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# Chlorophyll budget in a productive tropical pond: algal production, sedimentation, and grazing by microzooplankton and rotifers

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## Abstract

Chlorophyll *a* and pheopigment standing stocks and fluxes were used during a two weeks colonization experiment in a productive tropical pond (Layo, Côte d'Ivoire) in order to establish a chlorophyll budget. The experiment started from an azoïc state (the pond was dried, limed and progressively filled with ground water). Algal production was the only input to the phytoplanktonic system, while grazing and algal sedimentation were the main outputs. Chlorophyll *a* reflected the algal biomass, and degradation pigments were considered as an index of grazing by zooplankton (here, protozoans and rotifers). An estimation of the input through the algal growth rate was performed for the two main biological events observed during the study. The first algal bloom, with a large picoplankton participation, was mainly regulated by microzooplankton (increase of the peak) and rotifers (decrease of the peak). The second bloom (exclusively nanoplankton) was regulated by rotifers (increase) and by sedimentation of living cells (decrease). This last process was related to a sudden exhaustion of ammonia in the water column. Because of the time-lag between algal proliferation and zooplanktonic bloom, the phytoplanktonic biomass was able to be adjusted according to the availability of nutrients. This self-regulation took the form of sinking of active algal cells, resulting in a transient reduction of the food available for rotifers. This process had drastic consequences in these shallow waters, since a major part of the phytoplankton produced was removed from the pelagic system. For an optimal exploitation of the natural resources of an aquaculture pond, a study of the equilibrium nutrients-phytoplankton-zooplankton would provide a basis for artificial intervention, with a view to limit the impact of this mode of natural regulation.

## Introduction

Chlorophyll pigments are often used as estimates of phytoplankton biomass, in order to determine eutrophication levels in pelagic ecosystems. But these values correspond only to a standing stock, and their fluctuations on a time scale do not perfectly reflect the autotrophic activity. Variations of this algal biomass result from a dynamic equilibrium between inputs (primary production) and outputs from an ecosystem (mainly herbivorous grazing and cell sedimentation). Understanding these fluxes, and particularly the outputs, is necessary in order to establish a global budget for the algal biomass. Grazing is usually estimated from direct measurements (time variations of phytoplankton standing stock, gut fluorescence, labelled particle ingestion by zooplankton). Indirect methods can, to some extend, give separate estimates of grazing rates by microzooplankton (essentially protozoans) and by larger zooplankton (rotifers, copepods), from the size of the

pellets containing the degradation pigments (SooHoo & Kiefer, 1982a, b; Welschmeyer *et al.*, 1984; Welschmeyer & Lorenzen, 1985; Litaker *et al.*, 1988). But when such methods are used in open water, there is the complication of hydrodynamism and rapid changes of water. Working in closed shallow systems is a way of getting round this problem. From the chlorophyll standing stock variations, from these estimates of grazing and from the cell sedimentation rates, the parameters which reflect the algal biomass fluctuations (growth rate, doubling time and number of divisions per day) can therefore be assessed.

Such a study was carried out between March 15 (D1) and 31 (D17) 1988 (Arfi *et al.*, 1991), during the early stages of a natural recolonization of a productive tropical pond (Layo Aquaculture Station, Côte d'Ivoire). Working in an initially azoic system (resulting from drying the pond and lime spreading) have made possible to determine daily standing stock variations, input and output flux and the various modes of regulation of the algal biomass. In this shallow pond (0.6 to 1 m deep, for an area close to 600 $m^2$), the biological successions developing from the azoic state resulted within a few weeks in the development of relatively diversified planktonic communities (Legendre *et al.*, 1987; Bonou, 1990), which is a prerequisite for the introduction of new fry (Hem *et al.*, 1993). In this closed system, microalgal photosynthetic activity is the main way of production of particulate matter. Lateral inputs (banks, air-water interface) are very low, and there is no artificial enrichment as long as the pond is free of fry. Lateral outputs are impossible (banks), and the only output pathways from the phytoplanktonic compartment are grazing and sedimentation. In contrast to deeper systems, sinking material reaches rapidly the sediment, and is no longer accessible to the pelagic system, since vertical turbulence is limited (elevated banks surrounding the pond, attenuated local winds).

The purpose of the present study was to achieve a better understanding of the growth potential of phytoplankton, and to estimate the fraction of the stock leaving naturally the pelagic system by sedimentation, as opposed to through grazing activity. This budget would provide a basis for improving productivity in such aquaculture ponds by maximizing the utilization of natural resources, and limiting the artificial input of nutrients for plankton-eating fishes.

### *Outlines of ecological successions during the early colonization stages in the pond*

During each of the several colonization studies conducted in this pond (Legendre *et al.*, 1987; Bonou, 1990; Guiral *et al.*, submitted) as well as in the present study (Arfi *et al.*, 1991), a typical pattern was observed, characterized by successive peaks of pelagic organism. After the initial development of bacteria, a phytoplanktonic bloom begins usually 4 to 5 days after liming, in a context of very high nutritive potentialities. The decrease of the algal abundance is controlled by grazing, since this decay is concomitant with the successive developments of micrograzers (flagellates and ciliates) and rotifers. Later, cyclopid copepods present high abundances, some times accompanied by cladoceran. During these early stages of colonization, the developments of heterotrophic and autotrophic communities are thus first based on opportunist species favored by the initially high nutritive availability. This close link with the food induces also their rapid elimination, as soon as the trophic resources last out by overconsumption. These first steps are based on a catastrophic-type system, essentially controlled by bottom-up factors. Colonization is completed when secondary consumers, directly controlled through prey-predator relationships, are permanently installed.

## Materials and methods

### *Calculation of the chlorophyll budget*

Variations of the standing stock of chlorophyll in the water column expressed by time unit correspond to the input of new algal material into the

system, less the outputs (grazing and cell sedimentation). This is expressed by the formula:

$$dCHL/dt = CHL\,[\mu - g - G - SED]$$

where CHL (mg $m^{-2}$) represents chlorophyll *a* concentration in water, and $\mu$, g, G and SED ($d^{-1}$) respectively phytoplankton growth rate, grazing by microzooplankton (corrected from pheopigment photodegradation), grazing by rotifers and sedimentation rates. The coupled differential equations corresponding to this model (details in Welschmeyer & Lorenzen, 1985) give algal input ($\mu$) and output rates (g, G and SED) for the pelagic system. Table 1 gives the solutions for the differential equation. During the present study, micrograzers and rotifers were the only grazers present in the pond; at the end of the study, neither copepod nor cladoceran was observed in the water.

Grazing parameters are thus approached through variations and differential distribution of pheopigment concentrations in the water column and at the bottom. This method rests on several assumptions:

*Table 1.* Solution set for the differential equation (abbreviations and units in the text).

Instantaneous rates are deduced from the equation

$$dCHL/dt = CHL * [\mu - g - G - SED]$$

using these particular solutions:

$$SED = \frac{[\text{CHL-flux} * \ln(CHL_1/CHL_0)]}{[\Delta t * (CHL_1 - CHL_0)]}$$

$$G = \frac{[\text{PHEO-flux} * \ln(CHL_1/CHL_0)]}{\Delta t * (CHL_1 - CHL_0)]}$$

$g = g_1 * g_2/g_3$ with:

$$g_1 = [k * I * \Delta t] + \ln(CHL_1/CHL_0)$$

$$g_2 = PHEO_1 - PHEO_0 * \exp^{(-k*I*\Delta t)}$$

$$g_3 = \Delta t * [CHL_1 - CHL_0 * \exp^{-k*I*\Delta t}]$$

$$\mu = g + G + SED + [1/\Delta t] * ln(CHL_1/CHL_0)$$

– the only way to produce pheopigments is an acid hydrolysis of chlorophyll (pheophytin when the acid liberates Mg from the porphyrin ring, pheophorbide after further loss of the phytol chain). Herbivorous grazing is the basis of these processes in aquatic environments (Vernet & Lorenzen, 1987).

– it is known that protozoans produce fecal particles which are not membrane bound and rapidly disintegrate once emitted in water (Stoecker, 1984); some studies reported an increase in pheopigment concentration in grazing experiments (Daley, 1973; Goldman & Caron, 1985), while some other were less conclusive (Burkill *et al.*, 1987; Barlow *et al.*, 1988). In open water, photodegradation of these compounds leads rapidly to colorless residues which are no longer fluorescent. Based on light intensity, this process is supposed to be attenuated in more turbid waters.

– digestion processes and fecal production in rotifers is poorly understood. Edible particles (bacteria, microphytes) are concentrated in the mouth by the movements of the rotatory apparatus, ingested, broken in the mastax and digested in the digestive tractus in acid conditions. Pigmented degradation products accumulate in 'pellets' filling progressively the gut. At the end of the digestive process, these merely bound pellets are ejected in the water (Grassé, 1965).

– the amount of degradation pigments in a sample can give an estimate of the quantity of chlorophyll ingested, even if a more or less significant fraction of the chlorophyll may be metabolized in the digestive tractus of grazers (Dam & Peterson, 1988). Direct assimilation is known to occur (in particular for large grazers) but shows high variations, both within and across species (Lopez *et al.*, 1988). No precise information is available for this process in rotifers, but their intense metabolism (here enhanced by high water temperature) induced a very short gut evacuation time (5 to 10 minutes for *Brachionus plicatilis*, Pagano, unpublished data), thus minimizing the direct assimilation phenomenon. In a first approach basis, the molar conversion efficiency of chlorophyll *a* to pheophorbide in an ejected fecal

pellet by herbivorous rotifers will be here estimated to 0.66 (average value proposed by Dam & Peterson, 1988, from several literature experiments made on copepods).

– when pheopigments are measured by fluorescence, it is not possible to distinguish between pheophorbide *a* and pheophytin *a*. Since pheophorbide *a* is the dominant degradation product of chlorophyll *a* (Jeffrey, 1974), pheopigments will be considered at this preliminary stage as pheophorbide *a*.

– degradation pigments in small particles remaining in the water column can be mainly attributed to microzooplankton grazing, while pigments in large particles sinking to the bottom will mainly correspond to the larger zooplankton grazing (SooHoo & Kieffer, 1982a, b; Welschmeyer & Lorenzen, 1985). Pheopigments are expressed as equivalent-chlorophyll following the 1:1 weight ratio proposed by Conover *et al.* (1986) for fluorometer measurements.

– chlorophyll *b* can cause an underestimate of chlorophyll *a* concentrations and an overestimate of pheopigments (Lorenzen, 1981; Parsons *et al.*, 1984; Herbland, 1988), but spectrophotometric measurements of Layo samples showed very low values of chlorophyll *b*.

Estimating pigments fluxes from chlorophyll and pheopigments concentrations is then based on discussed assumptions. Several hypothesis can be accepted for our particular environment, but other assumptions cannot be verified. But owing to the simplicity of the technique and the intensity of the ecological phenomenons in the pond, assessment of respective importance of the input and of the output ways is still very informative for the management of such systems. In order to solve the differential equation and to calculate the instantaneous rates, several parameters had to be known, which were derivated from biological measurements in the pond.

*Pigments in the water column*

Water was sampled daily at the center of the pond (10 cm under surface, representative of the water column in this shallow homogeneous environment) and immediately filtered on a 63 $\mu$m screen. Particulate matter $<63\ \mu$m was retained on Whatman GF/F filters. Chlorophyll ($CHl_i$) and pheopigments ($PHEO_i$) concentrations were measured with a Turner 111 fluorometer after methanol extraction (adapted from Yentsch & Menzel, 1963).

*Algal sedimentation*

Vertical pigment fluxes (CHL-flux and PHEO-flux) were estimated with a sediment trap (area: 0.036 $m^2$) deployed daily at the sediment-water interface (dark part of the water column). Throughout the study, sediments were recovered at 8 am, and the trap rapidly replaced, after rinsing and filling with filtered pond water. Chlorophyll and pheopigment concentrations in the sedimented material were measured as above. Dividing the sinking chlorophyll flux (difference between two 8 am measurements, mg $m^{-2}\ d^{-1}$) by the initial standing stock in the water column (value measured at 8 am each day, mg $m^{-3}$) gave an estimate of the phytoplankton sedimentation rate (m $d^{-1}$).

*Grazing rate calculation*

Pheopigment provided an estimate of the grazing activity of herbivorous zooplankton. But some differences resulted from variations in grazer size and the corresponding dimensions of the defecated particulate material:

– samples taken in the water column corresponded mainly to pigments contained in small size particles, with a very low sedimentation rate (essentially products from small organisms or broken parts of larger pellets).

– samples taken in the trap corresponded to pigments contained in large size particles (here, essentially pellets from rotifers since no other large grazer was present in the pond during the study) with high sedimentation rates.

Because of the high water turbidity (light attenuation coefficients comprised between 2 and 3 $m^{-1}$, Arfi *et al.*, 1991) a limited fraction of the pigments was subjected to photodegradation in the euphotic layer, depending on the sinking rate of the particles, and the light intensity (I) to which they were exposed. With a very limited residence

time in the water column, the pigments contained in the sedimented particles were not subjected to photodegradation. The global incident irradiance was measured with a LiCor 200 SB pyranometer in the site and integrated daily. Photosynthetic Active Radiation (PAR) under the air-water interface was estimated to around 38% of the irradiance (Morel, 1978; Coté & Platt, 1983). In order to determine the photodegradation coefficient of pheopigments ($k$), incubations of water filtered on 10 $\mu$m screens (zooplankton elimination) were carried out 10 cm below the pond surface. The coefficient was calculated on the basis of the difference in pheopigment concentrations related to the available PAR (SooHoo & Kiefer, 1982a, b; Welschmeyer & Lorenzen, 1985). For the present study, and calculated after the first colonization days (chlorophyll > 1 mg $m^{-2}$), $k$ was estimated to 0.022 $m^{-2}$ mol.

*Zooplankton sampling*

Daily zooplankton sampling was carried out immediately after sunset (around 7 pm), with a 10 l bucket. Animals were retained on a 63 $\mu$m screen, and concentrated; neutralized formaline (4% final concentration) was added for sample conservation. Biometrical measurements were done to estimate an average biovolume for the species.

## Results

*Chlorophyll pigments*

*Pigments in the water column*

Chlorophyll *a* concentrations were close to 0 at the beginning of the study. They increased exponentially from D4 to D7 (Fig. 1), with a maximum of 14.3 mg $m^{-2}$. After that, values decreased until D10, when a second bloom started (maximum: 54.6 mg $m^{-2}$ on D12). Then, values decreased until the last day of observation (D17: 5.7 mg $m^{-2}$).

Pheopigment values (expressed as chlorophyll-equivalent) were high throughout the first bloom (maximum on D7, 10.1 mg $m^{-2}$), with degraded pigments constituting a high percentage of the total pigment concentrations. From D7 to D12, pheopigment values decreased to a minimum of

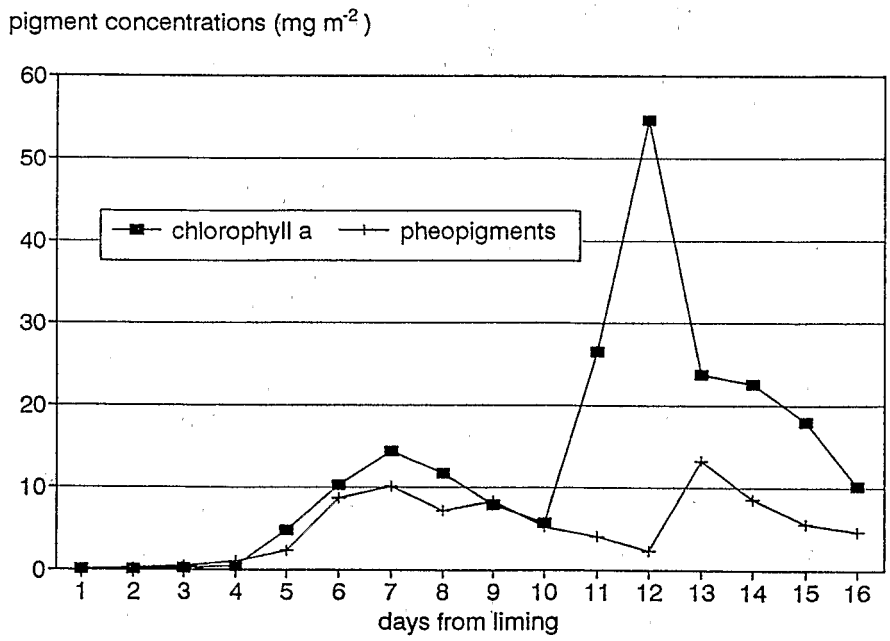


*Fig. 1.* Chlorophyll *a* and pheopigment concentrations expressed in chlorophyll-equivalents from March 15 and 30, 1988 (D1 to D16).

2.3 mg $m^{-2}$. At the end of the second bloom, an increase of these concentrations corresponding to the sharp chlorophyll decrease was noted (13.2 mg $m^{-2}$), but afterwards, values remained quite low, fluctuating around 5 mg $m^{-2}$.

*Algal sedimentation*

Very low at the beginning of the study, the chlorophyll flux toward the bottom followed closely the algal biomass variations (Fig. 2). Phases of increasing sedimented biomass (respective maxima 6.3 and 22.5 mg $m^{-2}$ $d^{-1}$ on D7 and D12) corresponded to the algal blooms. The same pattern was observed for the degraded pigments. Until D5, the chlorophyll standing stock was $< 1$ mg $m^{-2}$, and daily sinking rates of cells fluctuated between 0.11 and 0.36 m $d^{-1}$ (mean and standard deviation: 0.22 and 0.09 m $d^{-1}$). During the decreasing biomass periods, the sinking rate was higher. The average residence time of a cell in the water column was around 48 h during the first bloom, and 42 h during the second.

*Zooplankton*

During this study, the large zooplankton was only represented by the rotifers *Brachionus plicatilis* and *Hexarthra intermedia*. Some nauplii of cyclopid were observed at the end of the survey.

The first *Brachionus plicatilis* appeared on D3. This species showed high abundance during two sequences (Fig. 3): between D8 and D11 (8.3 $10^6$ ind $m^{-2}$, D9) and between D13 and D15 (5.6 $10^6$ ind $m^{-2}$, D14). The first *Brachionus* with eggs were observed on D6, but they were abundant only between D7 and D10 (1 to 2 $10^6$ ind $m^{-2}$), and again D13. The mean biovolume of *B. plicatilis* (considered as a sphere minus a spherical segment) was estimated as 1.71 $10^6$ $\mu m^3$ $ind^{-1}$.

*Hexarthra intermedia* was observed with low densities from D6, but from D12, its abundance was over $10^6$ ind $m^{-2}$, culminating on D15 (10.2 $\times$ $10^6$ ind $m^{-2}$). The average biovolume (a paraboloïd minus a parallelopiped) was estimated as $0.28 \times 10^6$ $\mu m^3$ $ind^{-1}$, 6 times lower than for *Brachionus plicatilis*.

*Input and output components of the chlorophyll budget*

Output components (g, G and SED) and growth rates ($\mu$) were estimated for the two algal blooms.

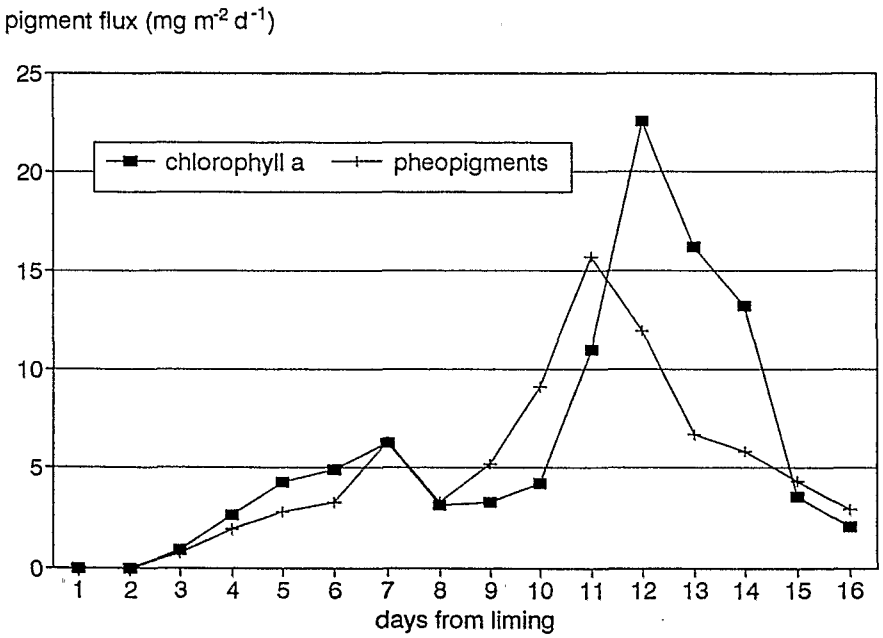


*Fig. 2.* Chlorophyll *a* and pheopigment flux toward the sediment.

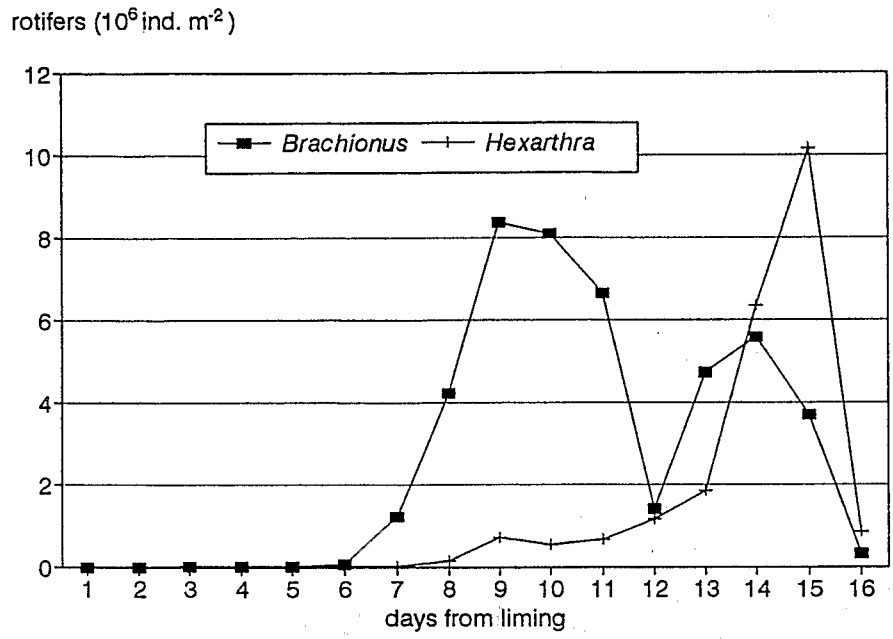


*Fig. 3.* Abundance of *Brachionus plicatilis* and *Hexarthra intermedia* in the water column.

For each of them, an increase and a decrease stage were considered. Parameters of the model were calculated from the relation between standing stocks and fluxes, giving instantaneous rates at the end of each stage (Table 1 and Fig. 4).

– The growth rate estimated for the increase stage of the first bloom (D4–D7) was high (4.16 $d^{-1}$, or 6 divisions per day), while the output components represented 72% of this input flux. The grazing activity of microzooplankton represented 44% of the output, completed for 34% by algal sedimentation. During the decrease

*Table 2.* Budget parameters during the four sequences studied.

| | g micro-grazing rate ($d^{-1}$) | G macro-grazing rate ($d^{-1}$) | Sed chlorophyll sedimentation rate ($d^{-1}$) | Total output ($d^{-1}$) | $\mu$ growth rate ($d^{-1}$) | Division per day | Doubling time (hours) | Output as percentage of input (%) |
|---|---|---|---|---|---|---|---|---|
| *First algal bloom* | | | | | | | | |
| Increase sequence, D4-D7 | 1.30 | 0.67 | 1.01 | 2.98 | 4.16 | 6.0 | 4 | 72 |
| Percentage of total output | 43.6 | 22.5 | 33.9 | | | | | |
| Decrease sequence, D8-D10 | 0.25 | 0.53 | 0.45 | 1.23 | 0.92 | 1.3 | 18 | 134 |
| Percentage of total output | 20.3 | 43.1 | 36.6 | | | | | |
| *Second algal bloom* | | | | | | | | |
| Increase sequence, D10-D12 | 0.03 | 0.57 | 0.35 | 0.95 | 2.08 | 3.0 | 8 | 46 |
| Percentage of total output | 3.2 | 60.0 | 36.8 | | | | | |
| Decrease sequence, D13-D16 | 0.14 | 0.27 | 0.52 | 0.93 | 0.51 | 0.7 | 33 | 182 |
| Percentage of total output | 15.1 | 29.0 | 55.9 | | | | | |

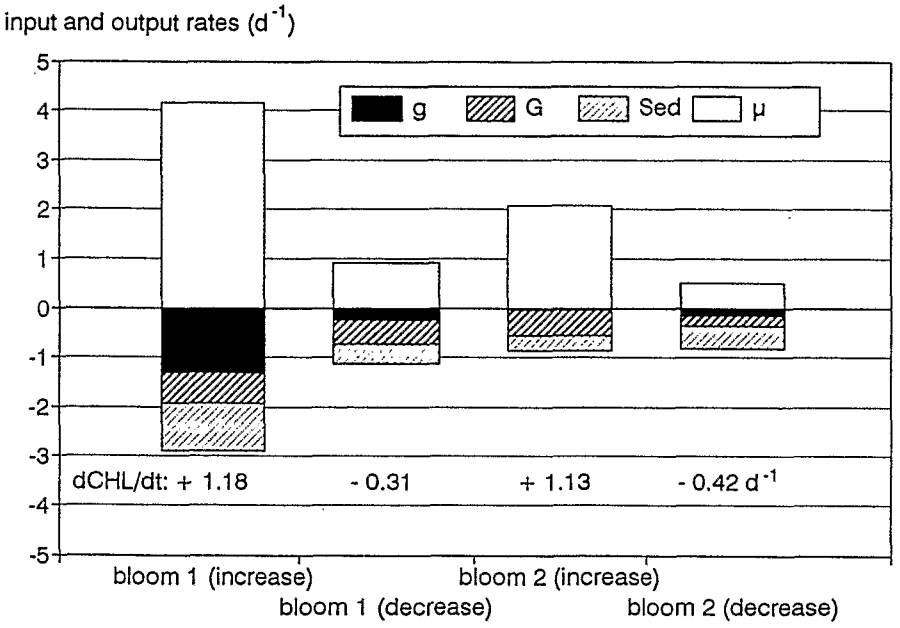


*Fig. 4.* Chlorophyll budget during the two algal blooms.

stage of this first phytoplankton bloom (D8–D10), output fluxes represented 134% of the input. The accumulation of microalgal materials observed from D4 to D7 was thus followed by a progressive decrease of the standing stock. Grazing by rotifers was the main output component (43% of the total output), and 37% resulted from cell sedimentation. During this sequence, the algal number of divisions per day was reduced to 1.3, and the growth rate to 0.92 $d^{-1}$.

– During the increase stage of the second algal bloom (D10–D12), the growth rate was 2.08 $d^{-1}$ (3 divisions per day). Sedimentation of ungrazed cells represented more than a third of the whole output, and the algal system was mainly regulated by rotifers grazing (60% of output flux). The decrease stage of the second bloom (D13–D16) was characterized by outputs representing 182% of the input flux. Cell sedimentation was the main factor responsible for this biomass decrease (56% of the total output), along with rotifers grazing (29%). During this last stage, the growth rate was low (0.51 $d^{-1}$, corresponding to 0.7 divisions per day).

## Discussion

### *Phytoplankton growth rate*

Variations of algal biomass in the pond during the 15 days following refilling featured two blooms, each made up of an exponential growth stage followed by a sharp decrease. The two periods of intensive development showed high growth rates (4.16 and 2.08 $d^{-1}$ respectively). These values are in the top range of growth rates for several algae (Bonin *et al.*, 1986). They also correspond to high temperature situations (30 to 36 °C in the pond).

### *Control of phytoplankton development by sedimentation*

Sinking rates of phytoplankton cells calculated during this study (0.11 to 0.36 m $d^{-1}$) come within the range noted in the literature for small cells (0.1 to 1 m $d^{-1}$, Lännergren, 1979; Bienfang, 1980; Burns & Rosa, 1980). There was no significant difference (Mann & Whitney non parametric test) between the average sinking rates

calculated for the two increase stages. However, the two algal communities were quite different, the first including 35% of picoplankton, the second quite exclusively comprised of nanoplankton (Arfi *et al.*, 1991). A preferential grazing of picoplankton by the microzooplankton present in the pond during the first algal bloom (presence of protozoans was deduced from the size class distribution of the particulate N in the water column, Arfi *et al.*, 1991) might explain this paradox. Since picoplankton cells sink more slowly than nanoplankton cells (Bienfang, 1980; Burns & Rosa, 1980), they remain longer in the water column; they are therefore more exposed to microzooplankton grazing. This would limit the proportion of picoplankton in the sinking cells, and thus explain the uniform sinking rates noted during the two blooms.

During recolonization, output of ungrazed cells by sedimentation represented 34 to 56% of the total output from the pelagic system. This percentage was first relatively constant (around 35% from D4 to D12), then peaked sharply during the decrease stage of the second bloom. The increasing importance of sedimentation in phytoplankton regulation might correspond to the sudden limitation of trophic resources in the pond (here a sharp decrease of $NH_4$-N availability, Arfi *et al.*, 1991). It is known that change in the cells' physiological state as a result of nutritive stress (Eppley *et al.*, 1967) can rapidly alter their buoyancy (Titman & Kilham, 1976), allowing more rapid movements toward the bottom. But in this shallow environment, lack of vertical turbulence makes sedimentation definitive for non-motile cells, which are then rapidly removed from the water column.

*Control of phytoplankton by trophic relationships*

The impact of grazing by microzooplankton on natural algal populations can be all the greater since protozoans have high metabolism and growth rates (Fenchel, 1982a, b; Azam *et al.*, 1983). In the pond, the microzooplankton grazing was important (44% of the output) only during the increase stage of the first algal bloom, where picoplanktonic cells represented a large part of the algal biomass. During the decrease stage of this first bloom, the proportion of outputs attributable to grazing by microzooplankton dropped from 44 to 20%. This decrease coincided with the appearance and the rapid development of rotifers in the pond which can graze on nanoplankton, but also take picoplankton (Boraas *et al.*, 1985; Caron *et al.*, 1985; Fahnenstiel *et al.*, 1986) and protozoans (Pourriot & Champ, 1982). With this increasing grazing pressure, the picoplankton community disappeared rapidly, and this in turn led to a gradual decline in the role of microzooplankton. The increase stage of the second bloom was dominated by nanoplanktonic cells, and the proportion of grazing attributable to microzooplankton was limited to 3% of the total output. The same process was observed during an other colonization study (Guiral *et al.*, submitted): protozoans (essentially Oligotrichs from the genera *Strombidium* and *Strombilidium*) were the first grazers to appear. They peaked simultaneously with the first phytoplankton bloom (here again characterized by a high percentage of picophytoplanktonic cells), and disappeared a few days later, when the algal biomass dropped to very low concentrations.

The proportion of outputs resulting from grazing by rotifers increased regularly, and culminated between D10 and D12 (Table 1). This percentage was low at first (22% of output flux until D7) compared to the microzooplankton activity, since rotifers were present with very low abundance. From D8, *Brachionus plicatilis* proliferation was largely responsible for the control of microalgal development (43% of outputs between D7 and D10, 60% between D10 and D12). Their impact was reduced (29% of outputs) between D13 and D16. The rapid development of the rotifer community was based on very short generation time. Availability of high trophic resources in the pond resulted in a rise of the metabolism in general (motility, filtration rate, weight acquisition: Pilarska, 1977; Waltz, 1983) and an increase of the adult fecundity rates. The high water temperature (30 to 36 °C in the pond), while probably close to the tolerance threshold for these organisms

(Allan, 1976), might also contribute to this increased metabolic rate. The intensive grazing activity of *Brachionus plicatilis* led first to a reduction in the growth rate of phytoplankton, then to a sharp decrease in the algal biomass. The maximum abundance of *B. plicatilis* was observed on D9 ($8.3 \times 10^6$ ind $m^{-2}$), while the chlorophyll biomass (17.1 mg $m^{-2}$) decreased by half compared to the maximum on D7. Related to the second algal bloom, a new development of zooplankton was noted from D12 (*B. plicatilis* and *Hexarthra intermedia*), with a maximum between D14 and D15. But, since the available algal biomass was suddenly reduced following a sharp decline in $NH_4$-N concentrations in the water (Arfi *et al.*, 1991), the rotifer abundance was drastically reduced.

## Conclusion

Although based on discussed assumptions, the model used in the present paper produced rates in good agreement with the processes observed in the pond. During the early stages of colonization of this productive tropical pond, regulation of phytoplankton communities was the work of both physical (cell sedimentation in a context of very reduced advection) and biological (herbivore grazing) phenomenons:

– in deep systems, sedimentation of ungrazed algae is considered as a minor pathway for exportation of algal material (Burns & Rosa, 1980; Lorenzen & Welschmeyer, 1983; Lorenzen *et al.*, 1983), since they are generally grazed during the sinking process. In shallow environments, when no resuspension is possible, sedimentation of intact cells (natural sinking, or related to a nutritive stress) can therefore remove an appreciable amount of organisms from the pelagic food web.

– output by sinking was completed by grazing, and a large proportion of the algal biomass produced in the pond was removed by planktonic herbivores. Grazing by microzooplankton was the main factor regulating the algal biomass when picoplankton was abundant, but since the ecosystem was essentially controlled by bottom-up factors, overconsumption of small cells led rapidly to the protozoans elimination. Afterwards, the nanophytoplankton regulation resulted from the grazing by rotifers. Sedimentation of pellets was also a major mean of transfer toward the sediment for biological material produced in the water column.

Combined with intact cell sedimentation, grazing had drastic consequences in these shallow waters, and a major part of the material produced was removed from the planktonic system in a very short time. For optimal exploitation of the natural resources of an aquaculture pond, a study of the equilibrium nutrients-phytoplankton-zooplankton would provide a basis for artificial intervention, with a view to limiting the impact of this mode of regulation.

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