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Planktonic primary production in a tidally influenced mangrove forest on the Pacific coast of Costa Rica

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Abstract: The seasonal variation of planktonic primary productivity was measured during one year in the main channel in the interior part of the mangrove forest of the Estero de Morales (Estero de Punta Morales), a mangrove system located in the Golfo de Nicoya at the Pacific coast of Costa Rica. Samples were incubated at the surface, 0.5 m and 1.0 m depth and the "light and dark bottle technique" was employed. The annual gross primary productivity (PPg) was 457 and the net primary productivity (PPn) was 278 g C m^{-2} a^{-1}. Daily PPg ranged from 0.29 to 3.88 and PPn from 0.12 to 2.76 g C m^{-2} d^{-1}. The highest rates observed in May and September were due to red tide blooms. The seasonal variation of primary productivity inside the mangrove forest depends closely on the PP in the adjacent area of the upper Golfo de Nicoya. Obviously the PP was light-limited since the compensation depth in the ebb current was found at only 1m depth. In the flood current it was somewhat deeper. The planktonic primary productivity inside the mangrove forest was completely restricted to the open channels. A simultaneous measurement demonstrated that PPn of the phytoplankton could not take place under the canopy of the mangroves. Additional studies on the time course of the oxygen concentration in the mouth of the main channel over 24 hrs demonstrated a relation between the O_2 and the tidal curves. The ebb current had always lower O_2 concentrations than the flood current, regardless of the time of the day. The difference to the foregoing high tide, however, was much smaller when the low tide occurred during the day. This indicates that under the canopy the net primary production and hence O_2 liberation of the attached macro- and microalgae, together with the high PPn of the phytoplankton in the channels, helped the oxygen concentration not to decrease as far as during the night. Nevertheless it shows that the consumtion of organic material in the submersed part of the mangrove forest exceeds always its production.

Key words: Primary productivity, phytoplankton, oxygen concentration, mangrove forest, Golfo de Nicoya.

In coastal areas, the import of allochthonous organic material (OM) may represent a substantial part of the carbon budget. This is especially the case with estuaries and semi-enclosed bights with shore lines which are covered with salt marshes and mangrove forests.

Mangrove forests are the dominating coastal ecosystems in tropical and subtropical regions where they cover from 60 to 75% of the coastline (Lalli & Parsons 1997). They are among the most productive marine ecosystems. Litter fall probably is the mayor source of nutrient and energy supply to the aquatic phase of these systems (Nixon 1980). In an *Avicennia germinans* mangrove forest in the Guayanas total litter fall was 1771 g m^{-2} a^{-1} (dry weight) with a leaf litter fraction of 61%

(Chale 1996). In a subtropical mangrove forest in Hong-Kong the annual total litter fall amounted to about 1770 g m^{-2} and the leaf litter fraction reached around 70% (Tam *et al.* 1998). In other regions the litter fall was somewhat lower (810 g m^{-2} a^{-1} in Florida, Twilley *et al.* 1986; 900 g m^{-2} a^{-1} in northern Australia, Mackey & Smail 1995), but in each case it is always a considerable amount of organic material that falls to the ground, leaves representing the highest fraction of it.

Depending on the hydrographical situation of the mangrove system (especially on the tidal currents), a part of the litter is exported directly or after its partial degradation to the neighbouring coastal areas (Odum & de la Cruz 1967). In a review about mangrove outwelling, Lee (1995) concludes that in the past the particulate organic matter export from the mangrove systems may have been overestimated sometimes, whereas the very important export of dissolved organic matter has not been taken into account until quite recently.

Due to its refractorial nature the organic material produced by mangroves, it is not used directly by most herbivores, instead it is channelled to decomposers (Lee 1990). Beside the production of organic material (OM) by the mangrove trees, a certain production of OM by planktonic algae also occurs in the inundated parts of the mangrove swamp. This fraction, however, has received little attention in past and current research even though it might be quite important, since more than half of the phytoplankton production (about 55% according to Cebrián & Duarte 1994) is directly accessible to higher trophic levels of the marine food chain (Duarte & Cebrián 1996). Therefore, if phytoplankton organic carbon is produced in the mangrove system and exported to the adjacent areas, this material is more important in the carbon fluxes of the receiving sytems than one would judge from its amount.

In the highly productive upper Golfo de Nicoya, which is located at the Pacific coast of Costa Rica, 68% of the shore line is covered by mangrove forests (Gocke *et al.* submitted), from which the gulf probably receives quite an important amount of particulate and dissolved organic material. The present study was performed as part of the determination of the primary productivity and the carbon flux of the upper gulf. The main objective was to determine how the seasonal variation and the magnitude of the planktonic primary production in a bordering mangrove forest are related to the primary productivity in the open areas of the upper Golfo de Nicoya.

MATERIALS AND METHODS

Study site: The study was undertaken in the main channel of the Estero de Morales (Estero de Punta Morales), a mangrove forest located at the eastern shore of the inner part of the Golfo de Nicoya on the Pacific coast of Costa Rica at 84°57’ N and 10°04’ W (Fig.1). The upper Golfo de Nicoya is a highly productive tropical estuary (Córdoba Muñoz 1998, Gocke *et al.* submitted), subjected to semi-diurnal tides with a mean tidal range of 2.3 m (Peterson 1958). Large mud flats exist on both sides of the upper gulf, and on about 2/3 of the shore line (excluding the islands) mangrove forests prevail (Wolff *et al.* 1988).

The mangrove forest of the Estero de Morales has an area of 327 ha (Fig. 1). The shore line of the outer region and the fringes of the entire channel system are occupied by *Rhizophora mangle*, and, on the landward side, by *Avicennia nitida*. *Laguncularia racemosa* and *Conocarpus erectus* occur infrequently. The mangroves of the Estero de Morales form a scrub vegetation not higher than 4-5 m with only few exceptions. This is quite unusual for the mangrove forests of the upper gulf, where the mangroves normally are large trees (Pool *et al.* 1977).

About 1/3 of the mangrove forest drains directly into the Golfo de Nicoya during ebb tide, whereas the larger portion is drained via the main channel system into the gulf. As shown in Fig. 1 fresh water enters by the Quebrada Grande, a small creek which is nearly depleted during the dry season usually lasting from mid-December till mid-April. The creek responds rapidly to rainfalls, rising and subsiding within a very short time. Even during the rainy season the main influence of the Quebrada Grande on the salinity is limited

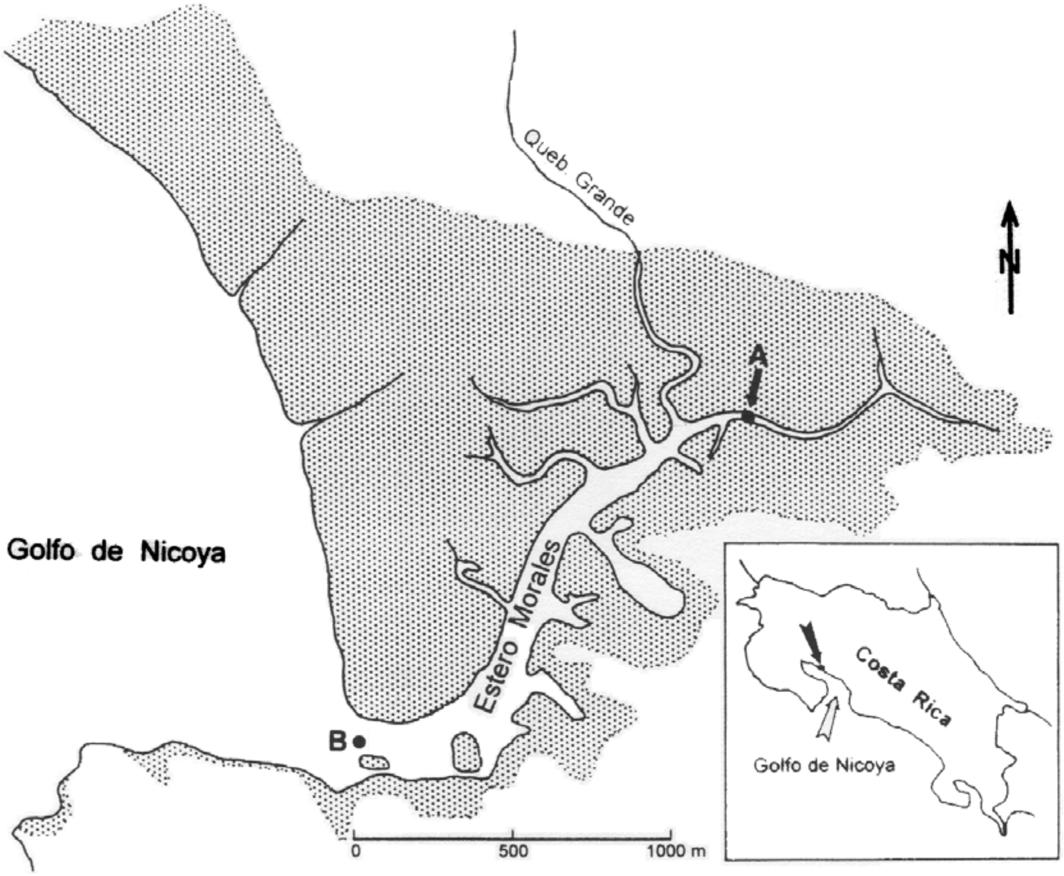

Fig. 1. Location of the study site. At station A the seasonal study was performed, station B was the location of the additional measurements.

to short periods after heavy rainfalls. The salinity values obtained lie between 25 and 35 PSU. In general, the salinity of the mangrove forest runs parallel to the salinity of the Golfo de Nicoya.

The determination of the planktonic primary productivity was performed in the upper part of the main channel, about 2 km from the mouth of the inlet (Fig. 1). At this location the depth of the channel at low tide was about 1.5 m. The additional measurements of daily variations of several variables were undertaken directly at the mouth of the main channel, where the depth at low tide was around 2 m.

Routine study: The Secchi depth was measured using a white plastic disc (20 cm diameter), which was heavily weighted to account for the sometimes very strong tidal currents.

The oxygen concentration of the water samples was determined by a micro-Winkler technique. Titrations were performed directly in the O_2 bottles (100 ml nominal volume) with a micro-burette of 0.5 ml total volume (Green & Carrit 1966, Bryan *et al.* 1976). Primary productivity was measured using the “light and dark bottle method” introduced by Gaarder & Gran (1927). Samples were taken twice per month in the center of the channel, first when the tide was coming in and one week later when the tide was going out. Those days were chosen on which high or low tide occurred roughly between 9: 30 and 10: 30. Two clear and one dark bottle of 100 ml nominal volume per depth were incubated at the surface, at 0.5 and at 1.0 m depth. The exposure lasted for 5 hrs and was always initiated around 8: 30. Oxygen concentration differences were converted into units of organic carbon produced or consumed applying a photosynthetic quotient of 1.20 and a respiratory quotient of 0.83 (Ryther 1956, Fogg 1963).

Additional study: The tidal curve was measured using marked poles firmly stuck in the bottom and read at short intervals. Total seston concentration was determined by filtering water samples (between 80 and 1000 ml according to the turbidity) through preweighed glass fibre filters (Whatman GF/F, 25 mm), previously combusted to 500 °C. After washing several times with small amounts of distilled water the filters were dried at 60 °C and weighed again. For determining the inorganic seston, the filters were afterwards combusted for 3 hrs at 500 °C, cooled at room temperature and weighed again. For measuring the Biological Oxygen Demand within 7 days (BOD_7) two 100 ml O_2-bottles were cautiously filled with the water samples taken at 1 m depth from the center of the channel. One bottle, which immediately received the oxygen reagents, was used to determine the initial O_2-concentration for the BOD measurement. It also served to determine the actual oxygen concentration of the water in the channel. The second bottle was incubated in the dark at room temperature (about 22 °C). After 7 days the final O_2-concentration of this bottle was measured. No attempts were made to account for the oxygen consume due to nitrification processes.

RESULTS

Seasonal study: The data obtained during the annual study showed a dependency of water turbidity (indicated by the Secchi depth) and oxygen saturation on the tidal phase (Table 1). The mean Secchi depth of the usually very turbid out-flowing water was only 40 cm, whereas the “cleaner” in-flowing water had a mean Secchi depth of 74 cm. The higher turbidity of the out-flowing water coincided with a somewhat lower oxygen saturation (53%) compared to 62% in the in-flowing water (mean values).

The respiration rates (R) of the suspended organisms in the in- and out-flowing waters differed, but not by very much. In the ebb current 45.6 mg O_2 was consumed per hour per cubic meter (annual mean), whereas in the flood current 35.6 mg O_2 m^{-3} h^{-1} were respired. (The strong red tide events in May and September were omitted from the calculation of the mean values).

TABLE 1

Annual means of Secchi depth and oxygen saturation in the flood and ebb tide (the ranges are given in parenthesis)

	flood tide	ebb tide
Secchi depth (cm)	74 (50-90)	40 (20-60)
Oxygen saturation (%)	62 (48-74)	53 (42-61)

We noted also a difference regarding the production of oxygen during the tidal phases. In the uppermost cubic meter of the out-flowing water a net production of 192 mg O_2 per hour occurred compared to 171 mg O_2 in the in-flowing water (annual mean value). The O_2-production in the clearer in-flowing water during the high tide phase, although a little bit lower per cubic meter than in the out-flowing water, was never restricted to the uppermost meter of the water column in the channel. On the other hand, oxygen production in the out-flowing water during low tide phases was in 6 of 12 measurements restricted to the uppermost meter, and, even when not restricted, it was always very low at 1 m depth. Thus, when taking the whole water column in the channel into account, more oxygen was produced during high tide than during low tide.

The depth distribution of the primary productivity demonstrated the strong influence of water turbidity and hence of the tidal phase on the optical properties of the water. Only during high tide a certain light inhibition of the PP in the incubation bottles at the surface was sometimes noted, whereas at low tide the PP at the surface was always lower than that at

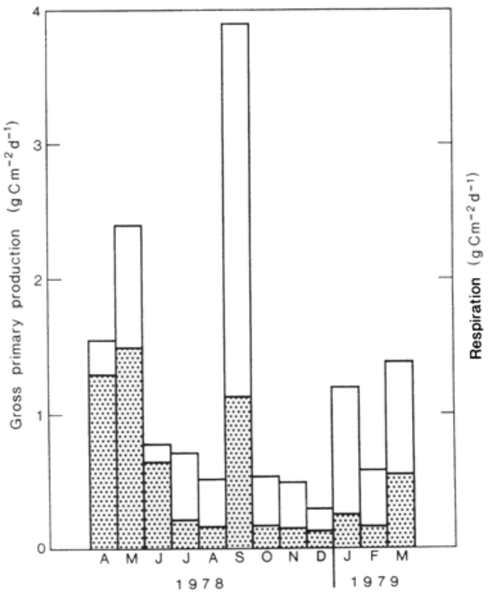

Fig. 2. Integrated gross primary production (PPg), net primary production (PPn) and respiration (R) of the photic layer (down to 1 m). PPg is represented by the total length, PP_n by the upper part and R by the dotted part of columns.

0.5 m. The euphotic zone, i. e. the layer above the compensation depth, reached always significantly deeper than 1 m during high tide as opposed to about 1m during low tide.

Figure 2 shows the seasonal distribution of the primary productivity. There was quite a strong scattering of the monthly values, in general, however, during the dry season and at the beginning of the rainy season the PP was significantly higher than during the peak of the rainy season. The highest values, which occurred in May and September, were caused by massive red tides. There was no fixed relation between gross primary production and respiration. In June already 85% and in January only 21% of the produced material were consumed in the euphotic layer.

The annual gross primary productivity (PPg) in the mangrove channel was 457 g C m^{-2} a^{-1}, the respiration (in the euphotic layer) amounted to 179 g C m^{-2} a^{-1} and the net primary productivity (PPn) was 278 g $Cm^{-2}a^{-1}$. These are conservative values, since our measurements did not take into account the layers below 1 m depth, where, at least during high tide, photosynthesis is still possible.

Additional study: During 24 h (almost two complete tidal cycles) the concentration of dissolved oxygen was measured at the entrance of the main channel (Fig. 1) at 1 m depth. The first study was performed on a day with a "normal" tidal range. It began at midnight. The second study began shortly after sunrise on a day with spring tides. The results are shown in Fig. 3. The curve of the oxygen concentration followed closely the tidal curve. Peaks in oxygen concentration coincided with high tides, the height of two subsequent peaks differed according to the daytime. When high tide occurred during the afternoon, its accompanying O_2 concentration was larger than that during night or shortly after sunrise (Table 2).

TABLE 2

Oxygen concentrations in mg $O_2\,l^{-1}$. Time of high tides in parenthesis

date		
31 May	6.35 (at sunset)	4.50 (early morning)
25 June	6.05 (afternoon)	4.65 (at night)

Figure 3 also shows that the decrease in oxygen concentration between high tide and subsequent low tide depended on whether the ebb under question fell into day- or nighttime. On 31 May when the ebb period roughly coincided with the first half of the light period, the decrease was only 0.60 mg O_2 l^{-1}. During the following tidal cycle, but with the ebb occurring in the dark period, the decrease amounted to at least 2.62 mg O_2 l^{-1}. The decrease was probably somewhat higher, because the lowest O_2 concentration was not yet reached since the study was finished shortly before low water. On 25 June the longer part of the ebb period occurred after sunset. Consequently the oxygen decrease was 3.15 mg O_2 l^{-1} (Table 3).

During the second 24 h study on 25 June the Secchi depth, the seston concentration and the BOD_7 in the main mangrove channel were

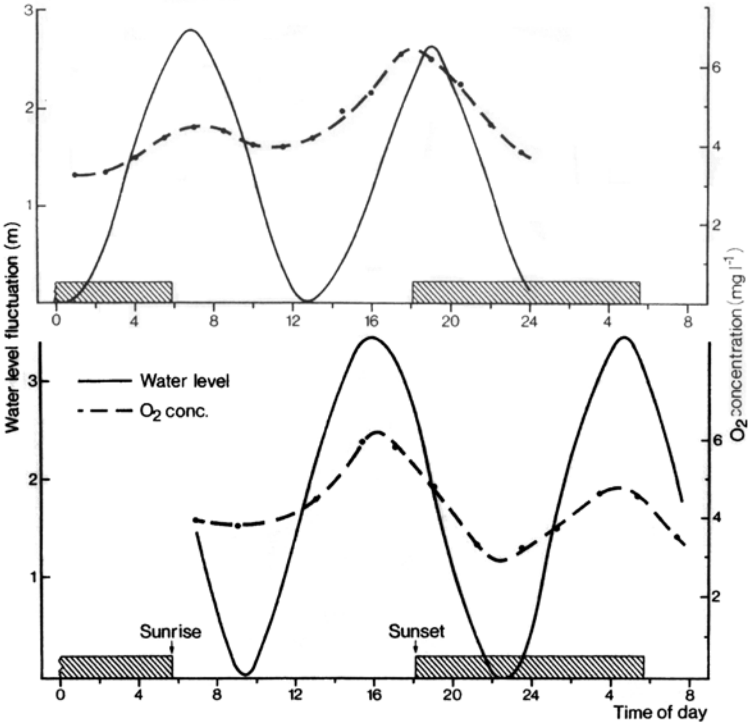

Fig. 3. Tidal variations of water level and oxygen concentration in the mouth of the main channel of a mangrove forest on 31 May (upper part) and 25 June (lower part).

determined in roughly two hour intervals. The results are shown in Fig. 4. The Secchi depth varied between 18 cm at low tide and 85 cm at high tide. The total seston concentrations were highest at low tide (83.7 and 63.0 mg dry weight per liter). A much lower seston content was observed at high tide (around 10 mg l^{-1}). The time intervals with very high seston values were short and almost restricted to the moment of the lowest water level and to the time shortly before it (Fig. 4). When the seston concentrations were highest, their organic fraction was lowest. The high amount of total seston at low tide consisted of 18 and 15% of organic matter, whereas at high tide the organic content increased to 26-28%.

The BOD_7 varied over the 24 h study between 2.61 and 1.00 mg O_2 l^{-1}. No clear relation to the tidal cycles could be detected. The high value of 2.61 mg O_2 l^{-1} coincided with the first (and highest) maximum of seston concentration. The second seston maximum, however, was not accompanied by a BOD_7 peak.

TABLE 3

Difference between O_2 concentrations (mg O_2 l^{-1}) at high tide and subsequent low tide. Time of tide in parenthesis

date	high tide	low tide	difference
31 May	4.50 (early morning)	3.90 (at noon)	0.60
	6.35 (at sunset)	< 3.72 (at night)	> 2.62
25 June	6.05 (afternoon)	2.90 (at night)	3.15

DISCUSSION

It is not known what percentage of the high tide water volume remains in the mangrove forest of the Estero de Morales at low tide. Since at low tide only the channels of the system are filled with water, this percentage

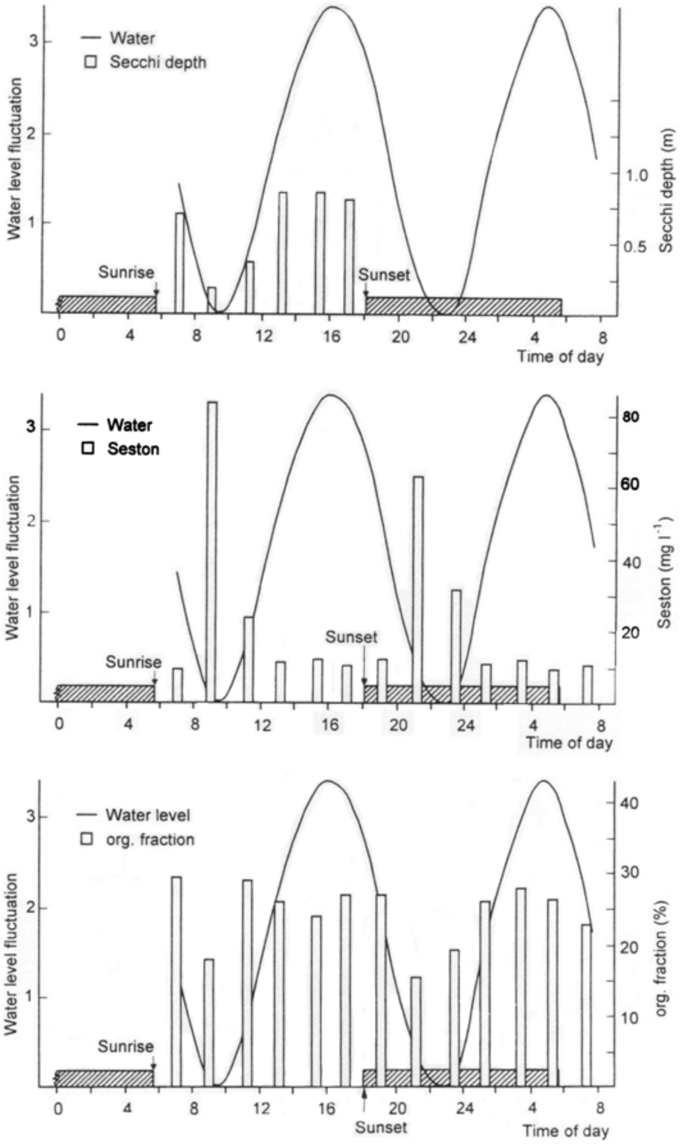

Fig. 4. Tidal variations of water level, Secchi depth (a), total seston concentration (b) and fraction of organic seston (c) on 25 June.

should be very low. Most probably more than 90% of the water volume are exchanged during an average tidal cycle. Hence, there is not enough time for the existence or development of a genuine phytoplankton population inside of the system. This means that the phytoplankton community of the Estero de Morales depends completely on the pelagic situation in the adjacent part of the upper Golfo de Nicoya. It is therefore not astonishing that the seasonal variations of primary productivity in the estero and gulf coincided almost completely. In both systems the highest primary productivity rates occurred during the dry season and at the beginning of the rainy season (Gocke *et al.* submitted).The very high PP, which was observed in September in the estero, was caused by a red tide bloom. This bloom also occurred in the gulf, but due to its patchiness it had no measurable effect on the primary productivity in the upper Golfo de Nicoya, since it simply was not sampled when the incubation was performed.

The magnitude of the primary productivity in the main channel of the mangrove forest inspite of its thin euphotic layer, is astonishing. In the Golfo de Nicoya the annual mean Secchi depth was 1.23 m (Gocke *et al.* submitted). In the Estero de Morales Secchi depth was only 0.57 m. The Secchi depth and the net primary productivity (PPn) of the estero reached 46% of the respective values of the gulf. Even if this exact correspondence may be somewhat accidental, it nevertheless shows that the phytoplankton in the estero is qualitatively connected with the gulf and that the quantitative differences between the PP are related to the optical properties of the water columns in both systems.

The community respiration (R) of the suspended organisms within the euphotic layer in the main channel of the mangrove forest was 179 g C $m^{-3}a^{-1}$. Due to the high turbulence caused by tidal currents, the respiration rates were nearly always homogeneously distributed over depth. Only when the red tides occurred in May and especially in September, R was much greater at the surface than at 0.5 and 1.0 m depth. The community respiration in the estero was higher than in the gulf, where it reached 107 g C $m^{-3}a^{-1}$ (Gocke *et al.* submitted). This is caused by higher turbidity in the estero due to resuspended sediment particles with their attached microorganisms. There is, however, no linear relation between respiration and turbidity (the latter taken as the inverse value of the Secchi depth). This is explained by the observation that the organic fraction of the seston increases more slowly than the absolute concentration. As shown in Fig. 4, the high seston concentrations, which were observed in the very turbid waters at low tide, had a smaller percentage of particulate organic material (around 15-18%) than the smaller seston concentrations in the less turbid waters during high tide (between 19 and 29%).

The gross primary productivity ranged from 0.29 to 3.88 and the net primary productivity from 0.12 to 2.76 g C m^{-2} d^{-1}. The annual values of 457 g C m^{-2} a^{-1} (PPg) and 278 g C m^{-2} a^{-1} (PPn) indicate that the main channel of the mangrove forest was highly productive. Very few data about planktonic primary productivity in mangrove forests were published till now, thus it is difficult to make comparisons. Córdoba Muñoz (1998) who performed measurements in the mouth of the main channel of the Estero de Morales, obtained the much higher annual PPn of 439 g C m^{-2} a^{-1} (PPn per day ranged between 0.69 and 2.53 g C m^{-2}). Her result, however, is not directly comparable with our value, since she made the incubations always at high tide at a much deeper station. Under these circumstances the PPn in the mouth of the channel is more similar to the situation in the open area of the upper Golfo de Nicoya than to the inner part of the channel system of the mangrove forest. Harrison *et al.* (1997), who studied the annual variation of primary productivity in two creeks in a mangrove covered region of the Indus River delta, found rates from 0.2 to over 1.0 g C $m^{-2}d^{-1.}$

An incubation of the flasks at high tide under the canopy of the bordering mangroves directly at the shore of the channel revealed a very low net primary production. Since this PPn was restricted to a thin surface layer, it follows that inside of the mangrove forest no net production of organic matter can exist due to phytoplankton and that the planktonic PP is virtually restricted to the open water areas of the channels. Since, however attached macroalgae were found on the prop roots of *Rhizophora* in the subtidal parts of the mangrove forest, a certain primary production due to epibiotic macroalgae occurs even under the canopy, since these algae are probably better adapted to low light intensities than the planktonic algae.

The oscillation of the oxygen concentration in the mouth of the main channel during a tidal cycle shows that the consumtion of organic material within the water column of the mangrove forest exceeds by far the production (Fig. 3). The graphic reveals that the oxygen concentration followed closely the variations of the water level. Even when the oxygen concentration of the water, which entered the system in the early morning, was quite low due to the oxygen consumtion in the gulf at night, it decreased still more inside the mangrove forest during high tide and the following ebb phase. This is in contrast to the open water of the upper Golfo de Nicoya, where the oxygen concentration increased strongly during the day, since there the production of organic material exceeded largely the consumtion in the entire water column (Gocke *et al.* 1990). Under the canopy of the mangrove forest, however, the respiration processes in the water were far greater than the processes, which lead to a liberation of oxygen, i. e. photosynthesis.

Oxygen consumtion occurs in the three compartments of the submersed system: in the water by suspended organisms (true plankton and resuspended small organisms), at the sediment surface by benthic organisms and on the prop roots and stems of the mangroves by epibiotic organisms and by the roots themselves (Gocke *et al.* 1981). Therefore, and since the oxygen liberation due to root attached macro- and microalgae cannot match the O_2 consumtion, the oxygen concentration of the out-flowing water must be lower than it was previously in the in-flowing water regardless of the time of the day and even under full sunshine. There was, however, an interesting difference between the ebb phases of day and night. Our measurements in the mouth of the main channel showed that the O_2 decrease from high to low tide was significantly smaller during the day (0.60 mg O_2 l^{-1}) than during night (around 3 mg O_2 l^{-1}, see Table 3). Obviously the primary production of the attached macro- and microalgae and especially the high PP in the channel makes up at least partly for the oxygen loss under the canopy. This means that the water which flows back into the open gulf (during the day) is higher saturated with oxygen than it was at the moment it left the shaded parts of the mangrove forest of the Estero de Morales.

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RESUMEN

Durante un año se midió la variación estacional de la productividad primaria planctónica en el canal principal al interior de un bosque de manglar del Estero de Morales (Estero de Punta Morales), un sistema de manglares ubicado en el Golfo de Nicoya, costa Pacífica de Costa Rica. Las muestras fueron incubadas en la superficie, a 0.5 m y 1.0 m de profundidad utilizando la técnica de “botellas claras y oscuras”. La productividad primaria anual bruta (PPg) fue de 457 y la productividad primaria neta (PPn) de 278 g C $m^{-2}a^{-1}$. La PPg diaria varió entre 0.29 y 3.38 y la PPn entre 0.12 y 2.76 g C $m^{-2}d^{-1}$. Las mayores tasas observadas en mayo y septiembre se debieron a florescimientos de marea roja. La variación estacional de la productividad primaria en el bosque de manglar depende estrechamente de la PP de las aguas abiertas de la zona superior del Golfo de Nicoya. Como se esperaba, la PP estuvo limitada por la luz ya que la profundidad de compensación durante la marea baja se encontró a sólo 1 m de profundidad. Durante la marea alta ésta se encontró a una profundidad algo mayor. La productividad primaria planctónica dentro del bosque de manglar estuvo totalmente restringida a los canales abiertos. Una medición simultánea demostró que no hubo PPn de fitoplancton bajo el follaje de los manglares. Estudios adicionales sobre el curso temporal de la concentración de oxígeno en la boca del canal principal durante 24 hrs, demostraron una relación entre el O_2 y las curvas de marea. Independiente de la hora del día, la corriente de marea baja tuvo siempre concentraciones menores de O_2 que la de marea alta. La diferencia con la marea alta precedente, sin embargo, fue mucho menor cuando la marea baja ocurrió durante el día. Esto indica que bajo el follaje la productividad primaria y por

lo tanto la liberación de O_2 por las macro y micro algas epibióticas, junto con la alta PPn del fitoplancton en los canales, contribuyen a que la concentración de oxígeno no disminuya tanto como durante la noche. Sin embargo, indica también que el consumo de material orgánico en la parte sumergida del bosque de manglar excede siempre su producción.

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