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**DETRITAL FOOD WEBS IN NEAR-SHORE WATERS,
MANGROVES AND ESTUARIES
A REVIEW**

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Abstract :

We try to organize the recent literature about organic-rich near-shore environments, in which sediment, shallow waters and riparian vegetation inter-act. We review the publications dealing with the effect of estuaries, and mangroves in particular, upon halieutics in the adjacent waters.

Several recurring themes emerge, which we shall list without priority as:

- * importance of heterotrophy, at all organizational and spatial levels (the microbial loop being only one aspect), and reduced role of autotrophs in optically deep waters,
- * importance of recycling processes (*f* ratio),
- * pervasive role of water body morphometry and bathymetry,
- * importance of processes at the interfaces, together with the difficulty of spatially defining these very interfaces,
- * blurring of frontiers: between oxic and anoxic, between auto- and heterotrophy, between autochthonous and allochthonous.



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Introduction :

Estuaries and coastal waters present the obvious feature that firm land is nearby. These mostly shallow waters can thus be influenced by riparian vegetation and by bottom. In several tropical estuaries, mangroves represent an environment where (coastal) seawater is submitted to the most varied interactions. An equally obvious feature of these aquatic environments is the presence of allochthonous organic matter. Detrital food webs should then be more important than classical ones, based upon *de novo* photosynthesis.

We became aware of these features while working on tropical estuaries, during studies aimed at the interactions between nutrients (and organic matter), bacteria and phytoplankton. The possible rôle of riparian vegetation was particularly obvious in two instances, with mangroves and with *Phragmites* swamps. The latter we found as relics in a then hyperhaline estuary. We started collecting reading notes, for a purely personal use. Once organized, these notes happened several times to be useful to colleagues, and might find some use here.

We present a limited review of recent publications dealing with mangrove production and its effects upon aquatic resources. Our aim is not to emulate exhaustive reviews such as Rollet's (1981), or that done by Hatcher et al. (1989) on the conservation aspect. We discovered too late the fine work on estuarine ecology by Day et al. (1989). We have limited our scope to mangrove biomass and production, and to some features of detrital food-webs and organic-rich environments. We shall also briefly consider the case of *Phragmites* swamps. Before that, we shall treat some -perhaps obvious- characteristics of estuarine and shallow waters, including some sedimentary processes. In this part, we have tried to stress those aspects which are more characteristic of tropical marshes, and to skip the general estuarine ones. As a matter of policy, we have used our own cross-reference, manual card system. Use of computerized information-retrieval systems (e.g. ASFA CD-ROM file) could constitute a *post hoc* complement. The fact that we centered our scrutiny upon recent literature does not imply a rejection of the pioneering studies done prior to the seventies.

A last word of caution: we did not try to write still another handbook on aquatic ecology. We have egotistically stressed those points which seemed us farthest from the (usual for us) deep-water domain. We have hence skipped several "evident" points (i.e. those we think we know), such as methods, or phytoplankton physiology. On this latter point, for instance, Harris (1986) wrote better than we ever could.

1. Physics and chemistry of shallow waters

1.1. : Physical characteristics

What follows is mostly reminders of those features, of sediment and of water, which may have more direct biological consequences. Light climate, in itself a physical factor, will be considered later on.

1.1.1. Water motions :

Tidal propagation in estuaries has been extensively studied. Tidal currents are asymmetrical, owing both to the reduced depth and to shore presence ; this last point is reinforced in mangroves by lateral trapping by riparian vegetation (Hatcher et al., 1989). Mangroves also have a particular bathymetry, with extensive shallow portions and a limited extension of deep, narrow tidal channels. This distribution of depths is also found in coastal plain salt marsh estuaries (see Day et al., 1989, p. 54). This structure enhances transverse motions during a tidal cycle (compare with Di Silvio & Fiorillo, 1981). Tidal pumping (i.e. net ebb or net flood in the deep or secondary channels, respectively) is frequent (Day et al., 1989, p. 62). Tidal mixing reflects the double influence of reduced depth (Wood, 1979 ; Longhurst & Pauly, 1987) and of shore presence (Pritchard, 1959 ; Hatcher et al., 1989).

High speeds, and turbulences, allow high loads of suspended matter (McCave, 1979; Rucker et al., 1990). The resulting high (inorganic) turbidity has an adverse effect on phytoplankton photosynthesis (see § 1.5). Conversely, tides represent a physical energy input which increases the overall estuarine productivity (Nixon, 1988) ; theoretical considerations also indicate that turbulence has a positive effect upon phytoplankton production (Margalef, 1989).

Lower current speeds, appearing either farther upstream or near the solid/liquid interface, allow sedimentation (for inorganic particles; Petticrew & Kalff, 1991) and settling of sessile organisms (Mullineaux & Butman, 1990). At a still lower speed scale, thermohaline circulation (see also § 1.2.) can appear in (relatively) shallow portions (Monismith et al., 90). In case of a "piston flow" (= "plug flow") regime, thermohaline circulation may exist also in ~~tidally-influenced portions of estuaries~~ (Wolanski, 1986).

As a whole, sediment transport is now reasonably well understood (Lerman, 1979; Dyer, 1979; Fisher, 1981; Falconer & Owens, 1990; West et al., 1990). Some difficulties may remain, especially in the erosion/sedimentation alternances found along some estuaries. Contrary to expectancies, sediment and salt may not travel in the same way (Schoer, 1990).

Grain size of suspended solids is a well-described function of current speed and turbulence (Lerman, 1979). Sediment characteristics in lakes can then be predicted to some detail from morphometry (Petticrew & Kalff, 1991). The phenomenon of "sediment focussing" has been described for lakes (see i.a. Caraco et al., 1992), but the analogous process of "shelf sweep" may be found in coastal waters (Archer & Devol, 1992).

1.1.2. Temperature :

Shallow waters have reduced thermal inertia against convective and radiative processes (Heath, 1977; Andersson & Rahm, 1986; Horsch & Stefan, 1988). While evaporation has a cooling effect, shallower -and warmer- waters evaporate more during the day. Shore proximity amplifies the "oasis effect" (Maglione, 1974, 1976). Intertidal sediment may again amplify these local processes with the right combination of tide and daylight : dark surficial soils may reach 60°C (Webb, 1958; Harrison, 1985).

1.2. Salinity :

Salinity most obviously results from the water (H₂O) budget, when considering an estuary as a whole. Intertidal and supratidal sediments play a role in this. While runoff coefficient - in its classical sense - is low, due to negligible slopes, rain collection is generally 100 % effective in marshes and swamps. (Gallaire, 1980 ; Sutcliffe & Parks, 1989 ; Vardavas, 1989).

Conversely, low-lying soil surfaces evaporate actively (Webb, 1958; Avissar & Mahrer, 1986; Baillie, 1986; Warrick, 1988). Capillary evaporation may lead to evaporitic brines (Swart et al., 1989) and to surface salt deposits (Hsü & Siegenthaler, 1969). Such deposits can then be flushed back to the water at first rains (Ridd et al., 1988). These salt movements result in a catena of soil facies : the european "schorre" and "slikke" are found, with somewhat different characteristics, under the aspect of the tropical "tannes" (the West-African name for salt flats; Marius, 1985; Twilley, 1985; see also § 3.1). Tidal flushing frequency governs the general distribution and level of salinity (Baillie, 1986; Twilley et al., 1986 ; Gordon, 1988). On a smaller time-space scale, pore water salinity may change rapidly, in submerged sediments, during a tidal cycle (Gordon, 1988 ; Richardson & Parr, 1988). ~~Since diffusion is controlled~~ also by porosity, exchanges will be slowed down in fine-grained sediments with high water and OM content (see § 1.3.1). In a somewhat different environment, Agosta (1985) showed that interstitial water in creek banks has a residence time of 1 to 15 days, with exchanges limited to a distance of 2 to 4 m from the low-water mark.

In the free waters, salinity distribution in an estuary is controlled by tide inside an overall, larger-scale framework defined by water balance, i.e. by climate. Modeling salinity distribution can be relatively simple on a small to medium spatial scale, although morphology and bathymetry may introduce some difficulties. Box models often remain highly effective (Officer, 1980; Miller & McPherson, 1991). A model for a whole estuary is still a major undertaking, especially with branched estuaries (Keiller & Close, 1985; Uncles & Stephens, 1990). Moreover, rain and evaporation may become as important as hydrodynamics in some shallow, far-strung estuaries (Pagès & Debenay, 1987; Savenije, 1988; Sutcliffe & Parks, 1989), while thermohaline circulation can accumulate dense deep waters (Phleger & Ewing, 1962; Wolanski, 1986; Stefan et al., 1989). Mangrove areas, which cumulate the above difficulties, still represent an arduous modelling problem (Kjerfve, 1990).

1.3. Organic matter

The subject of aquatic and sedimentary organic matter is currently a rapidly evolving field, as witnessed by the special issue of *Marine Chemistry* (39/1-3, September 1992). Apart from the recent controversy about DOC measurement, some of the difficulties may be illustrated by two citations: "... the complex and largely uncharacterized mixture of organic compounds that makes up pore water DOC" (Burdige et al., 1992) and "50 to 70 % of bulk organic matter remains unidentified at the molecular level" (Cowie & Hedges, 1992).

1.3.1. Sedimentary organic matter :

Knowledge about marine sedimentary humic substances was recently reviewed by Francois (1990). We shall not try to emulate this thorough review, but merely try to have a somewhat different viewpoint, also since we consider a slightly different environment.

Low current speeds and abundant riparian vegetation, as found in swamps or near-shore waters, combine to yield organic, and hence often anoxic, sediments. Sedimentation rates are naturally most variable; a moderate flux is about $1-5 \text{ g.m}^{-2}.\text{d}^{-1}$ (dry weight), corresponding to $10-100 \text{ mg C.m}^{-2}.\text{d}^{-1}$ (Wassmann, 84; Stoddard et al., 89; Childers & Day, 90; Fichez, 1990; Landing et al., 1991). A reasonable range for accumulation rates lies between 0.02 and 0.3 cm.yr^{-1} (Cooper & Brush, 1991; Dollar et al., 1991). An ample body of literature deals with sedimentation rate assessment from ^{210}Pb content (Carpenter et al., 1985; Burnett et al., 1989; DeLaune et al., 1989 b). On a shorter time scale, depletion of ^{234}Th is a good indicator of sedimentation rate (McKee et al., 1990). We may remark that, in the shallow waters we are dealing with, accretion (sedimentation) rates generally agree with organic fluxes at the interface. The problem is much thornier in deeper waters, through which settling particles travel for a

certain time. While benthic/pelagic coupling may work (Kamp-Nielsen, 1992), there are several instances where the flux through the water column differs from the accumulation rate on the bottom (Walsh et al., 1991; Calvert et al., 1992; Cowie & Hedges, 1992; Smith et al., 1992).

Organic matter (OM), expressed as carbon, generally represents between 0.5 and 10 % of dry weight (Edwards, 1978; Jahnke et al., 1990; Gonzalez-Prieto et al., 1989; Cooper & Brush, 1991; Archer & Devol, 1992). OM content increases with increasing water content and in increasingly fine sediments: in extreme cases, OM may amount to 20 % dry weight (in carbon; Moy & Levin, 1991). Some of the recently deposited OM undergoes decomposition (see § 2.2.1.). The OM percentage which is durably preserved increases also with increasing burial speed, i.e. increasing sedimentation rate; for a (rather low) rate of 1 mm.yr^{-1} , Chamley (1989) finds that 10 % of OM is durably conserved. In the same vein, Cocito et al., (1990) find high sedimentary C/N ratios at high OM percentages. Since buried OM undergoes diagenesis, OM content decreases in deeper sedimentary layers, while the proportion of labile components decreases (see Cowie & Hedges (1992) for amino acids).

A sizable proportion of sedimentary OM consists in particulate organic matter (POM), which may be "autochthonous", i.e. stemming from settled aquatic particles (Reimers et al., 1990). Much of sedimentary POM is "allochthonous", though, since terrestrial detritus is less labile (Knight & Bottorff, 1984; Hedges et al, 1988 a, b; Cowie & Hedges, 1992). In the particular case of marshes or swamps, use of the term "allochthonous" is somewhat misleading, since "riparian" vegetation (mangrove trees, or *Phragmites*, for instance) are a part of the said swamp (see Wetzel, 1992). However, the extreme illustration of "allochthonous" POM accumulation is lent by peat. Mangrove peats are found in Florida (Davies & Cohen, 1989) as well as in Senegal or in Viet Nam -among others-. The "sudds" of the Okavango delta (Ellery et al., 1990) or the papyrus swamps are intermediate examples of litter accumulation.

Dissolved organic matter (DOM) mostly stems from POM through very localized processes (Kelley et al., 1990). We shall see (§ 2.1.1) that (micro)biological processes are most active in this transformation. While overall DOM amounts are relatively low in the whole sediment, DOM concentration in pore water is about 20 mmol C.l^{-1} (Gadel & Texier, 1986). Highest concentration recorded in recent sediments was 70 mmol C.l^{-1} (Javor, 1989, p. 216). It may then diffuse back into overlying waters (see § 1.4 for the general process of sediment/water exchanges).

In the sediment, O_2 concentrations decrease rapidly, due to O_2 consumption for OM oxidation (Wilken et al., 1990; Sweerts, 1990; Brotas et al., 1990; see also § 1.3.2). Vertical profiles of sedimentary OM (be it POM or, more especially, DOM) reflect the respective

importance of import (= sedimentation), decay and diagenesis (Carignan & Lean, 1991). Anaerobic decay causes a gradual decrease in the proportion of labile components in the deeper layers (Francois, 1990; Cowie & Hedges, 1992), and hence a (generally slight) decrease in overall OM content (Martens, 1978, 1987; Klump & Martens, 1989; Kelley et al., 1990). We shall deal below with OM decay in some detail (see § 1.3.2.), but anaerobic OM utilization (oxidation) entails some chemical processes which modify sediments and correspond to loss, by the system, of either C, N or S. A thorough review of anaerobic carbon metabolism has been done by Capone & Kiene (1988; see also Hansen & Blackburn, 1991). We shall hence only briefly describe the three successive levels found at increasing depth into the sediment, i.e. at decreasing oxidation status and decreasing Eh:

- Nitrate reduction : dissimilatory NO₃ reduction differs from denitrification *sensu stricto* (Seitzinger, 1988). Anyway, these processes represent a serious N loss in cultivated (and fertilized) soils such as rice fields (Minzoni et al., 1988; El-Habr & Golterman, 1990). In *natural* environments at least, NO₃ concentrations are often low (Warwick & Hill, 1988; Sweerts & De Beer, 1989). Twilley & Kemp (1986) showed that denitrification rate is controlled by NO₃ concentration with Michaelis-Menten (first order) kinetics. Denitrification will thus be rather limited : highest rates are about 100 μmol NO₃-N.m⁻².hr⁻¹ (Vanderborght & Billen, 1975; Vanderborght et al., 1977; Kemp et al., 1990; Devol, 1991) or 2-3 mmol.m⁻².d⁻¹ (Dollar et al, 1991). Exceptional values of up to 1,000 μmol NO₃-N.m⁻².hr⁻¹ were observed by Seitzinger (1988). Twilley & Kemp (1986) found that maximum (potential) denitrification rate was a function of OC content. Sulfides (and especially the abundant FeS form) increase NO₃ reduction rate (Golterman, 1991 b). As other anaerobes, NO₃-reducers are highly sensitive to O₂ (Bonin & Raymond, 1990); concentrations must stay below 0.2 mg O₂.l⁻¹ (Seitzinger, 1988). A remarkable point is that nitrification and denitrification can take place simultaneously, at least at the human observational scale.

- Sulfate reduction : freshwater environments are relatively poor in SO₄, and sulphate reduction may be seasonally substrate-limited (Hordijk et al., 1989). In estuarine or marine environments, sulfate reduction can account for up to half of OM oxidation (Valiela, 1984, p. 300 ; Westrich & Berner, 1984; Martens, 1987; Sinke et al., 1992). With a rate of about 3 mmol.m⁻².d⁻¹, Dollar et al., (1991) estimate that sulfate reduction drives about 1/3 of benthic carbon metabolism in Tomales Bay. Strictly speaking, reduction of SO₄²⁻ does not lead only to sulfides (S²⁻), but to a whole assortment of reduced sulfur compounds, among which pyrite (FeS₂) (Fossing et al., 1992; Stoessel, 1992). Loosely speaking, then, "sulfide" production is a geochemical dead end (at least in a stable anoxic soil) since metals build insoluble compounds ; this can be interesting for heavy-metal scrubbing (Mc Lerran & Holmes, 1974; Silva et al., 1990). Humic substances increase metal immobilization in anoxic sediments (Francois, 1990).

Sulfide accumulation is indirectly important as a potential source of acidity in the case of ulterior aeration of sediment, or soil (Marius, 1985; Stoessel, 1992). Neutralizing this acidity is one of the major problems in mangrove soil management (van der Watt et al., 1991). Other reduced sulfur compounds ("carbon-bonded sulfur") are mostly recyclable (Hordijk et al., 1989; Spratt & Morgan, 1990), while some of them (thiophenes) are refractory, and constitute biological markers of hypersalinity (Damsté et al., 1990). A recent paper points out that SO₄ reduction may take place in oxic (hypersaline) environments (Canfield & Des Marais, 1991); we saw above an analogous case with denitrification, with the probable juxtaposition of oxic/anoxic "micro-niches" (see below).

- Methane production : this process is limited by availability of electron donors (volatile fatty acids, H₂), for which sulphate reducers are more competitive. Methane production is hence most active in freshwater sediments (Sinke et al., 1990), although it may be found in brackish and marine environments (Harris et al., 1982; Crill & Martens, 1983; see also reviews by Hobbie, 1988 and by Capone & Kiene, 1988). In hypersaline environments, specialized methane producers skip competition by utilizing methyl amines (King, 1988). In every case, a portion of CH₄ may be re-oxidized in the overlying oxic waters; the main part, though, escapes from the system together with some fermentative CO₂. A somewhat peculiar example of CH₄ production in reasonably oxygenated waters of Red Sea was recently found by Owens et al. (1991).

1.3.2. Organic matter at the interface :

The limit between dissolved and particulate is rather arbitrary (Ogura, 1970; Koike et al., 1990). This is particularly true in the case of the various colloids (Whitehouse et al., 1990; Benner et al., 1992), "flocs", "slimes" (Fry, 1987; Kirchman & Ducklow, 1987) and "marine snow" (Alldredge et al., 1990; Karner & Hendl, 1992). These amorphous jellies make the frontier between solid and liquid a somewhat murky zone, especially frequent in marshes. Daumas (1990) has reviewed the characteristics of this water-sediment interface. Conversion of DOM into POM is often biological (Camilleri & Ribí, 1986), but abiotic processes are possible: flocculation of high molecular weight (MW) DOM in oligo-haline estuarine waters is well known (Mantoura & Woodward, 1983). DOM can be converted into POM by bubbling under constant salinity and pH (Kepkay & Johnson, 1989). Bacteria synthesize high-MW compounds (Fry, 1987; Brophy & Carlson, 1989; Couch & Meyer, 1992). Settling particles add some POM. Conversely, POM is partly transformed into DOM (see § 1.3.2. and § 2.2.1.). The resulting OM accumulation - evidently more frequent in low-circulation waters - results in low oxygen content (Cappenberg, 1988). Oxygen gradients are steep (Archer & Devol, 1992); even in relatively quick-flowing waters, the oxygenated sediment layer is very thin (Sweerts, 1990;

Sweerts et al., 1986, 1989, 1991; Brotas et al., 1990). Despite these low O₂ levels, bacterial activity can be highest at the interface (Stephens, 1981; Craven et al., 1986; Archer & Devol, 1992); cellulose decomposition is most rapid in this interface (Schroeder, 1987). Micro-aerophilic bacteria occupy a very thin sediment layer (Ferrara-Guerrero & Bianchi, 1990); analogous micro-aerobic niches are found around POM (Paerl & Carlton, 1988; Paerl & Bebout, 1988; Boto et al., 1989). The switch from aerobic to anaerobic processes entails differing transformations of OM (Hansen & Blackburn, 1991; see also fig. 2.1.1). The floc layer at the water-sediment interface thus appears a very special environment, seemingly with even specialized bacteria (Beier et al., 1991; Orem et al., 1991).

Consumption of oxygen by sediment (including here the interface and the sediment itself) may amount to 40 mmol O₂.m⁻².d⁻¹ above organic shallow sediments (Officer et al., 1985; Sweerts, 1990). For comparison, Zeitschel (1981) found uptakes of 1-2 mmol O₂.m⁻².hr⁻¹ above profundal sediments. Archer & Devol (1992) found that O₂ consumption is controlled by O₂ concentration, but also by supply of labile organic carbon. This O₂ uptake corresponds mainly to direct bacterial uptake of the O₂ diffusing from water into sediment; recent micro-electrode studies have shown that O₂ diffusion is limited to some millimeters (Sweerts et al., 1986, 1989). Solid/liquid interfaces in general are thus high-gradient zones (at the scale of micro-organisms), even under high turbulence (considered at the human scale). The frequency of micro-niches, which was rather hypothetical (see i.a. Horrigan et al., 1990), has been proven by using micro-electrodes; for instance, nitrifying and denitrifying sites may be about 50 μm apart (Seitzinger, 1988). We have seen above (§ 1.3.1) several instances of "typically anaerobic" reactions in oxic waters.

An indirect O₂ consumption by sediment stems from chemical oxygen demand by reduced compounds (H₂S, CH₄, NH₄,...; Berounsky & Nixon, 1990; Hansen & Blackburn, 1991; Archer & Devol, 1992; Roden & Tuttle, 1992).

A last remark may be made here: Most of what we saw about O₂ exchanges, or about nutrient fluxes between sediment and water (see below) has been arrived at under rather static experimental conditions. Medium-scale water movements do exist in nature. Archer & Devol (1992) show that irrigation of sediments happen, the more so in presence of macrobenthic organisms, and can amount to some 10 cm³.cm⁻².d⁻¹.

1.3.3. Organic matter in the water :

Particulate organic matter in the (oxygenated) water column comprises also the living organisms, to be logical. In most cases, though, "POM" is equated with trypton. With this viewpoint, POM generally represents about 1/10 of total OM, with DOM making up the bulk of aquatic OM. A high DOM concentration is typically some 10 - 40 mg DOC.C.l⁻¹, found in

the forest "black waters" (Tan et al., 1990) and in the bogs (Davies-Colley & Vant, 1987; Wrigley et al., 1988).

The chemical nature of DOM is still vague; "humics" and "fulvics" are rather general operative terms. About half of DOM components are identifiable (Moran & Hodson, 1990 a). Even extracting DOM from water is a delicate task (Amador et al., 1990). DOM reacts abiotically as a chelator (De Haan et al., 1990) and as a substrate for photolysis (Kieber et al. 1990). Its biological role, as nutrient pool, is well studied (Moran & Hodson, 1989, 1990 a; some references in Pagès & Gadel, 1990). The multi-faceted chemical properties of humic substances have been reviewed by Francois (1990).

Depending upon catchment area and vegetation, compared with the importance of the aquatic domain itself, the bulk of aquatic OM may be allochthonous or autochthonous (Mantoura & Woodward, 1983; Levine & Weibezahn, 1986). Some DOM may also ooze back from the sediment ; re-suspension by wind action is another possible source of OM, both POM and DOM.

1.4. Nutrients (inorganic -) :

In the systems we have in mind, inorganic nutrients are often found in relatively negligible concentrations, compared with those of OM and those of biomass. In a somewhat symmetrical arrangement are found "high nutrients, low chlorophyll" upwelling systems (Probyn, 1988). Here, we would have "low nutrients, high biomasses" systems, at least when considering the customary inorganic nutrients. We have already stressed the importance of OM. Apart from the very nature of the substrates to be considered, studying the nutrients as controlling - or limiting - factors of production meets two kinds of problems. The first series of problems is the observational scale. Most (micro) organisms found here have developed an *r.* adaptation, to relatively ephemeral nutrient patches, which may be highly localized (Kilham & Hecky, 1988). The same problem has hampered the understanding of high-sea oligotrophic zones, with the additionnal difficulty of swindlingly low nutrient concentrations (Slawyk et al., 90). The second series of problems - which is related to the first one - is the utmost importance of assessing dynamical (or kinetic) fluxes, and not static concentrations. As an example of this second point, photosynthesis has been shown to increase with remineralization *rate*, and not with OM *concentration* (Kolber et al., 1990).

Another kind of problem in defining (primary) production control stems from physiology. Liebig defined his "law of minimum"; several authors have studied phytoplankton's reaction to one "limiting nutrient" (see i.a. review by Morrison et al., 1987). This 'limiting nutrient' concept, though useful and fertile, may provide a skewed perspective under natural

conditions. Between N and P, for instance, the important point is not so much their absolute concentration, but rather their ratio (Hecky & Kilham, 1988; Davies & Sleep, 1989; Quiros, 1990). In another setting, the same N:P ratio has been shown to control denitrifying bacteria (Twilley & Kemp, 1986). We shall not dwell upon the distinction between 'limiting' and 'controlling' factors.

After having tried to show that inorganic nutrients should be unfit as predictors of production, we must though remind that these small molecules are generally the obligate intermediary form of uptake. Since they also are those forms for which sensitive analytical methods have developed, they are - also in methodology, which is not a very scientific point of view - an obligate check-point.

1.4.1. Nitrogen :

Organic nitrogen, under the form of amino-acids (Am Ac), may be uptaken as such by bacteria, or they may be split and used either as energy (carbon) source or as nitrogen source (Hollibaugh & Azam, 1983; Tupas & Koike, 1990). Few studies were able to yield firm proofs of axenic AmAc uptake by phytoplankton (Palenik & Morel, 1990). Dissolved organic nitrogen (DON) in general is often neglected in N budgets, and not solely because of methodological problems. DON may though be a key component, as shown by two examples from high-sea studies: The first one is the "secondary bloom" developing on DON released by N₂-fixing blue-greens (Capone & Ferrier, 1992); the second one is the fact that DON re-exsudation is the only possible explanation for the gap between NO₃ disappearance and PON synthesis (Eppley & Renger, 1992).

In sediments - which we saw to be mostly anoxic -, ammonium represents about 5 % of total N (Simon & Kennedy, 1987; Gonzalez-Prieto et al., 1989). Pore water concentrations range between 1 and 10 mmol N.l⁻¹ (Klump & Martens, 1989; Wilken et al., 1990). Vertical profiles result from simultaneous production and uptake (Wilken et al., 1990). Ammonium production appears to be - also - temperature-sensitive (Hines et al., 1982; Klump & Martens, 1989). Uptake of NH₄ in the sediment is wrought by bacteria and by plant roots. Mangrove trees extract some 250 kg N ha⁻¹.yr⁻¹, according to Hatcher et al. (1989).

Exchanges between water and sediment (not considering NO₃ reduction) vary widely (Day et al., 89, p. 112 & 128; Daumas, 1990; Carignan & Lean, 1991). Gardner et al. (1991) showed an increased NH₄ diffusion in salt water, compared to that in freshwater. Under moderate to null stirring, NH₄ fluxes range between 10 and 300 μmol N.m⁻².hr⁻¹ in near-shore waters (Kemp et al., 1990; Falcao & Vale, 1990); deep-sea sediments, for comparison, release

5-30 $\mu\text{mol N}\cdot\text{m}^{-2}\cdot\text{hr}^{-1}$ (Zeitschel, 1981). After a period of wind-less weather, a wind event may propel large amounts of NH_4 (often mixed with CO_2 and H_2S) from surficial sediment and hypolimnion into the whole water column. We have mentioned above denitrification as the chief process in N cycle. Actual processes are more complicated, especially in poorly oxygenated environments at the sediment-water interface (Jorgensen et al., 1984; Downes, 1988). Inter-conversions between oxidized and reduced forms may lead to the apparent nonsense of NH_4 reduction into N_2 (Golterman, unpubl. results).

The NH_4 found in the water can then originate from sediment, or be produced from decomposing DOM (Hollibaugh & Azam, 1983). Another source of aquatic NH_4 is excretion : zooplankton produces about $1\mu\text{g NH}_4 - \text{N}\cdot\text{hr}^{-1}$ per mg dry-weight (Capblancq, 1990). Fishes excrete about $50\mu\text{mol NH}_4\text{-N}$ per g dry weight per day (Durbin & Durbin, 1983; Bray et al., 1986).

In the (mostly oxygenated) water column, the various forms of nitrogen (NH_4 , NO_2 , NO_3) can coexist. Their interconversion happens mainly through biological processes. Horrigan et al. (1990) showed that fluxes between the various dissolved compartments may be much higher than uptake into POM. Anyway, NH_4 may be found in oxygenated waters together with NO_3 . In what regards "primary" (autotrophic) production, the "conventionnal wisdom" was that NH_4 is preferentially uptaken, and thus inhibits NO_3 uptake (Wheeler & Kokkinakis, 1990). A particularly fertile notion is that NH_4 fuels the "regenerated" production while NO_3 fuels the "new" (exportable) production. The "*f* ratio" describes the relative contribution of "new" and "regenerated" building of POM (Eppley & Koeve, 1990; Dugdale et al., 1990, 1992). While upwelling areas have typical *f* values of 0.8 or more, the regeneration-based systems can show negligible *f* values (Harrison, 1990). Such a perception of the importance of "regenerated" production stems from studies of pelagic nitrogen metabolism. It seems that a similarly formalized, explicit view is rather unusual in other environments (Caraco et al., 1992).

Biological fixation of atmospheric N_2 (be it in the water or in the sediment) may be an important item in nitrogen budget. Howarth et al. (1988) cite some impressive figures, from $1\text{ g N (m}^2\cdot\text{yr)}^{-1}$ in some sediments to $2\text{ g N (m}^2\cdot\text{yr)}^{-1}$ in mangrove swamps, with an extreme value of $50\text{-}70\text{ g N (m}^2\cdot\text{yr)}^{-1}$ in cyanophyte mats.

1.4.2. Phosphorus

Since sedimentary OM is mostly detritical (in near-shore or estuarine waters at least), its C/P ratio is very high (Wassmann, 1984; Matson & Brinson, 1990). On whole sediment of natural environments, available ("exchangeable") P ranges between 1 and $20\text{ g P}\cdot\text{m}^{-2}$ (Holdren

et al., 1977; Gunatilaka, 1988; Sinke et al., 1990). Proportions of organic P vs inorganic P are highly variable (De Groot, 1990). As with NH_4 , higher plants represent the only export (neglecting for now recycled litter) of P : Hatcher et al., (1989) mention a figure of 20 kg P/ha.yr. Phosphate may diffuse through anoxic sediment (Den Oude & Gulati, 1988 ; Sinke et al., 1990), although some exceptions have been observed (Krom & Berner, 1980). The traditional view is that phosphate becomes practically sequestered in oxic sediments (Cerco, 1989 ; Curtis, 1989 ; Staudinger et al., 1990), but instances are known where aerobic sediment can act as a P source (Twinch & Peters, 1984; Jensen & Andersen, 1992). In the "classical" view, microphytobenthos and algal mats would then have a twofold blocking action upon PO_4 diffusion from sediment (Sundbäck & Granéli, 1988). Moreover, phosphate diffusion back into water is also hindered by SO_4 (Caraco et al., 1989).

Despite the above hindrances, phosphorus can become exported from sediments (Boers & van Heese, 88). Diffusive P flux toward water is often low: Caraco et al.(1992) estimate sedimentary contribution to $0.5\text{-}20 \mu\text{mol P.m}^{-2}.\text{d}^{-1}$ in an oligotrophic lake. In other environments, P flux can reach $2 \text{ mmol.m}^{-2}.\text{d}^{-1}$ (Twinch & Peters, 1984; Sinke et al., 1990; Carignan & Lean, 1991; Jensen & Andersen, 1992). This diffusion is controlled by SO_4 , and is hence more active in salt- or brackwater sediments (Jordan et al., 1991). Adsorption of PO_4 upon particles is a very active, and rapid, process (review by Froelich, 1988; Engle & Sarnelle, 1990). Combination of PO_4 with aquatic humics, also an active and frequent process, can have two opposite effects : PO_4 -Ca-humics effectively trap PO_4 , while PO_4 -Fe-humic complexes are weakly sequestering (Francko & Heath, 1983; Francois, 1990 ; De Haan et al., 1990). The high reactivity of PO_4 is also apparent in the various "organic P" compounds, in which P is - theoretically - not biologically available ; the answer to this problem are phosphatases, the first well-studied extracellular enzymes (Chrost et al., 1986).

In european (or westernized) countries, PO_4 is considered as the major cause of eutrophication in fresh water systems, with a major rôle of detergents (Golterman, 1991 a). In the Third World countries we saw (mostly West Africa), detergents are not yet phosphate-based, and sewage has relatively low PO_4 concentrations. The possible consequences of other anthropic PO_4 sources are offset or masked by other contaminants (fluorides in the case of phosphate mining).

1.4.3. Potassium

Aquatic biologists, and especially marine ones, never consider K as a possible limiting nutrient since it is always present in seawater at concentrations some orders of magnitude higher than N or P. In continental freshwaters, though, Golterman (1991 a) reminds that concentrations of practically all necessary elements (among which K) are much lower than algal

requirements. Waters with (relatively) high N and P loads could then be K-limited; this may happen, for instance, in effluent treatment ponds (Kroon et al., 1989). Rice fields are another problem, since reaped biomass exports about the same weight of P_2O_5 and of K_2O ; this amounts to about $50 \text{ mmol K} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, which must be replenished.

1.4.4. Silicium

Silicates are found in "average" organic matter at about the same atomic concentration as N (Day et al., 1989). Diatoms are the aquatic organisms most liable to be Si-limited. River waters show SiO_3 concentrations of $100\text{-}500 \mu\text{mol} \cdot \text{Si} \cdot \text{l}^{-1}$, while a typical "high" seawater concentration is $5\text{-}20 \mu\text{mol} \cdot \text{Si} \cdot \text{l}^{-1}$ (Harris, 1986 i.a.). Estuaries are often a sink for SiO_3 , through biotic and abiotic processes. Sediments act as buffers, receiving particulate silicates (sand grains or diatoms) and releasing dissolved SiO_3 (Schink et al., 1975; Yamada & d'Elia, 84; Falcao & Vale, 1990). Some Si may be sequestered as opal, under interaction with humic acids.

1.4.5. Sulfur :

Sulfur, like K, is practically never limiting in marine or brackish waters (about $40 \text{ mmol SO}_4\text{-S} \cdot \text{l}^{-1}$ in seawater) but might become limiting in very dilute, N- or P-enriched continental waters. Sulfur is necessary; it is found in organic matter at about the concentration of P (Harris, 1986). Aerobic $^{35}\text{SO}_4$ uptake has been proposed as an alternative to ^{14}C uptake for primary production measurement (Monheimer, 1978). We have mentioned above that SO_4 concentration regulates (directly or not) both N_2 fixation and PO_4 diffusion.

Sedimentary sulfur cycle is dominated by sulphate reduction, as seen above. Among the reduced compounds thus produced, carbon-bonded S and thiosulfates are recyclable in low-sulphate environments (Hordijk et al., 1989; Spratt & Morgan, 1990; Jorgensen, 1990). Sulfate flux toward the sediment is highly variable; one of the numerous factors is organic matter content and decay rate. Typical values are about $1 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ (Kelley et al., 1990).

Reduced organic sulfur compounds released in the water are potential electron donors for oxidation by bacteria and for anoxygenic photosynthesis, by some *Cyanobacteria* (Javor, 1989) and by bacteria (Steenbergen & van den Hoven, 1990; Overman et al., 1991).

1.4.6: Carbon:

Life (on Earth) is based upon carbon, which constitutes about 50 % of OM dry weight (see also § 3.2.2 and 4.1). Availability of inorganic carbon (be it CO_2 , HCO_3^- or CO_3^{2-}) is most often taken for granted. Dissolved inorganic carbon is never limiting in seawater. Freshwater plants may though be C-limited (see Day et al., 1989, their fig. 4.12). In natural brackish or fresh waters, DIC depletion can become apparent from pH increase in late afternoon. An extra supply of DIC can be necessary in high-density microalgal cultures (Goldman et al., 1981; Moulton et al., 1987).

The recent preoccupations about greenhouse gases have furthered the study of global carbon cycle(s). Sedimented POC represents a sink for carbon; there are though some leaks, since CH_4 and CO_2 may find their way back into the atmosphere (Carignan & Lean, 1991).

1.5. Light :

In terrestrial ecosystems, water and nutrients are the most evident limiting factors. In aquatic ecosystems, light was very soon identified as possibly limiting. We shall deal later on with photosynthesis-light models; we shall limit the present chapter to a quick description of underwater light field.

The laws of underwater light propagation are well known (Kirk, 1983; Spinrad, 1989). Waters in swamps, mangroves or estuaries are naturally not qualitatively different, but some quantitative aspects are particular. As a whole, these waters are optically deep, although their frequent shallowness may bring a portion of the bottom into the euphotic zone.

1.5.1. Components of light attenuation :

In clear waters, where absorption is more effective than diffusion, underwater irradiance decreases exponentially with increasing depth.

The simplest - and yet highly effective - description of transparency is Secchi disk depth, Z_s . An alternate way is assessment of underwater irradiance distribution (Jewson et al., 1984). Vertical attenuation coefficient for downwelling light, K_d (using Kirk's notation), is the most often measured coefficient. It results from the sum of *i*) K_b , biological attenuation by phytoplankton, *ii*) K_p , by total suspended solids (TSS, mostly inorganic) and *iii*) K_w , by dissolved substances (see Gallegos et al., 1990, for a general treatment). The relative importance of each component allows a classification of water types (Morel & Prieur, 1977; Kirk, 1983; Hojerslev, 1985; Mueller & Lange, 1989). The relationship between Z_s and K_d is characteristic of a given water type. A very rough approximation for inland waters is given by

$Z_s \cdot K_d = 1.44$ (Kirk, 1983, p. 96; see also Koenings & Edmundson, 1991); for oceanic waters, Balch et al. (1992) arrive at $Z_s \cdot K_d = 1.7$.

A: Biological component:

The ratio K_b/K_d represents the part of incident light actually harvested by phytoplankton. Absorption spectrum by phytoplankton shows two peaks, a major one at about 450 nm, a secondary one at 660 nm (at least in the most frequent case when chlorophyll *a* is the main pigment). Absorption in the PAR range (400-700 nm) is roughly proportional to biomass, but chlorophyll-specific attenuation, K_s , is not really constant. Bannister (1974) proposed a median value of $0.015 \text{ m}^2 \cdot \text{mg}^{-1}$. Ulterior work has shown that K_s is influenced by several factors, among which the "package effect" (Berner et al., 1989; Bricaud & Stramski, 1990; Gons & Rijkeboer, 1990; Sathyendranath et al., 1991).

B: Suspended solids

Suspended sediments have predominantly scattering properties (Bannister, 89; Gallegos et al., 1990).

Transparency, expressed by Z_s , is well correlated with TSS (total suspended solids) load across several orders of magnitude (Manheim et al., 1972). A turbid water may contain a TSS load of $50\text{-}200 \text{ mg} \cdot \text{l}^{-1}$ (Froelich, 1988 ; Kirk, 1983), which gives a Z_s value of $0.3\text{-}0.8 \text{ m}$. Underwater irradiance measurements, though, may give unclear results in very turbid waters. This is due to high back-scattering diffusion, which leads to high reflectance coefficients (Kirk, 1983; Bannister, 1990 a; Gallegos et al., 90). Determination of actual available light, and of euphotic depth, is thus complicated.

C: Dissolved components

Among the optically active dissolved substances, the most effective are humic substances (= DOM). Their collective names of "Gelbstoff" or "gilvin" (Kirk, 1983) reflect their (transmitted) yellowish colour when dilute. The high-DOM forest or bog waters appear reddish-black (Tan et al., 1990). This is due to a strong absorption in the blue-violet region (and a still stronger one in the UV range; Bricaud et al., 1981). A highly-coloured water contains $10\text{-}50 \text{ mg DOC C} \cdot \text{l}^{-1}$ (Pagès & Gadel, 90). Several components of DOM are fluorescent. This allows a detailed and sensitive assessment of DOM (Coble et al., 1990; Ferrari & Tassan, 1991; Moran et al., 1991 a).

1.5.2. Remote sensing applications :

Remote sensing generally demands high investments, but is often cheaper than traditional ground surveys, even on relatively easy ground. Tropical marshes and mangroves,

where ground travel is difficult at best, are an exemplary application field of remote-sensing techniques. We shall limit our present scope to passive sensors. Near-IR radiation can yield reasonably accurate surface temperature values (see Reynolds et al. (1989) for possible bias; for results on a global scale, see i.a. Strong (1989)). What follows is restricted to use of visible range radiation.

We have mentioned that high TSS loads cause high reflectances. Turbidity is probably the water feature which is most easily assessed by remote sensing (Sturm, 1981 ; Lindell et al., 1986 ; Curran & Novo, 1988 ; Stumpf & Pennock, 1989).

The upward radiance of a water body is also modified by bottom reflectance in optically shallow waters (Mobley, 1989). Exploration is limited to a water layer of about $1/K_d$ (remembering that light transmission is generally better in the blue-green window). This amounts to somewhat less than half Z_s . Several bathymetric mapping by satellite have been carried out, with self-obviously better results in clear waters (Topliss, 1984; Stumpf & Pennock, 1989; Ritchie et al., 1990). Inter-tidal and supra-tidal sediments are also amenable to remote sensing studies (Zbinden, 1983; Wang & He, 1988).

Assessing phytoplankton biomass by remote sensing appears a rather simple task in view of the very clear radiative signal (Kirk, 1983, p.155). There are indeed cases of Morel's "type I" waters where the chlorophyll signal is unadulterated (Galat & Verdin, 1988), but interferences are frequent, either by TSS or by DOM (Roesler et al., 1989 ; Smith et al., 1989 ; Vertucci , 1989; Ritchie et al., 1990). These interferences could sometimes be resolved: DOM interference with chl (Carder et al., 1986, 1989), DOM interference on seston (Winters & Buckley, 1980), interference of seston with chl (Brown & Simpson, 1990). Vertical chl distribution is sometimes a supplementary problem in pelagic tropical systems, where chl maximum is found at the basis of the thick mixed layer (Morel & Berthon, 1989). Such problem should not arise in the shallow environments envisioned here. Photosynthetic production can be inferred from remotely-sensed phytoplankton biomass and from the known [P vs I] relations (see Platt et al., 1988; Platt & Sathyendranath, 1988; Balch et al., 1992). Another, possibly more direct path (at least from a theoretical point of view) relies on assessment of solar-induced fluorescence at 683 nm (Stegman et al., 1992).

"Terrestrial" systems in marshy areas have also been mapped by remote sensing. Estimating vegetated surfaces is the most immediate application; a semi-quantitative assessment is possible with the various vegetation indices (Hodgson et al., 1987; Everitt & Judd, 1989; Crippen, 1990; Conner & Brody, 1990; Evans & Hill, 1990). Differentiating vegetations (for instance *Rhizophora* / *Avicennia* / *Nypa*) is sometimes possible (Dutrieux et al., 1990), although

radiative signals can be modified by water budget and climatic conditions. Ground-truth is always necessary.

1.6. Oxygen :

1.6.1: Oxygen budget

While oxygen does not belong to "nutrients" in the classical sense, the oxygenation status of a water determines its ability to support most life forms. O₂ concentration results from the equilibrium between production and consumption, since O₂ diffusion from air into water is of small importance, even under wind stirring (Talling, 1957; Gat & Shatkey, 1991). Oxygen is a by-product of photosynthesis; we shall hence have to mention here some (perhaps elementary) points about this process.

Oxygen sources are rather well defined. Some O₂ is brought down into the (relatively) deep sediment layers by macrophyte roots (Yamazaki, 1987; Seitzinger, 1988); this leads also to the "iron-pipe formations" around *Avicennia* roots (Marius, 1985; Thibodeau & Nickerson, 1986). The sole significant O₂ source in the water is then photosynthesis, both in the illuminated layers of the water column and on the bottom (Lindeboom et al., 1985 ; Jorgensen & DesMarais, 1990).

Photosynthetic O₂ production, representing "gross" photosynthesis, is a function of irradiance, at least in the simple case of an homogeneous water column. Several mathematical expressions have been proposed (see i.a. Jassby & Platt, 1976; Kirk, 1983). These various forms are in fact of equal theoretical value when the actual accuracy of experimental data is considered (Golterman, 1991 a; Balch et al., 1992). The main point for our concern is that gross O₂ production, A , decreases (along with irradiance) at increasing optical depth. Vertically integrated production ($R_z A$) is thus a function of attenuation coefficient K_d ; Talling's integral (1957) is the best known: $R_z A = (A_{max}/K_d) \cdot \ln(2I_0/I_k)$ (see Balch et al., 1992, for compared performances of various models of $R_z A$). Since gross production, A , is roughly proportional to phytoplankton biomass B (often estimated by chlorophyll concentration), and since B is often the main component of K_d , the homeostatic properties of phytoplankton gross production are apparent in the above integral.

Net oxygen production represents the difference between A and respiration (R). At the level of the whole water column, the decisive factor is the difference ($(R_z R_t A) - (R_z R_t R)$) between integrals over time and depth. "Classical" aquatic communities are based upon a predominant phytoplanktonic biomass. This means more or less implicitly a truly eutrophic system, where primary producers are not nutrient-limited and where (micro)heterotrophs are negligible. Anyway, phytoplankton respiration is often considered the main part of oxygen

consumption, and has been well studied. We shall only mention the notion of photo-respiration (see Grande et al., 1989). Beside this rather special effect, phytoplankton respiration may be roughly estimated at about $1/10$ of A_{\max} (Ganf, 1974 a; Talling, 1957; Grande et al., 1989; Grobbelaar, 1990; Grobbelaar et al., 1990). The other components of the aquatic (pelagic) community must also be counted in the total O_2 consumption: aerobic bacteria (Schwaerter et al., 1988; Cole et al., 1989; King & Palmer, 1989; Steenbergen & van den Hoven, 1990), zooplankton and fishes (see Mazumder et al., 1990 a, b for whole column O_2 budget). In most natural waters, net production can be positive or negative, but often hovers around zero. In a symmetrical way, carbon balance - at various depths or on the whole column - may be positive or negative (Hessen et al., 1990; Kelley et al., 1990; Jahnke et al., 1990). A rather special case is found in the man-made "High Rate Algal Ponds", in which bacterial respiration is a hefty proportion of total O_2 consumption (see i.a. Kroon et al., 1989).

We might conclude about O_2 budget with two remarks. Talling's model, as furthered by Vollenweider (1970), has been highly successful (Ganf & Viner, 1973; Ganf, 1974; Jewson, 1976; Platt, 1989). Most of these studies, though, were carried out on water bodies where bottom influence was negligible against the various processes in the water itself. We saw above (§ 1.3.2) that sedimentary O_2 uptake (or O_2 production by benthic microalgae) may be important in the overall O_2 budget. Another point must be recalled: In "classical" systems, the ratio of eutrophic depth to mixing depth is a reasonable predictor of net integrated production (Guildford et al., 1987; Smetacek & Passow, 1990, i.a.). This is true only when photosynthesis is the chief process. We shall see below (§ 2.3) some other cases.

1.6.2: Oxygen and biology

We may note that O_2 solubility decreases with increasing temperature, but mainly with increasing salinity (Weiss, 1970; Kinsman et al., 1974; Geddes, 1975; Sherwood et al., 1991). Since O_2 uptake by haemoglobin depends upon partial pressure, a lowered O_2 content at constant p_{O_2} should not be harmful to fishes. But increased temperature heightens metabolic rates against impoverished O_2 reserves, while increased salinity heightens osmoregulatory expenditure (we are alluding here to actual cases, with $T > 30^\circ\text{C}$ and $40 < S < 80 \text{ g.l}^{-1}$; Pagès et al., 1987). In less harsh conditions, Blaber (1985) did observe synergistic lethal effects of temperature and salinity on juvenile fishes.

Benthic fauna is often limited by O_2 content (see review on benthic macrofauna in muds, by Lopez, 1988). Its biomass is about $5\text{-}10 \text{ g dry weight m}^{-2}$ (see § 2.2). This supplementary oxygen consumption (above that of the sediment itself) is hence a not negligible

item in O₂ budget. Bioturbation increases O₂ consumption, by enhancing sediment-water exchanges (see i.a. Baudinet et al., 1990).

We have overflowed anaerobic processes in the sediment; we shall leave untouched the vast specialized domain of anaerobic, possibly chemiotrophic, bacteria (see some references in Javor, 1989, and in Sweerts, 1990).

2. Functioning and role of near-shore waters :

We have reviewed separately several physical and chemical factors which might characterize near shore, shallow, organic-rich waters. We shall now consider some peculiarities of the resulting food-webs of these environments, and their possible effects upon neighbouring systems.

2.1. Detrital food webs :

2.1.1. Litter decomposition processes :

We have seen above that organic matter (OM) gives off nutrients and energy, leading to heterotroph biomass and, indirectly, to autotrophic growth. We consider here the "practical" aspects of OM decay.

Most published results about OM decomposition rate are well described by first order kinetics with one homogeneous compartment (Bianchi & Findlay, 1991). This is true for natural DOM (Westrich & Berner, 1984; Kaplan et al., 1980 ; see also review in Pagès & Gadel, 1990) and for natural POM or detritus (Wetzel & Manny, 1972 ; Hart & Howmiller, 1975 ; De La Cruz & Post, 1977; Anderson, 1987 ; Blackburn, 1987). Some authors, though, identify a "refractory" compartment, especially in POM decay studies (Robertson, 1988 a; Gonzalez-Farias & Mee, 1988). The "multiple G model" considers several compartments in (sedimentary) organic matter (Burdige, 1991; Hansen & Blackburn, 1991); in the (too frequent) case of some scattering of experimental results, however, this model is equivalent to a refractory compartment (Carignan & Lean, 1991). We may remark as a mere detail that a system of two compartments, each with its exponential decrease, is analogous to Simpson & Dickey's model (in Cullen et al., 1992) for light attenuation in water. Decomposition rate of the more labile components is around 0.1 - 0.05 day⁻¹ for mangrove litter (Robertson, 1988 a). This rapid initial decay has been ascribed to leaching of DOM from litter in most cases (Benner et al., 1986; Moran & Hodson, 1990 b). In some other cases, weight loss was due to direct

attack and uptake, without any DOM intermediary step (Wilson et al., 1986; fig. 7.8 in Day et al., 1989). Decomposition rate for a given OM batch decreases with time, down to values of $0.01 - 0.001 \text{ day}^{-1}$ (see Hobbie 1988, p. 752). On the whole, turn-over times can thus be comprised between 2 months (Twilley et al., 1986) and more than 8 months (Wiegert & Murphy, 1970 ; Day et al., 1987 a).

Degradation rate is governed by several factors, which we may order into "intrinsic" ones, "environmental" ones, and "extrinsic" ones :

- we label as "*intrinsic*" factors nature, origin and composition of detritus. It has been long known in agriculture that manure - which is a form of litter - decomposes best at the "right" C/N ratio. In the same way, high C/N or C/P ratios lead to low decomposition rates (Benner et al., 1985 ; Robertson, 1988 a; Matson & Brinson, 1990). Bianchi & Findlay (1991) find decay rates sinking from 0.03 to 0.002 d^{-1} for increased C/N ratio. A remarkable fact is the increase of C/N during decomposition of POM (see below), due perhaps to N-scavenging by microbes but mostly to high carbon losses. In this instance, we may notice that some caution is required when using ratios, as stressed by Bianchi & Findlay (1991; p. 66). Lignins are rather refractory to biological attack (Moran & Hodson, 1989) and can hence be good markers of terrestrial organic matter (Gardner & Menzel, 1974; Moran et al., 1991 a, b). Tannins (and phenols in general) are often considered to be both refractory and inhibitory to (bacterial) attack (Gonzalez-Farias & Mee, 1988). As a whole, OM of terrestrial origin, with higher C/N ratios and more lignins, will be more refractory than "aquatic" OM (Prahel et al., 1980). As we mentioned above, diagenesis leads to a progressive alteration of bulk OM composition (Burdige, 1991; Cowie & Hedges, 1992; Burdige et al., 1992)

- the "*environmental*" factors may roughly be summed up by water availability. Higher humidity leads to higher decomposition rate in rain forests (Wiegert & Murphy, 1970) as well as in Mojave desert (Strojan et al., 1987). Rain accelerates the decay of standing dead reeds (Newell et al., 1985). In mangroves, high submersion frequency also promotes litter decay (Twilley et al., 1986 ; Robertson, 1988 a; Lee, 1989 a,b). Conversely, high salinities reduce litter decomposition in mangroves (Day et al., 1987 a; Snedaker, 1989) and DOM decomposition in salterns (Javor, 1989). Water content also controls - however remotely - oxygen availability. Anaerobic processes have often been shown to conserve carbon, being much slower than aerobic decomposition processes (Kepkay & Anderson, 1985; Benner et al., 1985, 1991). These latter are more efficient in terms of yield, either for ATP or for growth, at least from in vitro studies (Pirt, 1965; Hadjipetrou & Stouthamer, 1965 ; Oxenburgh & Snoswell, 1970; Payne, 1972). This lower efficiency of anaerobic bacterial processes would then lead to a higher consumption of substrate (Lee, 1992). But the very fact of a fundamental

difference between oxic and anoxic rates has been disputed when natural environments and populations are considered (Lee, *ibid.*). Hansen & Blackburn (1991) found unchanging hydrolysis rates of POM, while mineralization of the released DOM was lower under anaerobic conditions.

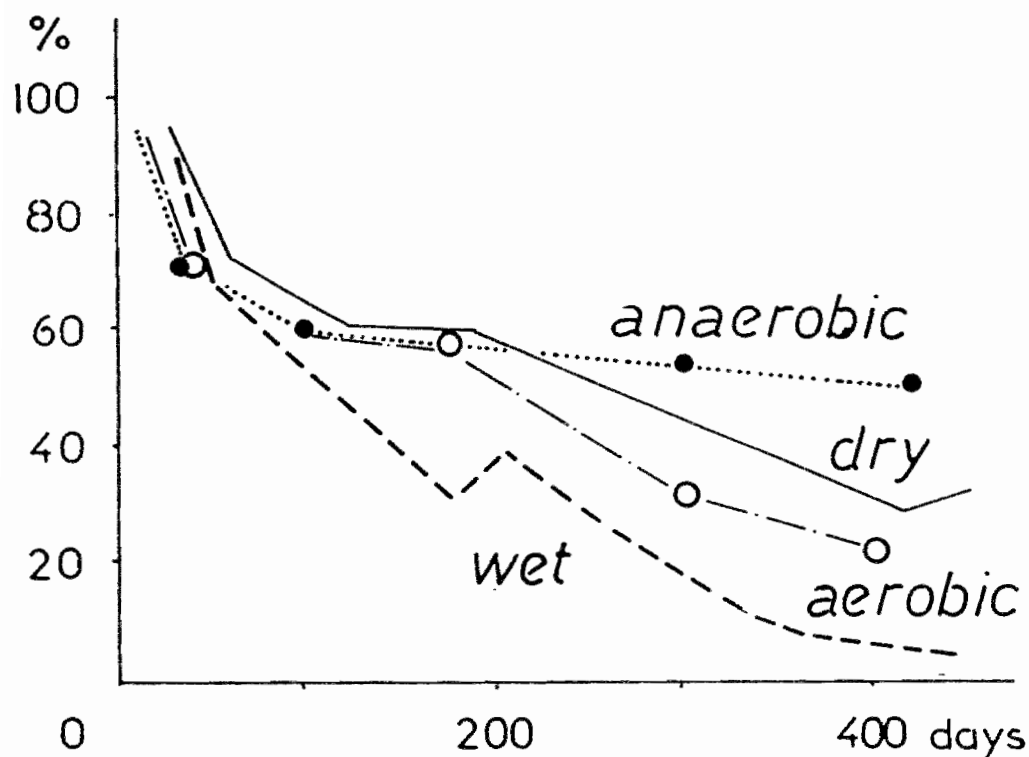


Fig. 2.1.1: Some examples of decomposition rates of plant material: Percent remaining dry weight as a function of time for *Rhizophora* leaves under dry (—) and wet (- - -) conditions, after Day et al. (1989), and for *Spartina* leaves with (o) and without (o) oxygen, after Valiela (1984).

Most of the above results stem from (more or less *in vitro*) experiments. An interesting possibility of artefact has been noticed by Gessner (1991), who found that dried (*i.e.* artificially so) leaves are prone to a much higher leaching than intact ones.

~~We order as "extrinsic" the various bio-degradation actions due to various organisms.~~
 Bacterial (or microbial) action would appear of paramount importance, as a first and obligatory step in OM decomposition (see partial review in Moran & Hodson, 1990 b; Couch & Meyer, 1992;). Weight loss of litter is not due solely to microbial attack, though; Moran & Hodson (1989) find that measured bacterial production accounts for only half the observed weight loss of *Juncus* litter. Occurrence and role of exo-enzymes appear larger than previously admitted (Chrost et al., 1986; Wetzel, 1991). Colonization of detritus by micro-organisms results in a

marked decrease in C/N ratio, whatever the precise causes (Moran & Hodson, 1989). This "conditioning" improves litter digestibility (Schroeder, 1987; Bowen, 1987; Crosby et al., 1990), although N-enrichment apparently has no effect per se (Schroeder, 1987). Mechanical comminution occurs at the next trophic levels, during feeding by small invertebrates of several phyla (Valiela, 1984; Warwick, 1987). Shredders in general markedly increase OM recycling (Cummins, 1988; Moran & Hodson, 1989). Small invertebrates accelerate pigment decomposition (Bianchi et al., 1988, 1991) and export of fine POM (Wallace et al., 1991). At a still higher trophic level, various crabs are very active; Hatcher et al. (1989) ascribe them up to 80 % of litter disappearance; Lee (1989 b) offers a more cautious estimate of 30 %. At the trophic level of fishes, importance of detritivory is (expectably) variable. Detritus may constitute a hefty proportion of the diet in juvenile fishes (Harrigan et al., 1989; Ahlgren, 1990 a,b; Davanzo & Valiela, 1990). Some opportunistic fishes, like the "tilapias", may turn to exclusive detritivory (Moriarty & Pullin, 1987; Edwards, 1988; Pauly et al., 1988). Actual detritus utilization may be low in some species (Deegan et al., 1990), also in relation with their enzymatic equipment. Valiela (1984) cites a peak value of 40 % utilization of detritus, while Mann (1988, p. 924) finds a yield of 30 % for a whole detrital food chain.

2.1.2. Detrital food webs and microbial loop :

Near-shore waters, estuaries or mangrove waters in an unpolluted state receive a relatively low amount of NO₃ or PO₄, despite occasional tides, while organic matter and NH₄ (either nearly autochthonous or really allochthonous) are abundant. Underwater light levels are often low owing to high attenuation, so that photosynthesis in the water tends to be - also - light limited. These conditions explain how recycling processes are predominant.

The classical food chain is rather linear, with phytoplankton producing organic matter and bacteria just cleaning up after fishes. With a growing number of studies showing a quantitative gap between (heterotrophic) predator biomass (and uptake) and primary production, a first answer was given by pico-plankton (see review by Stockner, 1988). Detrital food webs had been analyzed, but their scope, or their explanative value, was mostly limited to particulate (however fine) detritus and accompanying bacteria (Odum & Heald, 1975; Fenchel & Jorgensen, 1977; ; see review by Mann, 1988; Moran & Hodson, 1989). Riemann et al. (1990) cite Pomeroy (1974) as the pioneer of the "microbial loop", which accounts for production based on DOM (Jumars et al., 1989; Moran & Hodson, 1989). In this shunt, autotrophic (photosynthetic) processes contribute "only" O₂, and most biomass transfer is heterotrophic. Bacteria growing upon DOM are grazed by micro-heterotrophs (nano- and micro-flagellates), themselves grazed upon by ciliates (see i.a. McManus & Fuhrman, 1986; Bloem & Bär-Gilissen, 1989; Bennett et al., 1990; Hadas et al., 1990; Van Wambeke &

Bianchi, 1990). This mechanism and the more classical detrital food-webs fit nicely together into the rather peculiar environments we are dealing with.

Bacteria play a central role in the "microbial loop". They also do so in the parallel concept of "f ratio" (see also § 2.3). To the best of our knowledge, this "f ratio" idea was initially oriented towards free-water (and high-sea) systems near O₂ saturation (Eppley & Renger, 1992 i.a.). In near-shore waters, the substrate comes from a (relatively) low-O₂ environment and results into a high-O₂ one, since NH₄ (or DOM) fuels photosynthesis (see fig. 1 in Santschi, 1988).

The "microbial loop", as well as the picoplankton-based webs of oligotrophic waters, functions with small-sized organisms (Furnas et al., 1986). Size distribution has been a fruitful theme in studies of pelagic autotrophic organisms some twenty years ago (Sheldon & Parsons, 1967; Banse, 1976; Cousin, in Mann, 1988) and has had a continued success (Venrick et al., 1977; Furnas, 1983 a,b, 1987; Venrick et al., 1987; Suttle et al., 1990). Several studies show that size spectrum is a valuable indicator of "metabolic rate" for whole portions of food-webs (Sheldon et al., 1986; Yentsch & Phinney, 1989; Nielsen & Sand-Jensen, 1990; Suttle et al., 1990; Thingstad & Sakshaug, 1990), and especially for detrital ones (Kerr & Ryder, 1988; Mazumder et al., 1990 a,b) although some caution may be necessary (Lehman, 1988).

2.2: Yields and rates: figures and predictors:

Although "yield" often means "harvestable biomass production", i.e. seen from a human (and utilitarian) point of view, we shall briefly review the lower trophic levels of aquatic systems. Despite the importance of recycling, which we just stressed, and the subsequent feedback loops in the food web, we shall adopt below a very "classical" compartmentation along the linear hierarchy typical of an autotroph-based food chain.

2.2.1: Bacteria:

Methods for assessing bacterial biomass have improved a relatively long time ago (Gwynfryn, 1974; see Moriarty, 1987) but some problems remain (Ward & al., 1990). Viability, among others, may remain an unanswered question (Bergh et al., 1989). Bacterial abundance is still often given as cell number; while bacterial size is highly variable, a tolerable approximation would be about $2 \cdot 10^{-14}$ g C per cell (Couch & Meyer, 1992; Karner & Hendl, 1992). Figures for absolute bacterial biomass vary widely; a magnitude order could be between 1 and 100 $\mu\text{g C.l}^{-1}$, depending on the environment (Lind & Davalos=Lind, 1991; Eppley et al., 1992). Bacteria may amount to between 1 % and 10 % of phytoplankton biomass in eutrophic

waters (Cho & Azam, 1988), but can constitute up to 50 % of particulate organic nitrogen in oligotrophic waters (Eppley et al., 1992). Several authors find parallel distributions of bacterial abundance and of chlorophyll (Bird & Kalff, 1984; Malone & Ducklow, 1990), while others see no relation between both compartments, owing to allochthonous imports (Findlay et al., 1991). Anyway, a correlation does not explain the functioning of such complex systems, except in some "evident" cases (Robarts, 1988). Sorokin (1981) stressed the basic difference between biomass and actual production (at the bacterial level also). The ^3H -thymidine method -among others- has though facilitated the task of assessing bacterial biomass production (Fuhrman et al., 86). Several studies have quantified bacterial activity in various environments (Fuhrman & Azam, 1980; Williams, 1981 a; Azam et al., 1983; Ducklow & Hill, 1985; Servais et al., 1985; Baker & Farr, 1987; Bell & Ahlgren, 1987; Alongi, 1988; Horrigan et al., 1988; Schwaerter et al., 1988; Fuhrman et al., 1989; Bloem et al., 1989 a; Pett, 1989). The actual contribution of bacteria to upper-levels metabolism is still sometimes controversial (Moriarty & Pullin, 1987; Billen et al., 1990). Bacterial growth yield is naturally highly variable (see Pirt, 1965). An average value of 30 % has been found in several instances (Sorokin, 1981; Meyer et al., 1987), but yield is controlled by substrate nature. Humic DOC allows a yield of about 0.2 % (Leff & Mayer, 1991) while DOM exuded by healthy phytoplankton supports 50 % growth yield (Baines & Pace, 1991); aromatic hydrocarbons supported yields of 10-14 % in cultures (Beller et al., 1992).

Bacterial biomass may be controlled (like that of phytoplankton) either through "bottom-up" or through "top-down" processes. On one hand, axenic cultures are obviously controlled by substrate; this led to the well-known uptake (or growth) kinetics of Monod and of Droop (among the best known; see Morrison et al., 1987, for a review). On the other hand, natural bacterial populations may or may not be substrate-limited. These natural populations often have high production rates, owing to intense grazing. This top-down control has been more often deduced than proven, but remains a plausible and effective control mechanism for bacterial biomass (Pernie et al., 1990; Berninger et al., 1991; King et al., 1991). This again exemplifies the distinction (see above) between "static" biomass and "kinetic" production.

We have been dealing above with free-water bacteria (attached or free). Sedimentary bacterial biomass is often considered as an integral part of the said sediment. Sorokin (1981) gives a range of 1 to 5 mg per g of sediment. Several authors have indirectly assessed bacterial biomass, either through ATP determination (Christensen & Devol, 1980; Craven et al., 1986) or by other methods, and arrive at comparable magnitude orders (Bell & Ahlgren, 1987; Moriarty et al., 1991). Bacterial biomass may accumulate in anoxic sediments; since bacterial markers amount to 2-5 % of OM (Lee, 1992), the bulk of bacterial substance could amount to a very high proportion of sedimentary organic matter. Determination of bacterial production in

sediments is somewhat biased by the necessary use of slurries, and not of undisturbed cores (Tibbles et al., 1992).

As a last detail, we may notice that we have voluntarily skipped the field of aquatic fungi, molds and actinomycetes, which we have implicitly included on a functional level. These organisms may be highly active in POM decomposition (especially on "exotic" or toxic molecules), although they may also be surprisingly limited (Benner et al., 1984). In the water itself, both their low abundance and their slow growth make them negligible against bacteria.

2.2.2 : Primary production:

While phytoplankton is not always the main source of particulate organic matter, its role must though be recalled. Its biomass is routinely estimated in chlorophyll, although carbon is the more general "currency". The ratios C/N/P/chl/ATP often reflect nutritional status; among the numerous recent papers, see Minster & Boulaïdid, 1987; Kana & Glibert, 1987; Guildford et al., 1987; Davies, 1988; Bailey-Watts, 1988; Rivkin, 1989; Thompson et al., 1989; Prairie et al., 1989; Nielsen & Sand-Jensen, 1990). A medium-range phytoplankton biomass is about 15 mg chl. m⁻³ in estuarine waters. While production is highly variable (§ 1.5.2), an average figure for net production would be about 1 g C. m⁻².d⁻¹, amounting to some 250 g C. m⁻².yr⁻¹ (Day et al., 1989, p. 153). Photosynthetic yield (ratio of net, harvestable biomass to available solar energy) may reach 8-9 % in intensive microalgal cultures (Sukenic et al., 1987; Moulton et al., 1987; Vonshak & Richmond, 1988; Hartig et al., 1988; Fontes et al., 1989; Grobbelaar et al., 1990). Yields of about 4 % are still in the high range for natural waters with dominant photosynthetic biomass (Weidemann & Bannister, 1986; Barbosa et al., 1989). We have seen (§ 1.5.2) that quantum yield is also controlled by nutrient availability, or by recycling rate. In (artificial) fish ponds, energy may be added as inorganic fertilizers or as organic detritus. These additions represent an increase in O₂ demand, and will be rate-limited by oxygenation capacity of the pond (Moriarty, 1987).

Specific attenuation also decreases slightly at high biomass concentrations, indicating an increasing scattering of light by cells. Some of the highest biomasses, observed in intensive micro-algae cultures, are about 20 mg chl.l⁻¹, representing about 300 mg C.l⁻¹ (Boussiba et al., 1988). Vertically integrated biomasses seldom exceed about 800 mg chl.m² (Agusti et al., 1990). The ratio K_t/K_d is in rough agreement with the photosynthetic yield of the water body considered (Lemoalle, 1983; Bailey-Watts, 1988). Another effective parameter for primary production "prediction" is given by the optical depth of the mixed layer, represented by the ratio Z_{eu}/Z_{mix} (Kirk, 1983; Keller, 1988; Mueller & Lange, 1989; Smetacek & Passow, 1990; Grobbelaar, 1990). We have mentioned that light often limits photosynthesis; this explains how the ratio K_t/K_d can be a good predictor of global photosynthetic yield (Lemoalle, 83). In the

same vein, the ratio Z_{eu}/Z_{mix} correlates with productivity (Wofsy, 83; Harris, 86 (p.239); Gons & Rijkeboer, 90; Legendre, 90).

Prediction of primary production may be tricky; deterministic models have been tried, either for small systems or for whole upwelling zones, with heavy reliance upon nutrient supply and uptake rates ("bottom-up" control) and consideration of light limitation (Hecky & Kilham, 1988; Chalup & Laws, 1990; Bannister, 1990 b). For whole lakes, an ample body of literature has shown a strong correlation between production and PO₄ load (Vollenweider, 1976; but see Davies, 1988). Conversely, "top-down" control may be found, where high grazing rate leads (directly or not) to high recycling and production (Strom & Welschmeyer, 1991).

2.2.3: Benthos:

We are considering here "benthos" in the more usual perspective of the organisms living on (or in) the bottom. The benthic organisms in the mangrove (strictly speaking epibionts) will be dealt with in § 3.4.

Benthos in general represents an important component in shallow waters. Meiobenthos may represent 50-200 g.m⁻² (Sorokin, 1981). Macrobenthos biomass (as already mentioned) is in the range of 5-10 g (AFDW).m⁻². but may reach about 20-30 g.m⁻² on estuarine beaches (table 9.2 in Day et al., 1989) In Lake Chad, molluscs alone reach 4 g AFDW.m⁻² (one of the highest figures according to Lowe-McConnell, 1987(p. 60)), with a yearly production of 18 g AFDW.m⁻² (Carmouze et al., 1983). Day et al. (1989) cite biomasses of 2-17 g C.m⁻², with productions of 1-15 g C.m⁻².yr⁻¹ for epifauna, macro-infauna and meiofauna (see their tables 9.3 (p. 361) and 9.5). In a tropical brackish lagoon, Edwards (1978) gives a biomass of up to 50 g AFDW.m⁻² for infauna, with up to 30 g AFDW.m⁻² for the sole Cerithidae.

Bioturbation is an aspect which is difficult to assess. Its effect upon both water (through increased exchanges) and soil may be important (Pomroy et al., 1983). Mangrove crabs are an outstanding example of it (T.J. Smith et al., 1991).

2.2.4: Fishes:

From a strictly applied -if not materialistic- viewpoint, fish yield is the ultimate characteristic of a water body. Under natural conditions, fish biomass ("standing crop") ranges between 300 and 1000 kg.ha⁻¹ (Lowe-McConnell, 1987). Also under natural conditions, a low figure for yearly fish production is between 10 and 50 kg.ha⁻¹, corresponding to about 0.1-1.0 g C.m⁻².yr⁻¹ (Bayley, 1988). In sub-tropical and tropical estuaries, Day et al. (1989, table 10.3)

give a range of $10=70 \text{ g .m}^{-2}.\text{yr}^{-1}$ (i.e. $100=700 \text{ kg.ha}^{-1}$). Highest fish yields in managed systems reach about 1000 kg.ha^{-1} (Lowe-McConnell, 1987; Day et al., 1989), and intensive shrimp cultures have reached 3 tonnes per ha.

Prediction of fish yield is often considered one of the main aims of limno(oceano)logical studies, and the quest for "predictors" has long been active (Quiros, 1990). We shall review some of these, which may be divided between "external" factors, such as morphometry, and "internal" factors of functioning.

A: Morphometry and "external" predictors:

Morphometry has been correlated with production in lakes (Rawson, 1955). Depth in itself, and especially optical depth, has a direct effect upon primary production. We have seen that the ratio of mixing depth to euphotic depth is a good predictor (all other factors being equal) of integrated photosynthesis. Shallowness will amplify atmospheric effects, among which nutrient inputs by rain (Paerl et al., 1990) and, in the near-shore waters, aeolian litter transport (Cole et al., 1990). Shallow water bodies are sensitive to wind-induced turbulence, which may affect the whole water column (Carmack et al., 1986; Simon, 1989; Wainright, 1990). Resuspension of sediments - and of settled microorganisms - is relatively frequent, and important (Ganf, 1974; De Jonge & van den Bergs, 1987). Morphometry controls fetch, and hence the general characteristics and behaviour of sediments (Petticrew & Kalff, 1991). Shore-line development (Bailey-Watts & Kirika, 1987), another morphometric feature, also may have an effect upon over-all yield, especially with vegetated shores. Riparian forested wetlands have a positive action on fish yield (Lugo et al., 1988).

Depth and salinity are two of the most evident characteristics of a water body. Morpho-edaphic index (MEI) was pioneered by Schlesinger & Regier (1982) as an indicator of fish yield in temperate lakes (see Kerr & Ryder, 1988, for a review; Quiros, 1990). MEI has also been shown adequate for photosynthetic biomass prediction in tropical lakes (Lemoalle, 1983), and for benthic macroinfauna (Nixon, 1988). But MEI can only compare comparable things, and shows a strong effect of latitude (Schneider & Haedrich, 1989; Downing et al., 1990). This index has recently come under cross-fire from several directions. Theoretical aspects undermine the statistics (Jackson et al., 1990; Rempel & Colby, 1991), while the implicit relation between salinity (or conductivity) and nutrients is not always verified (Chow-Fraser, 1991). We are aware that MEI, and most of the above factors, have been employed to predict fish yield in lakes; there is no proof (at the best of our knowledge) that they might apply to estuarine or near-shore waters.

B: Functioning and "internal" predictors:

Primary production emerges as a good predictor of fish yield (Nixon, 1988). But we have seen that *i*) phytoplankton may not be the main constituent of fish diet and *ii*) photosynthesis can be controlled by the same regeneration processes that govern the whole food web. Whatever the pathway(s), primary production does appear correlated with fish yield (Day et al., 1989 (see fig. 2.2.4); Downing et al., 1990). We have mentioned above that size spectrum is a good predictor of food-web yield (Harris, 1986, p. 283; Mazumder et al., 1990 a,b). Recycling rate controls the fluxes, if not the biomasses (Harris, 1986, p. 84; Harrison, 1990; review by Capblancq, 1990; Eppley & Renger, 1992; Dugdale et al., 1992). Supplementary physical energy (tides, etc.) added from an external source appears to be "assimilated" by whole biological systems (Barber & Smith, 1981; Day et al., 1989; Margalef, 1989), although reduced mixing leads to phytoplankton blooms (Cloern, 1987, 1991).

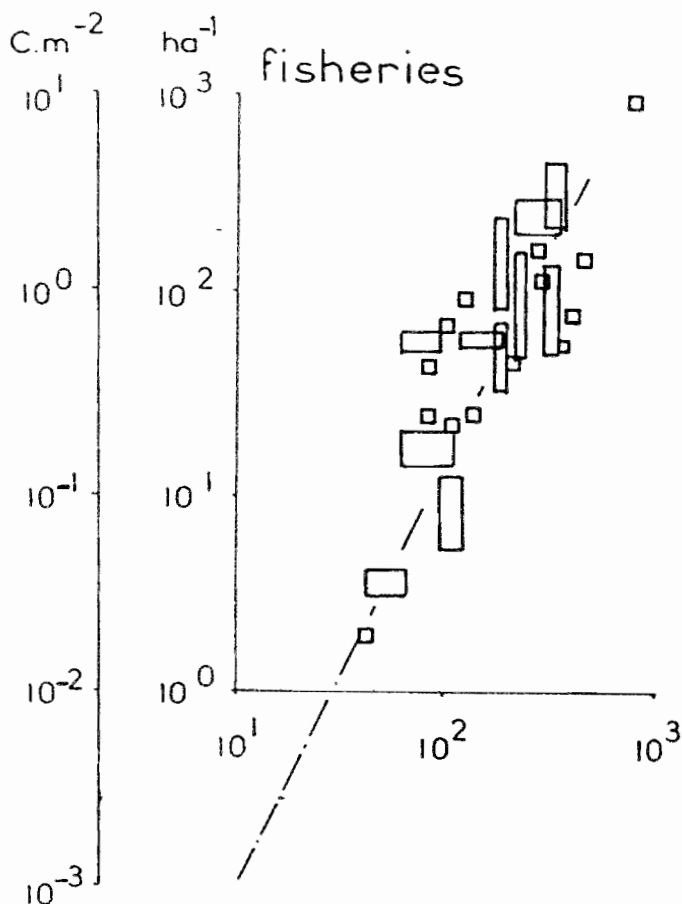


Fig. 2.2.4.: Relationship between fisheries yield and primary production (in $\text{g C.}(\text{m}^2.\text{yr})^{-1}$) in coastal and estuarine waters, after Day et al., 1989. Fisheries production given in two scales: the

right-hand one in $\text{g}\cdot\text{ha}^{-1}$ (from Day et al., *ibid.*), the left-hand one in $\text{g C}\cdot\text{m}^{-2}$, for comparison with primary production. Dashed line is a mere trend indication.

2.3: The many faces of "production"

Defining the "productivity" of near-shore waters meets several theoretical problems, owing to the intricate foodwebs found there.

One point is the juxtaposition of heterotrophic and autotrophic processes. Estuaries have been called "heterotrophic", since they import organic matter (Hopkinson, 1985; Dollar et al., 1991; Findlay et al., 1991; Moran et al., 1991 b; Smith et al., 1991). In the particular case of mangroves, net mangrove (terrestrial) production is much higher than aquatic photosynthesis (Clough & Attiwil, 1975; Ong et al., 1984) For near-shore freshwater margins, Wetzel (1990) argues that terrestrial OM is not "allochthonous", since the system should comprise both water and riparian vegetation. Anyway, in systems with high organic fluxes, Quinones & Platt (1991) show that f ratio and net/gross ratio become uncoupled. A negative net production (classically in terms of oxygen budget) is compatible with biomass exports.

A second point is the role of recycling processes effected by heterotrophs. Bacterial activity is only one side of this, since predation ("grazing") seems to be of paramount importance for actual recycling (Jumars et al., 1989; Andersen & Hessen, 1991). This leads to two further aspects. The first one is the quantitative importance of the microbial loop in the overall energy budget (Lind & Davalos-Lind, 1991). The second one is the much-debated question of bottom-up vs top-down control. Sterner (1990) and Sterner et al. (1992) show that both co-exist for phytoplankton; McQueen et al. (1986) showed that the importance of both varies according to the trophic level. Bacterial biomass may also be controlled from both directions (Berninger et al., 1991). In what regards bottom-up control, several studies have shown that the (static) concentration of a "limiting" substance is much less important than fluxes and ratios (Davies & Sleep, 1989; Prairie et al., 1989; Sterner, 1990).

A third point is the scale of observation. On a spatial scale, we have seen that processes at the interfaces, for instance, are seen in a different light when using micro-electrodes which work practically at the scale of micro-organisms. In what regards the time scale, important transient processes may be missed (Horrigan et al., 1990), so that repeated sampling is sometimes obligatory (Montoya et al., 1990). On a combined time-space scale, Horrigan et al. (1990) had to admit "circuitous 'food chain' processes" instead of "immediate (albeit bio-catalized) transformations" to explain highly active nitrogen fluxes between dissolved pools.

Quantifying fluxes in near-shore waters then appears particularly difficult, since these seemingly eutrophic environments often share many characteristics of oligotrophic waters.

Anyway, after having highlighted these problems, we shall try to describe two particular environments, the mangroves and the freshwater *Phragmites* swamps.

3. Mangroves:

3.1: General features:

Since our viewpoint is an hydrobiological one, we shall not try to review the extensive literature describing the wide variety of world mangroves from a botanical perspective; several detailed studies exist (Macnae, 1968; Chapman, 1976; see review by Rollet, 1981; Tomlinson, 1986). We shall limit ourselves to a sketchy description of the main features of mangroves, with some anecdotal personal observations from West Africa.

Mangroves, such as existing now, are relatively modern. The K/T boundary, 65.10⁶ year ago, would fit nicely (Wolfe, 1990), although *Nypa* existed at the end of the Cretacean (Rao, 1987; Tomlinson, 1986). *Pelliciera* and *Rhizophora* came later on, at the Eocene (30.10⁶ year; Tomlinson, 1986). Analogous formations existed as early as the Carboniferous, while swamp forests are present in comparable modern environments (Conner & Brody, 1990). Present-day mangroves are found along the coasts of the inter-tropical belt, in the tidal zone (Longhurst & Pauly, 1987, p. 23-26; see also Day et al., 1989, p. 192). Without entering the fray about the climatic (or not) character of mangroves (Uibrig, 1983 i.a.), we may recall that, according to Tomlinson (1986), mangroves are *r*-selective in finding their habitat, but are *K*-selective in maintaining it.

The highest specific diversity in mangroves is found in South-East Asia (Chapman, 1976; Tomlinson, 1986), while, West-African mangroves are much simpler (see below). We shall not risk a botanical description, but some simplistic morphological characters, taken from Chapman (1976; "C") and from Tomlinson (1986; "T"), are worth a reminder:

morphological characters of the main tree genera

character	genus
aerial roots:	
rounded	<i>Rhizophora</i> , <i>Bruguiera</i> (T)
flanged	<i>Ceriops</i> (T)
buttresses	<i>Heritiera</i> (T)
pneumatophores	(C)
thin, "pencil-like"	<i>Avicennia</i>
large and coarse	<i>Sonneratia</i>
bulbous end	<i>Xylocarpus-mekongensis</i> , <i>Laguncularia</i> (*)
knee-like	<i>Bruguiera</i> , <i>Lumnitzera</i>
sharp ridge	<i>Xylocarpus granatum</i> , <i>Heritiera</i>

(*) pneumatophores of *Laguncularia* are not always apparent, according to Tomlinson

A peculiar trait of mangroves, wherever in the world, is their zonation parallel to the water edge. A typical West-African profile (fig. 3.1) shows two tree sorts. In the intertidal strata, *i.e.* directly along the water front, *Rhizophora* sp. ("red mangrove" after Enos, 89) builds a dense barrier of stilt roots. Its lower branches mark the high-tide level. In the upper tidal strata, *i.e.* landwards, cylindrical pneumatophores sticking out of the mud identify *Avicennia* sp. (*A. africana* in Sénégal; "black mangrove" in America; "mangrove blanche" in French, after Marius, 1985). The "white mangrove" is *Laguncularia* (after Hicks & Burns, 1975). Back to our West-African profile: Still more landward, a bare mud expanse (the "tanne" in french-speaking West Africa; the term has been adopted by Twilley, 1985 b). These mud flats are often hypersaline even in the humid tropics (southern Vietnam for instance; Marius & Pagès, unpubl.), and often show a cover of *Sesuvium portulacastrum*. Analogous hypersaline bare flats are even found in New England salt marshes (Bertness, 1991 a). A peculiar detail of Senegalese mangroves is the occasional occurrence of baobab trees (*Adansonia digitata*) perched atop kjökkenmöddinger of shellfish remains. In other regions, well-developed mangroves show a more complex zonation (see fig. 3.4). *Avicennia* appears on the seaward side of the mangrove in Australia (Tomlinson, 1986) and in the "Indo-West-Pacific" (Macnae, 1968), as we saw in Vietnam.

Zonation of *Rhizophora* and *Avicennia* (to take only these two "typical" trees) appears to be controlled by several factors, among which seed predation (by crabs; Osborne & Smith, 1990) and light level (Smith, 1987). Propagule sorting (by tide and water level) has been shown to be very effective when salinity gradients are negligible (Rabinowitz, 1975; Tomlinson, 1986). The main zonation factor, though, appears to be salinity, against which *Avicennia* is more resistant (Jimenez & Sauter, 1991). This zonation of *Rhizophora* and *Avicennia* has its consequences upon soil properties in terms of oxygenation. We recalled above (§ 1.6) the "iron pipes" around *Avicennia* roots. The widely held view is that *Avicennia* oxygenates the soil through its pneumatophores, while *Rhizophora* allows fully anoxic soils (Marius, 1985; Thibodeau & Nickerson, 1986). It seems that effectiveness of oxygenation and generic differences must both be mitigated (Andersen & Kristensen, 1988; McKee et al., 1988).

The landward mangrove fringe may be occupied by *Nypa fruticans* where freshwater is abundant. This palm marks the transition zone submitted to the widest salinity range (Chapman, 1976; Dutrieux et al., 1990). We saw *Nypa* plantations thriving in a 0-28 g.l⁻¹ range in Vietnam. *Hibiscus tillaceus* marks the freshwater domain according to Chapman (1976), although we would consider that bamboos are a better hint of constant freshwater.

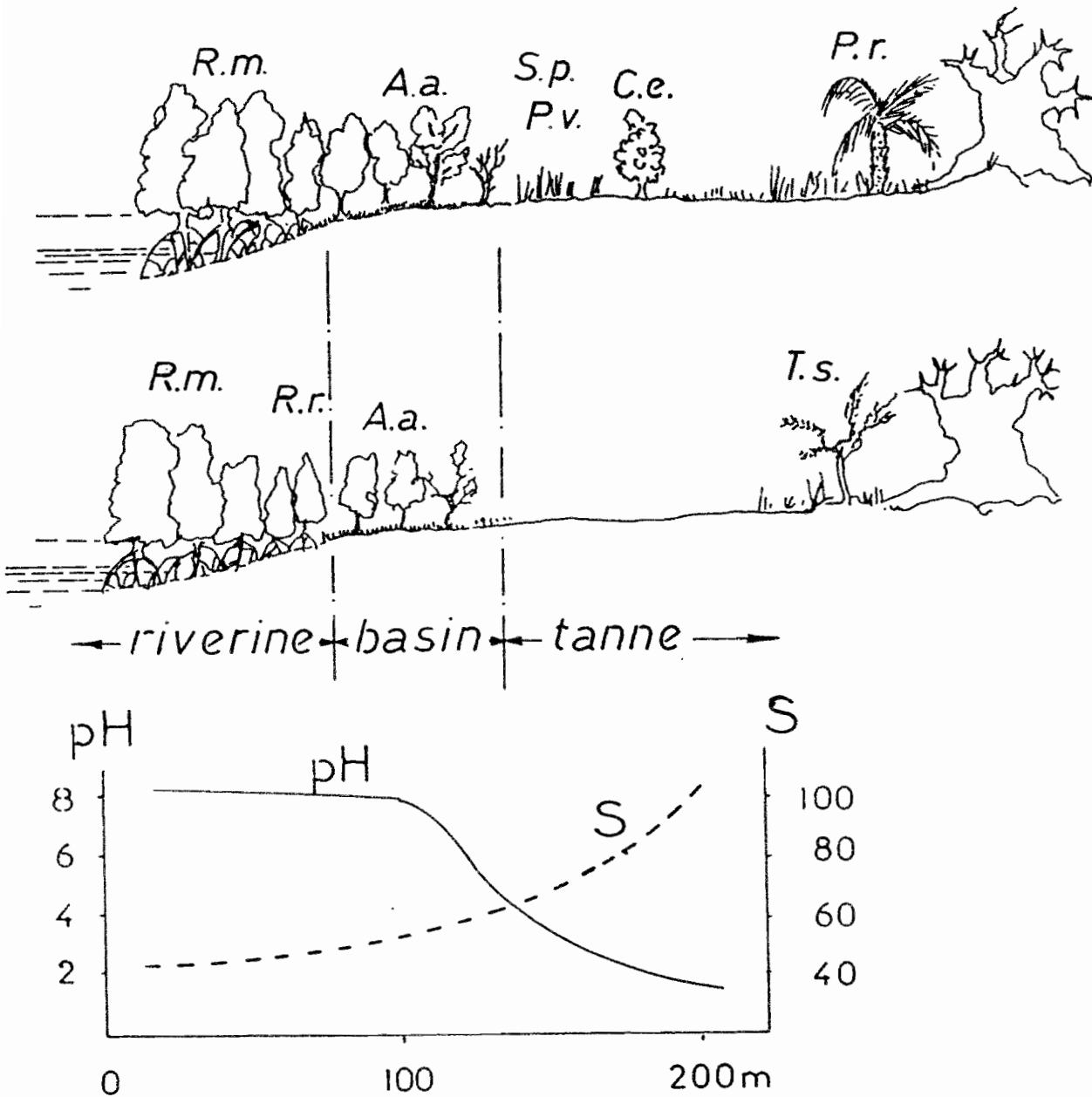


Fig. 3.1 : Schematic zonation of West-African mangroves, with either herbaceous tanne (above) or bare tanne (middle); on the far right, *Adansonia digitata* (adapted from Diatta et al., 1982). Below: salinity (g.l⁻¹) and pH of soil along a transect (approximate distances from water edge) on the Gambia River (after Twilley, 1985 b). Abbreviations: R.M.: *Rhizophora mangle*; R.r.: *Rh. racemosa*; A.a.: *Avicennia africana*; S.p.: *Sesuvium portulacastrum*; P.v.: *Paspalum vaginatum*; C.e.: *Conocarpus erectus*; P.r.: *Phoenix reclinata*; T.s.: *Tamarix senegalensis*.

Another general feature of mangroves is their overall bathymetry (or hypsometry; § 1.1.1). Although mangroves may also be found on hard coral (as in some points in New Caledonia), most mangroves grow on soft mud and in shallow waters. On a geochronological scale, mangroves expand during transgression episodes (Poumot, 1989). On a local scale, this corresponds to wide surfaces of very shallow waters against a very low percentage of deep tidal channels. These drainage creeks (Chapman, 1976) are called "bolon" in Senegambia (Marius, 1985; Twilley, 1985). This hypsometric distribution is naturally variable, also as a function of

tidal amplitude. This leads to various types of mangroves, as classified by Lugo et al. (1988) and Snedaker (1989). These various types correspond to different biomasses (see § 3.2.2). This most frequent correlation between shallow muddy environments and mangroves might be causal; the actual rôle of mangroves in promoting sedimentation is doubtful at best (Chapman, 1976).

3.2: Biomass and production of mangroves

3.2.1: Methods of assessment:

Biomass measurement seems easy, in principle if not in deed, in the case of macrophytes. But even in "simple" systems like *Spartina* salt marshes, the very methodology is a part of the problem (see fig. 5.12 in Day et al., 89). In mangroves, standing crop can be assessed by the obvious way of cutting down some mangrove stands, and weighing - with the equally obvious drawback of destroying the object of the study. Non-destructive, and hence repeatable, measurements use proxy estimators such as trunk diameter ("diameter at breast height", DBH) or total height (Cintron & Novelli, 1984; Komayama, 1989; Martin et al., 1990; Lee, 1990 a); such proxy estimators are also used in more classical forests (Ovington & Olson, 1970; Conner & Brody, 1990). Strictly speaking, regression between actual biomass and these indicators would be valid only for a given species in a given plot of land (Lee, 1990 a, b). In fact, the several uncertainty sources appear to cancel each other. The "structural index", which combines basal area, height and density, does give satisfactory results (Twilley, 85 b). Above-ground biomass can also be assessed by remote sensing (see § 1.5.3). Various vegetation indices have been employed on other forested landscapes, using the different wavelengths available in the different satellite-borne sensors (Linthicum et al., 1987). Another optics-based method utilizes sunlight attenuation by the canopy, under which irradiance distribution is curiously analogous to that of underwater light (see fig. 164-165 in Chapman, 1976). Irradiance at ground level is about 20% of incident irradiance, and can be an indicator of canopy density (Bunt et al., 1979, cited in Lee, 1990 a).

Determining mangrove production meets a two-fold problem: on the one hand, the problem seen above for biomass assessment (destructive vs repeatable methods), on the other hand the customary question of *gross vs net production* (see § 2.3). Among non-destructive methods, determination of gas exchanges (CO₂ or O₂) has been used, either in very large enclosures (Odum & Jordan, 1970) or above open forest patches (Yabuki et al., 1989). Litter production should be more easily assessed (barring sampling errors); detritivory by crabs can though seriously skew the observations (Lee, 1989 b; Robertson & Daniel, 1989 b).

3.2.2: Biomass: figures and factors:

While standing crop is highly variable, an indicative range lies between 500 and 5,000 g.m^{-2} (AFDW), or 5-50 tonnes. ha^{-1} . A New-Zealand mangrove stand showed an average of 680 g.m^{-2} , with a range of 400 to 10,000 (Woodroffe, 1985); several mangroves in South-East Asia have higher standing crops, ranging between 2,000 and 20,000 g.m^{-2} (Rao, 1987; Tanapermpool, 1989). For comparison, the Puerto-Rican El Verde rain forest had an average standing crop of 27,000 g.m^{-2} (Odum et al., 1970). The Nigerian mangrove standing crop corresponds to about 100 $\text{m}^3.\text{ha}^{-1}$ of timber (range : 50-250; Adegbehin & Nwaigbo, 1990). For mangroves in general, litter biomass is about 10-50 g.m^{-2} (Twilley et al., 1986), against 1930 g.m^{-2} in the El Verde forest (see above).

Distribution of biomass among the various organs has been described in several studies; Lugo et al. (1988) gives a summary of numerous results. The following table is only meant as an example.

Distribution of biomass in a *Rhizophora* mangrove
data from Silva *et al.* (1991), in kg. ha^{-1}

above ground		below ground	
flowers	22	fine roots	2,200
fruits	53	large roots	14,100
leaves	4,200		
branches	12,900		
prop roots	16,800		
stems	31,400		
total	65,400	total	16,300

The two general factors of biomass are latitude (which governs temperature and rain) and position relative to water level (which is related with tide). From what we saw in several places, but especially in West Africa, salinity appears to be of paramount importance, and results of the two above factors, which determine the water (and salt) budget. Mangroves do not exhibit a lower salinity limit as long as tide is felt. The upper salinity limit is ill-defined; growth rate and survival strongly depend on the temporal salinity régime, on a daily as well as seasonal scale. Gordon (1988) gives as absolute limit a salinity of 90 g.l^{-1} , while we observed in southern Sénégal that even *Avicennia* does not resist above a constant 60 g.l^{-1} . The physiological mechanisms of salt resistance have been well described (see for instance fig. 157 in Chapman, 1976). Standing crop should also be influenced by nutrient availability. Hatcher et al. (1989) review the evidence for N-limitation in the lower tidal levels, against P-limitation in the upper tidal levels. This contradicts Hicks & Burns (1975), who found a high landward

PO₄/Cl ratio. Generally, though, nutrient limitations in mangroves are masked by salinity (and/or tide) effects (see Hicks & Burns, *ibid.*).

The typology defined by Lugo & Snedaker (1974, in Snedaker, 1989) is founded upon tidal exchange rate, and has shown its worth. Some authors equate tidal régime with freshwater turn-over (Pool et al., 1975), but this appears to be a particular case of the more general point of water exchanges (or water residence time), whatever the average salinity (Hicks & Burns, 1975). The four (or six) classes defined by Lugo & Snedaker have been found to have a general validity (Pool et al., 1975; Lugo et al., 1988 ; Day et al., 1989).

Chemical composition of biomass should reflect nutrient limitations but, here again, other factors induce a much wider variation of the C/N/P ratio. Specific and anatomical characteristics (*Avicennia* vs *Rhizophora*, leaves vs wood, etc) are the main variability factors (Twilley et al., 1986). As a rule, though, mangrove plants, like most superior plants, have a high carbon content, with C/N ratios of 30-50 (at:at) and C/P ratios of 150-300 (Twilley *et al.*, *op. cit.*). Carbon constitutes about 50 % of dry weight, irrespective of taxonomy; leaves have a higher content in N and P (respectively 2.0% and 0.15%) than do branches (1.2% and 0.08%); dead wood has the lowest contents in N (0.6%) and P (0.03%) (Clough & Attiwil, 1975).

3.2.3: Production:

Primary production understandably varies still more than does biomass. An indicative range would be between 1.2 and 23 tonnes.ha⁻¹.yr⁻¹. (Twilley et al., 1986), which amounts to 5-100 mol C.m⁻².yr⁻¹. Day et al. (1987) give for net production a narrower range of 16-25 tonnes.ha⁻¹.yr⁻¹.

Litter production as related to typology; figures in g AFDW.m⁻²; upper line: annual litterfall, after Day et al., 1989; lower line: daily litterfall, after Pool et al., 1975

scrubhammock		basin	fringe	overwash	riverine
190+60		660+70	900+70		1300+100
0.2-0.3	1.8	2.0-2.3	2.0-2.6	3.0	3.0-3.6

As in aquatic systems, the main problem about "production" is the difference between net and gross production. Odum & Jordan (1970) found night respiration rates of 0.3-0.8 g C.(m².hr)⁻¹ in the El Verde rain forest. Some other figures are given below for comparison.

Comparison of net production and respiration. All figures in $\text{g C} \cdot (\text{m}^2 \cdot \text{d})^{-1}$, after Lugo & Snedaker (1975) and Hicks & Burns (1975; italics)

	net daytime	night
<i>Rhizophora mangle</i>		
sun	1.12±0.3 <i>0.7</i>	0.44±0.2 <i>0.5</i>
shade	0.75±0.1	0.46±0.1
trunks	-2.5±0.9	1.1±0.4
branches	0.001	0.007
prop roots	-0.04±0.3	0.08±0.05
<i>Avicennia germinans</i>		
sun	1.14±0.5 <i>1.6</i>	0.47±0.2 <i>1.2</i>
shade	0.7	2.3
trunks	-1.46±0.5	0.73±0.25
pneumatophores	0.05±0.04	0.26±0.10
<i>Laguncularia</i>		
sun	0.5±0.24 <i>1.8</i>	0.14±0.04 <i>1.6</i>
shade	0.5	0.35
trunks	-0.83	0.40

As a whole, mangrove production is controlled by several factors apart from specific differences (or anatomical ones; see below). Nutrients in the soil have been seldom considered. Salinity has a high impact upon production, as it does upon biomass, and each species has its optimum. Hicks & Burns (1975) showed that salinity in soil *and* in water interact to modify net production on all species.

Highest production rate is found in leaves and small debris, which represent only 10-20 % of biomass but 20-50 % of production. Litterfall amounts to 200-1,500 $\text{g (AFDW)} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, or about 0.5-2.0 $\text{g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ (Klinge & Rodriguez, 1968; Odum, 1970; Boto & Bunt, 1981; Twilley, 1985 a; Woodroffe, 1985; Twilley et al., 1986; Day et al., 1987 a; Woodroffe et al., 1988; Robertson & Daniel, 1989; Day et al., 1989; Lee, 1989 a, 1990; Flores-Verdugo et al., 1990; Shaeffer-Novelli et al., 1990). This litterfall cycles back nutrients: in non-mangrove forests, on a yearly basis and per m^2 , litter brings 4-10 g N (Klinge & Rodriguez, 1968) and 0.3-0.5 g P (Cole et al., 1990).

3.3: Exports from mangroves:

High organic matter (OM) production could mean that mangroves are a nutrient source for adjacent waters, provided that exportation does occur. In the somewhat analogous environment of salt marshes, several studies have shown a net OM export (Odum & Heald,

1975; Jordan et al., 1983; Valiela, 1984; DeLaune et al., 1989 a; see also review by Dale & Hulsman, 1990). In some cases, though, dissolved and particulate fluxes diverge: POM and phosphorus can be less exported than are DOM and carbon (Kaplan et al., 1980; Wrigley et al., 1988). Similarly, Whiting et al. (1989) find a higher export of PON than of DON. Several factors influence the direction of the net flux. Seasonal variations modify the available (exportable) biomass, so that the whole salt marsh acts as a flywheel for nutrients (Childers & Day, 1990). Morphology and typology ("age") of the marsh also have consequences upon the overall budget of nutrients and sediment (Heinle & Flemer, 1976; Jordan et al., 1983, 1989). A general ("universal") conclusion thus appears unreachable (Madden et al., 1988, p. 1,000) in these salt marshes, where even the spatial scale of observation plays a role (DeLaune et al., 1989 a). It is hence no wonder that the situation is far from clear for mangroves -even if Boto & Wellington (1988) caution against comparing these two ecosystems.

For mangroves, then, opinions differ about the sign and magnitude of net flux. Several studies find a net total organic carbon (TOC) export, ranging between 20 and 200 g C.m⁻².yr⁻¹ (Boto & Bunt, 1981; Twilley, 1985 a; Alongi et al., 1989). For comparison, floodplain forests yearly export about 3-15 g DOC-C per m² of watershed area (Meyer et al., 1987 and references therein; David et al., 1992). Other studies still arrive at a yearly export, but in much lower amounts and with marked seasonal variations (Boto & Wellington, 1988). Lastly, although working in seemingly ideal topographic conditions, Woodroffe (1985) cannot conclude about a positive or negative budget. In a similar vein, Silva et al. (1990) acknowledge such an uncertainty that "net import" remains a computational artifact.

This lack of a "universal" result may stem from several reasons. Methodology itself may play a role (see Day et al., 1989, p. 289). The customary eulerian approach may not be adequate for assessing a transport (Boto & Wellington, 1988). Rezenda et al. (1990) stress that a sizable proportion of DOM and POM travels alternatively out of the mangrove and back into it. We have mentioned the complexity of water movements in mangroves, with a-symmetrical flow/ebb fluxes (Day et al., 1989; see also Ong et al., 1991). In the "simple" case of a small woodland stream, Wallace et al. (1991) identify methodological pitfalls. Methodology can also intervene if either POM or DOM (but not both) is considered. Beside the variability of their ratio, the two forms can convert into each other (see § 1.3.2; Tranvik & Sieburth, 1989).

Apart from methodology, natural -and actual- variability also exists. Absolute C export and percent of litter exported are both positively correlated with tidal amplitude (fig. 3.3) (Twilley, 1985 b; Twilley et al., 1986; Lee, 1990 a, b; Rezenda et al., 1990; Alongi & Christoffersen, 1992). Exported forms (particulate or dissolved) also differ in the different types of mangroves (see last right column in table 1 of Snedaker, 1989). We have also seen that tide

acts indirectly upon mangrove standing crop, through salinity. Tidal amplitude -and elevation, relative to water level, of the considered mangrove stand- also controls decay rate and predation by macrofauna. Lee (1989 b) estimates that 30 % of daily litter

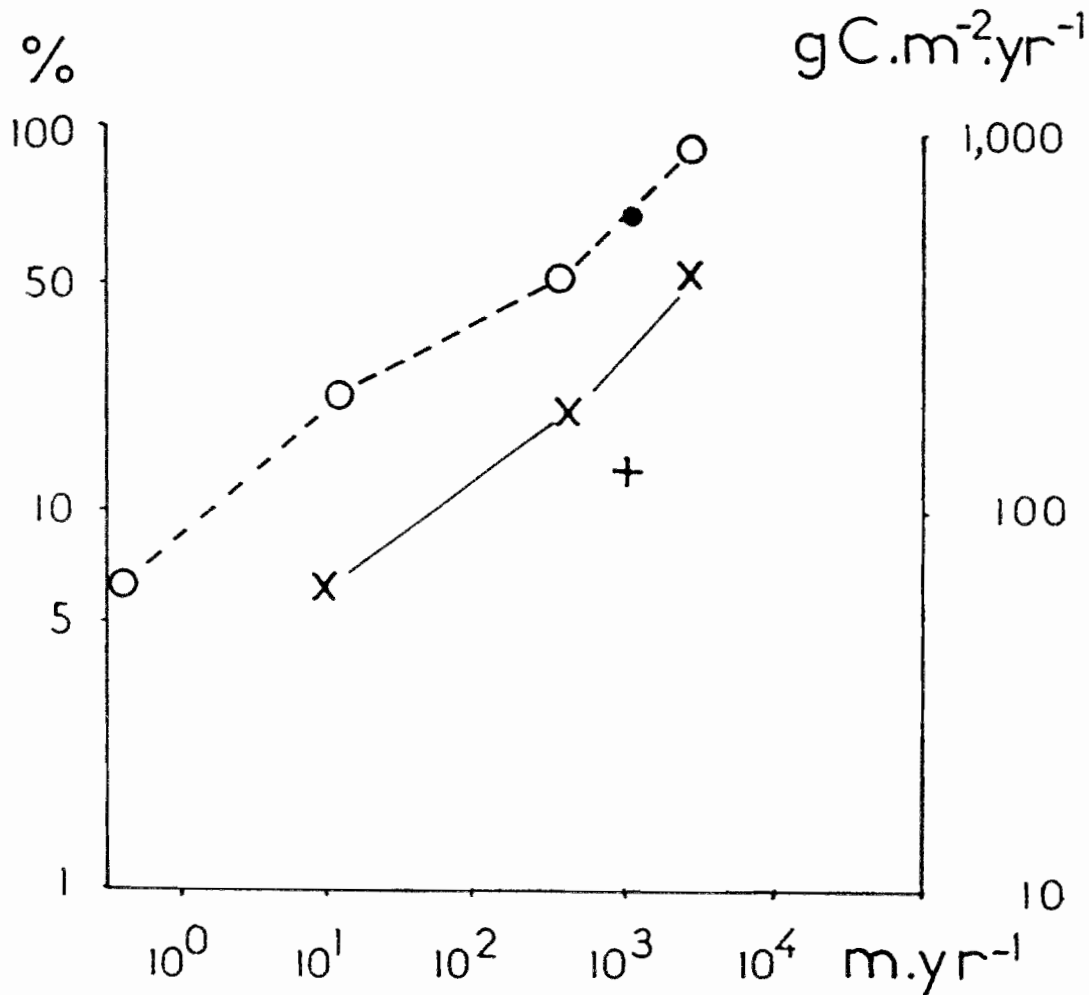


Fig. 3.3: Effect of yearly cumulated tidal amplitude (in m.yr^{-1}) on export of total organic carbon (circles) and on percentage exported (crosses). Data from Twilley (1985 b; o and x) and recalculated from Woodroffe (1985; o and +)

production is consumed, and thus escapes human assessment. Another "external" factor of export is rain, which increases exports from mangrove (Twilley, 1985 a) as it does in salt marshes (Whiting et al., 1989) and in other forested ecosystems (Lesack et al., 1986). The overall picture is hence far from clear. We may though notice that exports from mangroves actually happen (Gagan et al., 1987). Moran et al. (1991 a) do find terrestrial markers in coastal marine DOM more than 1 km away from mangroves.

We must address here the question of identifying "allochthonous", terrestrial components in general. At a macroscopic scale, the proposition is clear, but becomes murky at the molecular level. Stable isotopes, especially ^{13}C , may give good results (Rodelli et al., 1984; Gagan et al., 1987; Quay et al., 1992) but may present some pitfalls (Hedges et al., 1988 a;

Druffel & Williams, 1992). Fogel et al. (1992) show that $d^{13}C$ of estuarine phytoplankton may straddle the range of "terrestria" values. Amino-acid composition may give uncertain answers (Cowie & Hedges, 1992). Lignins seem a better bio-marker of terrestrial litter (Hedges et al., 1988 b; Alberts et al., 1991; Moran et al., 1991 a, b; Cowie & Hedges, 1992). Some truly typical hopane-like compounds have been used as tracers (Currie & Johns, 1989). It thus appears that identifying (if not always quantifying) terrestrial (and/or mangrove) exports is a difficult but feasible proposition.

We have up to now considered the "natural" exports. In what regards exploitation by man, we found annual exportations of 40-400 kg of timber per ha (Untawale, 1987; Robertson & Daniell, 1989) and of 8-12 tonnes of wood (Day et al., 1987). Regarding other mangrove products, the too classical item of "tanning barks" is brought down to proportions by Uibrig (1983): in relative weight units for an unspecified surface, we find:

construction timber	600
fuel wood	360
charcoal	30
tanning barks	1

3.4: Mangroves as biological systems:

Estuaries appear more productive, as a whole, than nearby coastal waters (Day & Yanez-Arrancibia, 1985; Madden et al., 1988). Fish biomass and production are often higher (Longhurst (1959) in Longhurst & Pauly, 1987, p. 127-129; Whitfield, 1983; Tabb & Roessler, 1989). Shrimps are also more abundant in (or off) estuaries (Longhurst & Pauly, 1987, p. 320; Snedaker, 1989). This special shrimp abundance has probably to do with their reproductive cycle. But the whole estuarine environment appears especially favorable for juvenile fishes (Pinto, 1987), so that estuaries are almost always nurseries (Madden et al., 1988; De Lafontaine, 1990). Nixon (1988) accounts for "more intense yield of fishes" by the added tidal energy (see also § 1.1.1).

These high biomasses and productions can be justified by shelter or by food. The shelter effect has been identified in pelagic environments (Kingsford & Choat, 1985; Longhurst & Pauly, 1987, p. 217). In estuaries, and especially in mangroves, shallow waters re-inforce shelter effects and attract juvenile fishes (Blaber, 1985; Deegan & Thompson, 1985; Ross & Epperly, 1985; Mann, 1988; Cyrus & Martin, 1991). Shelter effect in mangroves also applies to crabs (Wilson, 1989). Small tidal rivulets allow access to protective shallow areas (Freeman & Freeman, 1985; Rozas et al., 1988). In what regards food resources, litter can be more abundant than plankton (van Valkenburg et al., 1978), and may make up a hefty proportion of the diet of fishes (Harrigan et al., 1989; Ahlgren, 1990) and of prawns (Leh & Sasekumar,

1984). A synergistic effect of food and shelter exists in estuaries (Whitfield, 1983, 1984; Boesch & Turner, 1984; Parrish, 1990). In coastal waters, fish production increases with the ratio of marsh to open water areas (Deegan & Thompson, 1985; Deegan et al., 1985; Longhurst & Pauly, 1987, p. 127). In shallow mangrove margins, fish biomass is 5- to 10-fold that of adjacent waters (Blaber et al., 1989). In a somewhat similar setting, seasonally flooded forests appear to be a feeding -if not breeding- ground for fishes (see Lowe-McConnell, 1987 (p. 168 and 318) about forests around the Tonle-Sap). Several estuaries have been shown to be spawning grounds and/or nurseries "for numerous marine-related fishes" (Yoklavich et al., 1991). Mangroves, still more than other estuaries, have long been shown to increase secondary biomass and production, and hence fishery yields, in adjacent waters (De La Cruz, 1979). Mangroves are often attractors for fishes, adult ones as well as juveniles (Little et al., 1988; Morton, 1990).

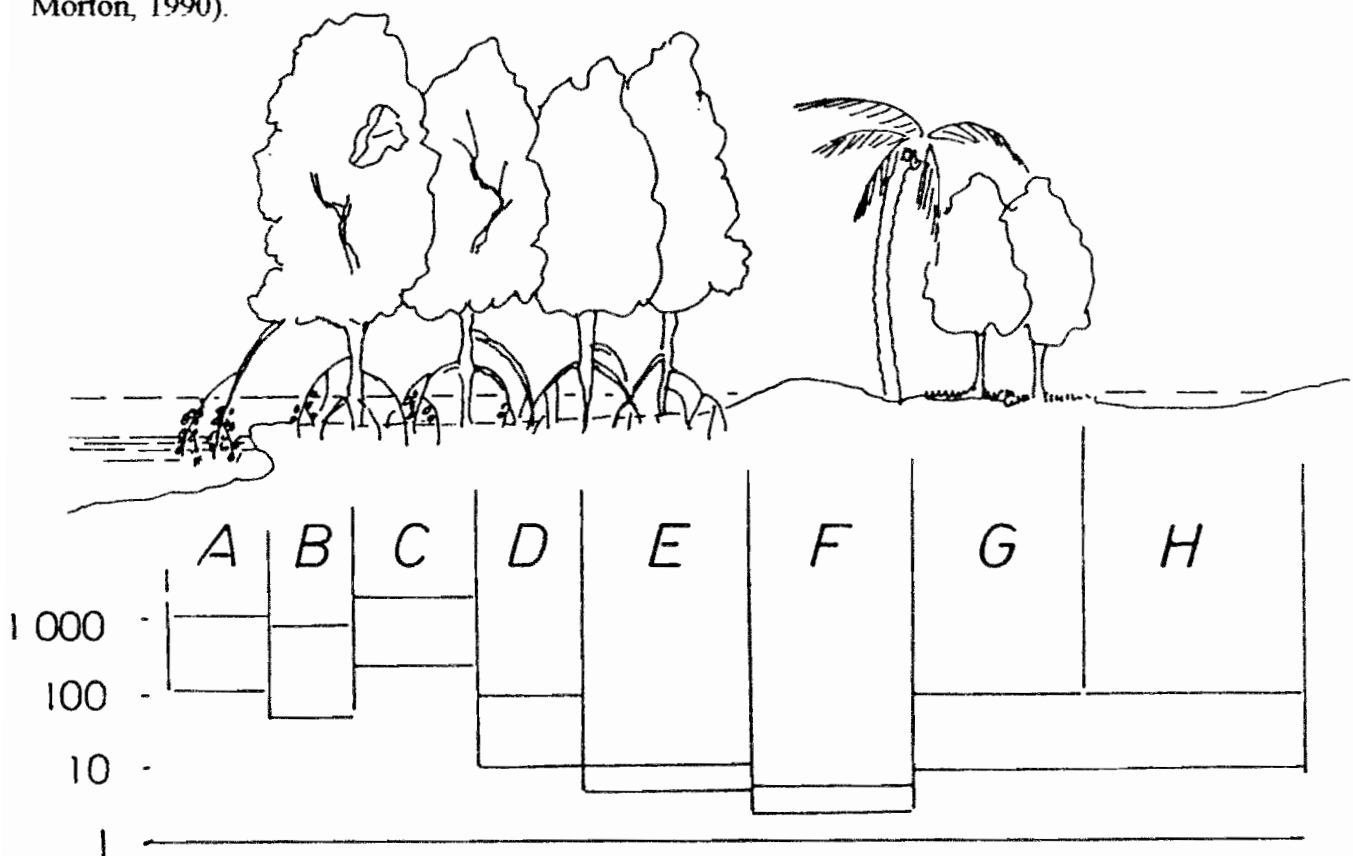


Fig. 3.4: Total biomasses across the schematic zonation of a well-developed *Rhizophora* mangrove, after Kolehmainen & Hildner, 1975. The approximate range of biomass is given (in g dry weight.m⁻²) under each zone. A: embayment; B: aerial roots; C: berm; D: *Bostrychietum*; E: central swamp; F: beach berm; G: mud flat, with *A. germinans*; H: saltern.

A quantified description of mangrove production has been tried by several authors after Odum & Heald (1975). Assessing both storage and flow for each compartment remains a major undertaking (see for instance fig. 22 in Lugo & Snedaker, 1975).

The bulk of references about mangrove productivity deals with fishes and shrimps. This may be due to methodological -or even psychological- biases, among which the fact that these "exploitable" species are caught in large amounts (up to 800 kg shrimps per ha. year; Day et al., 1989, p. 485). The possible supply of hard currency also plays a role. Secondary mangrove production is though not limited to fishes. As in other shallow waters, macrobenthos is often abundant. While some calm waters may have hypoxic "deep" layers, the frequent organic bottoms can feed a sizable benthic community (see § 2.2). Production figures are rather scarce, since most catches (mud-dwelling bivalves, especially) are consumed by local populations. Apart from its role as human food, macrobenthos recycles settled OM, and can make it again available to the planktonic food web; bioturbation is an important aspect of this recycling (Kristensen & Blackburn, 1987; Kemp et al., 1990).

Crabs are sometimes spectacularly abundant in mangroves. Their biomass can amount to 1-10 g (AFDW).m⁻², with an annual production of 1-15 g.m⁻² (Macintosh, 1984). Their feeding upon litter contributes to nutrient recycling (Lee, 1989 b, 1990). Among mangrove benthic animals, a particular place is occupied by mangrove oysters (*Crassostrea spp.*). Biomass figures for these particular oysters are rather scarce. Kolehmainen & Hildner (1975) give global "molluscs" biomasses of 60 to 500 g.m⁻². Interpolating data from a survey in Guinea (Marozova et al., 1991) yields biomasses of 112 g AFDW.m⁻², and 810 g AFDW "per metre" (probably per linear metre along mangrove channels). These figures compare well with those for oyster reefs: 200 g AFDW. m⁻² (Dame et al., 1984) and 160-970 g AFDW.m⁻² (Day et al., 1989, p. 363). Such figures, which visual inspection makes plausible, are especially impressive when compared with the effective water volume in mangrove channels: Muschenheim & Newell (1992) show that *Mytilus edulis* beds exploit a layer of water about 35 mm-thick. In other environments, suspension feeders, and particularly bivalves, can influence the general food web (Riemann et al., 1990; see review by Hobbie, 1988). Mangrove oysters can thus markedly modify the water in mangrove channels, both by their grazing upon seston and by their excretion (see Dame et al., 1989, for reef oysters). This two-fold effect of filter-feeders has been described in other environments with bivalves or fishes (Colman & Edwards, 1987; Pruder, 1987; Riemann et al., 1988; Mazumder et al., 1990; see also Gulati et al., 1990, on biomanipulation).

A last point rather characteristic of mangroves is the abundance of epiphytic organisms, in relation with the abundance of available substrates. In what regards bacteria, the old glass-slide method yielded results on the mode and rate of appearance of the first stages of bio-fouling. Bacterial production on macrophyte litter amounts to some 0.4 µg C.cm⁻².d⁻¹ (cm⁻² of detritus area; Moran & Hodson, 1989 a). To our knowledge, bacterial activity in the specific mangrove environment has not been studied in terms of biomass production per unit

area, while several studies have dealt with bacterial activity in mangrove sediments (Alongi, 1988; Alongi et al., 1989).

The other epiphytic organisms are micro-algae. The "Bostrychietum" is a well-described feature of mangroves. The role of micro-algae in general has been well studied in relation with sea grasses (see Day et al., 1989) or with other, mostly submerged, macrophytes (Burkholder & Wetzel, 1990) and often from the point of view of competition for available light (Twilley et al., 1985). As far as we know, epiphytes in mangroves have been mostly studied from a taxonomical point of view, while their functional aspect has been somewhat neglected. For a particular epixylic community taken as a whole, Couch & Meyer (1992) found biomasses ranging between 0.5 and 2 mg AFDW.cm⁻². Micro-phytobenthos growing on *Avicennia* pneumatophores show a gross production of some 500 mg C.hr⁻¹ per m² of sediment (Lugo & Snedaker, 1975). Most data on epibiotic microalgae stem from freshwater habitats; biomasses of 10-200 mg chl per m² of substrate have been measured (Baker & Orr, 1986; Hooper & Robinson, 1976; Bulthuis & Woelkerling, 1983; Palumbo et al., 1987; Hill & Boston, 1991; Boston & Hill, 1991; Turner et al., 1991).

Another set of figures may be sought with benthic microalgae, whose biomasses range between 15 and 125 mg chl per m² of sediment (Blanchard & Montagna, 1992). Benthic microalgal production (net) ranges between 10 and 30 mg C. hr⁻¹ per m² of sediment (Grant, 1986; Sundbäck & Granéli, 1988; Jönsson, 1991; Cahoon et al., 1992), with extreme values of up to 100-150 mg C. m⁻².hr⁻¹ (Pinckney & Zingmark, 1991). Gross productions range between 10 and 80 mg C. hr⁻¹ per m² of substrate (*ibid.*) and may reach 200 mg C.hr⁻¹ per m² of sediment (Heijs, 1987). We find again in this instance the wide difference between gross and net production (see figures in Lugo & Snedaker (1975) and in Turner et al., 1991). Anyway, epiphytic production is far from negligible from its sheer magnitude relative to free-water production. Apart from carbon fixation (or POC production in general), epiphytic organisms are also active in nitrogen (N₂) fixation (Van der Valk & Attiwil, 1984; Mann & Steinke, 1989; Paulsen et al., 1991). These effects of epibiotic communities find a pragmatical application with the West-African "acadja" fishing system (Hurault, 1964; Welcomme, 1972). Its efficacy is proven, although its mode of action is still largely hypothetical but probably relies both upon shelter effect and increased epibiotic biomass production.

3.5: Mangroves: why protect them ?

We are aware that this topic is awkward, and perhaps not really pertinent in such a paper with "scientific" pretensions. However, we came several times upon the question, be it in abstract terms or from an applied point of view. Scientists have been trying to protect mangroves for at least 30 years. Despite these efforts, and some success in public opinion, mangroves are being devastated at a dizzying rate around the tropical belt. Extolling the

qualitative value of a pristine environment does not cut much ice against majority's rule, a corrosive mixture of interests (or just greed) and neglect. This is compounded in developing countries by bare survival needs and "development" (whatever this might mean). We do not hope to turn the tide, since better and more authoritative voices have been trying to long before us. We only want to examine some of the reasons for protecting mangroves, including observations we made in some developing countries. The hub of our argumentation is that mangroves may have a low production but are better than nothing.

We have seen that mangroves export organic matter, while the exact amount is still undecided, and highly variable, biomarkers are found several kilometers away from mangrove stands. This gives a logical support to the presumed role of mangroves in fishery production. There are numerous hints, or even circumstantial evidence if not downright proofs, that yield is higher around mangroves. This may still be disputed, but often more out of personal conviction than for objective reasons. The role of mangroves (and estuaries) as nurseries is equally plausible- and equally disputed, with some arcane distinction between "truly estuarine" species and "opportunistic" ones. Anyway, this double role of mangroves, as shelter and as food source, has been often put forward with little actual effect: Clearing a mangrove brings immediate profit to a given collectivity, while decreasing fish yields strikes another community.

The protective role of mangroves against coastal erosion has been mentioned. While a fringe of *Rhizophora* may offer some protection against tidal turbulence, the reverse causative effect is more plausible (presence of *Rhizophora* because of low turbulence). There are numerous examples of alternating erosion/deposition cycles which control mangrove development, and a storm surge will not be halted by a mangrove. Against these negative views, we think that clear-cutting a mangrove may well be a one-way ticket toward local desertification. Evaporative losses may not be higher than evapo-transpiration, but it is plausible that a bare creek bank will tend to become hypersaline. Tree felling is often a preliminary to large scale works which deeply modify hydraulics and easily lead to acidification. There are some examples of successful exploitation of mangroves, but they are often due to autarcic, low-density native populations (Cormier-Salem, 1991). There are sobering -if not chilling- opposite instances of lasting destructions. In Guinea, some 60,000 ha of mangroves were cleared (for rice culture) then abandoned: 35,000 ha are definitively sterilized.

Mangrove production has often be cited as one of the good reasons for protecting them; the case was that mangroves are not a useless, unproductive (and possibly lethal) swamp. We deem this argument dangerous because easily contradicted. Biomasses and yield (of mangroves themselves) may look impressive at face value; we saw that annual yield is about 10 tonnes of wood and some 120 kg of timber. In what regards the latter, an analysis (Vincent, 1992) shows that timber is a poor prospect for sustainable development. In what regards fire wood, consumption is about 2.2 kg per head per day (one ha would supply 12 persons). These figures, albeit simplistic, indicate that mangroves remain a very localized commodity. The usual list of

tannins, dyes and exotic compounds do not really alter the picture. Against these negative remarks, we must stress the obvious fact that the above "negligible" yields are renewable, and available with a very small input, especially in what regards cash.

"Development" is one master word (even if its meaning is sometimes vague), and increased cash flow is generally *the* decisive index of development; increased yields (of anything) are also "good". So, mangroves must be replaced by something else. Freshwater backswamps can be coaxed into producing sago flour (Göhl, 1981) or even rice (we can remark that world market prices for edible carbohydrates are desperately low). But even such cultures need investments, water control, at least some fertilizers if not pesticides. Increasing yield needs energy, in several complementary forms, since "there is no such thing as a free lunch". Shrimp culture has exploded throughout the tropical zone, but shrimp farms can only succeed with heavy upstreal investments (water control, post-larvae rearing, feed production; see table 13-II, p. 77, in Untawale, 1987). We have witnessed extensive shrimp "farming" leading to devastated landscapes for a bare and ephemeral profit to a small minority of uprooted peasants. In all cases, as mentioned above, altered hydraulics can easily lead to intense soil acidification through even temporary oxygenation.

We hope having made our point that, in the absence of sizable investments and a well-directed application thereof, mangroves are the only (and hence the best) long-term bet, since some small production is better than none. Rubbish heaps are as objectionable in mangroves as anywhere else; the ultimate cost of destroying the environment is being rediscovered (Repetto, 1992).

4: *Phragmites* swamps:

These reed communities, and some other analogous ones, are widely found under various climates. They resemble mangroves and *Spartina* salt marshes in several aspects of their general functioning, layout and effect upon aquatic systems. Conversely, the main difference lies in the frequent (but not obligate) absence of tide, the effects of which have been mentioned above. We differentiate these *Phragmites* swamps chiefly for clarity's sake in the tables on biomass and production data. In these tables, we have incorporated figures from *Papyrus* or *Spartina* swamps, though being aware of size differences. These figures are meant to give orders of magnitude and comparison terms.

Zonation parallel to the water edge exists in the marshes occupied by these various macrophytes. Ostendorp (1988) showed a distinct pattern in *Phragmites* development. In a *Spartina* marsh, the distribution of species and phenotypes appeared to be controlled by

water/salt balance and by S^{2-}/O_2 proportions (Bertness, 1991 a, b; see also table 5.4 in Day et al., 1989).

4.1: Standing-crop biomasses:

Above-ground biomasses in *Phragmites* swamps range between 1,000 and 10,000 g (AFDW).m⁻². This represents a pool of phosphorus ranging from 100 to 2,000 mg PO₄-P.m⁻² (Gunatilaka, 1988). Underground biomass -alive and dead- is much higher, reaching up to 20 kg AFDW.m⁻² (Ostendorp, 1988). For *Spartina*, Gross et al. (1991) found less *live* biomass underground than aboveground..

Despite botanical differences, carbon constitutes about 50% of dry weight (Ostendorp, 1988), as it does in mangroves. Ash content is high; Si can amount to 10 % of dry weight (Viaroli & Fumagalli, pers. comm.). Nitrogen and phosphorus are relatively scarce, as in other "superior" terrestrial plants: atomic C/N/P ratios range between 520/18/1 and 3200/17/1 (Hocking, 1989 a,b). Clough & Attiwil (1975) found about 3 % N in *Phragmites* leaves. Phosphorus content ranges between 2-7 μmol P.g⁻¹ (Gunatilaka, 1988) and 0.14 % (w.w, i.e. about 50 μmol P.g⁻¹; Clough & Attiwil, 1975). Dead stems are expectably the most depleted organs. Internal translocation of nutrients takes place seasonally between rhizome and stem. Chemical composition of *Papyrus* stems is comparable: 1.2 % N, 0.16 % P in AFDW (Muthuri et al., 89). Emergent aquatic macrophytes in general have a C/N ratio of 40-50 (Bianchi & Findlay, 1991).

From the above string of figures, C/N/P ratios may appear rather indifferent. There is though a 'critical limit' for N and P content, under which no biomass increase may occur (Hough et al., 1989; Bradley & Morris, 1992). This limit reminds of Droop's 'cell quota' model for phytoplankton growth. Bradley & Morris (1992) find in *Spartina* an interesting positive correlation between water salinity and 'critical nitrogen content'. This may be a good illustration of the metabolic cost of osmoregulation.

Nutrient availability in the water, and thence in sediment, controls chemical composition and long-term biomass (Ulrich & Burton, 85). The same is true for sea grass (Powell et al., 89) and for terrestrial gramineae. Atmospheric nutrient sources (especially for N) can constitute a **high part of nutrient budget, with important inputs by rain and N₂ fixation (Ostendorp, 1988).** In the (very particular) case of inverse hyperhaline estuaries, *Phragmites* extension and biomass are also controlled by salinity incursions. As a whole, Day et al. (1989) identify three factors controlling production in intertidal wetlands: i) tidal range, ii) nutrient concentration in the sediment, iii) oxygen and drainage.

Continental and coastal swamps: Some standing stock data
figures in g (AFDW).m⁻²; C/N and C/P: atomic ratios

	organ. mat.	N	P	réf.
<i>Phragmites</i> biomass				
total	1,200			Lee, 90b
stems	900	3.9	0.2)
peat	5,500	229	22) Ostendorp, 88
total roots	4,300	49	4)
		C/N	C/P	
stems live	10,000	29	517)
stems dead	12,000	194	3230)
rhizomes	16,000	117	927)Hocking, 89,a,b
roots	3 000	58	1292)
<i>Spartina</i> biomass:				Day et al., 89, table 5.4
stream side	600-3000			
inland	260- 800			
average	300- 900			
<i>Ruppia</i> biomass				Edwards, 78
	200-1,000			
<i>Papyrus</i> (<i>Cyperus papyrus</i>)				
total	4,000-5,000) Muthuri et al., 89
above-ground	1,400)

4.2: Production:

The proportion of open waters and that of macrophyte-grown shallows control the share of truly aquatic production (by phytoplankton). In most lagoons or marshes, planktonic production represents a small part of whole-system yield (Flores-Verdugo et al., 1988; Lee, 1990 a). Aerial biomass production is highly variable under different climates. A median figure is about 1,000 g AFDW.m⁻².yr⁻¹ (Ostendorp, 1988; Lee, 1990 b). Underground production figures are seldom determined; an additional difficulty lies in separating true production (roots and rhizomes) from mere detrital accumulation (Ostendorp, 1988; Hocking, 1989).

Continental and coastal swamps: some production figures (in g .m⁻².yr⁻¹)

<i>Spartina</i> :			
	Valiela, 1984 (in carbon)	gross net	3,640 820
	Day et al., 1989 (AFDW)		above-ground 800-4,000 below-ground 1,000-5,000
<i>Phragmites</i> (AFDW)			
	Lee (1990 b)		2,200
	Ostendorp, 1988		1,025

Nutrient concentration, in water and in sediment, controls production. Phosphate uptake by *Phragmites* has been studied by Gunatilaka (1988). Apart from the customary nutrient uptake kinetics, uptake rate also depends on sedimentary characteristics, among which *i*) water logging, which is related with organic matter content, *ii*) salinity and SO₄ content, *iii*) oxygen concentration. These three factors are interwoven, and related with grain size. Oxygen depletion has a limiting effect and sulfides inhibit NH₄ uptake in freshwater plants (Koch et al., 1990) as well as in *Spartina* (Mendelssohn et al., 1981, cited by Day et al., 1989). Conversely, anoxic environments allow N₂ fixation in such marshes (Abd-Aziz & Nedwell, 1986). Nitrogenase seems associated with living roots, at least in papyrus swamps (Mwaura & Widdowson, 1992).

4.3: Exports:

Litter decay rate and nutrient liberation have been relatively seldom studied in the particular case of *Phragmites*. Complete disappearance needs 2-3 years in temperate climate (Ostendorp, 1988). Decomposition thus appears much slower than that of *Spartina* (Filip & Alberts, 1988, 1989). It is though probable that dead plants decay along the same general pattern, with an initial rapid leaching of low molecular weight components. In this perspective, rain appears to play a role in the decomposition of "standing dead" stems (Newell et al., 1985). Under typical tropical conditions, initial decay rates of 0.1 d⁻¹ have been measured in environments comparable with *Phragmites* swamps (Gaudet, 1977; Ellery et al., 1990). In an atypical (hyperhaline) environment, we observed seasonal bush fires extending into dried *Phragmites* marshes, thus accelerating remineralization (Pagès, unpubl.).

The (normally absent) tidal mixing can be replaced by wind-induced turbulence in these continental marshes. While a net exportation of litter would be difficult to assess, organic matter can thus be brought out of the macrophyte stands into the open waters (see Ellery et al., 1990, for comparable environments; see Wetzel, 1992, about the general features of land-water interfaces).

4.4: Side effects of *Phragmites* swamps:

At the level of the whole water body, the vegetative biomass probably partakes in the water budget through its evapo-transpiration. The main difficulty is that different authors arrive at diverging conclusions about the effect of plants (increase or decrease of total evaporation (Crundwell, 1986; Idso & Anderson, 1988; Koerselman & Beltman, 1988).

In another field, it is well accepted that macrophytes in general -and *Phragmites*- increase sedimentation rate by trapping fine suspensions. Their own POM production is a contribution to sediment accumulation. In the (very particular) case of saline incursions, flocculated DOM may be a further addition.

Shelter effects for fishes are exacerbated in the dense *Phragmites* stands growing in shallow waters. In comparable macrophyte stands, Dejoux (1983) found a three-fold increase in fish biomass compared with that in open waters of Lake Chad. Despite low irradiances at ground level, epiphytes still grow, and are an attractant for grazers. Riber et al. (1984) observed epiphytic biomasses of up to 400 mg chl per m² of sediment in a *Phragmites* stand. Rozas & Odum (1987) found an abundant nekton in analogous settings.

Avian fauna is also attracted -for opposite reasons- by these swamps, much more than by mangroves (Guillou et al., 1987). Predation on fishes by birds can amount to 1/3 to 1/2 of fish production (Winfield, 1990). Conversely, nesting birds can have a fertilizing effect (Oliver & Legovic, 1988; Powell et al., 1989; Winfield, 1990; Portnov, 1990). The overall effect of birds is an acceleration of nutrient turnover.

5 : Conclusion:

In what regards the functioning of detrital systems, a four-fold characterization emerges:

i) in estuarine systems, tide controls (directly or not) biomass, production and exports of riparian vegetation. In all systems, water régime is a controlling factor,

ii) sediments, and solid/liquid interfaces in general, are mostly a source of nutrients and - hence ?- a sink for oxygen;

iii) oxygen, which is controlled by underwater light availability, is necessary for all trophic levels except bacteria. It can be a limiting factor for loading rate (at the whole-system level) and for decomposition rate.

iv) recycling processes are predominant. "Residence time is the clue" to nutrient limitation (Pomeroy & Alberts, 88, p. 319). Despite high standing-stocks (even in nutrients), systems are frequently "crypto-oligotrophic", as witnessed by the small role of primary production (see Dortch & Packard, 89). Size-spectrum appears a good diagnostic tool (Mann, 88).

The present review originated from reading notes on two main subjects. The first one was the fate of detrital organic matter (DOM and POM) in aquatic environments, and this led

logically to anaerobic processes. The second subject was mangroves. In the resulting document, we preferred to separate the various components of the mangrove ecosystem, with the accessory chapter on reed swamps. Some themes were thus assigned somewhat arbitrary locations.

We voluntarily left aside several fields which would have been necessary, had we aimed at a handbook. Among the most conspicuous absentees are phytoplankton and nutrients (both uptake kinetics and limitation). This would have swollen an already bloated document. On the opposite, we did not limit our borrowing of data to near-shore, or estuarine, waters nor to the tropical zone; we also tried to find data from other forests than mangroves, thereby following the example of Lugo et al. (1988).

The main themes are expectably detrital matter and recycling. This stresses the fact that primary production is not the only pathway toward production of living particulate organic matter (by the way, the term "production" occasionally loses some sharpness). Anyhow, we see that heterotrophic processes can partake in the flux of matter and energy. The fertile concept of the "microbial loop" was developed for high-sea pelagic systems, but retains its usefulness in the rather special environments we dealt with. The stress on recycling (– remineralization) processes implies that we admit a bottom-up control for autotrophs, as well as for heterotrophs. In the same vein, studying "production" (of living POM, as said before) implies admitting a bottom-up control by available POM on the upper trophic levels.

We have noticed several points which are rather details, but which struck us either as recurrent themes (the key words were 'uncoupling' and 'discrepancy') or unexpected analogies. Among the divergences, we noted: *a*) uncoupling between hydrolytic activity and DOM uptake, as observed around marine snow (Smith et al., 1992; Karner & Herndl, 1992); *b*) uncoupling between production and consumption of NO₂ (Irrigan et al., 1990); *c*) uncoupling between *f* ratio, on one hand, and the net/gross production ratio, on the other hand (Quinones & Platt, 1991); *d*) discrepancy between water-column particle flux and bottom carbon decay (Cowie & Hedges, 1992; Smith et al., 1992). The analogy we noticed concerns C:N:P ratios. The concept of "critical nitrogen concentration" found for *Spartina* by Hough et al. (1989) fits well into the continuum observed in macrophytes by Duarte (1992). We already stressed (§ 1.4) the analogy with Droop's "cell quota" model. This brings again the nutrient limitation question (which we skirted) under the particular conditions of *terrestrial plants fighting against salinity*. This reminds of the summation by Lugo et al. (1973): "...nutrient availability [from terrestrial sources] is an important determinant of the vigor of a mangrove stand [...] and salinity adaptations represent the energetic cost of tapping these nutrient sources where competition is controlled (*i.e.* reduced) by other factors". This (perhaps lengthy) citation illustrates the energetic cost of osmoregulation, such as found under another form in the halotolerant *Dunaliella salina*.

Since a hefty portion of this document was devoted to litter, it was expectable that the subject of solid/liquid interfaces should often crop up (we left aside the air/water interface). We gathered the impression that interfaces (at any spatial scale) play an important role in nutrient fluxes (which is rather obvious) and that methodology is still more critical than in a "mere" liquid medium. We noticed the change of perspective brought by micro electrodes, but also the frequent disagreement between in situ and in vitro measurements in sediment/water exchanges. One series of artifacts is brought about by the use of a (Fickian) diffusion model to compute fluxes from vertical profiles, while direct measurements in benthic chambers give diverging results. A second artifact stems from static experimental conditions; while resuspension has been taken into account, the effect of irrigation is seldom quantified (see Archer & Devol, 1992). The mention of micro electrodes brings the whole problem of observational scale. Spatial and temporal variability have haunted aquatic sciences (among others) and lead to the whole field of sampling statistics. The observation of "transient processes" - and the very knowledge of their existence - is one big question mark in pelagic oligotrophic tropical waters. At a much smaller scale of time and space, it can be difficult to identify and quantify the exact pathways of nutrient fluxes between compartments: Horrigan et al. (1992) could not ascertain whether some nitrogen interconversions were merely "biologically mediated" or due to "circuitous 'food-web' processes". At about the same scale, the existence of micro-patches of nutrients has been hotly debated (Lehman & Scavia, 1984).

Another point worth underlining again is the relatively small meaning of absolute "static" concentration (or biomass) data compared with ratios and fluxes. In what regards ratios, the relative proportions of C, N and P are useful tools, be it to describe available nutrients or organisms. In litter decay processes, this C:N:P ratio is simultaneously a record of past history and a predictor of future fate; in a parallel way, production of a whole lake will be limited by either N or P according to the N:P ratio. In what regards fluxes, Pomeroy & Alberts (1988) stress that "residence time is the clue [...] to nutrient limitation". The speed of remineralization controls production (see also Ward & Twilley, 1986). Lastly, ratios of fluxes have proven effective diagnostic tools: the f ratio or the "relative preference index" describe the nutritional status of a population, while Istvanovics et al. (1992) showed that the ratio dC/dP is a good index of P depletion in phytoplankton.

One last series of remarks will deal with the general functioning of the systems described here, for which we propose the term "crypto-oligotrophic". We mean that an apparent richness masks truly oligotrophic features. It may seem that the term "eutrophic" has been satisfactorily defined (OECD, 1982). As we interpret it, a eutrophic system transforms high nutrient concentrations into high (exportable) biomasses. Comtois's model formalizes this

dynamic equivalence between biomass and nutrients. Another character of eutrophic systems (and probably a consequence of the above) is the preponderance of primary (photosynthetic) producers. On the opposite, the most evident features of classical oligotrophic systems are low biomasses and low nutrient concentrations. More basal features, though, are *i*) active recycling processes despite (or because of?) little, if any, export and *ii*) predominance of heterotrophic biomass (Dortch & Packard, 1989; Caraco et al., 1992; Li et al., 1992). We then see that, despite high concentrations of C, N and P (and high biomasses), the systems we have in mind actually behave as oligotrophic ones. The techniques, and the philosophy, developed for the study of oceanic oligotrophic waters might well be applied to mangrove waters !

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