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Phytoplanktonic biomass and production in a tropical hypersaline estuary, the Casamance (Senegal, West Africa)

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ABSTRACT

We use some results gathered in a West African "inverse estuary" (S > 150 g.l^{-1}) to illustrate some general problems found in near-shore waters.

Phytoplankton biomass (B) increased landward, owing to stability and hydraulic confinement. No nitrogen deficiency was apparent. Nightly in situ oxygen uptake was related to B, but also to allochthonous dissolved organic matter (DOM).

The two descriptors of the production/irradiance curve, α and P_m, were positively correlated. Gross production of the water column ($\Sigma_z A$; ^{14}C method) could not be modelled from maximum (sub-surface) production, due to frequent shallowness. Net areal production in the classical sense would appear negligible; by contrast, overall biomass production was probably maintained by heterotrophic bacterial activity

We compare these results with literature data for lakes, estuaries, coastal waters and oceanic oligotrophic regions. We also use some of our studies on lagoons or estuaries. Confined environments such as the Casamance show high sestonic biomasses of small-size organisms, and high energy flows. Recycling is preponderant, and f ratios are probably very low. While some features would outwardly correspond to eutrophic waters, these environments do show several characteristics of oligotrophy.

List of symbols

symbol	significance	units
A_{254}	in-vitro light absorbance at 254 nm	
A	gross production	µmol C.(l.hr)$^{-1}$
A_m	maximum (sub-surface) instantaneous production	µmol C.(l.hr)$^{-1}$
α	slope at origin of the P vs E curve ; in µg C.(µg chl.hr)$^{-1}$ (µE.m^{-2}.s^{-1})$^{-1}$	
α*	$P_m/E_d(0)$; minimum estimate of α	
B	phytoplankton biomass	µg chl.l^{-1}
C_p	particulate organic carbon	µmol C.l^{-1}
DIC	dissolved inorganic carbon	µmol C.l^{-1}
DIN	dissolved inorganic nitrogen	µmol N.l^{-1}
DOC	dissolved organic carbon	µmol C.l^{-1}
ΔDIC	increase of in situ DIC	µmol C.(l.hr)$^{-1}$
∇O2	decrease of in situ oxygen	µmol O2(l.hr)$^{-1}$
∇*C	dark ^{14}C loss	µmol C.(l.hr)$^{-1}$
$E_d(0)$	downwelling sub-surface irradiance	µE.m^{-2}.s^{-1}
$E_o(z)$	scalar irradiance at depth Z	µE.m^{-2}.s^{-1}
K_d	vertical attenuation coefficient (downwelling irradiance)	m^{-1}
K_s	chlorophyll-specific attenuation coefficient	mg^{-1}.m^2
P_m	chlorophyll-specific maximum production	µg C.(µg chl.hr)$^{-1}$
POC	particulate organic carbon	µmolC. l^{-1}
PQ	photosynthetic quotient	
R_z	irradiance reflectance at depth Z	
RQ	respiratory quotient	
S^*	spectrum slope	ln. nm^{-1}
$\Sigma_z A$	vertically integrated (="areal") production	mmol C.m^{-2}.hr^{-1}
$\Sigma_z A_h$	areal hourly production around noon	
$\Sigma_z \Sigma_t A$	areal daily production abbreviated as Σ A	mol C.m^{-2}.d^{-1}
$\Sigma_z \Sigma_t R$	areal daily respiration abbreviated as Σ R	mol O2.m^{-2}.d^{-1}
$\Sigma_{ph} R$	areal daily respiration by the sole phytoplankton	
Ψ	slope at origin of P vs E	g C.g chl^{-1}.E^{-1}.m^2
ξ	"compound factor"=$(B.E_o)/(K_d.10^3)$	
Z_{av}	averaged depth	m
Z_{eu}	euphotic depth	m
Z_s	Secchi disk depth	m

INTRODUCTION

Estuaries have attracted a great deal of interest in the last years. First, as an ecotone, they share the general attention given to such systems. On a trophic level, moreover, estuaries, or some bays, have been called "heterotrophic" (Smith et al., 1989, 1991; Dollar et al., 1991; Findlay et al., 1991, 1992; Howarth et al., 1992; Smith & Hollibaugh, 1993), since they often are fueled primarily by allochthonous organic matter flushed from terrestrial systems. A second point of interest, more mundane, is their high productivity in general, and their commercial yield in particular; this economic value is common to estuaries and coastal waters, while several studies have shown that estuaries are also nurseries for several fishes (Blaber, 1985; Ross & Epperly, 1985; Day et al., 1987; Parrrish, 1990; DeLafontaine, 1990; Yoklavich et al., 1991).

During the course of the study of a tropical estuary, the Casamance "river" (Sénégal, West Africa), we had the opportunity to deal with a system in which "productivity" (considered from a general, "fisheries production" angle) was not solely based upon the "classical" food-chain (with primary production at the start), but also upon organic matter imported from relic riparian macrophytes.

The concept of "net" production in such a system is notoriously ambiguous (Quinones & Platt, 1991). We found that high planktonic biomasses, with high gross production, were not always exploited at the tertiary level, so that photosynthesis was "running idle". Circumstantial evidence indicates that, at least in a first step, dissolved inorganic carbon is sequestered as particulate organic carbon (Pagès et al., in prep). Our data are though insufficient to decide whether the system is a net sink or a source for carbon on an overall basis.

Our study was not (could not) be devoted solely to primary production, since our resources (in manpower and material) were severely stretched in describing a system which was practically unexplored in terms of general functionning as well as in terms of environment. We were thus obliged to do a "quick and dirty" description, rather than a proper (in depth) study of the sole phytoplanktonic component.

We shall use, in our discussion, many references dealing with marine environments, either high sea or coastal (near shore) waters, as well as data, or results obtained in freshwater environments. Most problems are analogous in these aquatic environments, be it from the point of view of scientists trying to understand them or be it for the organisms trying to live (and prosper) in them.

1: BACKGROUND OF THE STUDY

The overall setting and some particulars of the Casamance estuary have been described elsewhere (Pagès et al., 1987). We shall have to recall, occasionnally at some length, those features which have a direct relation with the present subject. The main aspect of the estuary is its hydraulic régime.

The Casamance estuary (fig. 1) lies in a dry tropical area, along the southern border of Senegal. The rains last from mid-June to late October; annual rainfall varied between 800 and 1200 mm during the past 20 years (fig. 2). Yearly evaporation is about 1500 mm (fig. 2). Water temperatures have a rather narrow range (24°C in January, 30°C from July to September).

1.1: HYDRAULICS

The estuary is in fact a drowned river valley, under tidal influence along its whole length, up to about 260 km from the sea.

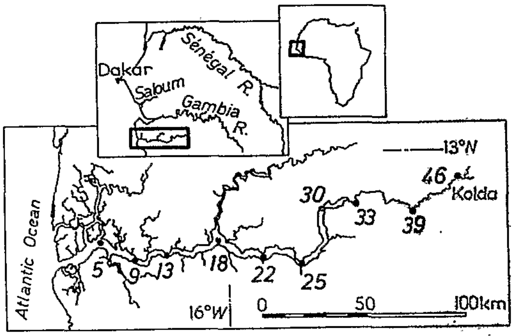

Figure 1. General setting of the Casamance estuary, with localization of some stations. Our station 13 is situated at Ziguinchor, the regional capital

The lowermost 90 km seaward stretch is bordered by mangrove swamps. Strong tidal currents (up to 1 $m.s^{-1}$) scour a narrow, relatively deep central channel, while wide shallows and mud banks are found on the sides. Tidal mixing is active up to st. # 18, some 100 km from the sea. Tidal amplitude is 0.6-0.8 m at the mouth (semi-diurnal régime), and decreases to practically nil in the uppermost reaches above st. #30.

In the upstream part of the estuary (st.# 30-41, 180 to 240 km from the sea), average depth decreases to 0.6-0.2 m, with occasionnal, very localized deeper channels (st. #25 and st. #30). Broad lateral marshes are occupied by the reed *Phragmites australis*. This riparian vegetation was well developped between st.#33 and st.#41 in 1984, at the beginning of our study. A brutal salinity surge in 1986 (see $ 1.2) led to a retreat of the reeds above st. #43, while dead reeds and litter was still found at the former locations in mid '87.

Since the yearly water budget is markedly negative (freshwater deficit of 300 to 800 mm per year), the net water motion during the dry season is a general upstream drift, at a rate of about 0.1 $cm.s^{-1}$. This drift occurs in a "piston flow" fashion with little longitudinal mixing (see for instance the sharp salinity gradients in fig. 4).

Freshwater discharge at Kolda (our st. #46) is low even at flood peak (6-10 $m^3.s^{-1}$) and has thus a small influence upon the overall water budget. We did not observe any measurable alteration (either in current speed or in water level or in water composition) during the flood period (August to November). Waters above the "salinity peak" (see below) have thus been trapped, and separated from the sea, for several years.

1.2: SALINITY

During its landward drift along the estuary, seawater becomes concentrated by evaporation. A "salinity plug" (to use the term coined by Wolanski, 1986) has been a permanent feature since 1968 (Brunet-Moret, 1970; Savenije & Pagès, 1992). At the end of the rain season, the maximum salinity values (≈ 60 $g.l^{-1}$)

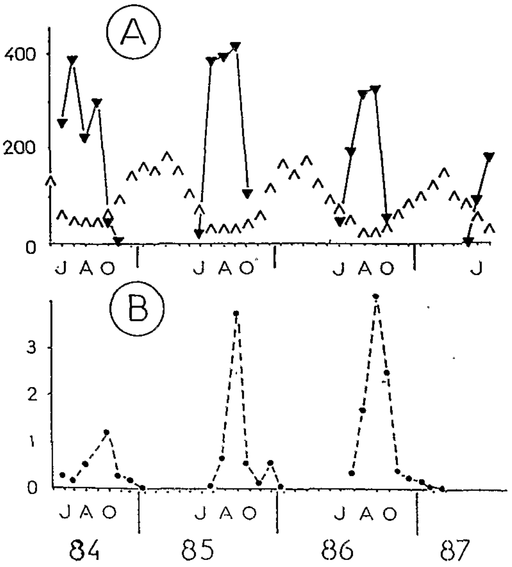

Figure 2: Elements of the water budget in the Casamance estuary during our study. A: Monthly data for evaporation (Λ) and rainfall (∇) at Ziguinchor (st. #13). B: Monthly averaged discharge at Kolda (our st.#46). Absence of symbol means zero. The months of June, August and October are indicated by their initials.

are found around st. #25, some 160 km from the sea. During the dry season, peak values increase and are found farther and farther inland. Salinities thus peak at around 150 g.l^{-1} at st.#38 at the end of the dry season; a record salinity of 202 g.l^{-1} was observed in June '86 at the same location.

This "salinity peak" is a convenient feature separating a "thalassic" downstream portion from what we call -somewhat improperly- the "a-thalassic" portion which contains mixtures of brine and freshwater. The thalassic waters are merely concentrated seawater in which major ions are mostly found in their original proportions (Jusserand et al., 1989). In June '86, however, a slight depletion in sulphate and calcium corresponded to gypsum crystals found on the bottom between st.#33 and st.#39.

We may note that the "salinity peak" has no intrinsic value as a marker of a given water mass, since it "travels" landward, like a wave, at a speed superior to that of the water itself. We must though stress that this "travelling" has nothing to do with tide, and this for several converging reasons: *a)* we were able to simulate satisfactorily the successive salinity distributions with a tidally averaged model; *b)* the simulated landward drift occured at about 0.1 cm.s^{-1}, while the salinity peak travelled at observed speeds of 0.3-0.7 cm. s^{-1}; *c)* tidal currents of about 20 cm.s^{-1} were measured 230 km away from the sea (st.#39) while the tidal wave has an observed speed of 150-200 cm.s^{-1} in this portion (LeReste, pers. comm., 1985).

1.3: NUTRIENTS

1.3.1: Dissolved inorganic carbon (DIC)

We observed a peculiar distribution of DIC concentrations ([DIC]) in the thalassic waters (fig. 5), with decreasing [DIC] in increasingly saline waters; from a classical value of 2.2 mmol C.l^{-1} at the lowermost stations, [DIC] decreased to about 0.5 mmol C.l^{-1} around the salinity peak. This negative correlation between salinity and [DIC] was linear, with a marked seasonal variation (for a given salinity, [DIC] increased during the dry season). In the a-thalassic portion, [DIC] increased again; mixing diagrams of [DIC] vs salinity indicate an occasional DIC input either from the Phragmites stands or from the continental waters.

1.3.2: Inorganic nutrients

All "classical" nutrients (NO_3^-, NH_4^+, PO_4^{3-}, SiO_3^{2-}) seldom showed any clear distribution pattern, either in absolute concentrations or in their ratios. The only reconizable pattern was an increase of dissolved inorganic nitrogen with increasing salinity in the thalassic part; however, this increase was not constant, and not statistically significant. The a-thalassic portion, conversely, often showed an outwelling of nutrients (mainly NH_4^+) from the Phragmites stands.

1.3.3: Dissolved organic carbon (DOC)

Concentrations of DOC increased landward (fig. 5), in a nearly exponential fashion, along the whole estuary, from 5-10 mg DOC-C.l^{-1} in the downstream portion up to 20-40 mg DOC-C.l^{-1} in the upper reaches. Here again, the Phragmites stands appear to be a permanent source of nutrients, with an occasionnal import from the continent at the first rains.

1.3.4: Oxygen and pH

As a rule, O2 concentrations were mostly between 70%

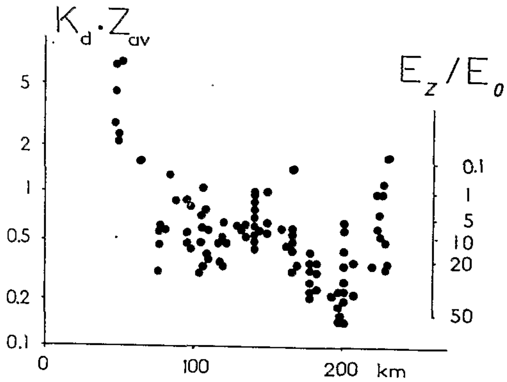

Figure 3. Underwater light climate as a function of distance to the sea (zero at mouth). Distribution of optical depth (attenuation coefficient, K_d, times averaged depth, Z_{av}). Right-hand scale shows the proportion of incident light reaching the bottom.

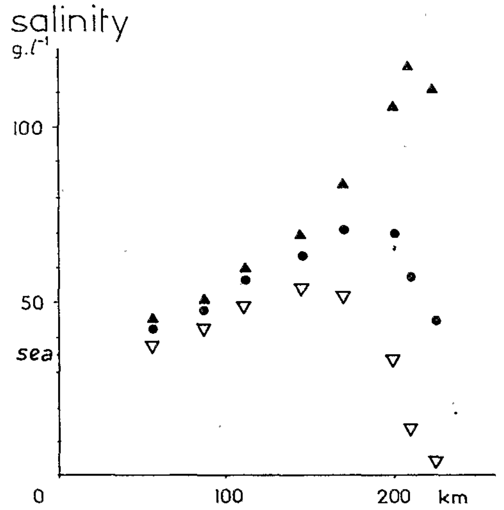

Figure 4. Seasonal averages of salinity (S, in g.l^{-1}) between 1985 and 1987. Typical situations in September-December, after the rains (V), in February-April (o) and in May-June, late in the dry season (Δ).

and 110% of saturation. We did observe some very low values (15-20% of saturation) during the early morning hours, in February-March, in the upper reaches (st. #38), with high phytoplankton biomasses (75-100 µg chl.l^{-1}; see below). We may note here, in relation with occasional oxygen depletion, that sulphate appear to be slightly more depleted than calcium, hinting at some sulphate-reducing activity.

Diurnal pH variations were small. Most pH values ranged between 7.25 and 7.75. An isolated series was found in June '86, with low readings (down to 6.3) in highly saline waters; this was due to glass junction error (Krumgalz et al., 1980). While diurnal O2 variations did correspond to biotic activities, in situ pH did not respond in a utilizable fashion to either photosynthesis or respiration.

1.4: LIGHT CLIMATE

Incoming above-water irradiance ($E'_d(0)$) showed the expectable annual variation with a trough caused by cloud cover during the rain season.

Underwater light climate was more complicated (fig. 3). Down-welling attenuation coefficient (K_d) showed lowest values (1.0-1.4 m^{-1}) in the median part of the estuary (st. #20-26, 110 to 150 km from the sea; see fig. 3). Inorganic turbidity was high in the downstream portion (K_d of 1.5-2.5 m^{-1} , with a Secchi disk depth Z_s of 1 to 2 m). The conjunction of turbidity and bathymetric (actual) depth led to optically deep waters ($K_d . Z_a$ = 1-5). The upstream waters, on the opposite, contained high organic loads; we observed K_d values of up to 12 m^{-1} and Z_s values as low as 0.15 m. The general upstream shallowness kept the optical depth to moderate values; if we consider averaged depth, Z_{av}, the product $K_d . Z_{av}$ remains between 0.2 and 1.0.

We shall see ($ 3.1.3.1) that light attenuation by phytoplankton represents but a small part of total attenuation. We have computed the attenuation coefficients for dissolved compounds,K_w, and for phytoplankton,K_b. The ratio K_w+K_b/K_d gives an estimate of *b/a*, ratio of diffusion to absorption (Kirk, 1983). This ratio *b/a* in turn indicates the contribution of back-scattered and reflected irradiance.

Upwelling attenuation coefficients (K_u) appeared plausible, but calculated irradiance reflectance (R_z) was mostly abnormally high against literature values (Kirk, 1983). Radiometer measurements (above water) in the 500-590 nm and 610-690 nm windows showed that bottom reflectance could reach 15 % (Pagès et al., 1990). A bottom effect upon R_z is thus present for waters shallower than about 0.5 m. Estimating scalar irradiance at a given depth ($E_o(z)$) is hence complicated by local bathymetry. We had to compute correction tables incorporating both measured K_d and bottom reflectance for estimating $E_d(z)$ and $E_u(z)$. Scalar irradiance was approximated by $E_o(z) = 1.5\ (E_d(z) + E_u(z))$. This (admittedly rough) approximation yielded a relatively homogeneous light field; "deep" layers (i.e. 0.6 m) were well into the euphotic zone.

2. MATERIAL AND METHODS

Between 1984 and 1987, a total of 24 field trips were done, but all parameters were measured only during 16 of them (see table I for calendar). Surveys were done in an 8 m open launch from the forward base of Ziguinchor, while the main laboratory was in Dakar (Fig. 1).

Bathymetry was surveyed with an echo sounder. At least one transverse profile was obtained at each station; some portions were charted with more detail (Debenay, 1984). Average depth (Z_{av}) was calculated for each "section" (i.e. station) by

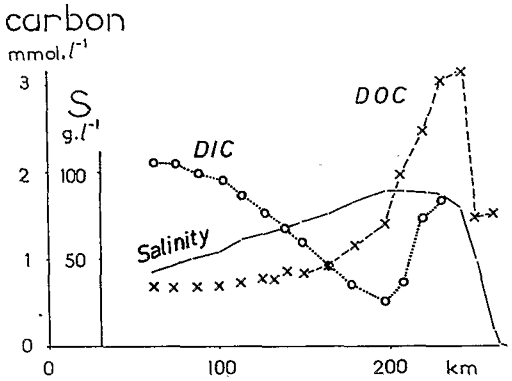

Figure 5: Survey of May 1987, with salinity (S), dissolved inorganic carbon (DIC) and dissolved organic carbon (DOC).

integration.

Salinity was measured in the field with a hand-held refractometer (Atago 20). Readings (in $g.l^{-1}$) were +/- 2 $g.l^{-1}$ accurate. Some samples were taken back to the lab for calibration with a Grundy A 230 induction salinometer.

Temperature was measured with a mercury thermometer (+/- 0.1°C).

pH was measured with a Cole-Parmer "Digi/sense" field pH-meter recalibrated about every hour with pH7 buffer. We used here the raw data, without correction either for temperature or for salt effect (Krumgalz et al., 1980).

Underwater light was measured with a flat LI 192 SB sensor aimed either at zenith or at nadir, attached either on a Niskin bottle or onto a rigid rod. Attenuation coefficients were calculated by linear regression of $ln(E_d(z)/E_d(0))$ *vs* Z.

Dissolved oxygen concentrations were measured with a YSI-57 oxymeter set at "Freshwater". The readings were corrected for salinity using extrapolated oxygen solubility equations (Weiss, 1970; Benson & Krause, 1984). Applicability of these extrapolations was verified a posteriori with the data of Sherwood et al. (1991).

Colour (in vitro spectral absorbance) was determined in the lab on GF/C-filtered samples. Spectra were scanned with a Bausch & Lomb Spectronic 2000 spectrophotometer fitted with a 1-cm (UV) or 10-cm (visible) cell. Correction for scattering in the visible was done according to Davies-Colley & Vant (1987).

Dissolved inorganic carbon (DIC) was determined by two methods. During the first three surveys considered here, we used the usual acidimetric method of alkalinity determination, with 0.05 N HCl titration monitored by pH-meter. For ensuing surveys, we used gas chromatography (Oudot et al., 1987). Eight-ml samples were poisoned with 1% (v/v) saturated $HgCl_2$. Determination was carried out on decanted 2-ml subsamples. After acidification with 0.2 ml pure H_3PO_4, the resulting gaseous CO_2 was determined by gas chromatography.

Dissolved organic carbon (DOC) concentration was monitored indirectly from light absorbance on GF/C - filtered samples (Pagès and Gadel, 1990). As a first approximation, DOC concentration (in mg $DOC\text{-}C.l^{-1}$) can be obtained from absorbance at 254 nm (A_{254}, in cm^{-1}) by: [DOC] = -1.25 + $65.7*_{254}$. In fact, carbon-specific absorption varies with molecular weight, which can be estimated from spectrum slope, S^*; our best estimate to date is: [DOC] = $1.370*A_{254}$ / (0.0411 - S^*). The labile portion of DOC was roughly estimated by long-term (2 months) in vitro incubations in the dark, with periodic monitoring of DOC decrease.

Major ions (Na, K, Ca, Mg, Cl, SO_4) were assessed in June '86 only. Samples had been $HgCl_2$-poisoned. Standard methods were used after suitable dilution with deionized water.

Nutrients were determined on GF/C-filtered samples preserved with $HgCl_2$. Nitrate, phosphate and silicate were measured on a Technicon AutoAnalyzer I using standard oceanographic methods (after Strickland & Parsons, 1968, and Parsons et al., 1984). Ammonium was determined manually, back in the laboratory, after unsuccessful tentatives in the field.

Chlorophyll was determined in routine by fluorimetry (Turner 110) on methanol extracts (24 hrs at 4°C, without grinding; Nusch, 1980), with calibration against trichromatic spectrophotometry. Routine checks were done on high-biomass samples using the specific absorption given by Javor (1989) for chlorophyll in methanol. Although acidification was carried out, we shall use here "total" chlorophyll figures, without correction for phaeopigments. Some high-biomass samples also underwent spectrophotometric measurements for chlorophylls and carotenoids (Jensen, 1978; Kirk, 1983; Parsons et al., 1984). We shall use the ratio of absorbances at 480 and 665 nm (noted "480/665") as an estimator of carotenoid/chlorophyll ratio.

Particulate organic matter (POC and PON) was assessed only during our May '87 survey. Precombusted GF/F filters were used. Measurements were done with a Hewlett-Packard HP 185B analyzer.

Photosynthesis was assessed by the ^{14}C method in "simulated in situ" incubations (Head, 1976) under natural light. Pyrex 250-ml screw-cap bottles were wrapped in several layers of tautly stretched plastic mosquito netting (transmittance of 55% as determined with a LiCor quantum meter). The Plexiglass incubator (0.4 x 0.8 m) was filled with river water. Samples were spiked with about 2 µCi of Na_2CO_3 in aqueous solution (CMM 53B from C.E.A., originally at 56.5 $mCi.mmol^{-1}$, diluted with H_2O at pH 9 and kept frozen in small portions). After incubation, sub-samples of 60-180 ml were filtered on 25 mm GF/C filters, which were rinsed with 10 ml of pre-filtered river water (we ascertained that counts were not significantly lowered by an ulterior treatment with HCl fumes). Dry-sucked filters were kept in plastic scintillation vials at 0°C (in the field) then at -20°C. The dried filters were counted by liquid scintillation (10 ml of either ReadySolv or the customary toluene-PPO-POPOP cocktail) on a Philips P4700 with external standard. Corrections (quenching, etc) were sometimes complicated by heavy inorganic loads. Calculation of ^{12}C uptake took into account the actual DIC concentration, but we disregarded possible effects of tracer uptake kinetics.

3: RESULTS

The general outstanding feature of the Casamance estuary is a pronounced longitudinal gradient. This gradient, found in most parameters, parallels that of salinity in the thalassic portion, but often diverges from it in the a-thalassic part. The distribution of most data is then strongly skewed, so that the risk of pseudo-correlations is high, and the basic requisites for parametric statistics are not met.

3.1: PHYTOPLANKTON BIOMASS

The bulk of data consists of chlorophyll concentrations, B, given in $\mu g.l^{-1}$, without correction for phaeopigments.

3.1.1: Spatial distribution

The permanent feature observed was an exponential increase of B in an upstream (landward) direction (fig. 6). While downstream and median portions harboured biomasses between 2 and 10 $\mu g.l^{-1}$, upstream values were mostly above 50 $\mu g.l^{-1}$; highest biomasses (250-350 $\mu g.l^{-1}$) were found in September '85.

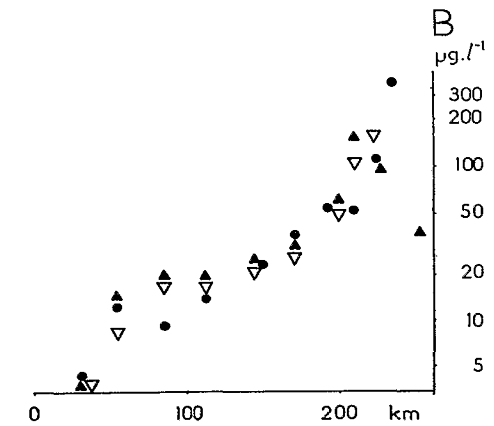

Figure 6. Distribution of phytoplankton biomass: Seasonally averaged chlorophyll concentrations (B, in µg.l^{-1} ; note logarithmic scale) in September-December (∇), in February-April (o) and in May-June (Δ). No significant seasonal effect could be shown.

Maximum B values were nearly always found at the farthest station occupied during a given survey, and this also during the rain (and/or flood) periods.

Seasonal effects were conspicuously absent. We could find no repetitive pattern throughout our 3-year study. Nor could we find any satisfactory correlation between B and environmental variables. Some positive correlations do exist, with the ratio Z_{av}/Z_s , with DOC concentrations, and with the morpho-edaphic index. There is nonetheless the distinct possibility that these correlations merely stem from the general longitudinal gradient, and are thus pseudo-correlations. This may also be the case for a weak corrrelation found between B and dissolved inorganic nitrogen.

Vertically integrated ("areal") biomasses, $\Sigma_z B$, gave comparable results. The median and lower portions of the estuary had areal biomasses of 10-20 mg chl.m^{-2}, while the stretch between st. #36 and st.#39-40 had the highest values (150-200 mg chl.m^{-2}) despite its shallowness.

3.1.2: Nature and composition of biomass

We have no taxonomic data for the study period, and we can hardly use the some observations made at a later time (Debenay et al., 1991). However, a particular situation was found in June '86, when strongly discoloured waters suggested a bloom of *Dunaliella salina* in the upper estuary. Ulterior measurements confirmed an increase in β-carotene proportion (estimated by the 480/665 ratio) in increasingly saline waters. Further measurements during later surveys confirmed this trend (fig. 7); surprinsingly, though, the June '86 survey gave the lowest 480/665 ratio.

3.1.2.1: Particulate organic carbon (POC) and carbon budget

Using the only series of POC measurements of the May '87 survey, a plot of POC vs B (fig. 8) shows a good agreement between both estimators; the remarkable exception is st.#39, then the only a-thalassic station. Excluding this station yields the correlation: POC = 129 + 6.01 . B (n=13, r=0.96; POC in µmol.l^{-1}, B in µg.l^{-1}). This would in itself indicate a high proportion of detrital POC. Closer inspection shows that POC/B ratios (in weight, this time) range between 80 and more than 300; lowest POC/B ratios are found at st.#35-37, where the peak of B is also located. POC/B values increase seaward (Spearman rank: rs=0.95, a<1%); the highest POC/B ratio (415 w:w) is found at st. #19.

Whatever its physiological state, seston POC represents between 100 and 700 µmol POC-C.l^{-1}. We may compare these amounts to the others carbon compartments during the same survey: DOC concentrations ranged between 700 and 3000 µmol.l^{-1}, while DIC represented between 2200 and 500 µmol.l^{-1}. The ratio DOC/POC is about 2.2 up to st.#26; it averages 2.5 around st.#30, then increases sharply to 3.9 and 5.6 at st.#33 and st.#39 respectively.

3.1.2.2: Particulate nitrogen (PON)

A plot of PON against B (fig. 8) shows a reasonable agreement, with the renewed exception of st.#39 (PON = 13.2 + 0.93 B (r=0.97; PON in µmol, B in µg)). Closer inspection of the plot shows two regions in the thalassic part: the upstream and median region (st.#26-37) contains rather less nitrogen, while the downstream half (st.#13-25) has PON/B ratios ranging between 2 and 6 µmol.µg^{-1} (mean 2.9 µmol.µg^{-1}). An overall linear relation between B and PON would then be illogical. We have used the inverse form employed by Dortch & Packard (1989), plotting the ratio B/PON against B (fig. 9). We obtain the regression: B/PON = 1.07 . B/(B + 14.2). While we are dealing with total N (and not

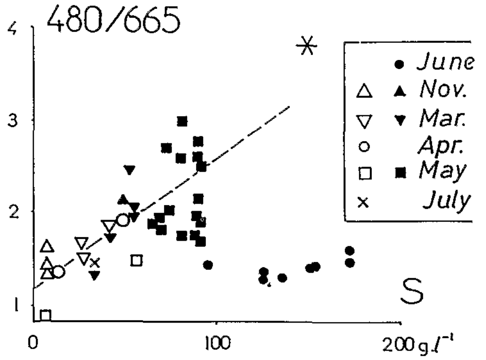

Figure 7. Increase of carotenoids under increasing salinity during several surveys, in the thalassic portion (filled symbols) and in the a-thalassic part (open symbols). The proportion of β -carotene against chlorophyll(s) is estimated by the 480/665 ratio. Asterisk is a non-axenic culture from water taken at st.#39 (salinity 150 g.l^{-1}) in June 1986.

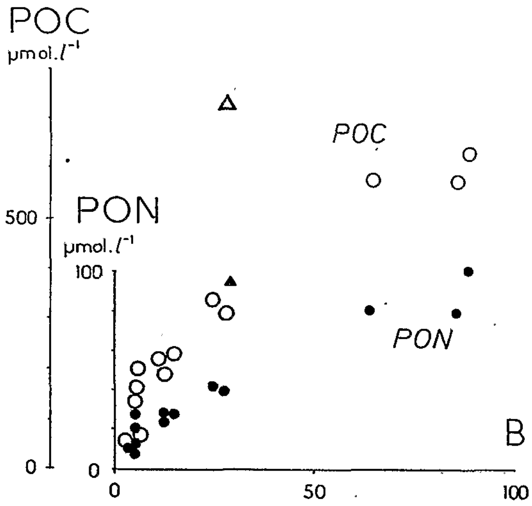

Figure 8. Comparison between chlorophyll (B), POC (white symbols), and particulate organic nitrogen (PON; filled symbols). Triangles indicate st.#39, in the a-thalassic portion.

protein N), we may make two provisional observations: *i)* our data points do show a relative decrease of PON at high B concentrations, and *ii)* the obvious outlier st.#39 has either "not enough" chlorophyll or "too much" nitrogen.

Plotting B/PON against POC/PON is statistically questionable. But this plot (not shown) indicates a landward increase of B/PON and a corresponding decrease in POC/PON. The seaward stations have a high POC/PON ratio (9 - 12 by atoms) while the upstream stations have lower POC/PON values (6 to 7 by atoms).

3.1.3: Effect of biomass upon environment

Most models of photosynthetic production are centered upon the negative feed-back of standing crop on the twin aspects of light attenuation and of respiration. Concerning the latter, some hypotheses are often implicit, the main one being that "biomass" is mainly phytoplanktonic: This is true in "eutrophic" systems. We shall try to show that other conditions may exist in the Casamance estuary, which has several features of oligotrophic systems.

We shall leave aside (at least here) the possible role of biomass as a nutrient pump, as explicited in Comtois's model (Morrison et al., 1987). We shall only adress a) the classical retroaction of phytoplankton upon light, b) the effect of respiration on O2 content, and c) the variations of DIC concentration.

3.1.3.1: Light attenuation

Since light is often the main limiting factor of aquatic production, we can try to estimate the attenuation due to phytoplankton itself, K_b, and its importance relative to total attenuation, K_d.

Several authors have determined the chlorophyll-specific attenuation coefficient, K_s. We shall ignore here any possible package effect and adopt for K_s the value of 0.015 $mg^{-1}.m^2$ found by Bannister (1974). We thus obtain an array of K_b values ranging between about 0.1 m^{-1} in the seaward portion and about 3.0 m^{-1} in the uppermost portion of the estuary (st.#36-41). We can use these figures in two ways. From a statistical point of view, first, total attenuation results from the sum of various attenuations. As expectable, K_b explains a small part of K_d variations ($K_d = 0.9 + 1.27 . K_b$; r = 0.73, n = 48). Including K_w (attenuation by DOM) improves the correlation ($K_d = 0.8 + 1.0 . K_b + 0.4 . K_w$; $r^2 = 0.50$, n = 36).

We can also try to estimate the fraction of light energy actually absorbed by phytoplankton, by utilizing the ratio K_b/K_d. This ratio ranges between 5% and 70%, without any recognizable seasonal trend. The spatial distribution of K_b/K_d (plot not shown) exhibits the expectable strong longitudinal gradient, with an obvious break (despite the low statistical significance) about 100 km from the sea (st.#19-20).

3.1.3.2: Oxygen uptake

We have monitored in situ O2 concentrations at several stations, during several surveys. We calculated nocturnal O2 consumption (∇O2 , in µmol $O2.l^{-1}.h^{-1}$) between sunset and dawn. We assumed that processes were linear in time; some intermediate measurements (not shown) showed this assumption to be acceptable. Comparing ∇O2 with biomasses (B, expressed in chl) gives a scattered plot (fig. 10) and a poor correlation: ∇O2 = 1.34 + 0.071 . B (r = 0.51*, n = 21). To express this in other units, we converted biomass (B) figures into POC ones on the

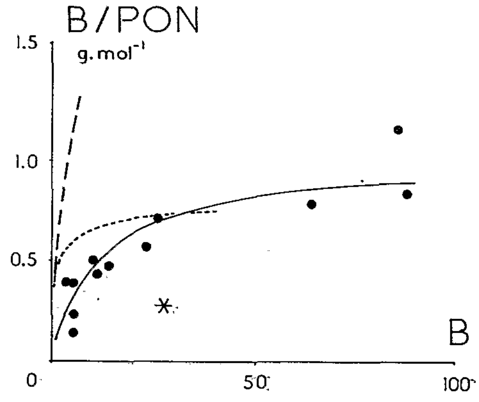

Figure 9. Increase of the ratio of chlorophyll to particulate organic nitrogen (B/PON) with increasing autotrophic biomass, B (in µg chl.l⁻¹), in May 1987. Asterisk indicates st.#39. For comparison, data from Dortch & Packard (1989) for the Peru upwelling (dotted curve) and for "normal" upwellings (dashed curve).

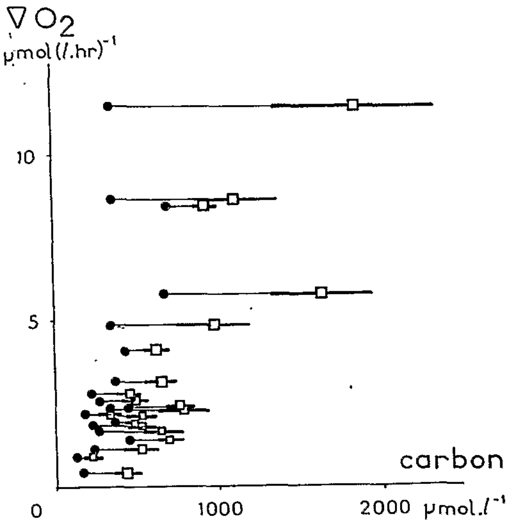

Figure 10. Oxygen uptake (nightly in situ consumption rate) compared with organic carbon concentrations. The black dots represent POC (calculated from chlorophyll). Corresponding amounts of DOC are indicated for each data set: squares were obtained with (POC + 1/2 DOC), while the thick horizontal lines stretch between (POC + 1/3 DOC) and (POC + 2/3 DOC).

basis of the overall linear correlation found for our May '87 data; the correlation is evidently equally indifferent when including all data. A more satisfactory correlation can only be arrived at by eliminating the upstream, high-biomass stations above (and including) st. #30; we then arrive at: $\nabla O2 = -0.15 + 0.0104 \cdot POC$ ($n = 19$, $r = 0.59^{**}$).

The high concentrations of DOC could have played a role, and should be taken into account. An approach by multiple regression would be more customary, but we preferred a more "mechanistic" approach, by "adding" variable fractions of DOC to the organic carbon pool (fig. 9). Adding an increasing proportions of DOC to POC gave better results than with only POC:

$(\nabla O2) = 0.0114 \cdot (POC + 1/10\ DOC) - 1.380$ ($r = 0.786$)
$(\nabla O2) = 0.0098 \cdot (POC + 2/10\ DOC) - 1.510$ ($r = 0.856$)
$(\nabla O2) = 0.0080 \cdot (POC + 3/10\ DOC) - 1.294$ ($r = 0.875$)
$(\nabla O2) = 0.0061 \cdot (POC + 1/2\ DOC) - 0.743$ ($r = 0.843$)
$(\nabla O2) = 0.0047 \cdot (POC + 2/3\ DOC) - 0.405$ ($r = 0.831$)

Since there is no a priori reason for DOC to be homogeneous across the whole estuary in what regards its labile or refractory character, we further tried to distinguish between downstream-median portion (st.#19-28) and upstream portion (above st.#30). This brought no real improvement, and correlation coeficients became non significant (but the small number of data may be one reason for this failure).

We shall discuss these results later on, but must proceed here to some further calculations on the slopes, after having again stressed that data distribution is so skewed that confidence intervals lose their meaning. Respiration rate with POC alone is of about 0.009 lmol O2.(lmol POC-C.h)$^{-1}$, while $\nabla O2$ is around 0.07 µmol O2.(µg chl.h)$^{-1}$. Including various fractions of DOC brings hourly respiration rates down to about 0.006 µmol O2.(µmol C)$^{-1}$, with "carbon" meaning now all available organic carbon.

3.1.3.3: *In situ variations of DIC*

In parallel with in situ O2 monitoring, we have some data on in situ DIC variations. These figures are less detailed, since we assessed DIC concentrations around dusk and at dawn on the following morning, without intermediate measurements. The nightly increase of DIC, ΔDDIC, agrees reasonably well with oxygen decrease: $\Delta DIC = 1.33 \cdot \nabla O2 + 4.95$ ($r = 0.904$). The paucity of data ($n = 6$) precludes any attempt of estimating a respiratory quotient.

3.2: PRODUCTION

We have done several incubation series at different irradiance levels. These incubations showed that photoinhibition seldom occurred. We shall then deal first with subsurface (maximum) measurements, which are more numerous, to explore possible correlations. We shall then deal with vertical photosynthesis distribution.

3.2.1: Subsurface production

3.2.1.1: Overall production: A_m

The general distribution of A_m is characterized by a marked landward increase. Seaward and median portions exhibit A_m values between 2 and 10 µmol C.(l.hr)$^{-1}$. A slight increase is observed between KP 140 and KP 200, and A_m reaches values of 15 to 20 µmol C.(l.hr)$^{-1}$. Peak A_m values of 105-110 µmol C.(l.hr)$^{-1}$ were observed at st.#38 in December 1984 and March 1985 only. This general trend can be described by the equation: $\log A_m = \log(1.78) + 0.0043 \cdot D$ ($r = 0.69$, $n = 101$) with distance to the sea, D, in km. These increasing A_m values parallel the evolution of B, with a proportionality coefficient of about 0.85 (B being expressed in µg chl.l^{-1}). We shall see below that specific production, P_m, differs widely from this value.

Several significant correlations were found between A_m and environmental descriptors. The annoying point is that we were unable to recognize any seasonal trend in A_m. We must then conclude that these correlations can represent a causal relation, but might also be due to a parallel distribution of various parameters along a strong longitudinal gradient. For instance, salinity is a good tracer of this longitudinal distribution of increasing confinement and increasing stability, and is correlated with A_m. In a more interesting way, we also found an effect of trophic characteristics. For instance, we obtained a negative correlation between A_m and seston composition (atomic C_p/N_p ratio), as measured during our May 1987 survey: $A_m = 47.8 - 5.0\ (C_p/N_p)$ ($r = -0.81$, $n = 12$).

We assessed dissolved organic carbon (DOC) production during a few incubations. Labelled DOC (DO^{14}C in acidified filtrates) amounted to between 6% and 8% of A_m in sub-surface samples. At lower light levels, DO^{14}C production reached 10 - 13 % of ^{14}C incorporation, but the absolute amount of DOC exuded became negligible. We can then consider that the high DOC concentrations measured in the upstream part of the estuary do not originate from phytoplankton excretion.

3.2.1.2: Maximum specific production: P_m

Chlorophyll-specific production values exhibit a very wide range, between 1 and 15 µg C.(µg chl.hr)$^{-1}$, around a median value of 4.5 µg C.(µg chl.hr)$^{-1}$.

The distribution of P_m along the estuary is rather featureless, with only a slight decrease in the median portion, about KP 180. We saw a gradual decrease in P_m values throughout the dry season 1984-85, but this decrease was not found again in the following dry seasons; no other seasonal effect emerges. No significant correlation could be found between P_m and any environmental parameter.

The overall proportionality between A_m and B (see above) would lead to a P_m value of about 10 µg C.(µg chl.hr)$^{-1}$. In fact, about the only satisfactory correlation found is a negative one between P_m and biomass B, at least in the thalassic portion: P_m = 1.50 - 0.72 . log B (r = -0.83, n = 47). This correlation confirms the absence of any seasonal trend.

3.2.1.3: Efficiency: α*

We have tried to obtain an approximation of the light utilization efficiency from our surface incubations, by the ratio of production (P_m) to available light ($E_d(0)$). The ratio thus computed represents a minimum value of the customary parameter α, "slope at origin" of the P-E curve (see below).

The values of α* range between 0.001 and 0.015 lg C.(lg chl.(lE.(m^{-2}.s^{-1}))$^{-1}$. Still more than with the other production descriptors, α* does not show any significant seasonal trend. Its decrease under high salinity or high biomass is not significant, either. By contrast, we did observe significant correlations between α* and three differing "metabolic" descriptors:

* with the P/N ratio of the dissolved fraction (total dissolved P and N) : a* = - 1.2 + 0.12 (TDP/TDN);

* with the C_p/N_p ratio in seston (May 1987 survey): the carbon-specific efficiency, a* , (and not, this time, the chlorophyll-specific one) shows a negative correlation: a* = 40.4 - 4.2 . (C_p/N_p) (r = - 0.80, n = 13);

* with various descriptors of bacterial mineralization. During the May 1987 survey, we measured glucose (U-^{14}C-glucose) uptake and DOC concentration, and we estimated assimilation and catabolism rates for glucose, total DOC and the labile fraction of DOC ("LOC"; see Methods). We obtain a series of positive correlations between α* and these rates:

assimilation	glucose	r = 0.65*
	DOC	r = 0.71**
	LOC	r = 0.71**
catabolism	DOC	r = 0.85***
	LOC	r = 0.77**

3.2.2: Vertical distribution of photosynthesis

We shall first deal with the results of our incubations, then convert these into vertical production profiles. Practically all our incubations were done under "simulated in situ" conditions in natural light (except the March 1986 survey, done with true in situ). Calculation of scalar irradiance was somewhat complicated by the strong reflectance of Plexiglass. This fact explains the frequently high irradiances found in our experiments; the "low irradiance" samples were often still in the range of 50-200 µE.m^{-2}.s^{-1}.

3.2.2.1: Incubations and P-E curves

In most incubations, specific production $P_{(z)}$ at a given level (of depth, or of irradiance) reacted to light intensity $E_{o(z)}$ in the customary way, with saturation at high irradiances (fig. 11). Photoinhibition was rare. The shapes of the P-E curves differ between surveys and between stations, without any obvious trend.

We shall describe these curves by E_k (irradiance at onset of saturation), P_m and α (initial slope). In view of the uncertainties on our $E_{o(z)}$ data, we did not seek an illusory "precision" using a computerized model fitting (see Frenette et al., 1993). Instead, we followed Mee's (1987) reasoning, calculating

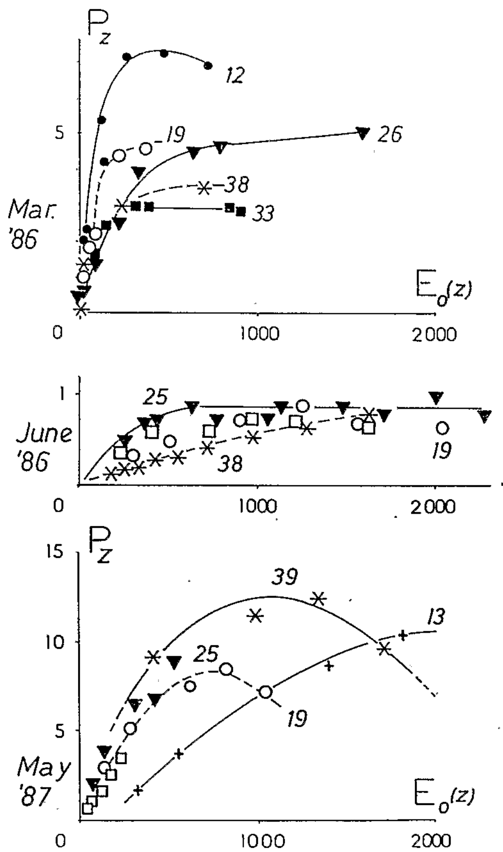

Figure 11. Variation of chlorophyll-specific production, P_z (in µg C.(µg chl.hr)$^{-1}$) with available light, $E_{o(z)}$ (in µE.m^{-2}.s^{-1}). Some typical surveys are shown, without any significant seasonal trend

E_k from the half-saturation irradiance E_x (at which $P_x = P_m/2$); E_x is 0.58 E_k. The slope α is P_m/E_k.

Our values of E_k range between 400 and 1000 $\mu E.m^{-2}.s^{-1}$. without any seasonal or spatial trend. These figures appear somewhat high, as we shall see later on. The initial slopes α of our curves range between 0.001 and 0.020 µg C.(µg chl.hr)$^{-1}$($\mu E.m^{-2}.s^{-1})^{-1}$. *Simplifying the various units used* yields the parameter Ψ, analogous to α but in g C.(g chl.E.m^{-2})$^{-1}$ (with the easily demonstrated conversion $\alpha = 277.778 . \Psi$). We then have Ψ values ranging between 0.4 and 6 g C.(g chl.E.m^{-2})$^{-1}$. We shall see that these values are somewhat high compared with other published results.

While searching for possible correlations, we remarked parallel variations of α and P_m. In fact, these parameters exhibit a positive correlation with each other (fig. 1). The entire set of experimental data yields the equation: $\alpha = 0.0047 + 0.0063 . P_m$ ($r = 0.87$, $n = 76$; line A in fig. 12). The uppermost (landward) and lowermost (seaward) stations often exhibit either very high P_m or very low α; discarding these extreme stations does not much modify the regression.

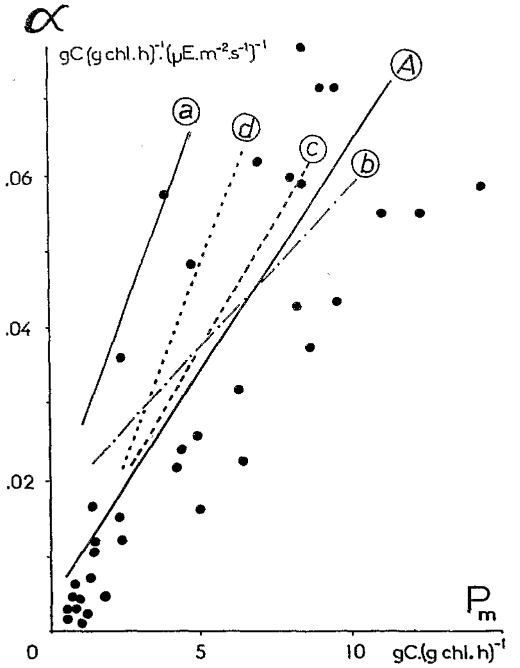

Figure 12. Correlation between maximum specific production, P_m (in µg C.(µg chl.hr)$^{-1}$) and initial slope, α (in µg C.(µg chl.hr)$^{-1}$($\mu E.m^{-2}.s^{-1})^{-1}$) in the Casamance (black dots and line A). Some other published data are shown: (a) from Prézelin, 1992; (b) from Jellison & Melack, 1993; (c) from Blanchard & Montagna, 1992; (d) from Hood, 1993.

3.2.2.2: Vertical profiles and integration

To transform our P-E curves into vertical ("in situ" underwater) profiles, we need to determine the "equivalent depth", Z_{eq}, such that $E_{o(Zeq)}/E_{d(0)} = 1.5$ (exp (- K_d . Z_{eq}). (1 + R), where R is the underwater reflectance coefficient, K_d the vertical attenuation coefficient, and $E_{d(0)}$ the downwelling irradiance just under the surface. The coefficient 1.5 accounts for the diference between downwelling and scalar irradiance (Kirk, 1983). All these corrections and calculations bring unavoidable uncertainties in the "equivalent depth" data. The vertical integration of our production profiles is further complicated by the fact that the actual depth (in fact, averaged depth Z_{av}) is occasionally shallower than the euphotic depth (Z_{eu}), especially in the upstream portion. We thus had to integrate production (by the customary parallelogram method) down to either Z_{eu} or to Z_{av}, whichever was the shallower to obtain an areal production, $\Sigma_z A$

The values of $\Sigma_z A$ range between 2 and 36 mmol C.m^{-2}.hr^{-1}. Again, no particular trend emerges, except an expectable (if slight) increase in the upstream portion. "Deep" stations, with high values of either Z_{eu} or Z_{av}, naturally give high $\Sigma_z A$ figures. These data are not particularly useful in themselves, but we can compare them with the results of two separate models, an analytical one and an empirical one.

Analytical modelling of $\Sigma_z A$

Following Megard (1973) and Lemoalle (1979), we shall define the quotient $Z_i = \Sigma_z A / A_m$. This quotient, which has the dimension of a depth, ranges between 1 and 2 m in the downstream and median portions of the estuary, then decreases down to 0.2 m in the upstream part. According to theoretical and empirical observations (Talling, 1957 a; Talling et al., 1973; Mee, 1987), Z_i should decrease when B, and/or K_d, increase; the product ($Z_i . K_d$) has a value of about 2.6 - 2.7.

We do obtain such a negative correlation between Z_i and B : $Z_i = 2.74 - 0.98 . \log B$ ($r = -0.60$, $n = 81$). Data points are widely scattered (fig. 12), but the main inconvenient is that our Z_i (and hence our $\Sigma_z A$) are lower than those predicted by Megard's (1972) relation for a given value of B. The very shallowness of the upper estuary is the only cause for the heavy discrepancy between theory (and empirical models obtained on deep lakes) and our observations.

Empirical models of $\Sigma_z A$

Several authors have tried an empirical modelling which is not explicitly based on the underlying P vs E mechanisms, but concentrates on bulk characteristics of the water (see paragr. 4.2.2) . All of these models have the common form: $\Sigma_z A = C . B . E_o / K_d$, C being a proportionality coefficient, and neglecting a possible constant term stemming from experimental regression equation. For ease of handling, we computed the expression $\xi = (B.E_o)/(K_d.10^3)$.

Plotting ξ against $\Sigma_z A$ yields widely scattered points (Fig. 14). In fact, two groups of stations may be distinguished:

- a first group shows high $\Sigma_z A$ values and relatively low ξ values; this group comprises all data obtained in August, September and October 1984, and in May 1987. These data are described by the regression: $\Sigma_z A = 1.20 . \xi + 3.36$ ($n = 23$, $r = 0.71$)
- a second group shows lower $\Sigma_z A$, and yields the

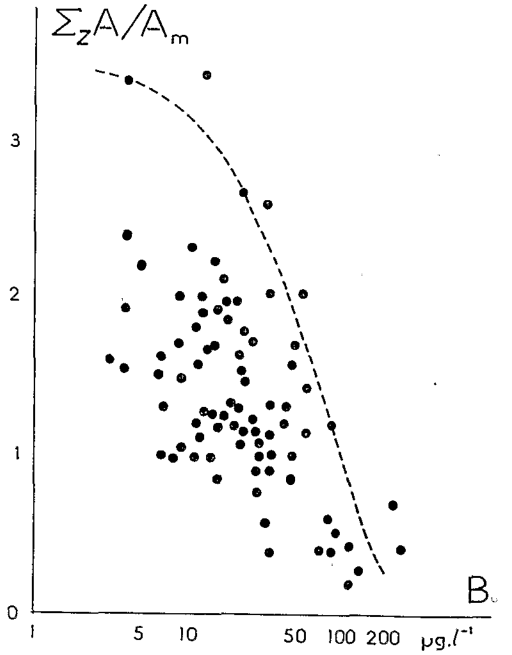

Figure 13. Decrease of integrated production ($\Sigma_z A$, in mmol C.m^{-2}.hr^{-1}), compared with maximum production (A_m, in µmol C.l^{-1}.hr^{-1}), with increasing biomass (B) in the Casamance. The dashed curve shows Megard's (1972) empirical relation.

regression: $\Sigma_z A = 0.40 . \xi + 2.25$ (n = 38, r = 0.83). We may notice here that Keller (1988 a) obtained in fully different environments a regression which would be, in our units: $\Sigma_z A = 0.30 . \xi + 2.27$.

3.3: OVERALL PRODUCTION

3.3.1: Daily gross production

Although our $\Sigma_z A$ values are thus severely cut off by shalowness, we shall try to further use them to estimate gross production in the whole estuary, by integrating the available hourly productions to the whole day. The proposition is complicated by the fact that our incubations were most often started whenever we arrived at a given station, i.e. at any time of the day between about 08:00 and 15:00. However, during this time, irradiances were mostly such that our surface samples stayed in the light-saturated part of the P-E curve. We could thus use the empirical relationships found by several authors , with the approached relation: $\Sigma_z \Sigma_t A = 10 . \Sigma_z A_h$, $\Sigma_z A_h$ being measured around noon (Ganf, 1975; Lemoalle, 1979; Mee, 1987; Keller, 1988 b).

We thus obtain daily productions ranging between 20 and 170 mmol C.m^{-2}.d^{-1}, with the highest values predictably coincident with highest biomasses.

3.3.2: Respiratory losses

Respiration can be looked at either as oxygen consumption, or as CO2 production, or as organic carbon oxidation. We have some data concerning these three processes, but these data are not precise, or numerous, enough to allow us to go much farther beyond an overall, much too general agreement about the magnitude of the abovre three processes. In particular, we shall not be able to estimate a respiratory quotient.

We have already seen that the in situ nightly oxygen consumption, $\nabla O2$, amounts to about 0.07 mol O_2.(g chl.hr)$^{-1}$ (or 2.2 gO_2.(g chl.hr)$^{-1}$) if phytoplankton is the sole consumer. Taking into account the existing DOC yields a consumption of 0.006 mol O_2.(mol AOC.hr)$^{-1}$, with AOC = POC + 1/2 DOC.

We have monitored in situ DIC concentrations on some occasions, and we can compute the nightly rate of increase of DIC,ΔDIC. As a first approximation, it shows a reasonable agreement with oxygen decrease: ΔDIC = 1.3 . $\nabla O2$ + 11.5 (n = 7, r = 0.896). Despite this, a comparison between ΔDIC and B yields no utilizable pattern (plot not shown). Plotting ΔDIC against "active organic carbon" yields a somewhat reduced spread of data points (plot not shown), but the correlation is poor : ΔDIC = 0.009 . AOC + 1.38 (n = 7, r = 0.50*). While the correlation is not statistically significant, we may at least note that the rate of DIC production is of the same magnitude as that of oxygen consumption.

A third estimate of phytoplanktonic respiration is its dark

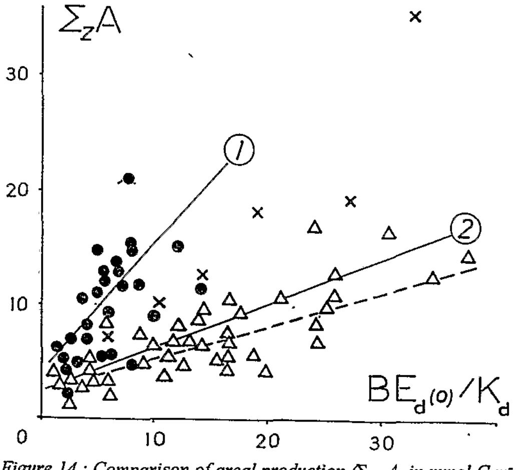

Figure 14.: Comparison of areal production ($\Sigma_z A$, in mmol C.m^{-2}.hr^{-1}) with the function $\xi = (B.E_o)/(K_d.10^3)$. Line (1) :surveys in August-October 1984 and May 1987 (o). Line (2) corresponds to the other surveys (Δ ; "second group" in the text), and is comparable to Keller's (1988 a) results (dashed line). The uppermost stations (st.#38-39) are designated by X.

carbon loss. This can be estimated from long ^{14}C incubations started during the day; an aliquot was filtered at sunset, another one at the following dawn. With some hypotheses, the nightly loss of carbon, ∇^*C, can be computed. From the few available data, we obtain: $\nabla^*C = 0.058 . B - 0.07$ ($n = 8$, $r = 0.984^{***}$). In theory at least (and putting aside the various assumptions made), this ∇^*C represents the respiratory losses of the sole autotrophic component of the planktonic community.

We may sum up the above results as follows:

	mol.(g chl.hr)$^{-1}$	mol.(mol AOC.hr)$^{-1}$
$\nabla O2$	0.07	0.006
ΔDIC	-----	0.009
∇^*C	0.06	-----

Since the above measurements were only done at some stations, we have extrapolated them to obtain an estimation of respiratory oxygen consumption, R, at every station where daily production ($\Sigma_z\Sigma_tA$) had been measured. We used the following two equations defining hourly respiration, R , and daily respiration, $\Sigma_z\Sigma_tR$:

a) $R = 5.1 * COA - 0.8$

with: $COA = POC + 0.5*DOC$ and : $POC = 5.9*B + 135$

b) $\Sigma_z\Sigma_tR = R * 24 * Z_{av}$

expressing R in µmol $O2.l^{-1}.hr^{-1}$; COA in mmol $C.l^{-1}$; POC and DOC in µmolC $.l^{-1}$, B in µg $chl.l^{-1}$; $\Sigma_z\Sigma_tR$ in mmol $O2.m^{-2}.d^{-1}$.

3.3.3: Net production and integration

The absolute values of $\Sigma_z\Sigma_tA$ and $\Sigma_z\Sigma_tR$ (abbreviated in $\Sigma\ A$ and $\Sigma\ R$ in what follows) present no clear trend when considering all data (plot not shown). A series of surveys (June, September and November, 1986) yields outliers with abnormally low $\Sigma\ A$. Another group of data points, with low $\Sigma\ A$ and high $\Sigma\ R$, corresponds to seaward stations (#11-13) but also includes the relatively deep st. #25. On the opposite side of the plot, the February '85 survey yielded systematically high $\Sigma\ A$ and low $\Sigma\ R$

Between these extremes, the bulk of data points represents stations in the median and upstream portions of the estuary, yielding the regression : $\Sigma\ A = 0.80 * \Sigma\ R + 7.8$ (n=59, r=0.76^{***}). The uppermost, shallower stations, could introduce a skewed distribution; excluding the st.#37-#39 portion gives the regression: $\Sigma\ A = 0.70 * \Sigma\ R + 14.0$ (n=49, r=0.67^{***}).

From these regressions, it appears that $\Sigma\ A$ (in mol $C.m^{-2}.d^{-1}$) is definitely smaller than $\Sigma\ R$ (in mol $O2.m^{-2}.d^{-1}$). That respiration is higher than gross production would mean that the Casamance estuary is heterotrophic. While plausible, this indication must be nuanced after closer inspection of the distribution of the ratio $\Sigma\ R / \Sigma\ A$, which is highest (between 2 and 3) in the seaward portion, and decreases to 1.0 or less in the uppermost stations. A plot of $\Sigma\ R / \Sigma\ A$ against salinity (figure not shown) shows that a break in $\Sigma\ R / \Sigma\ A$ generally occurs around the salinity peak, in the stretch st.#27-#31.

Several authors have found that net production is controlled by optical depth. We have hence compared $\Sigma\ R / \Sigma\ A$ with the quotient Z_{av}/Z_{eu}. Despite the wide scatter of data points (plot not shown), we obtained a significant correlation ($r = 0.64$ *** for $n = 45$). Deleting four outliers from to the seaward stations (st.#11-13, with high Z_{av}/Z_{eu}) lowers the correlation coefficient ($r = 0.54^{***}$); the regression becomes: $\Sigma\ R / \Sigma\ A = 1.32 * Z_{av}/Z_{eu} + 0.45$.

4: DISCUSSION

During this study of the Casamance estuary, our resources in material and manpower were severely stretched. This fact and the general material conditions obliged us to take several short cuts, and our study was not as "in depth" as we would have wished. In the following discussion, we shall try to compare our results with studies done in several different aquatic environments, including high sea. It may be felt that the bulk of references should stem from freshwater bodies. We do use studies done on lakes and brackish estuaries, but the Casamance is not a normal estuary. Its characteristics and functioning are much nearer to those of a brackish lagoon or a coastal marine environment. Conversely, despite its high salinity, the Casamance cannot be compared with a-thalassic salt lakes (which are mostly alkaline), while the various salterns throughout the world are again another environment. We shall make frequent comparisons with another hypersaline estuary, the Saloum, situated North of The Gambia (fig. 1), which closely ressembles the Casamance, and for which we have been gathering more detailed data on dissolved nutrients, and size and taxonomy in the seston (Pagès et al., in prep). We shall also refer to the brackish Ebrié lagoon (Ivory Coast), which we studied several years ago.

As a point of detail, our use of the term "upstream" may be misleading; we again stress that NO net freshwater flux existed in the Casamance estuary. "Upstream" merely designates the distal part, away from the sea.

4.1: PHYTOPLANKTON BIOMASS: DISTRIBUTION AND CONTROLS

The bulk of our biomass data consists of "total chlorophyll" figures. This calls for two rapid comments. First, assesment of phaeopigments, while theoretically possible by fluorometry, has been shown rather inaccurate (Hurley & Watras, 1991), especially under the instrumental conditions we were using (Baudouin & Scoppa, 1971). Inspection of our data confirmed the small value of computing "phaeophytins" (after acidification of the extract) and the calculations were discontinued. Our second comment concerns the use of chlorophyll as an estimator of biomass. Since our main aim was to assess the role of primary production, the choice of chlorophyll was logical. Alternately, from a "trophic web" perspective, other estimators of seston biomass could have been chosen (Lemasson et al., 1981; Mazumder et al., 1988), but practical methodological considerations led us to limit ourselves to 'chlorophyll' (B) as the main estimator.

4.1.1: General biomass distribution

In the Casamance, biomass concentrations increase "upstream" (fig. 5) to an average value of about 100 µg.l^{-1}, with the highest biomasses practically always at the uppermost station reachable by boat (st.#39 or 40). We have stressed that no seasonal variation was apparent. We observed an analogous distribution in the hypersaline Saloum estuary (Pagès et al., in prep.) and in the brackish Ebrié lagoon (Lemasson et al., 1980). The review by Javor (1989) gives few figures comparable to ours (owing to the descriptors used), but indicates a frequent increase of biomass in the distal portions of thalassic hypersaline water bodies. We must stress that, in the Casamance, these high upstream biomasses do not result from passive concentration of populations originating from the sea, as observed by Javor (1983) or by Alpine & Cloern (1992). In the Casamance estuary, transit times would be at least several months while these populations are in good physiological state. This permanent feature of high distal biomasses shows that floods did not appreciably flush out the plankton, as it happens in other, "normal" estuaries (Boyer et al., 1993). Here, the highest discharge during our study was about 1 $m^{-3}.s^{-1}$; with a wetted section estimated at about 50 m^2 (excluding the extensive reed marshes), such a discharge would translate into a net flow of less than 0.02 $m.s^{-1}$ during some few days at most.

The landward increase of B, in the Casamance as in other water bodies, has three possible reasons: nutrients, physical environment or confinement. As for the first possibility, in lakes of varying trophic status, numerous studies have confirmed the pioneer results of Sakamoto (1966, 1971) and Vollenweider (1976), both studying the effect of phosphorus load on eutrophication. This abundant literature has shown a causal relationship between biomass and nutrients (see review by Morrison et al., 1987), be it P (Lewis, 1990; Golterman, 1991) or N (Gowen et al., 1992). We shall have to come back to this point (paragr. 4.1.2), but we may remark here that, although nutrients (organic ones or not) do increase in the Casamance, they do not do so obligatorily in other hypersaline waters (Javor, 1989).

In what regards physical environment, the main longitudinal gradients in the Casamance concern bathymetry and tidal energy. The latter has been shown to represent (directly or not) a supplementary source of energy for phytoplankton (Nixon, 1988; Margalef, 1990). Increased mixing was found to favor diatoms in certains circumstances (Estrada et al., 1988). Ketchum (1954) had earlier shown the effect of estuarine circulation, while Barlow (1984) found that turbulence promotes a higher growth rate. Contrary to these findings, Monbet (1992) found systematically higher planktonic biomasses with lower tidal amplitude, while Cloern (1991a) observed high biomasses under low vertical mixing. This would fit in the Casamance estuary, with its strongly dampened tides. Another physical feature is depth, and particularly optical depth, which may play a role. Production (C and N uptake) and/or biomass have been found to increase at decreasing depth (Fee, 1979; Perry & Dilke, 1986; Owens et al., 1986). Also in relation with depth, several studies found a relationship between biomass (or fish production) and the morpho-edaphic index (MEI, ratio of conductivity to mean depth) in lakes ((Ryder, 1965, in Schneider & Haedrich, 1989; Lemoalle, 1979; Straskraba, 1980). As far as we know, the MEI concept has not been used in estuaries; however, in the Casamance, the hydraulics are such that successive portions can be equated to separate basins, as shown by stable isotopes distribution (Jusserand et al., 1989). We did obtain a very good description of B distribution in the thalassic portion from the MEI values (plot not shown). However, recent studies have shown that the MEI concept, while broadly effective in comparable lakes, actually coincides with nutrient distribution (Deegan & Thompson, 1985; Pridmore et al., 1985; Perry & Dilke, 1986; Chow-Fraser, 1991; Rempel & Colby, 1991). We are thus back to nutrient limitations.

Several authors have found a positive correlation between biomass and/or production and the quotient Z_{eu}/Z_{mix} (Grobbelaar, 1985; Harris & Trimbee, 1986; Powell et al., 1989; Cloern, 1987, 1991 b; Gons & Rijkeboer, 1990; Cole et al., 1992; Grobbelaar, 1992; Lind et al., 1992). This effect of vertical optical/physical structure has also been described in lakes (Hawkins & Griffiths, 1993), but especially in the open sea (Garside & Garside, 1993) following the early studies by Ryther Ryther, 1956; Ryther & Yentsch, 1957). In the Casamance, since we seldom found any vertical stratification, we may admit that the whole water column belongs to the homogeneous layer ($Z_{mix} = Z_{av}$). We saw that the product $K_d.Z_{av}$ decreases down to about 0.25-0.5 in the median and upper portion of the estuary. This translates into a quotient Z_{eu}/Z_{mix} of between 9 and 18 for the upper half of the estuary, against a Z_{eu}/Z_{mix} of about 2 in the seaward portion. This is very far from the critical Z_{eu}/Z_{mix} value of 0.16 given by Alpine & Cloern (1988), or 0.2 (Cloern, 1987) ; there is then a distinct possibility that the increase of B in the upper Casamance may be due at least in part to optical shallowness . This would though implicitly mean that available irradiance is the main limiting factor of photosynthetic biomass.

Along this path of reasoning, we can recall the homeostatic functioning of phytoplankton in which biomass exerts a negative feed-back on its own density through light attenuation. In the Casamance, we have seen that K_b (attenuation due to chlorophyll) is seldom more than 50% of K_d. To compute K_b , we took for K_s (specific attenuation coefficient) a value of 0.015 $m^2.mg^{-1}$, thereby following Bannister (1974). Other determinations of K_s have yielded values between 0.007 and 0.04 $m^2.mg^{-1}$ (Ganf, 1974c; Gieskes et al., 1979; Laws & Bannister, 1980; Oliver & Ganf, 1988; Chalup & Laws, 1990). Platt et al. (1989) found a specific absorption coefficient of 0.04 $m^2.mg^{-1}$, which implies a higher attenuation coefficient (see also Oliver & Ganf, 1988; Marra et al., 1993). However, the average K_s value we chose is not too under-estimated, since we arrive at a peak K_b/K_d ratio of 80% . This homeostatic loop leads to a determination of the theoretical maximum possible content of chlorophyll in the euphotic zone. Following various pathways of reasoning, and several empirical relations, maximum integrated biomass may reach between 300 and 450 mg $chl.m^{-2}$ (Talling, 1965; Ganf, 1974c; Jewson, 1976; Oswald, 1988; Robarts & Zohary, 1992).

Lastly, the distal increase of B observed in the Cassamance might also be an automatic consequence of "confinement". We designate a water body as "confined" when its exchanges with the sea are reduced, or restricted, by any cause. The salinity of a 'confined' water body can increase or decrease, relative to that of the sea, depending on the local water budget. In the present case of the Casamance estuary, increased salinity illustrates the increased residence time under a negative water budget, and the decrease of exchanges with the sea. One well-described consequence of confinement (and not merely of salinity) is the decrease in taxonomical variety, such as described by Por (1979) in hypersaline coastal lagoons (see also Herbst & Bromley, 1984). We are dealing, in the Casamance like in other 'confined' systems, with environments which have a high stability (on the time-scale of phytoplankton, at least). High abundances of organisms balance the low species number Bailey-Watts, 1986). We are aware of the qualitative nature of these considerations. The very notion of *confinement* has remained (to our knowledge) semi-quantitative at best. Many studies were focused on biological data, with a heavy stress on taxonomy (Phleger & Ewing, 1962; Hedgpeth, 1967; Evans et al., 1973), while benthos was often privileged (Guelorget & Perthuisot, 1983). Against such abundant biological data, the complementary aspect of hydrodynamics is often neglected, so that no hard data on residence time may be compared with taxonomic impoverishment.

4.1.2: Nature and composition of biomass

We have no routine taxonomical data for the Casamance estuary. We could several times observe phosphorescent waters in the lower seaward portion, around st.#5; such occurrence is rather common (Smayda, 1980), but no positive identification is available in our case. More interestingly, we could identify a proliferation of *Dunaliella salina* in June 1986 from the pronounced reddish discoloration of the waters. The high proportion of carotenoids is typical of this alga (Ben Amotz & Avron, 1983, 1989, 1990; Borowitzka & Borowitzka, 1988). The increased ratio of absorption at 480 and 665 nm under increasing salinity (fig. 7) illustrates the role of carotenoids as a protection against various hostile conditions (Bianchi & Findlay, 1990; Sosik & Mitchell, 1991), among which high irradiance (Berner et al., 1989; Borowitzka & Borowitzka, 1988). Most studies on this point have centered upon nutrient stress; nitrogen depletion, and/or a high C/N ratio, have been related to a high carotenoid/chlorophyll ratio in phytoplankton in general (Watson & Osborne, 1979; Moed et al., 1988; Lewitus & Caron, 1990; Heath et al., 1990). In a related way, the ratio of β-carotene to chlorophyll has been found negatively correlated with growth rate in nitrogen-limited *D. tertiolecta* (Sosik & Mitchell, 1991). In our case, we shall see below that the POC/PON ratio does not correspond to a severe nitrogen deficiency; the increase in 480/665 values in the upstream waters has hence no clear origin. As a last remark, the presence of *D. salina* in hyperhaline waters is well known (see review in Javor, 1983), so that its presence in the Casamance estuary is relatively normal; on the opposite, its absence in the comparably hyperhaline Saloum estuary is surprising.

The chemical composition of seston in the Casamance appears rather indifferent at first view, since particulate organic carbon (POC) and nitrogen (PON) are reasonably correlated with B throughout the estuary (fig. 8). The distribution of the two ratios POC/B and POC/PON, which both increase seaward, may indicate either a high proportion of detritus or a nitrogen depletion in the lower part of the estuary. That estuaries and/or coastal marine waters are N-limited has long been a standard view, despite some exceptions (Krom et al., 1991). However, recent developments have shown that "the paradigm of N limitation in the oceans requires qualification" (Hecky et al., 1993). In the Casamance, the very high values of POC/PON (11.8 mol:mol) and of POC/B (>300 by weight) observed in the seaward portion are more typical of detrital particulate matter; comparable values have been found elsewhere in terrestrial macrophyte litter (Wetzel & Manny, 1972; Aziz & Nedwell, 1986; Jordan et al., 1989; Moran & Hodson, 1989; Cifuentes, 1991; Duarte, 1992). In the upstream portion of the Casamance, POC/PON reaches nearly normal values, around 7 mol:mol. These relatively low figures are somewhat unexpected, since the dominant *D. salina* should contain a hefty proportion of glycerol at the salinities of up to 90 $g.l^{-1}$ found there (BenAmotz & Avron, 1983; Gilmour et al., 1984, 1985; Moulton et al., 1987; BenAmotz & Avron, 1989, 1990). The moderate POC/PON ratios hint at a sufficient N supply in the upstream part of the Casamance. The ratio POC/B calls for a further comment: Malone (1982) found a negative correlation between POC/B and B (POC/B = 150 $(B)^{-0.41}$) and recalls the well-known fact that high POC/B can also stem from high irradiances, while Chalup & Laws (1990) showed that POC/B decreases at high growth rates.

The ratio B/PON we observed (fig. 9) appears somewhat low, especially at low B concentrations, since most B/PON found in the literature are around 1 $g.mol^{-1}$ (Laws & Bannister, 1980; Blasco et al., 1982; Prezelin, 1982; Herbland et al., 1985; Hager et al., 1984; Ward & Twilley, 1986; Guildford et al., 1987; Glibert et al., 1988; Rivkin, 1989; Thompson et al., 1989; Marra & Ho, 1993). In the Casamance, since POC/PON are about normal in the high-B waters, we must admit that chlorophyll is less concentrated than it "should", relative to PON. Dortch & Packard (1989) found an analogous situation (in differing environments) and interprete it as an "inverse trophic pyramid" with "too much" heterotrophs relative to autotrophs (by the way, the exact value of the parameters in their B/PON vs B equation is moot, especially since the regression equation is calculated from 1/x vs 1/Y; see Dowd & Riggs, 1965). In the Casamance, we probably have a high proportion of micro- or nano-heterotrophs, since meso-zooplankton abundances sharply decrease above st.#18 (Diouf & Diallo, 1987). An increased proportion of (small) heterotrophs is most often a characteristic of oligotrophic waters (Fuhrman et al., 1989; Dortch & Packard, 1989; Simon et al., 1992). Thus, despite its high B concentrations and its sizeable nutrient stocks, the Casamance estuary (and especially its upstream portion) would exhibit some features of an oligotrophic water body. The Saloum estuary, which we have already mentioned, is also in such a situation, with still lower B/PON ratios along with B values of up to 20 $\mu g\ chl.l^{-1}$ (Pagès et al., in prep). This Saloum estuary further shows a strong increase of small-size organisms (<2.7 µm) with increasing salinity, and increasing distance to the sea. Small-size dominance is another acknowledged feature of oligotrophic waters (Yentsch & Phinney, 1989; Iriarte, 1993; Jochem et al., 1993; Owens et al., 1993).

These subjects of chemical composition and oligotrophy lead us to deal with possible nutrient limitations on biomass in the Casamance estuary. A first point is the low proportion of nutrients present in an inorganic form, compared with dissolved organic matter (DOM). We shall try to illustrate this with DON compared with dissolved inorganic nitrogen (DIN). In the Casamance itself, we did not measure DON concentrations, but we can try to estimate them roughly from DOC, which was present in concentrations ranging between 500 and 1500 $\mu mol\ C.l^{-1}$. If we admit that the C/N ratio in such DOM is around 30 (mol:mol), we would have between 17 and 50 μmol DON-N.l^{-1}, against between 5 and 20 μmol DIN-N.l^{-1}. In this latter DIN, nitrate (in fact NO3+NO2) was predominant only in the seaward part, while NH4 represented most of DIN in the median and upstreal portions. In the Saloum estuary, DIN amounts to about 30 % of total dissolved nitrogen (TDN), and the oxidized forms (mainly NO3) constitute less than 50% of DIN. We can thus verify that NO3 alone is a poor estimator of the "richess" (=trophic state) of a water body as soon as imports of DOM are possible. We shall again find this importance of NO3/DON ratio when dealing with "regenerated production" and the *f* ratio.

Apart from these questions of chemical form (inorganic/oxidized versus organic/reduced), the total amount of nutrients could be biomass-limiting. We have already recalled the classical opposition between marine and fresh waters, with the (once well-accepted) view that lakes are P-limited while estuaries are N-limited (McCarthy & Goldman, 1979; Hecky & Kilham, 1988; Caraco et al., 1989, 1990; Fisher et al., 1992; Levine & Schindler, 1992; Magnien et al., 1992 and references therein). Some early studies had cautioned against possible over-simplifying (Lange, 1973). Recent studies have shown how specific processes differenciate fresh and salt water systems, for P (Caraco et al., 1990) or for N (Gardner et al., 1991) but we have recalled the warning of Hecky et al. (1993) about N limitation in salt water . Parallel to this latter precautionary note, recent papers have stressed that the absolute concentration of nutrient(s) plays a much lesser role than the N/P ratio (Hecky & Kilham, 1988; Davies & Sleep, 1989; Elser et al., 1990; Prairie et al., 1989; Marra et al., 1990; Krom et al., 1991; Smith et al., 1991), or other nutrient ratios (Fisher et al., 1992; Sieracki et al., 1993). In the Casamance estuary, the inorganic forms of N and P (which are the only available figures) showed no definite N/P trend. In the Saloum estuary, we observed a definite increase of DON/DOP and TDN/TDP ratios in the upstream direction. In an interesting way, such an evolution of the N/P ratio defines, again better than absolute concentrations, the limit between eutrophy and oligotrophy, with a high N/P in oligotrophic systems (Downing & McCauley, 1992).

4.2: PRODUCTION

We shall see later on that this term may have different true meanings. Here, though, we shall give it, from the very methodology (^{14}C method) we used, the meaning of gross short-term photosynthesis. Numerous studies on reasonably rich waters were carried out with the oxygen method and incubation bottles. Other studies assessed the bulk changes occurring in the water column, monitoring either oxygen concentration (Bender et al., 1987; Roos & Pieterse, 92) or DIC or alkalinity. We mostly used ^{14}C measurements during our study on the Casamance estuary; the immediate reason was a purely practical one, namely that a synchronous study of continental shelf productivity was under way. We are aware of the numerous pitfalls of the ^{14}C method in particular (Gieskes et al., 1979; Peterson, 1980; Dring & Jewson, 1982). Besides, tracer uptake kinetics are still a general problem despite numerous studies (Bernhardt et al., 1975; Goldman et al., 1981; Marra et al., 1981; Smith & Horner, 1981; Dring & Jewson, 1982; Geider, 1988; Marra et al., 1988).

4.2.1: Reaction to light: P-E curves

Our incubations yielded few instances of photo-inhibition despite the occasionally very high irradiances. We may note that photoinhibition, while rather often reported, has stirred a mild controversy about its actual existence under "normal" (i.e. natural) conditions. Some authors consider photoinhibition as a physiological reaction which must be incorporated in the P-E models (Megard et al., 1979; Platt et al., 1980; Belay, 1981; Gallegos & Platt, 1981). On the opposite, there is some evidence that experimental (and hence artificial) conditions may be the main cause of photoinhibition (Behrendt, 1989; Mallin & Paerl, 1992; Nixdorf et al., 1992).

A special P-E equation was proposed by Blackman (1905; in Harding et al., 1982, and in Bendall & Gray, 1988), with a discontinuous function. Various mathematical forms have been proposed to describe the variation of photosynthesis (P) under increasing irradiance (E). The main parameters of these P-E curves are their slope at origin, a , and the maximum production, P_m. The half-saturation irradiance, E_k, is defined by $a = P_m/E_k$. Several other equations do not account for photo-inhibition.

Among these seemingly widely differing expressions, Frenètte et al. (1993) remind that the integrals (4) and (5) stem from two possible approximations of a same differential equation. Vollenweider (1965) had also shown that Smith's equation could be integrated along various developments. Fitting experimental data to any mathematical expression is also fraught with mathematical or statistical pitfalls (Dowd & Riggs, 1965; Golterman, 1991). From another perspective, Golterman (*ibid.*) soberingly reminds that the unavoidable experimental errors strongly decrease the importance of the exact mathematical form used (in Golterman's argument, forms (1) and (6) were compared). Jellison & Melack (1993) found coefficients of variation of up to 38 % for both P_m and α. A somewhat comparable point has been made in the (somewhat remote) field of tracer kinetics: While the analytical solution of an n-compartment system is theoretically feasible, experimental

Table A: Various P - E equations:

1: $P = P_m * \alpha * E / (P_m^2 + (\alpha * E)^2)^{1/2}$
2: $P = P_m * \alpha * E / (P_m + (\alpha * E))$
3: $P = \alpha * E * \exp(-\alpha * E / P_m)$
4: $P = P_m [1 - \exp(-\alpha * E / P_m)]$
5: $P = P_m * \tanh(\alpha * E / P_m)$
6: $P = P_m * E / (K_E + E)$
6': $P = \alpha * k * E / (k + E)$
7: $P = \alpha * E / (bE + c)$
8: $P = E / (a * E^2 + b * E + c)$
9 $P = \alpha * E - ((\alpha * E)^2 / 4 * P_m)$ for $E < 2E_k$
$P = P_m$ for $E > 2E_k$
10: $P = P_m * E_{opt}/E * ln((E/E_{opt})+1)$

sources: 1: Smith, 1936; 2: Baly (1935; in McBride, 1992); 3: Steele (1962); 4: Webb et al., 1974 (after Frenette et al., 1993; attributed to Platt et al. (1980) by Blanchard & Montagna, 1992; attributed to Peterson et al.(1987) by Cloern, 1991 b); 5: Jassby & Platt, 1976; 6: Monod (in Golterman, 1991); 6': Marra et al., 1993; 7 : Eilers & Peeters, 1988; 8 : BenZion & Dubinsky (1988); Megard et al., 1985; 9 : Platt et al;, 1975 ; 10: Bush (in Oswald, 1988, and in Oh-Hama & Miyachi, 1988) uncertainties set a practical limit at three comparrtments (Wilkinson, 1961; Sakoda & -Hiromi, 1976 Li, 1983). In oppbsition to Golterman's views, Frenette et al. (1993) show that different models yield different values of a (and, to a lesser degree, of P_m). As a last point, several models were found of comparable (if not equal) value in what concerns their fit or their predictive power (Harrison et al., 1985; Balch et al., 1992; McBride, 1992). Jassby & Platt (1976) found that Smith's model was second best to their own. In the face of these variagated , but generally pessimistic views, we did not try to fit our data to a specific model but merely estimated P_m and α by "subjective analysis" (Frenette et al., 1993). This amounts implicitly to Blackman's formulation.

The parameters α and P_m of our P-E curves have unremarkable values when compared with some published data originating from other environments (table B), since our P_m figures range between 1 and 13 g C.(g chl.hr)$^{-1}$, while our α values are between 0.005 and 0.07 g C.(g chl.hr)$^{-1}$.(µE.m^{-2}.s^{-1})$^{-1}$.

As remarked, our E_k values seem rather high compared with most figures found by other authors, which often range between 100 and 200 µE.m^{-2}.s^{-1}. Since the uncertainty on our P_m values is low, we must infer that we have somewhat under-estimated our α slopes for want of data under very low irradiances.

Against the rather indifferent absolute values that we found for α and P_m, a remarkable point in our results is the correlation between α and P_m. A rapid survey of the literature would indicate that these parameters are essentially independent, especially since the determination of their quotient (E_k) has been considered of paramount importance by most scientists since Talling (1957). Chalup & Laws (1990) found no correlation between α and P_m. Despite the frequently showed variability of E_k, we did find some other studies which concluded at a P_m-α correlation (table C) while Cole et al. (1992) found α and P_m "highly correlated", without giving a regression equation.

These correlations often diverge, from ours (fig. 12) and between them. A few of the starker discrepancies might probably stem from oversights, especially when converting α^b into Ψ, or from shear errors in decimal point. Apart from this, a basic difference in E_k would be the most immediate explanation for the disagreement, but this is excluded in some studies which explicitly sought to show different light adaptations (Hood, 1993). We are thus left with an array of very real correlations, which are sometimes too wide apart, but also are often tentalizingly coùmparable.

In what regards the distribution of our P_m and α values in the Casamance, we found that they did not correlate with

Table B: Spread of published values of P *vs* E parameters (references in alphabetical order)

maximum production : P_m
in g. (g chl.hr)$^{-1}$
* medium values:
1 - 10 (C; *ref. 2, 4, 5, 6, 7, 9, 10, 15, 19, 20, 23, 24)*
2.5 - 27 (O2; *ref. 16, 22)*
* low values: 0.2 - 0.5 (C ; *ref. 3, 11, 14)*
* high values:
15 - 25 (C; *ref. 1, 8, 12, 14, 21, 24)*
60 (O2; *ref. 25)*

slope at origin
α in g C.(g chl.hr)$^{-1}$.(µE.m^{-2}.s^{-1})$^{-1}$
Ψ in g C.g chl^{-1}.E^{-1}.m^2
* medium values
α : 0.02 - 0.06 *(ref. 5, 7, 12, 13, 18, 19, 23)*
α : 0.05 - 0.16 (in g O2). *(ref. 16, 25)*
Ψ : 5.5 - 15 *(ref. 6, 22)*
* low values:
α : 0.01 *(ref. 3, 19)*
Ψ : 1.0 *(ref. 20)*
* high values
α : 0.1 - 0.2 *(ref. 21)*
Ψ : 20 - 30 *(ref. 14, 18)*

references: 1: Blanchard & Montagna, 1992; 2: Chalup & Laws, 1990; 3: Cole et al., 1992; 4: Di Tullio et al., 1993; 5:Dower & Lucas, 1993; 6: Fahnenstiel et al., 1989; 7: Frenette et al., 1993; 8: Glover, 1980; 9: Grobbelaar, 1992; 10: Grobbelaar et al., 1992; 11: Hill & Boston, 1991; 12: Hofman & Ambler, 1988; 13: Iriarte & Purdie, 1993; 14: Jellison & Melack, 1993; 15: Keller, 1988 b; 16: Kroon et al., 1992; 17: Langdon, 1988; 18: Lohrenz et al., 1991; 19: Platt et al., 1992; 20: Prasad & Hollibaugh, 1992; 21: Prézelin, 1992; 22: Roos & Pieterse, 1992; 23: Schofield et al., 1990; 24: Sukenik et al., 1987; 25: Szyper et al., 1992.

Table C: Correlations between P_m and α

A) explicitly mentioned by authors
$\alpha = 0.0075 * P_m + 0.0010$ (Blanchard & Montagna, 1992)
$\alpha = 0.0013 * P_m$ (Steenbergen et al, 1989)

B) recalculated
(alphabetical order of authors)
1 $\alpha = 0.0046 * P_m + 0.0008$
2 $\alpha = 0.0024 * P_m + 0.0002$
3 $\alpha = 0.0334 * P_m + 0.0004$
4 $\alpha = 0.0032 * P_m + 0.0029$
5 $\alpha = 0.011 * P_m - 0.007$
6 $\alpha = 0.0045 * P_m + 0.016$
7 $\alpha = 0.003 * P_m$
8 $\alpha = 0.0021 * P_m + 0.007$
9 $\alpha = 0.010 * P_m + 0.019$
10 $\alpha = 0.064 * P_m + 0.032$

1: (r=0.81) Boston & Hill, 1991 ; 2 : Cole et al., 1992 (recalculated from means; n=12,r=0.91) ; 3 : Dower & Lucas, 1993: n=21, r=0.85; 4 : (r = 0.72) Hill & Boston, 1991; 5 : Hood, 1993; 6 : Jellison & Melack, 1993; 7 : Marra et al., 1993; 8 : Platt et al., 1992 (2 groups only); 9 : Prézelin, 1992; 10 : Steenbergen & van den Hoven, 1990.

environmental (i.e. "static") characteristics, but only with B and with regeneration rates. This absence of correlation with environment resembles the unpredictability of ϕ_m found by Schofield et al. (1993), or the absence of environmental control observed by Booth & Beardall (1991). On the opposite, several authors found that P_m was a function of temperature (Harrison & Platt, 1980; Jellison & Melack, 1993), while we did not find any seasonal variation, either for P_m or for α. The negative correlation between P_m and B in the Casamance can be compared with the findings of Findenegg (1965) and of Jellison & Melack (1993), or with an analogous relation (P_m proportional to 1/B) found by Westlake et al. (1980). In the same direction, Fisher et al. (1992) found that P_m could limit the accumulation of B. All these observations are justified by the Contois model (in Morrison et al., 1987), which explicitly states that biomass represents sequestered nutrients which are then not available for further production. In an analogous way, Fuhrman et al. (1989) suggest a sequestration of nutrients in (bacterial) biomass. As a last point, Capblancq (1990) reminds that oligotrophic systems are characterized by the storage of nutrients inside biomass. In the case of the Casamance, we might have a problem on this particular point, since we noticed that the ratio DOC/POC strongly increased landward. But this concerns only the carbon cycle (and the DOC fraction is mostly allochthonous). In what regards the "classical" nutrients (N and P), both the Casamance and the Saloum estuaries do show an increased ratio of biomass to nutrients in the upstream portion.

A negative correlation between P (P_m in our case) and B is thus plausible -- as long as we deal with a closed system, analogous to a batch culture in which a finite amount of a given nutrient has to be distributed among various compartments. If this was the case, high biomasses would need high fluxes, just to maintain steady state, while both specific production and net production would be low. We must remember that we deal here with two different things: our measured P (or P_m) represents carbon fluxes, while Contois's model deals with a possibly limiting nutrient (N or P). We thus find again the need of considering parallel, but separate, cycling of C and N (or P) which was stressed by Platt et al. (1989) and Quinones & Platt (1991).

Admitting that high biomasses may sequester nutrients and thus limit production implicitly means that nutrient concentrations are truly limiting production (see formal treatment in Chalup & Laws, 1990, i.a.). Such an assumption of bottom-up control by nutrients is frequent, but not always founded (Agusti et al., 1990). We have recalled above some comments about N or P limitation in general. We may here note that absolute concentrations are poor predictors (apart from Droop's "cell quotient" concept) because kinetic flows are much more important (Ganf, 1974b; Kolber et al., 1990; Chalup & Laws, 1990; Harrison, 1990). Especially in oligotrophic systems, recycling rates determine limitations. It is thus highly plausible that our P_m are correlated with various estimators of (heterotrophic) regeneration. We found a similar relationship in a comparably 'confined' brackish lagoon (Pagès & Lemasson, 1981). In a similar way, Verity et al. (1993), studying hydraulically trapped coastal waters, showed that recycled nitrogen allowed a continued high production (but a constant biomass), and concluded that "conditions [were] in some ways similar to the oligotrophic zone of ocean gyres".

This importance of nutrient recycling in the control of primary production leads to a double comment. The first aspect is the functional relationship between heterotrophs and autotrophs. We have seen (paragraph 4.1.2) that the Casamance estuary exhibits B/PON ratios corresponding to an "inverted trophic pyramid" such as found in oligotrophic systems (see also Simon et al., 1992). We noticed that P_m (and A_m) was positively correlated with the PON/POC ratio. Such a correlation can express the role of remineralization by heterotrophs, but may merely correspond to the interaction between growth rate and cell quota (Sharp et al., 1980; Chalup & Laws, 1990; Laws & Chalup, 1990). The second aspect of regenerative processes is the relative importance of "new" production compared with "regenerated" production. This theme, which introduces the *f* ratio, will be dealt with below.

4.2.2: Vertically integrated production

We have dealt up to now with maximum (or "optimum") photosynthesis. However, on the scale of a water body, the important point is areal production integrated across the whole water column. This problem has been studied by numerous authors along two paths, either by analytical modelling or with empirical models. The analytical models were pioneered by Talling (1957) and furthered by Vollenweider (1965). The aim was to integrate the P-E relationship across the exponential underwater light field. A general form of these integrations may be written as: $\Sigma_z A = A_m . Z_{eu} . F(E)$, with *F(E)* describing the P-E relation. Talling (1957) used Smith's formulation and arrived at the well-known expression : $\Sigma_z A = A_m \; ln \; (2.E_o/E_k) \; / \; K_d$. Vollenweider (1965) showed that the *ln* form is but one of the several possible integrals. Mee (1987) used the equivalent integral arctang. Anyway, these "$P_m{}^b/K_d$ algorithms" (Balch et al., 1992) perform satisfactorily in most cases (Platt, 1986) but rely explicitly on the determination of specific properties of phytoplankton. The value of $ln(2.E_o/E_k)$ was empirically determined in several water bodies, mostly in lakes (Talling, 1957); its average value of about 2.6 agrees with the coefficient of semi-empirical models like that of Jones (1977), who found the relation: $\Sigma_z A = 2.4 \; . \; A_m/K_d$.

Another path, the empirical one, uses bulk properties of the water column, without explicitly considering the characteristics of the P-E reaction. Several authors have used this approach, arriving at the general form: $\Sigma_z A = k.B.E_{d(o)}/K_d$ (Cloern et al., 1985; Cloern, 1987; Cole & Cloern, 1987; Keller, 88 a, b; Powell et al., 1989; Boyer et al., 1993). It is noteworthy that the "compound function" (Keller, 1988 a) $B.E_o/K_d$ stems from the double integration of a P-E function ($P_z = P_m.(1-exp(a.E_z))$ and of a E-Z function ($E_z = E_o.exp(-K_d.Z)$), which yields the approximation $\Sigma_z A = 0.99 \; . \; \alpha.P_m.(B.E_{d(o)}/K_d)$ (Peterson et al., 1987; Cloern, 1991b). Published regression equations often have a constant term originating from statistical processing of experimental data. Anyhow, these empirical models imply that, at least on the scale of the system under study, the phytoplankton reacts uniformly to light, whatever its nutrient status may be; the good fit found by Keller (1988 a,b) across a sharp trophic gradient testifies of the robustness of such empirical models. The variety of units used by the authors does not facilitate a serious comparison between published regressions:

1 : $P = 0.70 \; . \; B.E_o.Z_{eu} + 220$

2 : $P = 2,7 \; . \; B.E_o/K_d + 198$

3 : $P = 3{,}4 . B.E_o/K_d + 150$
4 : $P = 5.16 . B.E_o/K_d$
source and notes: 1 : 24-hr production; Keller (1988a); amounts to $P = 3.22.B.E_o/K_d$; 2 : "daily production", Keller (1988b); P in g $C..m^{-2}.d^{-1}$, E_o in $E.m^{-2}.d^{-1}$; 3 : Powell et al (1989); 4 : Cloern, 1991 b; (P in mg $C.m^{-2}.d^{-1}$, E_o in $E.m^{-2}.d^{-1}$)

We mentioned above (paragr. 4.2.1) that our E_k values appear too high. An indirect confirmation of our over-estimation of E_k is lent by the value of the expression $ln(2.E_0 /E_k)$ ($= Z_i.K_d$). This expression appears in Talling's (1957) model; its empirical value is about 2.6 (Talling et al., 1973: Jewson, 1975). With our data, we arrive at $ln(2.E_o /E_k)$ ranging between 0.7 and 2.2, indicating over-estimated E_k's (since E_o is reasonably accurate). This indicates that K_d is not solely due to biomass in the Casamance estuary. Another hint stems from the product ($Z_i . K_d$), which is lowest in the uppermost stations. All this could indicate the role of dissolved (organic) matter (DOM) in the attenuation of light, since particulate inorganics are very low in the upstream portion. This observation leads us to another possible explanation of the low Z_i values. We have plotted the product ($Z_i . K_d$) against the ratio (Z_{av}/Z_{eu}). We obtain a positive correlation (figure not shown) which clearly indicates that very shallow stations ($Z_{av}/Z_{eu} < 0.3$) have a much too low value of R_zA, without any optical effect of DOM.

We may note here that such an expression appears to pose a problem of dimensions, since Σ_zA is in $g.m^{-2}.hr^{-1}$, while the compound factor $B.E_o/K_d$ will be in $(g.m^{-2}).(g.m^{-2}.s^{-1})$ if we transform the irradiance in its caloric equivalent. Since biological attenuation, K_b, is by definition equal to $B.K_s$, we can write $\Sigma_zA = C'. E_o.K_b/K_d$, with $C' = C/K_s$. The proportionality coefficient then integrates the specific attenuation of chlorophyll. The main point, though, is that integrated production, Σ_zA , is strictly proportional to the fraction of available light which is actually absorbed, without any explicit influence of either phytoplankton physiological properties (apart from Platt's (1986) model) or of environmental characteristics (nutrients, etc). In fact, though, the inclusion of B in the empirical equations does implicitly incorporate an effect of the past nutrient history of the population under study.

4.2.3: Extrapolated daily production

The determination of daily production from a series of short incubations appears a rather simple problem, since the variation of available irradiance should be known, either from theory (Kirk, 1983) or by measurement. In some cases, an integral across time (Σ_tA) can be obtained by a straightforward equation, like that found by Talling (1957; see also Jones, 1977), incorporating the P-E curve and either cumulated irradiance (Hammer et al., 1973) or daylength (Talling, 1957). However, several problems can crop up at various levels (Vollenweider, 1965; Hammer et al., 1973). The underwater light field is modified in function of the solar zenith angle (Kirk, 1983) while the reaction of phytoplankton to light may show diel periodicity (Prézelin & Matlick, 1980; Harding et al., 1982; Prézelin, 1992; Sommer et al., 1992). We have already mentioned some problems due to tracer uptake kinetics; the non-linearity of 14C uptake, as well as that of O2 production, has been highlighted by various authors (Harris & Piccinin, 1977; Marra, 1978 a, b; Hesslein et al., 1980; Goldman et al., 1981; Malone, 1982; Jensen, 1985). Several authors have tried to establish empirical relations between instantaneous production (as measured by incubations of varying duration) and daily (=day-light) production (Williams, 1981a; Harding et al., 1982; Mee, 1987; Platt et al., 1988; McBride, 1992). Most of these relations show that daylight production ($\Sigma_z\Sigma_tA$) can be extrapolated from the hourly production around noon (Σ_zA_h) with the approximation $\Sigma_z\Sigma_tA = 10 . \Sigma_zA_h$ (Ganf, 1975; Lemoalle, 1979; Mee, 1987; Keller, 1988b). This simple conversion concerns only the daylight hours; a daily (24 hrs) production (Σ_zA_{24}) must account for the nightly period with its respiratory lossses. We shall deal with this aspect later on but we can already note that Malone (1982) showed that, at least in a given case, Σ_zA_{24} was about equal to Σ_zA_h, the latter being measured by a 2-hr incubation. In the case of the Casamance, protracted incubations showed a constant photosynthetic rate (either as O2 production or as 14C uptake), without any noticeable decrease due to possible depletions. We may then accept the above extrapolation between Σ_zA_h and $\Sigma_z\Sigma_tA$.

Our values of $\Sigma_z\Sigma_tA$ range between 20 and 170 mmol $C.m^{-2}.d^{-1}$ (i.e. 0.2 - 2.0 g $C.m^{-2}.d^{-1}$). These are rather moderate figures compared with productive natural waters (Talling et al., 1973; Bindloss, 1976). We may recal that the upper limit of photosynthesis seems to be around 30 g $C.m^{-2}.d^{-1}$ (Robarts & Zohary, 1992).

4.3: RESPIRATORY LOSSES

Our figures of "production" for the Casamance estuary were mostly based on ^{14}C measurements after relatively short incubations, and correspond thus to gross production, i.e. gain of carbon . We shall here consider the various losses, which we tried to evaluate using several methods and approaches. We shall distinguish, in a somewhat artificial way, phytoplankton losses from community respiration.

4.3.1: Phytoplanktonic respiration and losses

The fact of dark carbon loss by phytoplankton is well known (Eppley & Sharp, 1975) and has been equated to respiration ((Rivkin, 1989). For all practical purposes, in our experiments, we may admit that this loss concerns solely autotrophic organisms, since we added $H^{14}CO_3^-$ and incubation duration did not allow heterotrophs to accumulate significant amounts of ^{14}C (see also Schweizer & Heusel, 1992). Aside of that, the significance of dark ^{14}C loss is far from clear-cut. A part of this loss can represent DOC exudation, which is well known since the pioneering studies by Fogg (1952; see also Samuel et al., 1971, and Fogg, 1983). Wood & van Valen (1990) have shown that DOC excretion is a physiological process which makes sense, and occurs in perfectly "healthy cells" (Bjornsen, 1988). In the Casamance estuary, we measured a negligible DOC excretion, and shall hence admit that most of dark carbon losses do correspond to respiration. An analogous view of low direct DOC release is held by several authors (Jumars et al., 1989; Fuhrman et al;, 1989; Malone & Ducklow, 1990). Translating a loss of ^{14}C into a ^{12}C oxidation rate obliges to some hypotheses, the main one being a uniform labelling of the whole phytoplaktonic compartment; we are aware of the approximative character of this hypothesis, since specific activity varies between the various cell components (see i.a. Fahnenstiel et al., 1989). A portion of the respired ^{14}C could also be recycled, by renewed uptake, at low DIC concentrations, while a part of the recently fixed ^{14}C may be excluded from respiration (Bidwell, 1977, in Chalup & Laws, 1990). Despite these several objections, admitting a uniform specific activity is reasonably justified (Dring & Jewson, 1982), and yields a dark carbon loss rate (∇^*C) which agrees reasonably well (r = 0.94) with in situ oxygen deepletion rates, $\nabla O2$. Our data did not allow a comparison between ∇^*C and the in situ DIC increase, ΔDIC. In a parallel way, our rates of ΔDIC and $\nabla O2$ give at first sight a reasonable agreement (r = 0.90), with a slope of 1.3 mol C.(mol O2)$^{-1}$. These few data do not allow the calculation, however tentative, of a respiratory quotient. We can however remark that the regression between ΔDIC and $\nabla O2$ shows a significant constant term; such an excess of DDIC may be due, as found in several other studies, to other electron transfers (SO_4 reduction, etc) beside O2 reduction (Caraco et al., 90; Mattson & Likens, 1993).

The reasonable agreement between ∇^*C on one hand, Δ DIC and $\nabla O2$ on the other hand, prompts to a further comment, namely a question of scale. Platt et al. (1989) duly stress that, in the particular case of *f* ratio determinations, bottle incubations may seldom be extrapolated to a whole oceanic region. In our case, we have tried to compare bulk measurements (ΔDIC and ∇ O2) with in vitro data (∇^*C). That we obtained an agreement better than an order of magnitude is in itself noteworthy.

Neglecting for a while the contribution of DOC to nightly O2 consumption, we arrived at an O2 uptake rate of 0.07 mol O2.(g chl. hr)$^{-1}$, or 2.2 g O2.(g chl. hr)$^{-1}$. This rate is roughly comparable to those found by other authors working in different environments (Ganf, 1974 a; Jones, 1977; Martinez, 1992; Langdon, 1988; Grande et al., 1989; Weger et al., 1989; Westlake, 1980; Daneri et al., 1992; Grobbelaar et al., 1992; Kroon et al., 1992; Markager et al., 1992). By contrast, though, some published respiratory rates are much higher, around 1 mol 02.(g chl. hr)$^{-1}$ (Grande et al., 1989; Szyper et al., 1992).

Beside these results, expressed as chlorophyll-specific respiration rates, some authors compare respiration (R) with production. Talling and his school admit that R amounts to 10% of P_m, while Findlay et al. (1992) and Cole et al; (1992) indicate that R is about 5 % of P_m . Morrison et al. (1987) found a still lower respiration rate, amounting to 3-4 % of net production, contrasting with very high respiration rates (20 % of P_m) found by Malone (1982). Daily (24 hrs) carbon loss represents between 6 and 19% of photosynthetic (12 hrs) carbon fixation (Rivkin, 1989), but night-time respiration may reach 25 % of "measured [?] production" (Keller, 1988a). Published biomass-specific rates range between 6% d^{-1} (Grobbelaar, 1985) and 9 % d^{-1} (Morrison et al., 1987). Carbon-specific respiratory losses, determined as ∇^*C, may reach 5-10% hr^{-1} (Geider, 1988) but may also be as low as 1-5 % hr^{-1} (Martinez, 1992). All these published figures show that phytoplanktonic respiration rates cover a very wide range. We can then merely say that our results are plausible, without being able to evaluate them in a more precise way.

4.3.2: Community respiration

As recalled above, we had seen that $\nabla O2$ appeared to be better explained when we also considered DOC concentrations, thus defining an "Active Organic Carbon" (AOC) pool comprising a fraction of DOC. This calls for several comments. First, on a purely statistical level, the distribution of our data is such that we should normalize them by a log transformation. This unfortunately leads to the physiological nonsense of a specific respiration rate which increases sharply with increasing carbon concentrations (calculations not shown). Further, we did not use the customary approach of two-variable regression because we have seen that biomass (B or POC) and DOC do not vary independently (whatever the cause may be). A second comment concerns the proportion of DOC which is involved in respiration. It is self evident that DOC does not "respire", since it is merely the substrate of bacterial activity. While "adding" increasing proportions of DOC to POC improves the correlation between ∇ O2 and AOC, this improvement is partly artificial and due to the extension in range of the high-AOC figures. Despite this, we can see that at least 1/10 of DOC contributes to oxygen consumption. Our long-term in vitro incubations showed that labile DOC (the fraction which disappeared after 1-3 months) represented between 5 and 15% of total DOC (Pagès & Gadel, 1990). If we take into account the ratio of DOC to POC in the Casamance, the above 1/10 DOC included in the AOC pool represents between 10% and 50% of POC. These percentages indicate that heterotrophic (bacterial) respiration may reach about one third of total oxygen uptake in the upper portion of the Casamance estuary. Although we must take these figures with caution, their magnitude fits well with other published estimations of bacterial respiration (Schwaerter et al., 1988; Cole et al., 1989; Smith et al., 1991). They also agree with the refractory/labile character of natural aquatic DOC (Hobbie, 1988; Deuser, 1988; Kirchman et al., 1991). Lastly, we arrive at an hourly oxygen consumption rate of about 0.06 mol O2 per mol "active organic carbon"; this figure again agrees broadly with published results.

4.3.3: Extrapolated respiratory losses

Our data are based on measurements taken at surface or sub-surface during the night. To compute a daily respiration in the whole water column ($\Sigma_z\Sigma_t R$), we have admitted that respiration (say $\nabla O2$) was constant with time and depth. This double hypothesis needs some examination.

In what regards diel variation of respiration, we are obliged to neglect possible intrinsic rythms (Jones, 1977; Sommer et al., 1992) or the effects of growth rate (Langdon, 1988; Martinez, 1992). Apart from these rythms, some authors found an heightened respiration rate under light, relative to dark respiration (Ganf, 1974 a; Humphrey, 1979; Grande et al., 1989; Daneri et al., 1992; Markager et al., 1992; Szyper et al., 1992; Szyper & Ebeling, 1993; Rivkin, 1989; Weger et al., 1989). A few studies show a lower diurnal respiration (Roos & Pieterse, 1992). Photorespiration appears to occur frequently (Burris, 1981; Raven & Beardall, 1981; Bender et al., 1987; Grande et al., 1989; Birmingham et al., 1982) but this reaction to light is not a rule (Harris & Piccinin, 1977; Bender et al., 1987; Grande et al., 1989). Booth & Beardall (1991) could find no evidence of photorespiration in *Dunaliella salina*, while Imafuku & Katoh (1976) even found inhibition of respiration under light, and Jones (1977; p. 574) concluded that "information [was] insufficient". Another question mark for our intended extrapolation of $\nabla O2$ to daily respiration is the possible exchanges between water and atmosphere. Most authors monitoring in situ O2 concentrations correct their O2 budget for air/water exchanges (Roos & Pieterse, 1992; Howarth et al., 1992; Teichert-Coddington & Green, 1993). However, Gat & Shatkay (1991) have shown that brines (such as we had in the Casamance) have a low diffusion coefficient for gases. We hence decided against any correction of our O2 data. We did not, either, try to account for tidal excursion after considering both actual tidal excursion (see paragraph 1.1) and longitudinal oxygen gradients, both of which were negligible.

Vertical integration of $\nabla O2$ raised some more questions about possible pelagic inhomogeneities (see for instance Jewson & Taylor, 1978) and about bottom processes. On this latter point, from the few measurements we had done, sediment had an O2 consumption ranging between 10 and 60 mg $O2.m^{-2}.hr^{-1}$ (at st.#19 and st.#25-#30-#34 respectively). These uptake rates are plausible when compared with other published data on benthic respiration (Dollar et al., 1991; Kemp et al., 1992; Devol & Christensen, 1993). Contrasting with these high O2 consumptions, we found in the Casamance that vertical homogeneity (both for DIC and for O2) was the rule rather than the exception. The seldom cases were observed in the shallow stretch between st.#37 and st.#39, bordered with dense reed swamps, and only when exceptionally high plankton biomasses were present (this would follow the long-term relation between benthic fluxes and pelagic production, as observed by Dollar et al., 1991). Anyway, the frequent vertical homogeneity observed in the Casamance would indicate that efficient , if slow and local, mixing processes ensured vertical homogeneity; a transverse thermo-haline circulation is the prime suspect. Anyhow, the main point is that we can accept a vertically uniform respiration rate, so that we may integrate surficial $\nabla O2$ figures across the average depth at each station. From the above considerations about daily variations, we can also extrapolate $\nabla O2$ for 24 hours, thus arriving at a set of $\Sigma_z\Sigma_t R$ values.

4.4: NET PRODUCTION, ENERGY AND MATTER BUDGET

Net photosynthesis (in an aquatic system for instance) primarily depends on the "outcome between light-harvesting efficiency and respiratory (and excretory) losses" (Langdon, 1988). We shall try to evaluate and comment the relative importance of these opposite processes in the case of the Casamance estuary. This will lead to some comments about the role of organic matter, and further to the characteristics of eutrophic and oligotrophic systems.

4.4.1: Net production

4.4.1.1: Molecular quotients

The simplified equations of photosynthesis and respiration give the impression of opposite equimolar fluxes of carbon and oxygen, so that both respiratory quotient (RQ) and photosynthetic quotient (PQ) are equal to unity. In what concerns PQ, Burris (1981) has shown its wide range, while several aauthors show (or remind) that PQ value is strongly conditionned by the end-products of photosynthesis and by the source of nitrogen. This latter point leads, by the way, to the problem of competition for reductants (and ATP) between NO3 uptake on one hand and carbohydrate synthesis on the other hand (Megard et al., 1985). In what regards RQ, the range of published values is somewhat narrower thant that of PQ, but nonetheless rather wide (Langdon, 1988; Langdon et al., 1992; Szyper et al., 1992; Szyper & Ebeling, 1993). In our case, we have assumed that PQ and RQ are equal to 1.0 when comparing O2 and C data (see for instance paragraph 4.3.1). We reasonned that other uncertainties, of potentially comparable magnitude, made any attempted 'correction' a rather illusory search for pseudo-accuracy.

4.4.1.2: Vertical integrations: rationale and problems

Such questions might have been debatted above, when discussing our computation of $\Sigma_z A$ and $\Sigma_z\Sigma$, but the main point here concerns both aspects since we shall examine bathymetry and hydrodynamics. The Casamance estuary exhibits a somewhat peculiar hypsometry, with extensive shallows and a relatively narrow and deep channel (paragraph 1.1). Such a distribution of depths is found in some lagoons (Venice lagoon for instance; see Di Silvio & Fiorillo, 1981) or coastal plain salt-marsh estuaries (Day et al., 1989, p. 54), but appears mainly in mangrove environments (Kjerfve, 1990). To take this hypsometry into account, we have calculated for each station an average depth, Z_{av}

Computing a vertical integral ($\Sigma_z A$ or $\Sigma_z R$) across this Z_{av} implies that every water particle has an equal probability of staying at any depth between surface and Z_{av}. In fact, however, a water mass in a shallow zone will be constantly well-illuminated during the day, while a water column in the "deep" channel includes an important bottom layer outside the euphotic domain. Such a deep water column will then systematically show a negative net production. An analogous situation has been described in at least a turbid estuary, where an overall positive production was only possible with exports from the shoals (Cole et al., 1992). Another example of the role of shallows in the general balance of biomass may be found along the Nile river (Talling, pers. comm., 1993), where lateral shallow coves harbour blooms which re-seed the main channel. In any case, such exchanges necessitate lateral transport. We have already evoked the possible "lateral non-tidal circulation" due to thermal (or even thermo-haline) density gradients; these processes have been observed in fresh-water systems (Horsch & Stefan , 1988; Stefan et al., 1989) and are a strong possibility in saline sabkhas (Lemoalle, pers. comm., 1992). In the Casamance, saltier brines were occasionally observed in deep portions of the central channel and could have resulted from night-time cooling of evaporated near-shore waters.

4.4.1.3: Net production: elements and factors

Assessing whether net production is positive or negative has a twofold rationale. On a daily scale, a negative balance leads to oxygen depletion, with the subsequent (and rather rapid) risks for the whole system. On a longer time-scale, a positive balance is necessary for maintaining the carbonaceous biomass.

The sign (<0 or >0) of net production has mostly been related to light availability in the water column. Some authors have considered compensation depth, either in freshwater (Talling, 1957; Jewson & Taylor, 1978) or in seawater (Sverdrup, 1953; Smetacek & Passow, 1990). The concept of compensation irradiance is equivalent (Alpine & Cloern, 1988; Langdon, 1988; Carpenter et al., 1993). Other authors have more explicitly focused upon the vertical hydrological structure, with special consideration of the ratio Z_{eu}/Z_{mix}. This ratio has a critical value of 0.16, below which no net production is allowed (Grobbelaar, 1985; Alpine & Cloern, 1988; Cole et al., 1992). In the case of the Casamance estuary, we saw that $\Sigma_z\Sigma_t R/\Sigma_z\Sigma_t A$ was systematically higher at the seaward stations, while $\Sigma\ R\ /\Sigma\ A$ (to use an abbreviated notation) was lower in the upstream portion. We have also seen that $\Sigma\ R\ /\Sigma\ A$ shows a positive correlation with Z_{av}/Z_{eu}. That relative respiratory losses increase with increasing optical depth sounds plausible, according to the various studies cited above. However, our relation between $\Sigma\ R\ /\Sigma\ A$ and Z_{av}/Z_{eu} is seriously undermined by two kinds of objections.

The first one stems from statistics. Our $\Sigma_z\Sigma_t R$ was computed as a vertical integration of a respiratory rate, r, and has thus the general form $\Sigma_z\Sigma_t R = k * Z_{av}*r*(B+b)$, with k being a constant, and b representing DOC contribution. We saw that $\Sigma_z\Sigma_t A$ has been found by several authors to be proportional to $B*E_o/K_d$ and can be hence expressed as $\Sigma_z\Sigma_t A = k'*B*E_o*Z_{eu}$. Our ratio $\Sigma\ R/\Sigma\ A$ has then the general form $\Sigma\ R/\Sigma\ A = k''*(Z_{av}/Z_{eu})*(1+(b/B))$. It is thus highly objectionable to compare $\Sigma\ R/\Sigma\ A$ with the same quotient Z_{av}/Z_{eu}. A second objection to the regression of $\Sigma\ R/\Sigma\ A$ against Z_{av}/Z_{eu} is much more functional. Our values of the ratio $\Sigma\ R/\Sigma\ A$ range between 0.3 and 2.0 (mean: 1.1) although Z_{av}/Z_{eu} ranges between about 0.2 and 1.5. The light climate is thus generally very favourable, compared with the critical value (see above) of 0.16-0.20 for the inverse ratio Z_{eu}/Z_{mix}. It appears that the magnitude of our $\Sigma\ R/\Sigma\ A$ is unrealistically high, not in itself (since a negligibly small net production is fully possible) but in comparison with the low Z_{av}/Z_{eu} ratios. However, the importance of Z_{av}/Z_{eu} (or Z_{eu}/Z_{mix}) as a diagnostic tool has been proven in estuaries, or in water bodies in general, in which phytoplankton was the main component for light absorption and respiration. This is not really the case in the Casamance estuary. We can try to estimate the amount of respiration due to the sole phytoplankton, using the respiration rate of 0.07 mol O2.g $chl^{-1}.hr^{-1}$ found before. The integrated phytoplanktonic respiration, $\Sigma_{ph}R$, does not yield any better plot of $\Sigma_{ph}R/\Sigma A$ against Z_{av}/Z_{eu} (plot not shown) but the ratios $\Sigma_{ph}R/\Sigma A$ range between 0.1 and 0.8, being thus much more typical for well-illuminated waters. We then see that one of the most usual determinant of net production, namely the optical depth of the mixed layer, emerges as a week predictor in the particular case of the Casamance estuary. The difference ($\Sigma\ A - \Sigma\ R$), or the quotient $\Sigma\ R/\Sigma\ A$, is not really determined by depth.

The relative magnitude of net and gross production has also been compared, in other environments, with either "production" or biomass. In the first instance, several natural water bodies exhibit an inverse relation between net production ($\Sigma\ A - \Sigma\ R$) and gross production (the 'Eppley curve'; Dortch & Whitledge, 1992; Smith & Hollibaugh, 1993). In intensive algal cultures, maximal biomass production (i.e. maximal net photosynthesis) is obtained by manipulation of density and water depth to arrive at an optimal "areal biomass" (Raven, 1988; Oswald, 1988; Boussiba et al., 1988). Sukenik et al. (1991) found an optimum around 0.6 g $chl.m^{-2}$, giving a net production of 9 $gC.m^{-2}.d^{-1}$.

This aspect of net production calls for a last remark. Net production can be defined as "the part of total production in excess of local community metabolism" (Sathyendranath et al., 1991). This definition is at the same time very precise and very broad. Its explicit mention of 'community' reminds that phytoplankton is not the sole active component; 'production' is not obligatorily equivalent to 'photosynthesis', and any synthetized particulate matter can be preyed upon, whatever its origin (see Williams, 1981a). Further, in the above definition, no particular element (C, N or O2) is mentioned. The notion of 'net production' was more or less explicitly coined for O2 and/or C cycles. As already remarked, this implies a predominance of phytoplankton, so that we deal with a linear food chain (not a food web), in an autotrophic and often eutrophic system. Now, studies in oceanography have led to a progressive shift in emphasis, focussing upon the nitrogen cycle and the opposition between new and recycled production. This change led to a closer inspection of related subjects among which *a*) recycling processes (*f* ratio), *b*) nutrient imports (allochthonous matter, lateral imports), and *c*) role of heterotrophs. The notion of *f* ratio was heralded by the numerous studies of the "relative preference index" (comparing the uptake of NH4 and NO3) (McCarthy et al., 1975, 1977; Axler & Goldman, 1981; Glibert et al., 1982; Harrison et al., 1992). Among the abundant literature dealing with the *f* ratio and its consequences, we shall merely recall that a high *f* ratio (i.e. high 'new' production and low regeneration) corresponds to high biomasses with a relatively low production (Platt et al., 1989; Harrison, 1990). Apart from the important diagnostic value of the *f* ratio, we find again the basical difference between biomass and production (see also Harrison, 1990, and Verity et al., 1993).

4.4.2: Role of organic matter

In most aquatic environments, especially in the pelagic ones far awazy from terrestrial influences, DOC production is mainly -or exclusively- based upon phytoplankton, whatever pathways ultimately lead to DOC (Jumars et al., 1989; review by Lee & Henrich, 1993). In the case of the Casamance estuary, however, several converging hints indicate that most of the abundant DOC found in the upstream reaches originated from the wide reed marshes stretching above our st. #33. It may be debatted whether these riparian macrophytes belong to the ecosystem or not (Wetzel, 1979), so that the exported organic matter might not be really 'allochthonous'. Anyway, the utilization of organic matter of terrestrial origin by aquatic ecosystems has prompted several authors to consider the latter as heterotrophic systems, be they rivers (Howarth et al., 1992) or large streams (Findlay et al., 1991) or coastal bays (Smith & Hollibaugh, 1993). Even the whole Ocean might be considered as heterotrophic in this respect (Hedges, 1992; Smith & Hollibaugh, 1993).

In several tropical estuaries, the mangrove is the most conspicuous, and characteristical, riparian vegetation, and numerous authors have confirmed Odum's "outwelling hypothesis" (Odum & Heald, 1975; review in Pagès, 1992). In a tropical brackish lagoon, the Ebrié system, the shear width of the water body strongly diminished the possible role of the riparian vegetation (Lemasson & Pagès, 1981). In the particular case of the Casamance estuary, the role of the mangrove as a source of organic matter is strongly limited by local factors (low mangrove biomass and broad tidal channel), while equally local features enhance the contribution of the Phragmites swamps (high biomass, narrow and shallow channel). Furthermore, in the upper Casamance, hydraulic containment leads to a closed system in which terrestrial matter (be it called 'allochthonous' or not) is effectively trapped. Although this is a mere detail, these upper reaches are functioning like a "terminal lake" (*sensu* Gonfiantini, 1980), but with a double aspect: for salt and stable isotopes, the opening faces seaward, while the estuary is opened in the landward direction for organic matter.

Anyway, terrestrial contributions to the upper Casamance system may be divided between the 'conventional' nutrients (N, P, possibly Si) and carbon. Among nutrients, we routinely leave aside potassium, since we are dealing with seawater, in which K is never limiting; the problem might arise in freshwater systems (Golterman, 1991; Talling, 1992). The few data we have about silicates show the customary paucity of SiO3 in seawater. In what regards nitrogen, we have already signalled the predominance of its reduced forms (DON and NH4) against the oxidized forms (mainly NO3). This fact should indicate low *f* ratio values (Platt et al., 1989; Dugdale et al., 1992) and a high proportion of "regenerated" production (Williams, 1981 a). By opposition, though, lateral advection of any form of nitrogen may promote "new" production (Platt et al., 1989).

In what regards carbon cycling, and organic matter in general, the Phragmites stands along the upper Casamance usually dried out during the dry season, with a short greening after the rains. Such 'old' particulate matter can still give off DOM which is utilizable by bacteria (Findlay et al., 1992). The organic carbon cycle (in the Casamance as in other systems) has several aspects. In relation with nutrients, "luxury uptake" of carbon has sometimes been observed (Lehman, 1978; Lemasson et al., 1980; Istvanovics et al., 1992; Sambrotto et al., 1993). Furthermore, the presence of micro-aerobic zones, in relation to abundant organic matter (either POM or DOM), may lead to a control of nutrients (especially of N) by the carbon cycle (Smith et al., 1992). Oxidized nitrogen would then be further depleted. Also on the subject of carbon vs nutrients, several authors found that heterotrophic bacteria may be limited les by nutrients (N or P) than by energy source (Cotner & Wetzel, 1991; Keil & Kirchman, 1991).

Another aspect of the carbon cycle in the Casamance is its overall balance. We have mentioned that DIC concentrations decrease with increasing salinity. We ascribe this abnormal behaviour to a biological (phytoplanktonic) sequestration of DIC in the form of sedimented POC (Pagès et al., in prep.). The upper Casamance would then appear to act as a carbon sink, but the ultimate fate of the settled POC may be either a long-term sequestration or a recycling as CO2 or CH4. For the former possibility, definitive burial rate has been shown to increase with sedimentation rate and pelagic production (Chamley, 1989; Cocito et al., 1990; Calvert et al., 1992; Kamp-Nielsen, 1992; Bertrand & Lallier-Vergès, 1993). For the latter possibility, methanogens were found in the Casamance sediments (Jacq, pers. comm., 1986) while a slight deficiency in SO4 indicated sulphate-reducing activity (Pagès et al., 1993). The question thus remains open as to whether the Casamance acts as a source or a sink for carbon.

A complementary aspect of the organic carbon cycle is its trophic role in the aquatic system, and its contribution to the overall "production" in the Casamance - considering as "production" the synthesis of new POM, be it phytoplanktonic or bacterial. In the particular case of the Casamance, our few measurements of ^{14}C-glucose uptake (Pagès, unpublished) showed a high heterotrophic activity, but these data are insufficient to quantify bacterial activity. We may though try to estimate it from our respiration measurements, with the hypotheses that: *i)* about 2/10 of DOC "respires" at a rate of 0.01 mol O2.mol $C^{-1}.hr^{-1}$; *ii)* DOC amounts to 1-2 mmol $C.l^{-1}$; *iii)* bacterial growth yield is 50%. With these figures, we arrive at a bacterial production of 50-100 $\mu molC.l^{-1}.d^{-1}$, against a photosynthesis (^{14}C) of about 50-200 $\mu molC.l^{-1}.d^{-1}$ (data from the May '87 survey). These admittedly rough calculations lead to a triple remark. The first point is that bacterial production is of the same magnitude as photosynthesis. Analogous results have been obtained in several water bodies (Lind & Davalos-Lind, 1991; Findlay et al., 1991, 1992). The general importance of the microbial loop (Azam et al., 1983) is thus again underlined. We may recall that, according to some authors, the microbial loop has a high regeneration activity but a low transfert efficiency toward higher trophic levels (Iverson, 1990; Goldman & Dennett, 1992), while a somewhat different view has also been defended (Williams, 1981 b). The second point is the relationship between bacteria and phytoplankton. The abundances of these two components are notoriously parallel (Fuhrman et al., 1980; Bird & Kalff, 1984; Malone & Ducklow, 1990; Morales-Zamorano et al., 1991; Morris & Lewis, 1992; Simon et al., 1992). This parallelism has been ascribed to "trophic status" . A closer look at published data shows however that the relationship is far from uniform (Letarte & Pinel-Alloul, 1991; Kirchman et al., 1993); here again, eutrophic and oligotrophic systems show a profound organizational difference (Cole et al., 1988, Simon et al., 1992). Our third point deals with the energetics of the purported relation between phytoplankton and bacteria, which has been often ascribed to a "bottom-up" control of bacterial biomass through phytoplanktonic DOM production (Bjornsen et al., 1989; Wood & van Valen, 1990; Eppley & Renger, 1992; Sell & Overbeck, 1992; Ducklow et al., 1993). Bottom-up control has indeed been proven, especially in eutrophic waters (Horrigan et al., 1988; Billen et al., 1990; Pernie et al., 1990; Cotner & Wetzel, 1991; Letarte & Pinel-Alloul, 1991), but top-down control can also (co-)exist (Tranvik, 1988; Berninger et al., 1991; Leibold & Wilbur, 1992; Psenner & Sommaruga, 1992). The difference between eutrophic and oligotrophic systems surfaces again (Sanders et al., 1992; Gasol & Vaqué, 1993). Whatever the case, our results for the Casamance point out that the DOC flux required for bacterial production cannot stem only from autotrophic production, so that an external source of DOC must exist. An analogous conclusion has been reached by several authors in various environments (Hedgpeth, 1967; Baines & Pace, 1991; Lind & Davalos-Lind, 1991; Findlay et al., 1991, 1992; Ducklow, 1993; Kirchman et al., 1993). In a somewhat parallel way, riparian macrophytes contribute a sizable portion of the overall "production" in some estuaries (Ong et al., 1984; Flores-Verdugo et al., 1988; Lee, 1989, 1990). The "heterotrophic" feature of nearshore waters is thus doubly illustrated. Finally, really autotrophic systems would appear rather seldom (Bush & Fisher, 1981).

4.4.3: Eutrophic *vs* oligotrophic systems

We have noted several times that eutrophic and oligotrophic systems correspond to different trophic webs. Following the generally accepted view, the most obvious criterion defining oligotrophy would be chlorophyll concentration. Even at this basic stage, some relativity exists, since Balch et al. (1992) consider that a eutrophic oceanic water contains more than 1 µg chl.l^{-1}, while the eutrophy limit is set above 20 µg chl.l^{-1} for lakes (Carlson, 1977; Wofsy, 1983; Yoshimi, 1987; Golterman & de Oude, 1991). An areal (*i.e.* integrated) biomass of 30 mg chl.m^{-2} defines a mesotrophic ocean (Jacques, 1993). In view of these figures, it may sound somewhat unexpected to evoke oligotrophy for the waters of the Casamance estuary, with sometimes 50 to 200 µg chl.l^{-1}, or in the Ebrié lagoon, with 15 to 40 µg chl.l^{-1} (Lemasson et al., 1981). In the same vein, oligotrophy is often defined by a total dissolved phosphorus (TDP) concentration lower than about 5 µg P.l^{-1} (Golterman, 1991). In this respect, too, the estuaries or lagoons that we studied would seem ill-fitting into the oligotrophic category, with between 0.5 and 4 µmol TDP-P.l^{-1} (Lemasson et al., 1980; Pagès, 1992; Pagès et al., in prep.).

Despite this, while the most immediate (or obvious) features of oligotrophic waters are low concentrations of biomass and nutrients (Beers et al., 1982; Seip et al., 1992), a whole array of related features is characteristical of oligotrophic systems. These traits have been recently reviewed by Capblancq (1990); some other complementary details may be added (table D).

Table D: Typical features of oligotrophy

character	trend	reference
* biomass		
+ total	low	a
+ % small sizes	high	a, g
+ % heterotrophs	high	d, e
* nutrients		
+ N/P	high	h
+ relative distribution		
inorganic,dissolved	low	
organic particulate	high	a
DON/DIN	>> 1	f
+ regeneration	high	a,i
turn-over time	low	a, b
f ratio	< 0.1	f
+ losses		
sedimentation	low	a
terminal PO4 burial	high	c
denitrification	low	a
* production		
+ total	variable	
over-estimation by short 14C method	strong	a
+ net	low	a

references and notes:
a: Capblancq, 1990 ; b: especially for phosphorus ; c: Gächter & Meyer, 1993 ; d: Dortch & Packard, 1989; Sanders et al., 1992; Simon et al., 1992 ; e: Currie, 1990; Beers et al., 1982 ; f: Harrison et al., 1992 ; g: Painting et al., 1992; Jochem et al., 1993; Wehr, 1993; Probyn, 1992; Probyn et al., 1990 ; h : Elser et al., 1990; Downing & McCauley, 1992 ; i: Carlsson et al., 1993

The various estuaries we studied fit perfectly the whole above description, except for the first line ("low total biomass"). This is why we coined (Lemasson & Pagès, 1983) the perhaps unnecessary neologism of "crypto-oligotrophy" for such seemingly eutrophic waters. The fact, if not the term, has been observed elsewhere (Verity et al., 1993) with the same conclusions.

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