this material to the deeper waters of the study area. This phenomenon, defined as sediment focusing i.e. greater sedimentation in the deeper basins than in shallower areas of enclosed systems, has been described in detail by HAKANSON (1977) and HILTON (1985) for lakes. The present site thus seems to be an area of sediment focusing as it also represents the deepest section of Guara-pina Lagoon, the slopes of the basin are steep and the sediments have in comparison to the remaining areas a higher content of organic matter. Resuspension and secondary sedimentation of matter by tidal intrusion must also be considered.

NUTRIENTS, PRIMARY PRODUCTION and PHYTOPLANKTON

The phenomenon of nutrient accumulation in stagnated, bottom waters for sub-tropical and tropical lagoons has been

documented by several authors (BEERS and HERMAN, 1969; MEE, 1978; OKUDA, 1981; SMETACEK et al., 1981).

The availability of these nutrients to primary producers depends upon the depth of the stagnated bottom water within the water column and the magnitude and location of stratification within the water column. These factors determine the intensity and duration of wind mixing and also temperature convection needed to dissolve stratification in order to liberate and transport the accumulated nutrients from the bottom to the surface layer. In the present study, wind speeds of 4 to 8 ms⁻¹ during several days were sufficient to cause a marked erosion of the shallow lying halocline but insufficient to cause its dissolution. This was not due to the lack of wind energy per se (SINCLAIR et al., 1981) but more due to the renewal of marine water which enabled the maintenance of the halocline over time. However, salt entrainment to the surface layer occurred sporadically during the events when mixing was strongest and tidal intrusion lacked during the sequence of the tidal cycle, i.e. phase IV.

The comparison of TIN concentrations between the bottom and the surface also revealed that a great fraction of the TIN accumulated at the bottom during stagnation (phase I) was advected out of the basin during tidal intrusion (phase II) due to marine water proliferation via a 1.5 m channel towards the middle reaches of the lagoon (KNOPPERS et al., 1986). For example 54 mgatm⁻³ of ammonia accumulated during phase I at the bottom and during tidal intrusion the concentrations declined to 3 mgatm⁻³. The ammonia injected to the surface was 17 mgatm⁻³. The basin, although small, should thus not be neglected as a nutrient source to primary producers at least for the middle reaches of the lagoon, particularly during summer when periods of stagnation may be prolonged due to longer outflow conditions caused by rainfall mediated water level elevations (KNOPPERS, TURCO and MOREIRA, unpubl. data). Decline of water levels would

enhance tidal intrusion and thus enhance nutrient advection.

The high N:P ratios in the bottom water (35-70:1) and the surface sediment pore water (30:1 for 0-1 cm and 9-10 cm depths) indicated that decomposition of organic nitrogen was preferential to phosphorus and that ammonia release rates from the sediment must have surpassed those of phosphate. Redox-state related differences in the adsorption and desorption behaviour between the elements (BREZONIK, 1972; ROSENFELD, 1979) with the sediment or processes of phosphate precipitation as well as the specific characteristics of the clay sediments highly rich in organic matter (20% DW) were probably responsible for these values. These values are high if compared to the general N:P composition of 10 to 20:1 of organic matter in pelagic and benthic systems (REDFIELD et al., 1963; POLLEHNE, 1980; PARSONS et al., 1984) and to some studies conducted with sub-oxic and anoxic clay sediments which were characterized by a nitrogen to phosphorus release rate of about 10:1 (POLLEHNE, 1980; BALZER, 1984). The sediments of the latter study exhibited an organic matter content by a factor of five lower than in the present study.

If an N:P ratio of 16:1 is assumed to be the demand of primary producers (REDFIELD et al., 1963), the range of N:P values of 10 to 20:1 as well as the absolute concentrations encountered in the surface layer imposed no limitation to primary production. Phosphate retention by the sediment is probably compensated by fresh water sources (KNOPPERS et al., 1986). Primary production within the surface layer did not seem to be light limited. Light harvesting efficiency of the phytoplankton population which mainly consisted of the cyanophytes *Synechococcus* sp and nanoflagellates was higher at 1 m depth than near the surface. Light intensities of 150 $\mu\text{Em}^{-2}\text{s}^{-1}$ yielded production rates of 10 $\text{mgCm}^{-3}\text{hr}^{-1}$ in 1 m depth and 700 to 1400 $\mu\text{Em}^{-2}\text{s}^{-1}$ at 0.1 m depth 25 to 40 $\text{mgCm}^{-3}\text{hr}^{-1}$. WOOD (1985) reported light saturation intensities for oceanic *Synechococcus* species around 200 $\mu\text{Em}^{-2}\text{s}^{-1}$ which

is similar to the limit for warm water oceanic phytoplankton (HARRIS, 1978). However, production rates and efficiency, the latter as based upon the assimilation number (mgChr-l/mgChl.a , Table 2), were relatively low (range 1.12 to 2.25) in comparison to those found in other sub-tropical/tropical lagoons (SUBBA RAO, 1981). The author documented a range in assimilation numbers between 1.3 and 24 which corresponds to values of marine phytoplankton in general (PARSONS et al., 1984). Further information on the characteristics of the prevailing phytoplankton population are depicted in Table II. The values for phytoplankton carbon (PPC) and the ratios production: ppc, productio: Chl. a, PPC: Chl. a and total carotenoids: Chl. a are shown for a 14-day period.

Table II - The temporal variation of Phytoplankton biomass (PPC) in mgC m^{-3} and the ratios between Primary Production and Phytoplankton biomass (P/PPC) and Chlorophyll a (P/Chl), Phytoplankton biomass and Chlorophyll a (PPC/Chl), and total Carotenoids and Chlorophyll a (CAR/Chl).

Day	PPC	P/PPC	P/Chl	PPC/Chl	CAR/Chl
1	918.6	0.38	1.12	33.0	0.94
3	732.4	0.72	1.86	28.4	0.99
5	763.4	0.51	1.82	39.3	1.11
7	1008.5			40.0	0.83
9	274.3	0.94	1.60	18.7	0.85
11	719.4	0.62	2.24	39.7	1.08
14	478.9	0.70	2.25	35.6	1.32

With the exception of day 9 and 14 PPC values remained relatively constant. However, changes in population

composition did occur. *Synechococcus* sp, contributed up to 85% of total biomass during the first three days of the study. During phase II its contribution declined to 40% which was paired with an increase in nanoflagellates up to 45% of PPC. The remaining population consisted mainly of *Trichodesmium* sp and the dinoflagellate *Prorocentrum minimum*.

The rough indicators for the assessment of the physiological state of the population, the PPC:Chl. a and CAR:Chl. a ratios, did not reveal any substantial changes during the entire study. This is surprising as species composition changed and the impact of physical forcing varied considerably. This suggests that the cyanophyte population and the nanoflagellates exhibited similar ratio values and wind induced mixing at windspeeds around 3ms⁻¹ (phase I) and at 4 to 8ms⁻¹ (phase II) had a similar effect upon the population. This was also substantiated by the assimilation numbers and the low variation in production rates. However, the PPC:Chl. a and CAR:Chl. a ratios were by a factor of 1.5 to 2 higher than observed for sound growing nanoflagellates in the tropics and in temperate areas (SMETACEK, 1975; ODEBRECHT, 1981; KNOPPERS, 1982; KNOPPERS et al., 1984). However, as no information is available on the behaviour of these ratios for Cyanophyte populations under changing environmental conditions interpretations should be regarded as limited.

If the assimilation numbers are truly low and the PPC:Chl. a and CAR:Chl. a ratios are on the high side they imply, that in spite of sufficient nutrient and light availability, the population was subject to stress conditions due to the short temporal variations in physical forcing and high turbulence. The relationship between production efficiency and magnitude of turbulence is still difficult to assess as turbulent motions in surface layers exist over a variety of scales. MARGALEF (1978) proposed a scheme relating survival strategy of life-forms to turbulence and nutrient availability, in waters. Fertile and turbulent waters enhance diatom growth

whereas exhausted and stratified low turbulent environments favour dinoflagellate growth. Enriched and low turbulent environments favour small celled life forms.

HARRIS and LOTT (1973b) state that wind speeds in excess of 4ms⁻¹ are critical in the propagation of organized flow structures or Langmuir Vortices which enhance strong vertical mixing within a shallow water body. Thus, taking into consideration that small celled species and considerable turbulence prevailed and that the physiological parameters do not clearly indicate sound growing conditions, it is assumed that the dynamic physical forcing during the study imposed stress upon the phytoplankton population.

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