Biogeochemistry **14**: 129—148, 1991

Metabolism of a subtropical Brazilian lagoon

J. P. CARMOUZE, B. KNOPPERS AND P. VASCONCELOS
Deptº de Geoquímica — UFF — Morro do Valonguinho 24210 Nitéroi R.J., Brazil

Accepted 6 June 1991

Key words: coastal lagoon, autotrophic activity, heterotrophic activity, community metabolism, total CO_2 method

Abstract. Total community, planktonic and benthic metabolisms were measured by using the carbon dioxide production and consumption, the 'diurnal curve' method and the in situ bottle incubation technique over an annual cycle in two sublagoons of the Saquarema Lagoon, Brazil. Metabolic rates of the phytoplankton-based lagoon were characterized by considerable daytime and daily variability in production and respiration, by a seasonal shift between net autotrophy and heterotrophy and by an annual balance of production ($P = 105 \pm 65$ mmoles/m^2/day, $n = 25$) and respiration ($R = 102 \pm 50$ mmoles/m^2/day, $n = 25$). Total community metabolism was similar throughout the lagoon, but phytoplankton assimilation rates and benthic respiration showed spatial differences. Bottle incubations compared to total community free water respiration suggested that the pelagic community was 2—5 times more active than the benthos.

I. Introduction

Considerable effort has been spent on measurements of hourly, daily, and annual rates of phytoplankton primary production in tropical and subtropical coastal lagoons (Gilmartin & Relevante 1978; Qasim 1979; Rao 1981; Nixon 1982). Most studies have been conducted using in situ dissolved oxygen and carbon-14 incubation techniques (Alem & Samaan 1969; Tundisi et al. 1973; Gilmartin & Revelante 1978; Mee 1978; Arenas 1979; Day et al. 1982; Pàges et al. 1981; Vaulot & Frisoni 1986; Randall & Day 1987; Flores-Verdugo et al. 1988; Sandoval-Rojo et al. 1988; Moreira & Knoppers 1990). Less attention has been given to the assessment of the basic community parameters of production and respiration using diurnal curve 'free water' measurements of dissolved oxygen and carbon dioxide (Odum & Hoskin 1958). Few authors have applied in situ incubation techniques with free water measurements in phytoplankton-based coastal lagoons (Park et al. 1958; Qasim et al. 1969; Sournia 1977;

Sournia et al. 1981; Reyes & Merino 1990). The advantage combining both techniques is that, together, they furnish information on total primary production, total system metabolism and the relationship between pelagic and benthic metabolism to total metabolism of the system. These aspects are now of particular interest in view of the discussion on whether coastal systems are autotrophic or heterotrophic (Smith & MacKenzie 1987; Smith 1988; Reyes & Merino 1990).

In this study we report measurements of free water changes in carbon dioxide consumption and production over an annual cycle in the Saquarema Lagoon, Brazil. Studies on primary production in the region are scant and have been determined only by standard incubation techniques (Machado & Knoppers 1988; Costa-Moreira 1989; Moreira & Knoppers 1990).

II. Study area

The lagoon is situated along the subtropical coastline of the State of Rio de Janeiro which harbours a series of shallow mesotropic to hypereutrophic lagoons subject to either natural or cultural eutrophication.

The lagoon (28°S and 42°W) has a surface area of 23.4 km^2, a mean depth of 1.15 m, and is composed of a series of four sublagoons. They are from east to west: Fora (7.4 km^2), Boqueirão (0.6 km^2), Jardim (2 km^2) and Urussanga (12.6 km^2) (Fig. 1). Urussanga has more fresh water influence ($S‰ = 5.8 \pm 3.5$, $n = 133$) than Fora, which communicates directly with the ocean ($S‰ = 14.5 \pm 6.3$, $n = 133$). The lagoon is weakly influenced by tide. The mean tidal range is 0.01 m in Urussanga and 0.04 m in Fora (Knoppers et al. 1991, this issue) and may be defined as a 'choked' system in accordance with the classification scheme proposed by Kjerfve (1986). Anthropogenic perturbation is characterized by agricultural activities in the drainage basin on Urussanga and by domestic sewage effluent discharge into Fora.

III. Methods

This study was carried out from August 1988 to July 1989 at two stations, one in Urussanga and one in Fora. Depths of these two stations were, respectively, 1.10 ± 0.20 m and 0.90 ± 0.20 m ($n = 133$). Twenty-five surveys with five to six free water measurements over a diurnal cycle at 18.00, 06.00, 10.00, 12.00, 15.30 and 18.00 hrs were performed. Temperature, salinity, pH, alkalinity, and dissolved oxygen were monitored at 0.10 m from the surface, at mid-depth, and above the bottom. Water

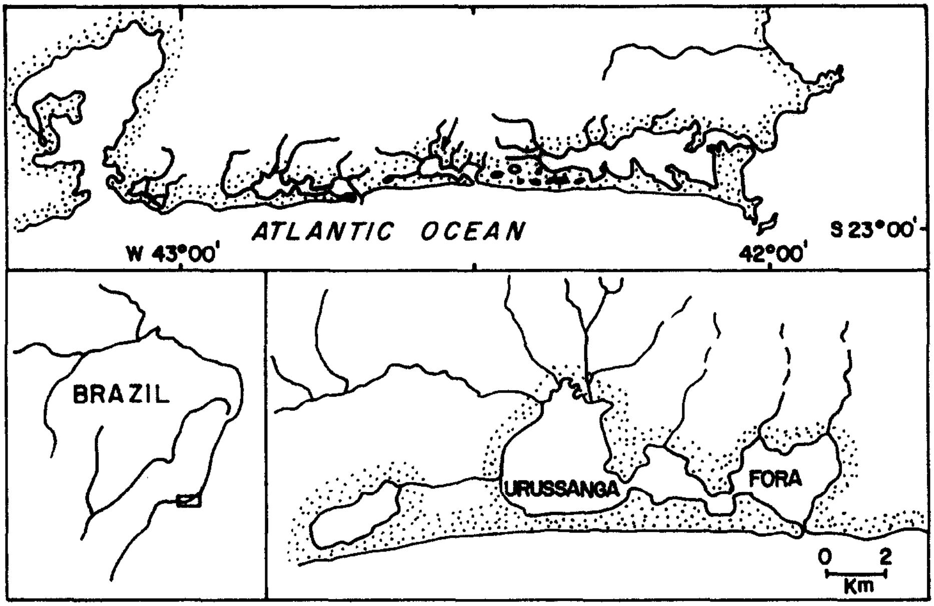

Fig. 1. Map showing location of the Saquarema Lagoon in Brazil.

samples for analysis of nutrients and chlorophyll-a were collected at 18.00 only. Simultaneously, water samples were collected and incubated in borosilicate bottles (300 ml) at the respective depths. During the period of high biological activity in summer and autumn, one nighttime incubation (18.00 to 06.00 hrs) and four daytime incubations (06.00 to 10.00, 10.00 to 12.00, 12.00 to 15.00, and 15.30 to 18.00 hrs) were performed, while during the period of low biological activity in winter, one nighttime incubation and three daytime incubations (06.00 to 10.00, 10.00 to 14.00, 14.00 to 18.00 hrs) were conducted.

Temperature and salinity were measured by a YSI salinometer, Model NCT, dissolved oxygen by a polarographic sensor (YSI Model 58) with a resolution of 0.3 μM, and pH with a 0.001 high resolution unit (Metrohm pHmeter 654) and a high precision pH electrode assembly (Metrohm No. 65102). Alkalinity was determined by sulfuric acid titration using Gran's function (Gran 1952). Total dissolved carbonates and total carbon dioxide (TCO_2) were assessed by the pH-alkalinity method, using an ionic association model (Carmouze 1984). Samples for ammonia, nitrate, nitrite, and orthophosphate were filtered and frozen at −18 °C before analysis by Standard Methods (Strickland & Parsons 1972). Particulates for chlorophyll analysis were retained on Whatman GFC filters and held at −18 °C until analysis in the laboratory (Lorenzen 1967).

The daily metabolism of most ecosystems is characterized by alternating periods of net production and net respiration. The period of net production does not always overlay the photoperiod. The period of net respiration may include not only the night time but also the early morning or late afternoon. For that reason, the metabolism has been characterized by the net community production rate, P, relative to the daily period rate, R, corresponing to the night period and eventually the photoperiod of net respiration. Both rates have been measured

- by diurnal changes of TCO_2 contents in the water column (free water technique) and
- by changes of TCO_2 concentrations in-situ bottles (incubation technique).

The former approach, introduced by Odum (1956) measures the whole system (pelagic + benthic metabolism) while the latter procedure, detailed by Vollenweider (1974), measures only pelagic metabolism. Both techniques present some limitations. The incubation technique yields measurements performed on isolated samples of natural communities where biological activities are altered. The applicability of the free water technique is discussed by Hall & Moll (1975). Its major shortcoming is due to unmeasured estimates of exchange at the air-water interface.

Transfer of gases has been described by a model of two-diffusion films, one in the liquid phase and one in the gas phase (Kanwisher 1963; Liss 1973). Only the liquid film appears to control CO_2 exchanges and Fick's first law may be used to calculate the flux, F:

$$F = D/z \times \Delta C = K \times \Delta C,$$

where K denotes the mass transfer coefficient of CO_2, D the diffusion coefficient for the film thickness, z and C the concentration difference across the film. Diffusion of CO_2 is slow compared to its reaction with H_2O and OH^- to form H_2CO_3, HCO_3^-, and CO_3^{2-}. As HCO_3^- and CO_3^{2-} are formed (or consumed) at rapid rates compared to that at which CO_2 moves through the interface, the flux must also include the diffusion of these ions. Thus, the pertinent concentration difference across the diffusion layer is that of total carbonic species, TCO_2: $\Delta C = [TCO_2]_s - [TCO_2]_{eq}$, $|TCO_2|_s$ and $|TCO_2|_{eq}$ which are respectively the total carbonic species concentration at the surface water and the total carbonic species which is in equilibrium with pCO_2 (Stumm & Morgan 1981; Nishimura et al. 1984).

The transfer coefficient (D/z) is calculated as a function of wind speed. Of the many relations available for CO_2, we have chosen the relation recommended by Weiler (1975) for field measurements: A correction factor was introduced to take into account the fact that the effective molecular diffusion coefficient, D, to be considered is not that of CO_2 ($1.9 \times 10^{-5} cm^2 s^{-1}$) but rather that of HCO^2 ($1.2 \times 10^{-5} cm^2 s^{-1}$), as the latter is the dominant component at pH 7—9 (Lerman 1979). Finally, the adopted values of D/z as a function of wind speed, V, are:

— for $V < 2$ m s^{-1} and when the surface water is unruffled D/z (cm h^{-1}) = 1.05;

— for $V > 2$ m s^{-1} D/z (cm h^{-1}) = $0.35 \times V^2$; (V in m s^{-1}).

The data were supplied by the meteorological station of Saquarema.

IV. Results and discussion

Physical and chemical setting

Saquarema Lagoon, with its sub-tropical humid climate, exhibited a dampened bimodal seasonal pattern in rainfall during the study (Fig. 2a), and unimodal patterns in water temperature (Fig. 2b) and insolation (Fig. 2c). Typical dry and wet seasons often encountered in tropical and subtropical regions were less apparent because of the frequent passage of polar fronts throughout the year. These fronts, which are the principal meteorological feature of the region, cause marked short-term meteorological changes resulting in temperature decrease, rainfall, river flooding, marine water intrusions to the lagoon, and strong vertical mixing of lagoon waters (Costa-Moreira & Carmouze 1991).

Mesohaline conditions with salinities ranging from 5 to 25% (Fig. 3a), prevailed over the year, with values usually being 2—3 times lower in the Urussanga section relatively to the Fora section. Uniform water masses with low salinities throughout the entire lagoon were only encountered over short periods of the year, when rivers flooded. The flushing half life, which expresses the hydrodynamic turnover time, is 23 days in Urussanga and only 6 days in Fora (Knoppers et al. 1991, this issue). A distinct seasonal trend was seen in Secchi-disk depth and phytoplankton chlorophyll-a biomass (Fig. 3b and 3c, respectively). The unimodal pattern of highest chlorophyll-a in summer and autumn was inverse to that for Secchi depth. Short-term changes in both variables were marked during the passage of cold weather fronts and subsequent input of clay riverborne matter and resuspension of the organic rich flocculent material from the lagoon bottom. Higher chlorophyll-a concentrations and lower Secchi-disk values were observed throughout the year in Urussanga than in Fora.

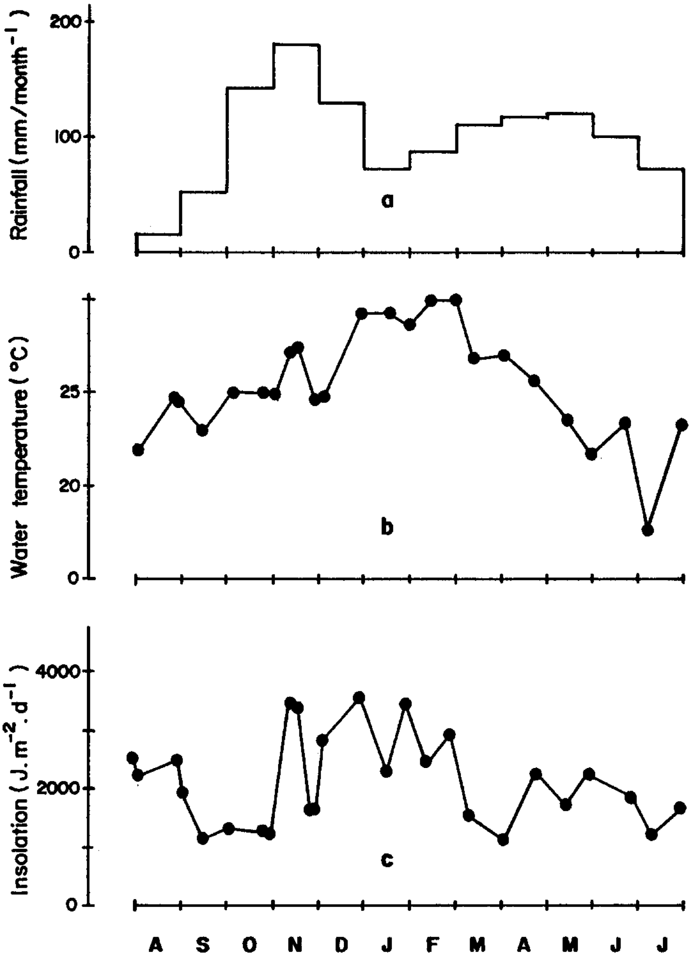

Fig. 2. Rainfall distribution in the Saquarema Lagoon from August 1988 to July 1989 (*a*), temperature (*b*) and solar insolation (*c*) on sampling days. Insolation values were computed from hours of insolation (Brichambaut & Lamboley 1968).

Domestic nutrient pollution is higher in Fora than in Urussanga. Areal loading of dissolved inorganic phosphorous, total phosphorous and dissolved inorganic nitrogen was 60, 400, and 450 mmoles m^{-2} day^{-1}, respectively, in Fora and 30, 100, and 75 mmoles m^{-2} day^{-1} in Urussanga (Knoppers et al. 1991, this issue). In spite of these regional differences in nutrient loading, nutrient concentrations in the water column were similar in both sections, with a mean annual dissolved inorganic nitrogen concentration of 3.5 ± 1.8 μM and dissolved inorganic phosphorous of 0.65 ± 0.35 μM (n = 45). Well-defined seasonal patterns were absent. Differ-

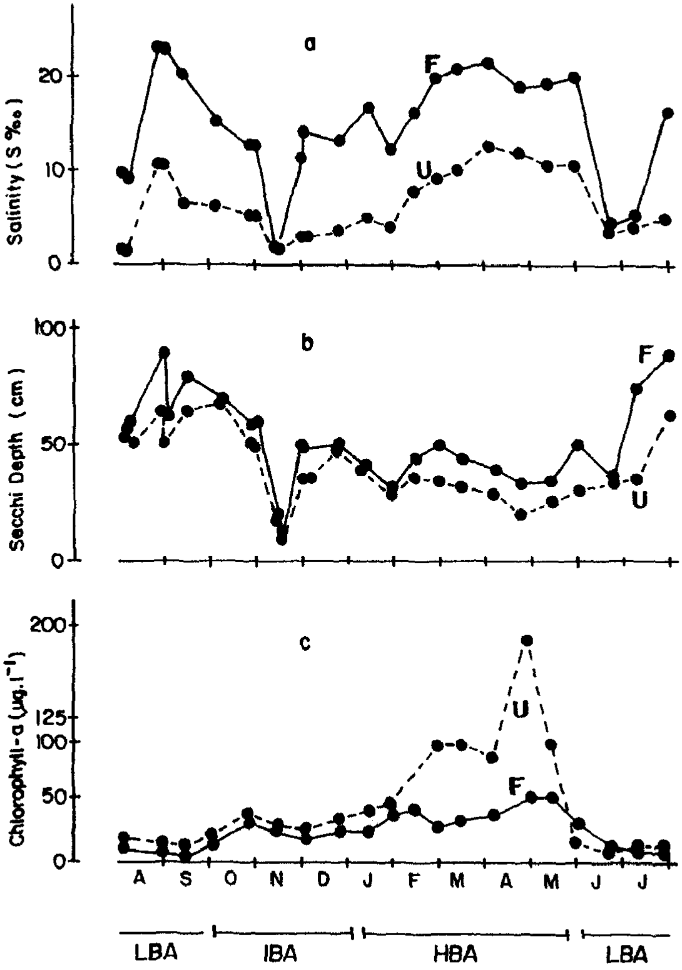

Fig. 3. Salinities (*a*), Secchi depths (*b*) and chorophyll-a concentration (*c*) in Urussanga (U) and Fora (F) sublagoons during the periods of biological activity (LBA) in Winter, of intermediate biological activity (IBA) in spring and early summer and of high biological activity (HBA) in late summer and autumn.

ences in flushing times in addition to biological uptake are assumed to be the main factor regulating nutrient concentrations.

Total community metabolism

Saquarema Lagoon is a phytoplankton-based system with a negligible contribution of benthic micro- and macro algae at its lateral periphery. The total system metabolism is thus primarily governed by phytoplankton and that of pelagic and benthic heterotrophs. This simplifies the distinction between autotrophic and total system metabolisms.

The study revealed three distinct temporal features in metabolic rates:

— considerable daytime and daily variability in production and respiration,
— seasonal shifts between net autotrophy and heterotrophy, and
— an annual equilibrium between production and respiration.

Variability of metabolic rates over the photoperiod is demonstrated by the magnitude of the standard deviations of daytime cumulative total CO_2 consumption (Fig. 4). Net respiration may occur in early morning and/or in late afternoon and frequently, over a period of 48 hrs, net respiration doubled while net production remained equal or vice-versa. Some examples are given in Fig. 5.

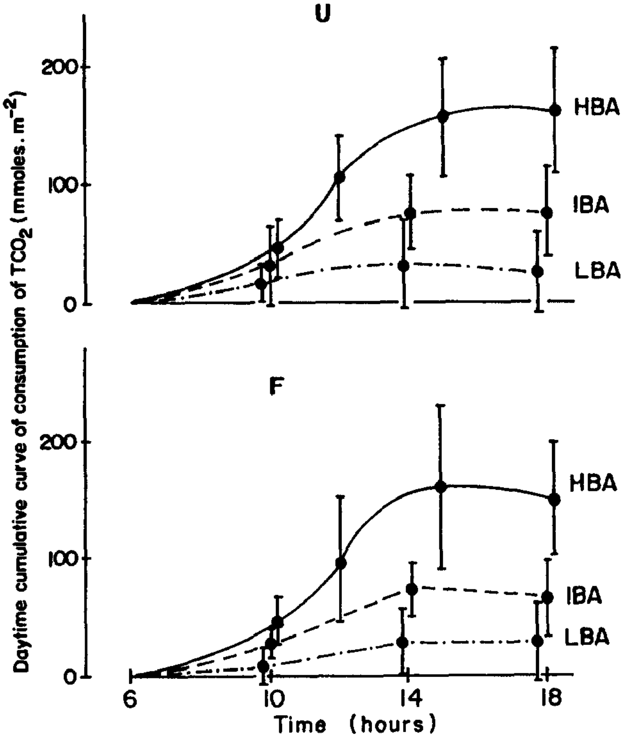

Fig. 4. Daytime cumulative curve of total CO_2 consumption in Urussanga (U) and Fora (F) sublagoons during the periods of low biological activity (LBA) in winter, of intermediate biological activity (IBA) in spring and early summer and of high biological activity (HBA) in late summer and autumn (free water technique).

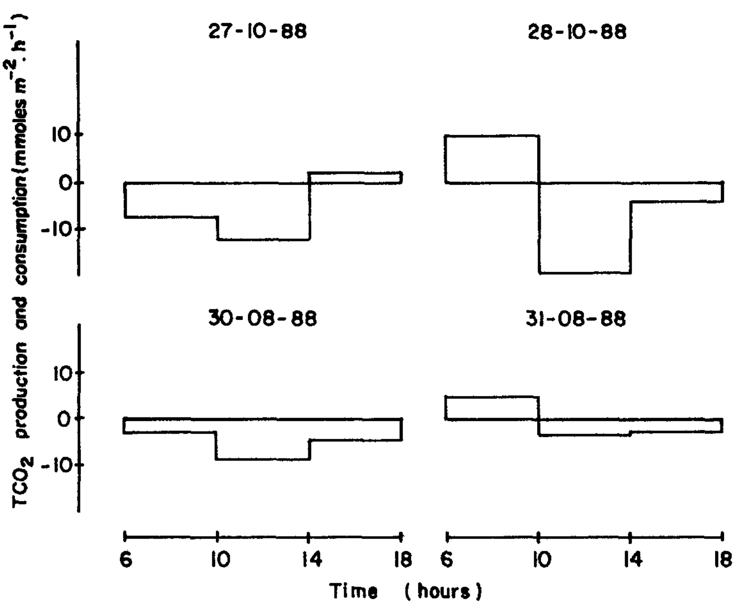

Fig. 5. Two examples of changes in total CO_2 production and consumption during the photoperiod.

Despite these short-term changes, there are seasonal patterns of net daily production and respiration rates (Fig. 6). Three periods were distinguished:

- a period in winter, from mid-May to mid-September, with the lowest biological activity (LBA),
- a period in spring and early summer from mid-September to mid-January, with intermediate biological activity (IBA), and
- a period in late summer and autumn, from mid-January to mid-May, with high biological activity (HBA).

The net daily production and consumption of CO_2 are given in Fig. 6, the net daily metabolism in Fig. 7 and the seasonal ranges in Fig. 8. In both sublagoons, net heterotrophic metabolism dominates during winter (LBA) while net autotrophic metabolism occurs in summer and autumn (HBA). The difference between P and R is statistically significant only for the HBA period (Student's t-test). The seasonal trends are confirmed by seasonal differences of average daily CO_2 saturation of surface waters, expressed as the difference between TCO_2 of surface waters ($[TCO_2]_s$ and the corresponding TCO_2 in equilibrium with atmospheric CO_2 ($[TCO_2]_{eq}$) (Fig. 9). During the heterotrophic LBA period, $[TCO_2]_s - [TCO_2]_{eq}$ was > 0 indicating that the waters were supersaturated with respect to atmos-

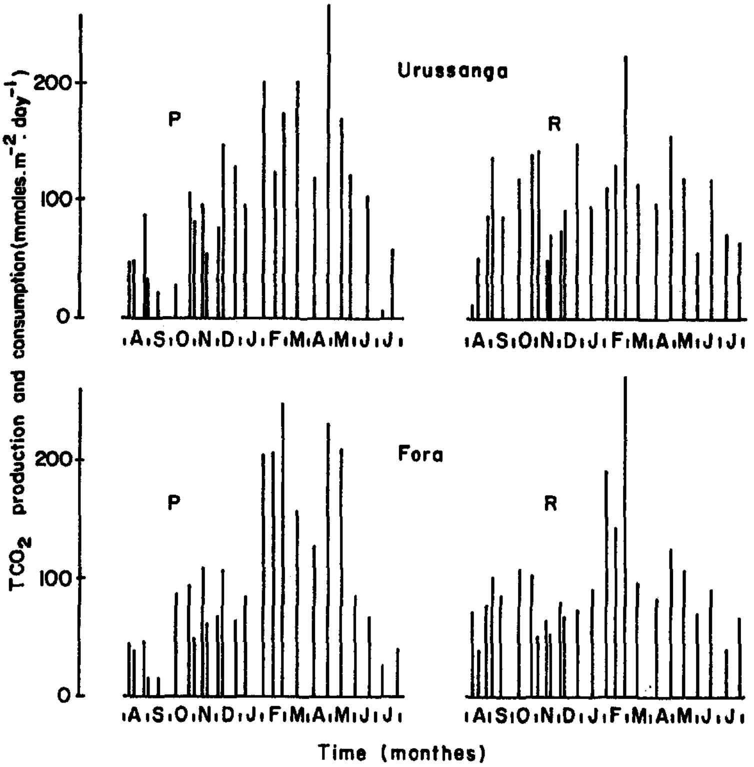

Fig. 6. Daily consumption and production of total CO_2 reported as net production (P) and respiration (R) in Urussanga (U) and Fora (F) sublagoons over an annual cycle.

pheric CO_2. Carbon dioxide transfer was from water to the atmosphere. The fact that surface waters are maintained supersaturated implies that the frequency of days when $R > P$ is higher than that of days when $P >$ R. During the autotrophic HBA period $[TCO_2]_s - [TCO_2]_{eq}$ was < 0. The CO_2-H_2O system was undersaturated because days with $P > R$ were more frequent.

Classical environmental forcing variables and some physical and chemical characteristics of water which have been presented, partly explain the principle features of the lagoon metabolism. The seasonal pattern of temperature with a warmer season from mid-December to mid-March (water temperature = 28.2° ± 2.2, $n = 12$) and a colder season from June to August (water temperature = 22.6° ± 2.2, $n = 14$) coincide quite well with the respective HBA and LBA periods. This result confirms the well-established influence of temperature on metabolic rates (Sieburth 1967; Harris & Puccini 1977; Tison & Pope 1980; Carmouze & Caumette 1985). Furthermore, production rates are enhanced in the late

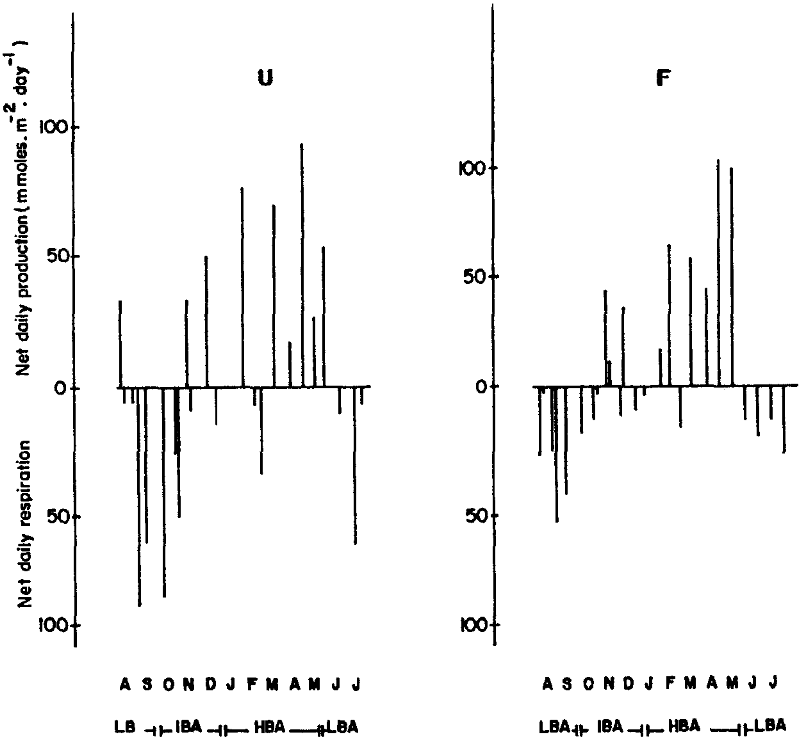

Fig. 7. Net daily consumption or production of total CO_2 reported as net production (P) and respiration (R) in Urussanga and Fora lagoon over the year.

summer-autumn period of HBA by significantly higher values of insolation (1655 J m^{-2} day^{-1}) than in the winter period of LBA (1395 J m^{-2} day^{-1}). As a response to these climatic changes, average chlorophyll-a concentrations increased from 14 $\mu g\ l^{-1}$ in the winter period to 39 $\mu g\ l^{-1}$ (Fora) and 94 $\mu g\ l^{-1}$ (Urussanga) in the summer period. However, no significant correlation between the mentioned environmental variables and *P* and *R* is apparent. This is probably due to the fact that:

- seasonal trends are severely dampened by the passage of polar fronts throughout the year, and
- biotic factors, such as structure and physiological state of the plankton community in the case of primary production, may strongly influence total community metabolism.

The seasonal shift from auto to heterotrophic metabolism, might be linked to a greater susceptibility of autotrophic processes to environmental variables than heterotrophic processes, i.e. favourable summer conditions stimulate and unfavourable winter conditions inhibit primary production

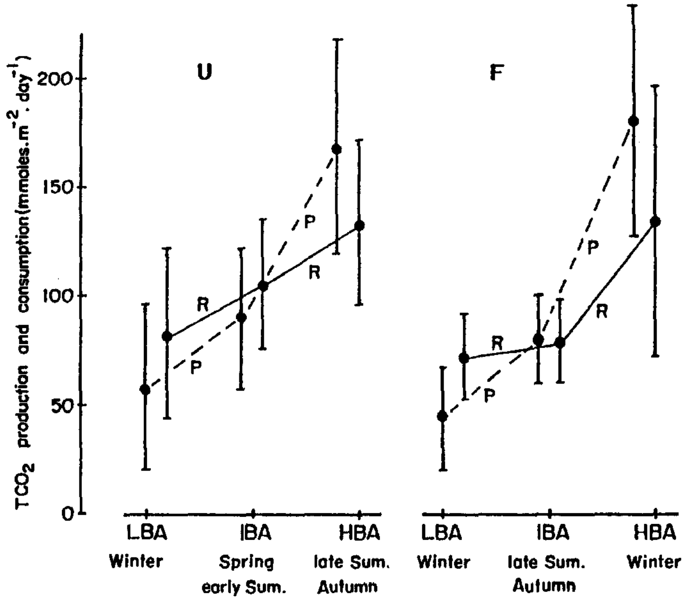

Fig. 8. Seasonal ranges of daily production (P) and respiration (R) rates during the periods of low biological activity (IBA) in spring and early summer and high biological period (HBP) in late summer and autumn ($n = 8$, 9 and 8, respectively).

more than total organism respiration. Net production was higher during periods of high turbulence in summer and autumn ($P > 200$ mmoles m^{-2} day^{-1} on 1/02/88, 20/04/88 and 9/05/88 with wind speeds > 8 m s^{-1}). However, nutrient enrichment of the water from pore water mixing was not observed probably because of the rapid biological uptake. Similar results were obtained by Knoppers & Moreira (1988) in the adjacent shallow eutrophic lagoon of Guarapina.

In spite of the high short-term and seasonal variability in metabolism, autotrophic and heterotrophic metabolisms were balanced over the year in both sublagoons. According to the free water technique: $P = 107 \pm 68$ mmoles m^{-2} day^{-1} and $R = 107 \pm 50$ mmoles m^{-2} day^{-1} in the Urussanga section and $P = 104 \pm 68$ mmoles m^{-2} day^{-1} and $R = 98 \pm 49$ mmoles m^{-2} day^{-1} ($n = 25$) in the Fora section. Thus, on an annual basis, an equivalent amount of produced organic matter was respired.

Because autotrophic and heterotrophic activities are balanced on an annual basis, one would expect a relationship between P and R in individual samples. This was not always the case. In Fora, the coefficient of correlation between P and R from both free water and incubation techniques were 0.75 and 0.70, respectively, whereas in Urussanga, the

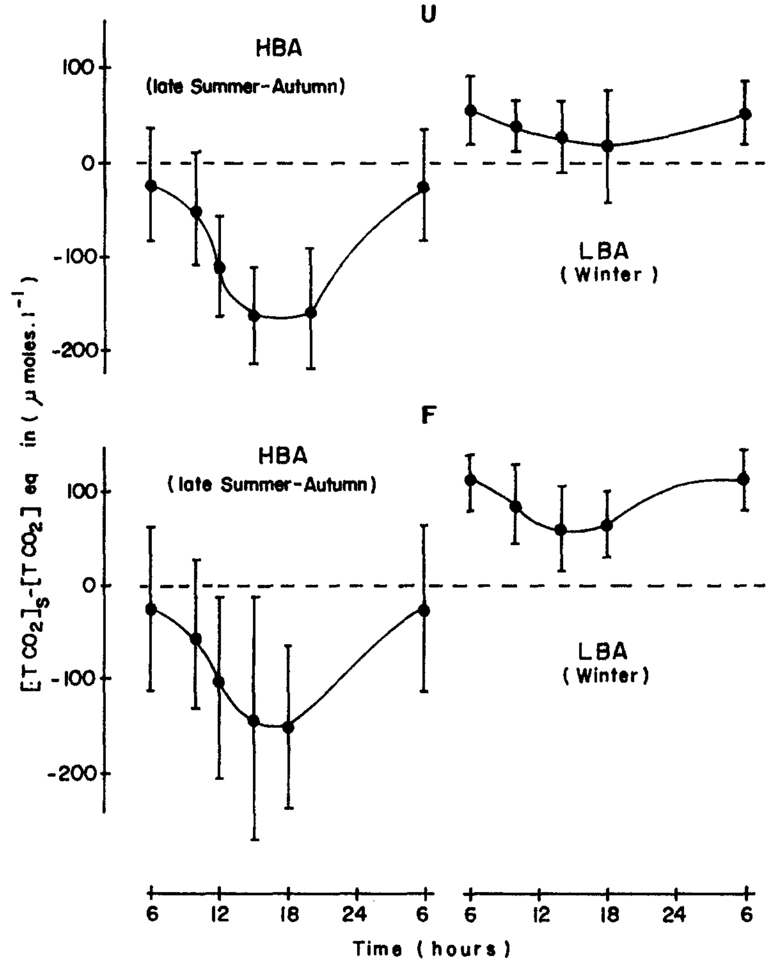

Fig. 9. CO_2 saturation levels over 24 h, expressed as the difference between the concentration of total CO_2 of surface water (TCO_s s) and its equilibrium level relative to atmospheric pCO_2 (TCO_{2eq}) in Urussanga (U) and Fora (F) sublagoons during periods of low intermediate and high biological activity (LBA, IBA and HBA; $n = 8$, 9 and 8, respectively).

corresponding values were 0.44 and 0.30. Presumably, there were differences in the nature of available substrate to the heterotrophic community of the two sublagoons. Although there is no direct evidence, the predominance of terrestrial-borne organic matter in superficial sediments of Urussanga in comparison to Forga suggests that allochthonous input of organic matter in the former is more important than in the latter. Superficial sediments of Fora appear to consist primarily of autochthonous matter derived from algae (Gadel, pers. comm.).

Regional differences in metabolism

Although an annual equilibrium between produced and respired carbon prevailed in the Saquarema Lagoon, some regional differences between the interconnected Urussanga and Fora sublagoons were apparent:

- salinities were 2—3 times lower in Urussanga,
- flushing time is about 4 times faster in Fora,
- domestic discharge of total phosphorous and dissolved inorganic nitrogen is 5 times higher in Fora,
- Secchi-disk depths are lower in Urussanga during the period of high biological activity.

It is therefore highly surprising that net daily P and R values were similar during the three metabolic periods in both sections (Fig. 7). Domestic pollution in Fora did not appear to increase biological activity. However, in autumn, the photosynthetic efficiency of phytoplankton was 2—3 times higher in Fora (3.5 μmoles C per μg Chla per day) than in Urussanga (1.5 μ mole C per μg Chla per day). The shorter residence time of water with its diluting effect in conjunction with a larger input of new nutrients from effluent discharge in Fora, presumably furnished more favourable conditions for phytoplankton growth and thus the maintenance of a better physiological state of phytoplankton populations.

Planktonic and benthic metabolism

The importance of planktonic community metabolism relative to whole system metabolism may be assessed by comparing P and R values obtained simultaneously from free water (FW) and in situ incubation (INC) techniques. Benthic metabolism can be estimated from the difference between whole community respiration and pelagic respiration.

Microphytobenthic activity is assumed to be negligible in the Saquarema Lagoon because the Secchi depth measurements were generally less than 40 cm and resuspension of organic rich flocculent sediments from the bottom was a frequent event. Thus, net daytime production given by the free water technique (P_{FW}) should be less than or equal that from in in situ incubation (P_{INC}) technique, and the difference between P_{INC} and P_{FW} should represent daytime benthic respiration. In fact, on many occasions the opposite was observed. This is shown in Fig. 10 by the percentage difference of the two production measurements relative to their mean value.

During IBA and HBA periods, P_{FW} values were significantly higher than those of P_{INC} (Student's t-test, $p = 0.05$) in contrast to the LBA

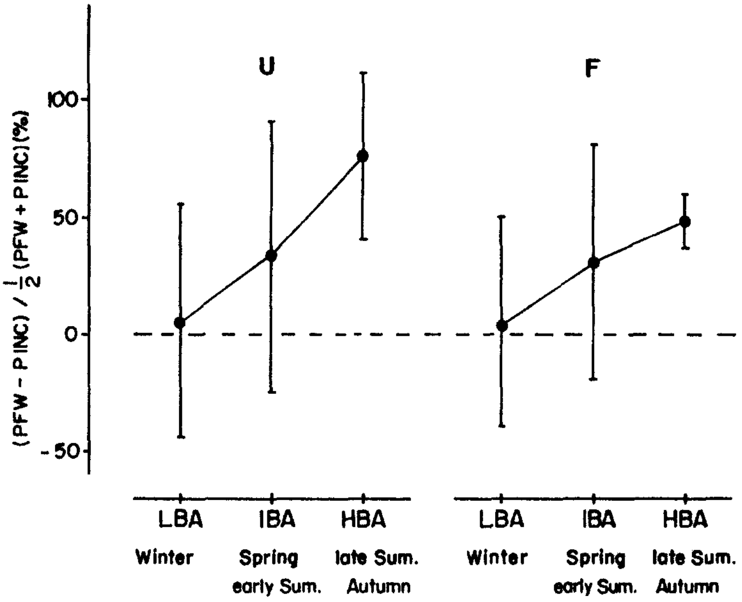

Fig. 10. Differences in percentage of the free water and incubation evaluations of net productions (respectively, P_{FW} and P_{INC}) relatively to their mean values ($\frac{1}{2}(P_{FW} + P_{INC})$, in Urussanga (U) and Fora (F) sublagoon during the periods of low, intermediate, and high biological activity (LBA, IBA and HBA; $n = 8, 9$ and 8, respectively).

period with no significant differences. As benthic autotrophic activity is not likely to be important, the discrepancy during IBA and HBA periods may be attributed to an increase of microbial activity during the incubations (2—4 h). Some authors have reported considerable 'bottle effects' (Zobell 1946; Kunicki-Goldfinger 1974) but others failed to detect it (William & Gray 1970; Fuhrman & Assam 1980). Maximum discrepancies between P_{FW} and P_{INC} occurred during the HBA period in the Urussanga section and coincided with low Secchi depths and high chlorophyll-a concentrations (Fig. 3b and 3c, respectively). The lack of vertical mixing of phytoplankton during incubation is one possible explanation, but additional in situ experiments using plexiglass tubes isolating the entire water column with and without the inclusion of superficial sediments, clearly showed that the elimination of nutrients liberated from the bottom considerably reduced net production (Pereira-Canterle, pers. comm.). Thus, a principal factor limiting autotrophic activity in isolated bottles during the summer period of high nutrient demand was probably the interruption of nutrient advection from bulk water and sediments. Such conditions may immediately change metabolic rates (Jannash 1967).

Benthic respiration during the daily period of net respiration (which includes night and, in some cases, early morning or late afternoon), in the Saquarema Lagoon, represents an annual mean of 37 ± 16% ($n = 50$) of total community respiration. Pelagic respiration thus accounted for at least half of the total respiration. However, this relationship was subject to marked regional and temporal variations, particularly in the more organic-rich Urussanga section. Average values for both Urussanga and Fora ranged from 36 to 50% during LBA and IBA periods; but during the HBA period, benthic respiration declined towards 17% in Urussanga and remained at 53% in Fora (Fig. 11). The predominance of pelagic respiration during this latter period in Urussanga coincided with highest phytoplankton biomass in the lagoon which was greater by a factor of 3 than in Fora. Pelagic micro-heterotrophs probably also encountered favourable growth conditions during the increase of phytoplankton production and biomass. The differences observed between Urussanga and Fora during the HBA period with regard to the importance of benthic respiration may be enhanced by the fact that particulate and dissolved organic material may more readily flocculate in Fora during mixing with sea water (Sholkovitz 1975).

The calculations of the contribution of benthic respiration are minimum estimates because it is quite likely that planktonic respiration was overestimated because of bottle effects in the long incubation period used. However, benthic respiration of the Saquarema Lagoon was well within the range from estuarine and coastal systems (Nixon 1981; Florek & Rowe 1983, 1985; Balzer et al. 1986; Machado & Knoppers 1988). In a

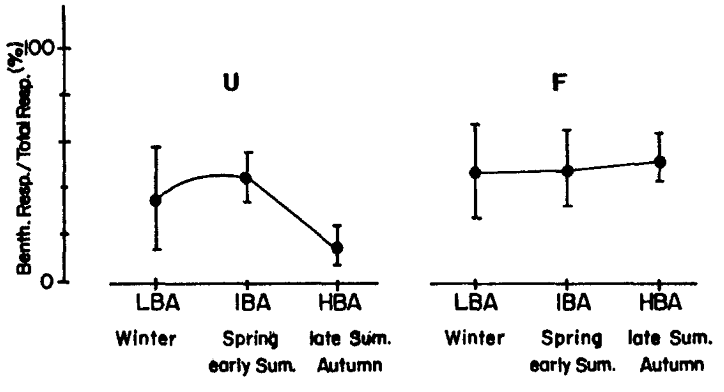

Fig. 11. Benthic respiration over total respiration, expressed in percentage in Urussang (U) and Fora (F) during the periods of low, intermediate and high activity (LBA, IBA and HBA; $n = 8, 9$ and 8, respectively).

review, Nixon (1982) reported that up to 50% of the supply of organic matter is respired at the bottom of these systems.

The annual balance between autotrophic and heterotrophic metabolism encountered in Saquarema Lagoon does not seem to be a common feature applicable to all coastal lagoons. Net heterotrophy has been established for Bissel Pond, USA (Nixon & Oviatt 1973) and the El Verde Lagoon, Mexico (Flores-Verdugo et al. 1988). Net autotrophy was detected in the southern part of Laguna Madre, USA (Odum & Wilson 1962; cited in Reyes & Morino, in press) and the Bojorguez Lagoon, Mexico (Reyes & Merino, in press). Balanced metabolism was observed in the Terminos Lagoon, Mexico (Day et al. 1988). Smith and Mackenzie (1987) argue that, with some exceptions, shallow water systems tend towards net heterotrophy. We think that in view of the wide array of methological approaches in use, the diversity of plant communities involved, and the scarcity of studies on lagoon metabolism, a common pattern of metabolism is still difficult to attribute to these habitats. However, a principal feature of tropical and subtropical eutrophic lagoons with seasonal changes in climate, seems to be a seasonal shift between autotrophy and heterotrophy.

References

Aleem AA & Samaan AA (1969) Productivity of Lake Mariut, Egypt. Part II. Primary production. Internationalen Revue der gesamten Hydrologie 54: 491—527

Arenas V (1979) Balance anual del carbono orgánico, nitrógeno y fósforo en el sistema langunar Huizache-Caimanero, México. PhD dissertation, Universidad Nacional Autónoma de México

Balzer W, Pollehne F & Erlenkeuser H (1986) Cycling of organic carbon in a coastal marine system. In: Sly PG (Ed) Sediments and Water Interactions (pp 325—330). Springer Verlag, Berlin

Brichambaut P & Lamboley G (1968) Le rayonnement solaire au sol et ses mesures. Cahier de l'AFEDES, INRA, Paris, 120 pp

Carmouze JP (1984) Généralisation d'une méthode de détermination du carbone minéral total par pH-métrie dans les eaux. Rev. Hydrobiol. Trop. 17: 175—189

Carmouze JP & Caumette P (1985) Les effets de la pollution organique sur les biomasses et les activités du phytoplancton et des bactéries hétérotrophes dans la lagune Ebrié (Côte d'Ivoire). Rev. Hydroboil. Trop. 18(3): 183—211

Costa-Moreira AL (1989) Estados tróficos da laguna de Saquarema num ciclo anual. Tese de Mestrado. Dt° de Geoquímica, U.F.F. Niteroi, RJ, Brazil

Costa-Moreira AL & Carmouze JP (1991) La lagune de Saquarema: Hydroclimat, seston et éléments biogéniques au cours d'un cycle annuel. Rev. Hydrobiol. Trop. 24(1): 13—23

Day JW Jr, Day RH, Barreiro MT, Ley-Lou F & Madden CJ (1988) Primary production in the laguna de Terminos, a tropical estuary in the southern Gulf of Mexico. Oceanologica Acta Sp No 5: 269—276

Florek RJ & Rowe GT (1983) Oxygen consumption and dissolved inorganic nutrient production in marine coastal and shelf sediments of middle Atlantic Bight. Int. Revue Gess. Hydrobiol. 68(1): 73—112

Flores-Verdugo FJ, Day JW Jr, Mee L & Briseno-Duenas R (1988) Phytoplankton production and seasonal biomass variation of Seagrasses, Rupiamaritima L., in a tropical Mexican lagoon with an ephemeral inlet. Estuaries 11: 51—56

Fuhrman JA & Azam F (1980) Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica and California. Appl. Environ. Microbiol. 39: 1085—1095

Gilmartin M & Revelante N (1978) The phytoplankton characteristics of the barrier island lagoons of the Gulf of California. Estuarine and Coastal Marine Science 7: 29—47

Gran G (1952) Determination of equivalent point in potentiometric titration. Analyst 77: 661—671

Hall CAS & Moll R (1975) Methods of assessing aquatic primary production. In: Lieth AJ & Whittaker RR (Eds) Primary Production in the Biosphere (pp 19—53). Springer-Verlag, New York

Harris GP & Puccini BB (1977) Photosynthesis by natural phytoplankton populations. Arch. Hydrobiol. 80: 405—457

Jannash HW (1967) Growth of marine bacteria at limiting concentrations of organic carbon in sea water. Limnol. Oceanogr. 12: 264—271

Kanwisher J (1963) On the exchange of gases between the atmosphere and the sea. Deep. Sea Res. 10: 195—208

Kjervfe B (1986) Comparative oceanography of coastal lagoons. In: Wolfe DA (Ed) Estuarine Variability (pp 63—81). Academic Press, New York

Knoppers B & Moreira PF (1988) Materia em suspenção e sucessão do fitoplancton na lagoa de Guarapina, RJ Acta Limnológica Brasiliense III (2): 291—317

Knoppers B, Kjerfve B & Carmouze JP (1991) Trophic state and water turn-over time in six choked coastal lagoons in Brazil. Biogeochemistry 14: 149—166 (this issue)

Kunicki-Goldfinger WJH (1974) Methods in aquatic microbiology. A story of apparent precision and frustrated expectations. Pol; Arch. Hydrobiol. 21: 3—17

Lerman A (1979) Geochemical Processes (pp 74—120). Wiley, New York

Liss PS (1973) Processes of gas exchanges across an air-water interface. Deep Sea Res. 20: 221—238

Lorenzen CJ (1967) Determination of chlorophyll and pheopigments: Spectrophotometric equations. Limnol. Oceanogr. 12: 343—346

Machado EC & Knoppers B (1988) Sediment oxygen consumption in an organic rich subtropical lagoon, Brazil. Science of the Total Environment 75: 341—349

Mee LD (1978) Coastal lagoons. In: Riley JP & Chester R (Eds) Chemical Oceangraphy 7 (pp 441—490). Academic Press, New York

Moreira PF & Knoppers B (1990) Um ciclo anual da produção primaria e nutrientes na Lagoa de Guarapina, RJ. Acta Limnologica Brasiliensia III: 275—290

Nishimura H, Naksjima M & Kumagai M (1984) Exchange of oxygen and carbon dioxide across the water surface during algal blooms in a pond. Water Res. 18(3): 345—350

Nixon SW & Oviatt CA (1973) Ecology of a new England salt marsh. Ecological Monographs. 43: 463—498

Nixon SW (1981) Remineralization and nutrient cycling in coastal marine ecosystems. In: Neilson & Cronin LE (Eds) Estuaries and Nutrients (pp 111—138). Humana Press, Clifton, New Jersey

Nixon SW (1982) Nutrients, primary production, and fisheries yields in coastal lagoons. Oceanologica Acta sp N° 5: 357—371

Odum HT (1956) Primary production in flowing water. Limnol. Oceanogr. 1: 102—117

Odum HT & Hoskin CM (1958) Comparative studies on the metabolism of marine waters. Publ. Inst. Mar. Sci. Univ. Texas 6: 159—170

Pagès J, Lemasson L & Dufour P (1981) Primary production measurements in a brackish tropical lagoon. Effect of light, as studied by the 14C method. Rev. Hydrobiol. Trop. 14: 3—15

Park K, Hood DW & Odum HT (1958) Diurnal pH variation in Texas bays, and its application to primary production estimation. Publication Institute Marine Science University of Texas 9: 404—453

Qasim SZ, Wellershaus S, Bhattathiri PMA & Abidi SAH (1969) Organic production in a tropical estuary. Proceedings Indian Academy of Science, Section B 59: 51—64

Qasim SZ (1979) Primary production in some tropical environments. In: Dunhar MJ (Ed) Marine Production Mechanisms (pp 31—69). International Biological Program-IBP, 20 Cambridge

Randall J & Day JW Jr (1987) Effects of river discharge and vertical circulation on aquatic primary production in a turbid Louisiana (USA) estuary. Netherlands Journal of Sea Research 21: 231—242

Rao SDV (1981) Spacial and temporal variation of phytoplankton production in Lagoons. In: Coastal Lagoon Research, Present and Future. UNESCO Technical Papers in Marine Science 33

Reyes M & Merino M (1991) Primary production and eutrophication in Bojorguez lagoon, Cancun, Mexico (in press)

Sandoval-Rojo LC, Flores-Verdugo FJ, Araujo UZ, Day JW Jr & Mercado AE (1988) Phytoplankton productivity in Barra de Navidade Coastal lagoon on the Pacific Coast of Mexico. Rev. Hydrobiol. Trop. 21: 101—108/173—189

Sieburth JMcN (1967) Seasonal selection of estuarine bacteria by temperature. J. Exp. Mar. Biol. Ecol. 1: 98—121

Sholkovitz ER (1975) Flocculation of dissolved organic and inorganic matter during the mixing of river water and sea water. Geochim. Cosmochim. Acta. 40: 831—845

Smith SV (1988) Mass Balance in Coaral reef dominated areas. In: Janson BO (Ed) Coastal-Offshore Ecosystem Interactions. Lecture Notes on Coastal and Estuarine Studies 22 (pp 209—226). Springer-Verlag, Berlin

Smith SV & Mackenzie FT (1987) The ocean as a net heterotrophic system: Implications from the biogeochemical cycle. Global Biogeochemical Cycles. 1(3): 187—198

Sournia A (1977) Analyse bilan de la production primaire dans les récifs coralliens. Annales Institut de Monaco, nouvelle série 53: 47—73

Sournia A, Delasalle B & Ricard M (1981) Premiers bilans de production organique et de calcification d'un récifbarriére de la Polynésie Française. Océanologica Acta 4: 4236431

Strickland JDH & Parsons TR (1972) A Practical Handbook of Seawater Analysis, 2nd edn. Bull. Fish. Res. BD Canada, 167, 319 pp

Stumm W & Morgan YY (1981) Aquatic Chemistry, 2nd edn. Wiley Interscience, New York, 780 pp

Tison DL & Pope DH (1980) Effects of temperature on mineralization by heterotrophic bacteria. Appl. Environ. Microbiol. 39: 584—587

Tundisi J, Tundisi TM & Kutner MB (1973) Plankton studies in a mangrove environment. VIII. Further investigations on primary production, standing stock of phyto- and zooplankton, and some environmental factors. Internationalen Revue der gesamten Hydrobiologie 58: 925—940

Vaulot D & Frisoni GF (1986) Phytoplankton productivity and nutrients in five Mediterranean lagoons. Oceanologica Acta 9: 57—63

Vollenweider RA (1974) A manual in Methods for measuring primary production in aquatic environments. IBP Handbook N° 12. Blackwell Scientific Publications. Oxford

Weiler RR (1975) Carbon dioxide exchanges and productivity in lake Erie and lake Ontario. Verh. Internat. Verein. Limnol. 19: 694—704

Williams PJLeB & Gray RW (1970) Heteretrophic utilization of dissolved organic compounds in the sea. J. Mar. Biol. Assoc. UK 50: 871—881

Zobell CE (1946) Marine Microbiology. Cronica Botanica, Waltham, Mass