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PRELIMINARY EXPERIMENTS ON PHYTOPLANKTON PRODUCTION ECOLOGY IN LAKE TANGANYIKA

by
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PREFACE

The Research for the Management of the Fisheries on Lake Tanganyika project (Lake Tanganyika Research) became fully operational in January 1992. It is executed by the Food and Agriculture Organization of the United Nations (FAO) and funded by the Finnish International Development Agency (FINNIDA) and the Arab Gulf Programme for United Nations Development Organizations (AGFUND).

This project aims at the determination of the biological basis for fish production on Lake Tanganyika, in order to permit the formulation 0f a coherent lake—wide fisheries management policy for the four riparian States (Burundi, Tanzania, Zaïre and Zambia).

Particular attention will be also given to the reinforcement of the skills and physical facilities of the fisheries research units in all four beneficiary countries as well as to the build— up of effective coordination mechanisms to ensure full collaboration between tha Governments concerned.

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1. INTRODUCTION

In large lakes, phytoplankton primary production is the main source of energy for the secondary production, including pelagic fish production. Thorough knowledge of the primary production processes is thus necessary for a comprehensive understanding of the biological basis of fisheries yield. The main objectives of the carbon-energy subcomponent of the Lake Tanganyika Research Project, as outlined in a previous technical document (Salonen & Sarvala, 1994), are (1) to obtain a more reliable estimate for phytoplankton primary production in Lake Tanganyika and (2) to evaluate the importance of dissolved organic matter (DOM) for the planktonic food chains of the lake. The methodology required for the primary production measurements was explored in preliminary experiments in April 1994 (Salonen & Sarvala, 1994). In September - October 1994, further experiments using the radiocarbon method were performed by the local LTR staff in Kigoma, and the results were counted in Finland. In November – December 1994, during the visit of the consultant JS to Kigoma, still further experiments were arranged in cooperation with the local staff. Here we report the results of these experiments. Based on our experiences so far, we also propose a tentative working plan for the carbon-energy subcomponent for the first research cruise with the *R/V Tanganyika Explorer*.

2. METHODS

2.1 Chlorophyll and nutrients

Vertical distribution of phytoplankton and its diurnal changes were estimated from the *in vivo* fluorescence of chlorophyll *a* using a Turner 10-AU field fluorometer operated by a 12 V battery. Measurements were made during three days (2, 4 and 7 December 1994). All water samples were taken with a darkened Limnos sampler. Sampler contents were drained through the fluorometer by connecting the draining tube of the sampler to the black inlet tube of the fluorometer. Flow rate was kept stable and slow by adjusting the height of the outlet tube end. Fluorescence values were recorded during the throughflow of water after the reading had stabilized. Fluorometer settings were as follows: LOW (AUTO) (RAW) TIME CONST 2 (SEC).

The fluorometer readings were calibrated against extracted chlorophyll in one vertical series extending from the surface down to 100 m (5 December 1994; 10-m sample intervals down to 60 m; thereafter 20-m intervals). Two replicate samples were taken from each depth. In the laboratory, two litres of water were filtered using low vacuum (about 20 kPa) through Whatman GF/C filters. The filters were dried in dark, packed in sealed plastic bags and transported to Finland. At Lammi Biological Station, chlorophyll *a*, total organic carbon, total phosphorus and total nitrogen were measured from small circular subsamples of the filters (total filter area 1134.10 mm^2, subsample area 49.02 mm^2). Chlorophyll was determined after ethanol extraction (ISO 10260, 1992; without acidification) with a fluorometer. Total nutrients

were determined after simultaneous peroxodisulphate digestion using standard chemical methods.

A zooplankton sample for carbon and nitrogen determinations was also taken off Kigoma in the morning of 6 December 1994 as a composite of three vertical hauls with a 100-µm plankton net from 100 m to surface. The sample was preserved in 0.25 % glutaraldehyde in the field. In the laboratory, after sedimentation overnight, excess water was decanted off and the animals were transferred to a 100-ml bottle with some extra glutaraldehyde added, and transported to Finland for analyses. Due to delays in the installation of a new carbon-nitrogen analyzer in the University of Turku, the carbon results are not yet available.

A water sample for nutrient analyses was taken into an acid-washed plastic 250 ml bottle from 30 m depth on 7 December 1994 at 9.20, and transported to Finland for analyses at Lammi Biological Station, University of Helsinki. The results are not yet available.

2.2 Primary production

Phytoplankton primary production was measured using the ^{14}C-method with acidification and exchange of the residual $^{14}CO_2$ with air (Niemi *et al.*, 1983; Salonen & Sarvala, 1995). Water samples were taken with a Limnos sampler from different depths, and two 20 mL glass liquid scintillation vials for each depth were filled with water. After filling the vials were kept under aluminium foil to avoid damage of phytoplankton by bright light. When sampling was completed, 80 µL (88 kBq or 2.4 µCi; 40 µL = 44 kBq or 1.2 µCi in the September–October experiments) of radiocarbon solution ($Na_2{}^{14}CO_3$) was added into each vial. One vial of each pair was covered with a double layer of aluminium foil. Then vials were attached from their plugs in a horizontal position to a suspending array and lowered to the same depth from which the water was sampled. The assembly hanging vertically from a buoy was left freely floating in the lake for the time of incubation. After the incubation, a drop (0.3 mL) of concentrated formaldehyde was added to each vial. Then the vials were wrapped in aluminium foil and transported to the laboratory.

Several series of primary production measurements were carried out off Kigoma by Mr. M. Kissaka with the help of Ms. Heini Kurki in September–October 1994 as follows:

Date	*Time*	*Weather*	*Depth*
21 Sept.	09.05–11.10	Clear	1–80 m
23 Sept.	07.47–09.50	From slightly	1–40 m
	10.30–12.30	cloudy to clear	1–40 m
30 Sept.	07.35–09.35	Extensive cloud	1–40 m
	10.30–12.35	coverage	1–40 m
	13.05–15.05		1–40 m
	08.05–18.15		1–40 m
1 Oct.	09.25–11.30	Full cloud coverage	1–80 m

Strong winds caused difficulties during these experiments, and one series was completely lost. Moreover, all of the vials incubated at 60 m or deeper, and several of those incubated at 40 or 50 m, lost their bottom during the incubation. There were also further problems with these data: the dark values showed a clear increase with time from 21 September (49–65, average 57) to 1 October (152–246), suggesting a severe contamination of the radiocarbon stock solution. Thus, only the results of the first series (21 September 1994) were useful; even this series contained some deviating values (negative net dpm at two depths). Additional faith on the results from 21 September is given by the fact that the dark counts in this series showed quite normal variability and their average level was in good agreement with dark counts from the successful vertical series on 7 December, taking into account the lower biomass and productivity in September.

A diel time series off Kigoma on 2 December 1994 comprised four successive 2-hour incubations starting from the sunrise and ending close to the sunset, and, in addition, one long incubation extended from the beginning of the first short-term experiment to the end of the last one. The incubation times (with notes on the weather) were as follows:

Short-term incubations	*Long incubation*
07.50 - 09.57 (cloudy)	7.50 - 17.35
10.32 - 12.40 (rain)	
13.00 - 15.00 (partial sunshine)	
15.25 - 17.30 (bright sunshine)	

Also in this series, two of the vials incubated at 40 m lost their bottom during incubation or in the later treatments.

In the first short-term incubation, several of the dark bottles lost their foil cover (vials suspended at 1, 20 and 40 m), only those from 5 and 10 m were intact. Likewise, in the long incubation, only the dark vial from 10 m was intact, the 5-m vial had partially retained its cover. In the later short-term incubations the foil was attached with water-resistant tape, and no further losses of cover occurred. However, as became evident from high activity counts, most of the vials had still received light. Therefore, in calculating net production, average dark counts from the later vertical experiment were used. This introduced extra uncertainty as to the absolute level of the results, but the relative differences between depths should remain approximately correct (on 7 December the dark bottles gave quite even values at all depths).

The detailed vertical distribution of primary production was measured in a 2-hour incubation in the morning of 7 December 1994 at the depths of 1, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50 and 60 m. Water samples were taken between 7.40 and 8.40, and the incubation was started at 8.55 and ended with formaldehyde addition at 10.55-11.12. In this series, the dark vials were more completely wrapped in aluminium foil, and then no tape was required to hold the cover. In this series, the radiocarbon dose was erroneously introduced into the vials immediately after they had been filled. Thus the first samples stayed with added

radiocarbon under the aluminium foil for up to one hour. Two control samples were killed with formaldehyde before the addition of radiocarbon, and incubated in water bath on board of the research vessel.

In the TAFIRI laboratory, a 6-mL subsample was pipetted into an empty plastic 20-mL liquid scintillation vial, and acidified to pH < 2 with a drop of orthophosphoric acid. Later in Finland, any possibly remaining traces of inorganic radiocarbon were removed from this water by an exchange with atmospheric CO_2 during two days. To remove inorganic radiocarbon bound by carbonates and possibly retained by filters, the opened liquid scintillation vials were kept 10 min under the fuming of strong hydrochloric acid. After these treatments 10 mL of Wallac HiSafe 3 scintillation fluor was added to each vial and mixed thoroughly. The radioactivities were measured with Wallac Ultrobeta 1200 liquid scintillation counter.

Results of the vertical series were calculated by subtracting the dark results for each depth from the corresponding light results; for unknown reasons, the radiocarbon controls were unrealistically high and thus useless. Because of problems with the dark vials, the results of the diel series were calculated subtracting from the light results the average dark results obtained in the vertical series.

2.3 Culture experiments

Size-fractionated culture experiments were performed on 4–7 December 1994. Water was taken in the afternoon 4 December 1994 (about 16.30) from 20 m depth off Kigoma from four different locations situated about a hundred meters apart. In the laboratory, the four samples were sequentially filtered through a 50-µm nylon net and a 2-µm Nuclepore filter, and each fraction divided into two 0.5-L experimental bottles so that each bottle received about as much water from each sample. Experimental setup consisted of three light and three dark bottles as follows:

Light	**Dark**
control (no filtering)	control (no filtering)
<50 µm	<50 µm (nylon net)
<2 µm	<2 µm (Nuclepore)

The bottles were attached symmetrically to a system constructed locally by Eero Seppälä and a metal workshop, and suspended in water in front of TAFIRI. Light bottles were suspended at 20 m (the same depth from which water was taken). Because of shortage of rope, the dark bottles were suspended above the light bottles at 10 m. The distance between bottles was so high that any shading was improbable.

Experimental bottles were subsampled every evening and morning by taking, after mixing, 60 ml of water with a pipette. These samples were fixed in acid Lugol and transported to Finland for further treatment. Because the treatment of the samples requires

extensive microscopical counts with a fluorescence microscope, the results are not yet available.

2.4 Light-induced decomposition of organic matter

Experiments on light-induced decomposition of organic matter were also arranged. 56 mg of preweighed fulvic acid was dissolved in 1 litre of freshly distilled and cooled water. Quartz glass and usual glass tubes plus five oxygen bottles, all with ground glass stoppers, were filled with this preparation. Three tubes were also filled with lake water (from 20 m) filtered through a 0.2 µm Nuclepore filter. Glass tubes and oxygen bottles were covered with aluminium foil. The oxygen bottles representing the starting situation were stored in the refrigerator. With the aid of a system constructed by Eero Seppälä, the light and dark tubes were suspended in a horizontal position in the lake off TAFIRI at the depths of 5 cm, 1, 2, 5 and 10 m. Two separate series were prepared, and both were set at 15 m depth on 4 December 1994 at 19.30. One series was taken from the lake next evening (5 December 1994 at 18 o'clock), and one of the lake water tubes was darkened by wrapping it in aluminium foil. All recovered tubes were marked, wrapped in aluminium foil and stored in the refrigerator. The second series was likewise recovered after three days (7 December 1994 at 18 o'clock). All tubes and bottles were transported in hand-baggage to Finland for further treatment. Whenever possible during the longer stopovers (Bujumbura, Brussels) the tubes were stored in a refrigerator. At Lammi Biological Station water colour was measured, and the dissolved inorganic carbon and volatile organic carbon determined with a sensitive carbon analyzer (Salonen 1979, 1981).

3 RESULTS

3.1 Chlorophyll

In the morning of 2 December 1994, the vertical distribution of relative fluorescence showed relatively even high values from the surface down to the depth of 30 m, with a possible weak minimum at 20 m (Fig. 1). From 30 to 80 m the relative fluorescence declined in a smooth exponential way. Later during the day, there was a considerable decline of fluorescence at the surface to almost half of the morning values. A less pronounced decreasing trend was evident at all depths, except at 10 m where the highest values were recorded in early afternoon. Values measured at 20 m were consistently lower than those at 10 or 30 m. The difference between the surface values measured in the beginning and at the end of the first morning series mainly indicates the influence of horizontal variation. The weather was at first cloudy, with partial dim sunshine in late morning. In the afternoon, full sunshine started before 15 o'clock. The increasing radiation was immediately followed by a rapid inactivation of phytoplankton chlorophyll: the relative fluorescence of surface water kept in a tub on the deck decreased from 0.076 to 0.037 between 14.05 and 14.48:

time	fluorescence
14.05	0.076
14.30	0.072
14.40	0.057
14.48	0.037

In the morning of 5 December 1994, the fluorescence maximum was at the depths of 10–20 m (Fig. 2). There was again a steep decrease in the surface fluorescence during the one-hour sampling period, whereas at 10 m the values slightly increased. The decreasing trend of fluorescence towards depth was interrupted by a weak increase at 40 m. The morning weather was clear, but after 12 o'clock the weather turned cloudy and finally rainy.

In early morning of 7 December 1994, the vertical fluorescence profile was exceptional in having its maximum at the surface, with slowly declining values down to 10 m (Fig. 3). One hour later, fluorescence maximum was broader, extending from 1 to 10 m, and the values had slightly increased. From 10 to 60 m there was an approximately linear decrease, with a slight twist at 40 m (Fig. 3). Later during the day, the fluorescence at 1 m declined steeply, and some decrease was evident at all depths; the local maximum at 40 m was now clearer. At 1 m, there was a significant decrease from 0.170 to 0.138 already during the 45 min required for sampling the whole vertical profile. It is noteworthy that the fluorescence values measured in this series were clearly the highest hitherto recorded off Kigoma. Weather was clear and sunny, but the previous day had been cloudy with abundant rain.

In the vertical series taken on 5 December 1994, there was a fairly close linear correlation between the fluorescence values and the extracted chlorophyll (Figs 4 and 5), a fluorescence reading of 0.100 approximately corresponding to 0.85 mg m^{-3} of chlorophyll *a*. However, towards the higher end of the range there was more divergence (values from 10 and 20 m depth; Fig. 5), which may derive from the species composition of the phytoplankton community.

3.2 Primary production

In the two-hour morning incubation on 21 September 1994, the maximum primary production was found at 30 m, but results from 15–20 m were not very far from each other (Fig. 6; data for the uppermost 10 m are lacking; the negative value for 25 m indicates some technical failure). From 30 m production declined towards depth, but zero production was not reached until at 50 m. The great depth of the maximum production level and the deep productive layer both conform to expectations based on the high radiation from the clear skies and the high transparency of water. Judging from the low net counts, the production level seems to have been fairly low.

In the diel series of 2 December 1994, the maximum production was recorded at 5–10 m depth, and production at 40 m was close to zero (Fig. 7). The estimates of daily net production obtained from the long incubation and from the sum of the short-term incubations were approximately similar at 1 m, but at deeper

levels the sum of the short-term experiments considerably exceeded the values from the whole-day incubation (Fig. 7). Both series showed prominent surface inhibition at 1 m depth. In the first short incubation in the morning, the production estimates obtained were fairly similar at all depths (a negative value for 10 m must be due to a technical error), but later during the day, clearly highest values were obtained at 10 or 5 m (Fig. 7). The noticeable difference in the production level between the morning and afternoon incubations directly reflects the difference in irradiance conditions: the morning was cloudy and rainy, but the afternoon was sunny. The results are also in accordance with the relative fluorescence measurements, which showed an increase in fluorescence at 10 m from the morning to the early afternoon.

In the detailed vertical series, the highest net production was measured at 15 m, but the values were quite similar from 1 to 15 m (Fig. 8). From 15 m there was a steep decline to almost zero at 30–40 m. Samples from 45 and 50 m showed somewhat higher values, but these may be erroneous.

3.3 Particulate nutrients

The vertical distributions of particulate organic carbon (Fig. 9), particulate nitrogen (Fig. 10) and particulate phosphorus (Fig. 11) in the morning of 5 Dec. 1994 resembled the distribution of chlorophyll (Fig. 4). Surface values were clearly depressed, and the highest particulate nutrient values were observed at 10 m, with a secondary peak at 30 m. At greater depths, particulate nitrogen decreased continually, but phosphorus levels were about similar from 60 to 100 m, and carbon seemed to increase at 80 and especially at 100 m. Because of the simultaneously increasing interreplicate variance of carbon, this latter trend is somewhat uncertain. The high carbon values in the deepest samples might have been due to scattered large zooplankton individuals, but the very high C:N and C:P ratios make this explanation unlikely.

From the surface to 60 m, the ratio of particulate organic carbon to chlorophyll *a* varied between 100–200 (by mass), with a slightly decreasing trend towards depth and (Fig. 12). At greater depths the ratio increased steeply. Carbon to nitrogen ratio varied around 10 (by atoms) from 0 to 50 m, with slightly higher values at 0 and 30 m (Fig. 13). Towards greater depths the ratio increased, especially steeply below 80 m. The vertical profile of the carbon to phosphorus ratio was quite similar to that of the C:N ratio, but the surface and 30-m peaks were more prominent (Fig. 14). The particulate atomic N:P ratio decreased from 14–16 in the epilimnion to about 8 at 100 m (Fig. 15). The average atomic C:N:P ratio from our study was 161.9 : 12.3 : 1 (62.8 : 5.6 : 1 by mass). For the productive layer (0–40 m) the atomic C:N:P ratio was 132.6 : 13.6 : 1 (51.4 : 6.2 : 1).

The levels of particulate carbon, nitrogen and phosphorus correlated strongly with chlorophyll (Figs 16, 17, 18), suggesting that most of the particulate nutrients were bound into biomass (this need not necessarily be true, if total seston also correlates with chlorophyll); the correlation was weakest for

carbon. Excluding the deviating 100-m sample, the intercept of the regression of organic carbon on chlorophyll was relatively small, suggesting that phytoplankton was the major component of the particulate organic matter. The N:P ratio increased linearly with increasing chlorophyll up to a maximum at about 0.8 mg m^{-3} of chlorophyll, and then declined slightly at the highest chlorophyll levels (Fig. 19). The slope of the relationship between particulate nitrogen and carbon was close to one (Fig. 20), although the deepest sample was a clear outlier, and the same was true of the phosphorus and carbon relationship (Fig. 21).

3.4 Light-induced decomposition of organic matter

Already after one day in the light, practically all colour visible in the field had disappeared from water in the experimental tubes. Water in the darkened tubes had also lost its colour, presumably because light could penetrate from the stopper end (it was difficult to construct such a suspending system that would have endured the wave action and at the same time retained the tubes in a horizontal position). However, the visually observed loss of colour may have been partly reversible, because later laboratory measurements showed that the maximal loss of colour after three days at the surface was not more than slightly over 50 %. The loss of colour was a decreasing function of both depth and time (Fig. 22). Both relationships seemed to be nonlinear. After one day, about 30 % of colour was lost at the surface, but only 5 % at 10 m depth. After three days, >50 % of colour had been lost at the surface and about 20 % at 10 m depth. The original idea was to quantify the decomposition rate by following the increase of dissolved inorganic carbon formed in the process (as the difference between the light and dark tubes). Unfortunately, probably due to the long transport involving strong mechanical disturbance and pressure changes, the initial values obtained for the dissolved inorganic carbon were too variable for any meaningful comparisons. However, the levels of volatile organic carbon, also derived from the light-induced decomposition, were measurable, and showed a nonlinear (probably exponential) decrease with depth and time (Fig. 23). The volatile organic carbon was probably mostly carbon monoxide, although it was not identified.

The colour decrease and the volatile organic carbon formation thus showed that light is a strong agent of organic matter decomposition in the conditions of Lake Tanganyika. The strength of the solar radiation could be clearly seen also in the transformations of the aluminium foil which was used for darkening the tubes and primary production vials: in the uppermost 20 m the foil completely changed appearance becoming faded and fragile. At deeper depths and inside a protective cover the foil surface retained its original appearance.

4. DISCUSSION

4.1 Methodological considerations

The experiments performed by the local staff in September–October 1994 revealed several practical problems, which must be taken into account when carrying out the routine measurements. Considering the possibility of rough weather, it is advisable to minimize the work to be done on boat. The dark incubations require a more reliable darkening system: the aluminium foil must be replaced by dark containers. The unexpected breakage of vials suspended in deep water does not much harm the program, because the productive layer seems to be practically restricted to the uppermost 40 m. On the other hand, the rapid contamination of the radiocarbon stock solution seems to be a real problem at Tanganyika. This is certainly partly due to the high temperatures, generally enhancing bacterial growth. Moreover, because the pH of Tanganyika water is high, the natural bacteria from the lake may easily adjust themselves to the alkalic conditions of the radiocarbon solution. The contamination problem can be avoided through adjusting the radiocarbon ampoule size so that a new ampoule can be opened for each measurement series.

In the December experiments the volume of radiocarbon solution added into the vials was doubled to 80 µL in order to increase the resolution, but still the final counts of radioactivity remained somewhat low. For reasons of working safety and water chemical considerations it is not possible to increase the radiocarbon dose much more. Therefore, to attain better reliability of the primary production results, it is advisable to increase the incubation time, although this alternative eventually leads to other problems, e.g. to a stronger enclosure effect.

The methodological experiments performed hitherto give a good basis for the routine primary production measurements planned for the three main field stations of LTR (Bujumbura, Kigoma and Mpulungu; Salonen & Sarvala, 1995). Simultaneous measurement of chlorophyll and irradiance data will greatly increase the precision of primary production estimates obtained.

4.2 Nutrient ratios

Particulate nutrient composition ratios present a relatively simple method of determining the nutrient status in lake waters (Hecky *et al.*, 1993). There are no earlier data on the particulate nutrient ratios in Lake Tanganyika, although total and dissolved nutrients have been measured on several occasions. The particulate carbon, nitrogen and phosphorus concentrations observed off Kigoma were not very far from values reported for the offshore areas of Lake Malawi, although much lower than those in other deep African lakes (Kivu, Victoria and Albert; Hecky *et al.*, 1993). However, the particulate nutrient ratios now observed in Tanganyika seem to resemble more marine than lacustrine values (Elser & Hassett, 1994). The particulate nitrogen to phosphorus ratios off Kigoma were lower than in lakes in general (Elser & Hassett, 1994). They were also lower than those given for the African lakes Malawi and Kivu, but higher than those reported for

the lakes Victoria and Albert (Hecky *et al.*, 1993). Our values were somewhat lower than the Redfield ratio (16:1 by atoms), suggesting that nitrogen might be the limiting nutrient in Tanganyika. However, according to published work, inorganic fixed nitrogen and phosphate are regenerated in Tanganyika in near-Redfield proportions (Edmond *et al.*, 1993), which suggests that the nutrient limitation, if any, should not be severe (Hecky *et al.*, 1993). The lower nitrogen to phosphorus ratio in our deepest samples is consistent with the suggested minimum due to denitrification around the oxycline (Hecky *et al.*, 1993). The carbon to nitrogen ratios of about 10 in the epilimnion also suggest moderate nitrogen deficiency (lower limit C:N>8.3; Healey & Hendzel, 1980). The high deep-water ratios reflect nitrogen depletion in the anoxic layer. Although higher than the Redfield ratio, the carbon to phosphorus ratios off Kigoma were low compared to most lakes, showing relatively good availability of phosphorus. Yet two of the epilimnetic values exceeded the limit suggested to indicate moderate phosphorus deficiency (lower limit C:P>129; Healey & Hendzel, 1980), and our average C:P ratio for the productive layer was very close to this limit. On the other hand, according to the criteria of Healey & Hendzel (1980), the average carbon to chlorophyll ratio in the productive layer (12.0 µmol μg^{-1}) was indicative of severe general nutrient deficiency (lower limit given as >8.3). However, the low levels of chlorophyll, leading to high values of this ratio, may be the result of the often light-saturated conditions in the clear waters of Tanganyika. Our results thus suggest moderate nitrogen and possible phosphorus limitation of phytoplankton in Tanganyika. Further work on the regional and temporal variation of the particulate nutrient ratios in Tanganyika clearly seems to be worthwhile.

4.3 Mechanisms regulating primary production at tanganyika

Due to the changing methodological details and various technical problems at this early exploratory and training stage, we refrain from far-reaching comparisons of the primary production results. However, there are certain recurring features in the data that warrant preliminary conclusions. The strong surface inhibition of chlorophyll and primary production, observed at Tanganyika in April 1994 (Salonen & Sarvala, 1994), was evident also in the present data. In September, close to the end of the windy dry season, the productive layer was deep, with maximum production at 30 m. Later, during the rainy season, the surface inhibition was less pronounced. In December, the chlorophyll and primary production maxima were closer to surface than in April, and on one occasion the morning maximum was observed at the very surface. The chlorophyll levels were also clearly higher than in April. Interestingly, the highest chlorophyll values were recorded after an especially dark and rainy day. This observation, together with our earlier data, gives rise to some theoretical perspectives on the regulation of primary production in Lake Tanganyika.

On sunny days, the solar radiation reaches very high intensity, and values exceeding 1000 µE m^{-2} s^{-1} are common. Irradiance levels exceeding about 500 µE m^{-2} s^{-1} are known to be harmful to

phytoplankton (e.g. Kirk, 1983). In the clear waters of Tanganyika, the deleterious effects of excess light are expected to extend to the uppermost 10–20 m. The observed downward spread of the chlorophyll decline, if real and local and not produced by horizontal displacement of different water masses, can be explained by vertical mixing of the epilimnetic waters.

On moderately cloudy days, in contrast, the optimum light conditions for photosynthesis are found close to the water surface. This may enable a rapid accumulation of phytoplankton biomass, because during the daytime the uppermost 20 metres are usually practically devoid of grazing zooplankton (Vuorinen and Kurki, 1994). Phytoplankton at 20 m and deeper down may be heavily grazed by copepod nauplii and other herbivorous zooplankton, thus preventing the increase of algal biomass. Too dark clouds may, however, reduce the irradiance below the optimum required by phytoplankton, as was evident in our experiments on 2 December. The phytoplankton photosynthesis– irradiance relationship is humped, and the irradiance conditions at the surface of Tanganyika may vary on both sides of the maximum during a single day. Therefore, the primary production may show at times positive, at times negative correlation with increasing irradiance, depending on whether the starting point is on the ascending or on the descending arm of the relationship.

Rainy days may make the nutrient conditions more favourable for the phytoplankton. It has been earlier proposed that phytoplankton production in Lake Tanganyika may be at times limited by the availability of nitrogen (Hecky, 1991), and our own results on the composition of particulate matter also suggest moderate nitrogen limitation. The rains are usually associated with thunderstorms, and thus they replenish the inorganic nitrogen stores of surface water (Hecky *et al.*, 1991), enhancing primary production. The rainwater is also slightly colder than the lake surface water, which might induce deep mixing of epilimnion during heavy rain. This mixing would bring new nutrients from the deep water to the euphotic layer. Hecky *et al.* (1991) concluded that due to denitrification at the oxic-anoxic interface, the monimolimnion of Tanganyika cannot supply inorganic nitrogen to the mixolimnion. However, the nutrient profiles measured by LTR clearly show occasional intrusions of nitrogen-rich deep water into the epilimnion (Plisnier, 1994).

Thus, there seem to be several mechanisms making the conditions for primary production at Tanganyika more favourable during moderately cloudy days and immediately after rain than on clear, sunny days. These mechanisms can be formulated into a simple model which should enable a fairly realistic simulation of the vertical and temporal dynamics of phytoplankton primary production, starting from the weather conditions, solar radiation, epilimnetic mixing and zooplankton biomass.

5. CARBON/ENERGY SUBCOMPONENT ON THE RESEARCH CRUISES

The routine measurements of chlorophyll and primary production at the three intensively studied field stations are designed to give a view of the temporal development of productivity, and to

provide the basis for calculations of annual production levels. With extensive measurements during the research cruises with the *R/V Tanganyika Explorer*, on the other hand, we are able to assess the spatial variation, possible regional patterns, as well as the representativeness of the intensive stations. The cruises also offer an excellent opportunity to study experimentally the importance of nutrients and dissolved organic matter in the productivity of Lake Tanganyika, utilizing even such technically demanding methods as cannot be included into the routine sampling program of the field stations. In the following, we clarify the aims of the carbon/energy subcomponent on the research cruises and propose a working plan for the first cruise. The program for the later cruises must be modified according to results to be obtained from the first cruise.

5.1 Aims

The main objectives of the carbon/energy subcomponent during the research cruises of the *R/V Tanganyika Explorer* are:

(1) to provide lake-wide information on the vertical and horizontal distribution of chlorophyll to form a basis for primary production simulations;

(2) to work out a primary production *vs.* chlorophyll and irradiance relationship for the primary production simulations;

(3) to provide information on the nutrient ratios in different components of the pelagic food web;

(4) to perform exploratory experiments on the role of nutrients in the regulation of primary production in Tanganyika;

(5) to provide information on the concentrations of dissolved organic carbon in Tanganyika;

(6) to provide information on the level of bacterial activity in the plankton of Tanganyika;

(7) to train the local personnel to use the primary production methodology.

The activities of this subcomponent will be usually combined with the hydrodynamics, limnology and zooplankton studies on *R/V Tanganyika Explorer*. The measurements and water samples required for this subcomponent can be taken during the stops for hydrodynamic measurements or limnological sampling, and thus they do not increase the duration of the cruise. More restricted fluorometer and irradiance measurements should be included in the program of all cruises.

5.2 Equipment and personnel

Equipment:

- Limnos sampler (small and large; with messengers)
- Plastic bucket (20 L) for making composite samples

- Vacuum pump and bottle plus filter holder for chlorophyll samples
- Nylon sieves (25, 50, 100, 200, 500 µm mesh cloth pieces or small nets) for size-fractionation of plankton
- Whatman GF/F and GF/C filters (diameter 47 mm)
- Nuclepore filters (pore sizes 1 or 2 µm and 0.2 µm) and appropriate filter holder
- Plastic minibags for storing filters
- Plastic 100-mL bottles for phytoplankton and bacterioplankton samples
- Plastic 250-mL bottles for zooplankton samples
- Field fluorometer (Turner Designs 10-AU-005, with pump and bubble trap chamber)
- Primary production equipment, plus in addition the on-board incubator
- Li-Cor underwater radiation (PAR) measurement system (sensor, cable, datalogger, sensor housing for measurements in air)
- Zooplankton sampling net, mesh size 50 µm
- Dissection microscope for handling zooplankton
- Chemicals for nutrient addition experiments (nitrogen, phosphorus, and carbon sources; doses prepared beforehand)
- Glutaraldehyde (25 %) for preservation of zooplankton biomass samples

Personnel:

Consultant(s) from Finland (Salonen and/or Sarvala or Järvinen), local LTR staff (as considered suitable); counterparts from each country: training is given during the first cruise, and if required, on later cruises.

5.3 Chlorophyll

Horizontal variation

Fluorescence should be measured with the field fluorometer from surface samples whenever possible, together with irradiance measurements with the Li-Cor system. Preferably the fluorometer should be connected to a computer for continous monitoring of surface fluorescence during travel. Surface water is lead through the fluorometer via a bubble trap chamber, and the results are logged to a computer file with the same program as reads the weather station. The surface readings give meaningful information on the spatial distribution of chlorophyll during the night, in the morning and on cloudy days. On sunny days, the surface inhibition should become evident. Irradiance is continuously logged by the weather station so that it can be related with the diel variations in fluorescence.

Vertical distribution

During stops longer than 1 h, vertical distributions of chlorophyll fluorescence are taken with the fluorometer from samples taken with the Limnos sampler from 0, 5, 10, 20, 30, 40, 50, 60, 70, 80 and 100 m. Vertical attenuation of light is measured with the Li-Cor system. At limnological vertical sampling sites (B) the fluorescence is measured from the same

samples which are used for the determination of chlorophyll by filtering and extraction (Whatman GF/F filtering of 3 litres per depth, from 0 to 300 m, the number of depths determined by the limnological sampling). The relationship between chlorophyll *a* and fluorescence can be established from these data. The same filters will be used for nutrient ratio and chlorophyll determinations (perhaps in Finland, because the measurement of chlorophyll from subsamples of the filters may require higher sensitivity than is obtainable with a spectrometer; dry filters can be transported). Nitrogen and phosphorus may be determined in the field laboratories.

5.4 Primary production

Phytoplankton primary production is determined using an on-board incubator at different light intensities, measured with Li-Cor radiation meter. For the incubations, composite samples are combined from samples taken from the depths of 5, 10 and 20 m (later experiences may necessitate further depths, but this is a convenient array for start). In the incubator experiments the light saturation curve of primary production will be determined under 6 illumination levels covering the range from ca. 50 µE m^{-2} s^{-1} (ca. 5 % of surface light level) to ca. 400 µE m^{-2} s^{-1} intensity. Incubations are usually made in the morning and in the afternoon; the total number of incubations during a cruise may be 20–30. Vertical in situ incubations (5, 10, 20, 30 and 40 m) will be made along the incubator experiments during longer (>4 h) stops at the north, central and south basins.

A nutrient enrichment experiment will be arranged two times, with samples from the north and south basins. The experimental setup is: no addition, nitrogen addition (175 µg L^{-1} N as NH_4Cl), phosphorus addition (25 µg L^{-1} P as $KHPO_4$), carbon addition (250 µg L^{-1} C as glucose), and all combined. Incubations last 2 days and each treatment is duplicated (altogether 30 glass liquid scintillation vials). The vials are kept in the incubator.

5.5 Nutrient ratios

Total particulate nutrient (C, N, P) ratios are obtained from glass fiber filters prepared for chlorophyll determinations (see above).

Nutrient ratios in different fractions of plankton are obtained from three areas (north, center, and south basins). Nutrients in bacterioplankton are determined from 1-µm Nuclepore filtrate filtered onto GF/F filters. Rather monospecific fractions of zooplankton are obtained by sieving through a series of 500 (*Tropodiaptomus*), 200 (*Mesocyclops*), 100 (*Tropodiaptomus*) and 50 µm (nauplii) mesh nets.The composition of the fractions is checked with a dissection microscope. For nutrient ratios, qualitative samples are sufficient. The samples are stored in a desiccator.

Nutrient ratios should also be determined from larger components of the pelagic system (medusae, atyid shrimps, fish larvae, larger fish).

Zooplankton samples are preserved in glutaraldehyde for later determinations of individual carbon and nitrogen biomasses in Finland.

5.6 Dissolved organic carbon

Dissolved organic carbon (DOC) is one potential source of energy for the pelagic production in Lake Tanganyika. Accurate measurements of the DOC concentrations are thus one important goal of the LTR project. No suitable carbon analyzer is available locally, and therefore the samples must be transported to Finland for analyses with a very sensitive analyzer (Salonen 1979). Samples from 0, 40, 80, 140, 200 and 300 m are taken from the north and south basins (sampling sites B for the vertical limnological sampling) into 25-mL ground glass bottles. Samples are transported to Finland for dissolved (DOC) and volatile organic carbon (VOC, mainly methane) determinations.

5.7 Bacterial studies

To estimate bacterial production, leucine incorporation experiments (Chin-Leo & Kirchman, 1988) will be performed at the north, central and south basins (0, 10, 20, 40, 80, 140, 300 m; the vertical limnological sampling sites B). Isotope dilution assay will be made once to determine the saturation concentration for leucine uptake (range 1–100 nM leucine). Biomass samples are taken from the vertical series at the same locations. If the same water mass can be sampled by day and night, exploratory samples will also be taken for the determination of diel changes in bacterial numbers.

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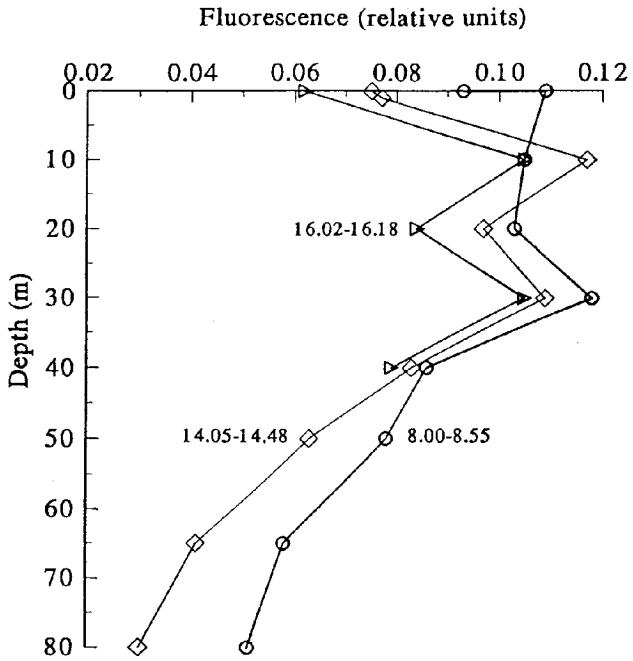

Fig. 1. Diurnal variation in the vertical distribution of relative fluorescence off Kigoma 2 Dec. 1994. The two replicate surface values of the first series show the extent of variation caused by the shifting location of the drifting boat.

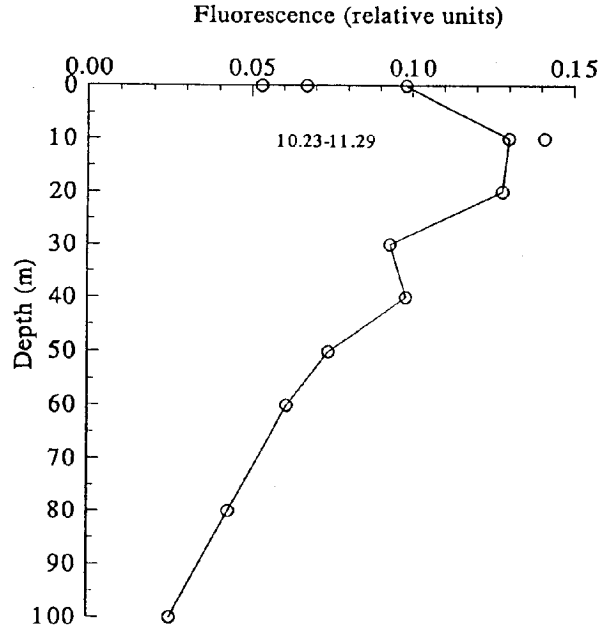

Fig. 2. Vertical distribution of relative fluorescence off Kigoma 5 Dec. 1994. Replicate values (single circles) at the surface show the decrease during the sampling period (about 1 hour). Although part of this change may be due to shifting water masses, most of the variation was probably due to the adverse effects of bright sunshine, since changes at 10 m depth were much less pronounced.

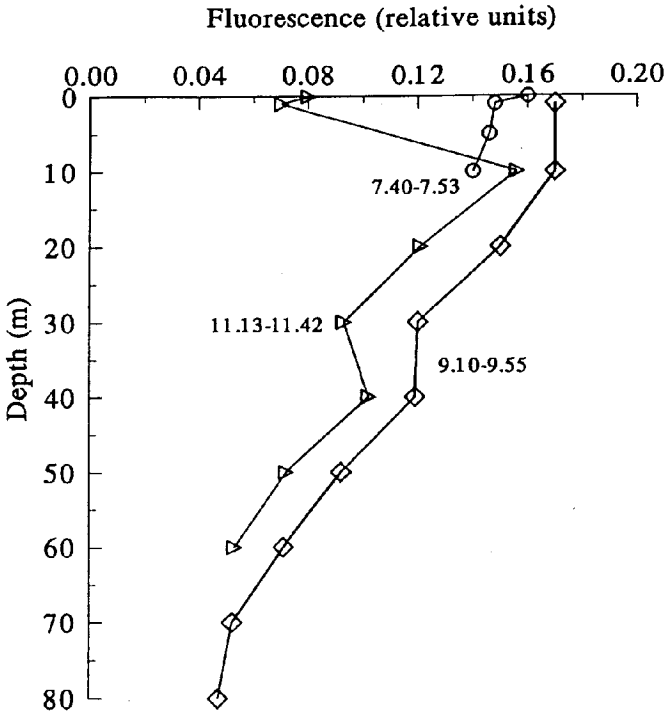

Fig. 3. Diurnal variation in the vertical distribution of relative fluorescence off Kigoma 7 Dec. 1994.

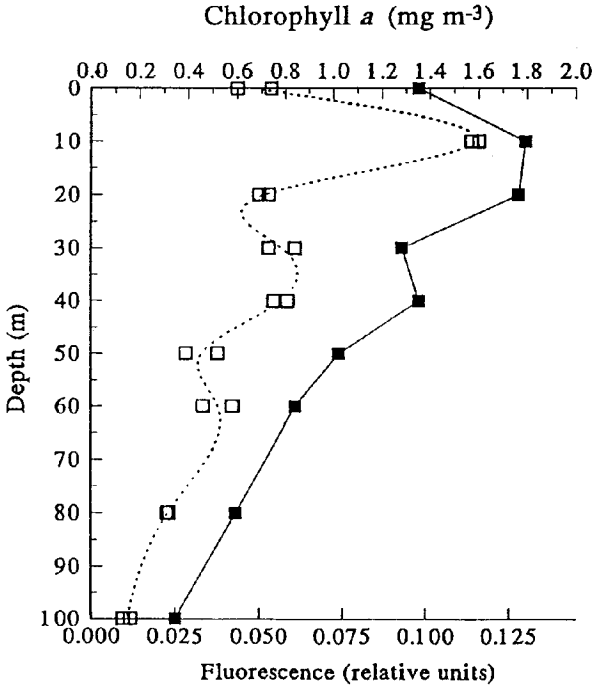

Fig. 4. Vertical distribution of relative fluorescence (black squares) and chlorophyll *a* (open squares; Whatman GF/C filtering of 2 litres, ethanol extraction, fluorometer measurement) off Kigoma 5 Dec. 1994. Both measurements derive from the same water sample.

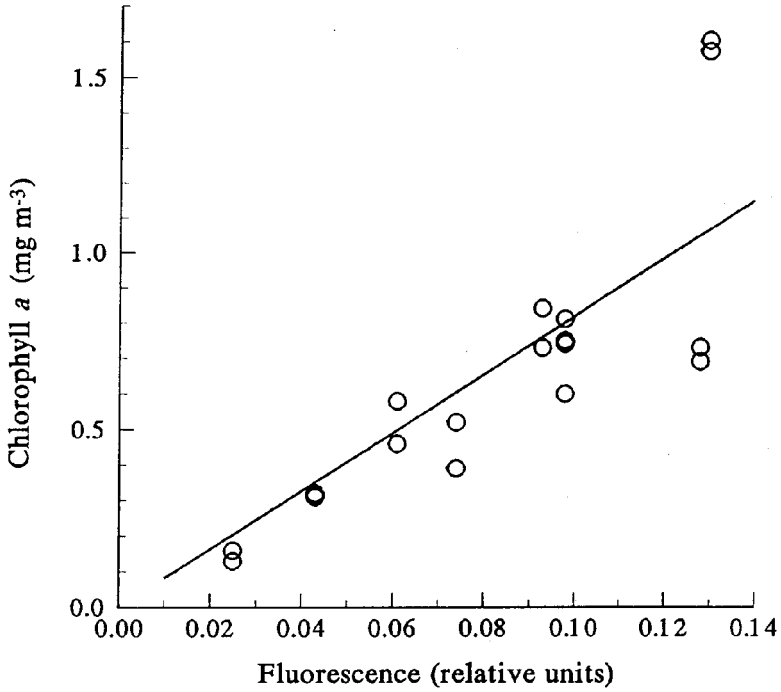

Fig. 5. Relationship between extracted chlorophyll and field measurements of relative fluorescence off Kigoma 5 Dec. 1994 (samples from 0–100 m depth). The regression line was forced through the origo.

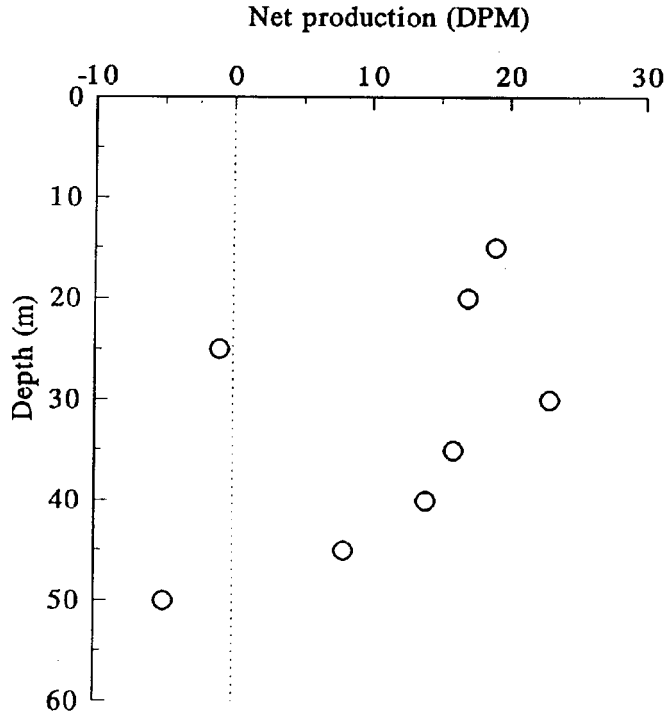

Fig. 6. Vertical distribution of relative primary production (in net dpm units) off Kigoma 21 Sept. 1994 (measurements by Mr. Kissaka and Ms. Kurki).

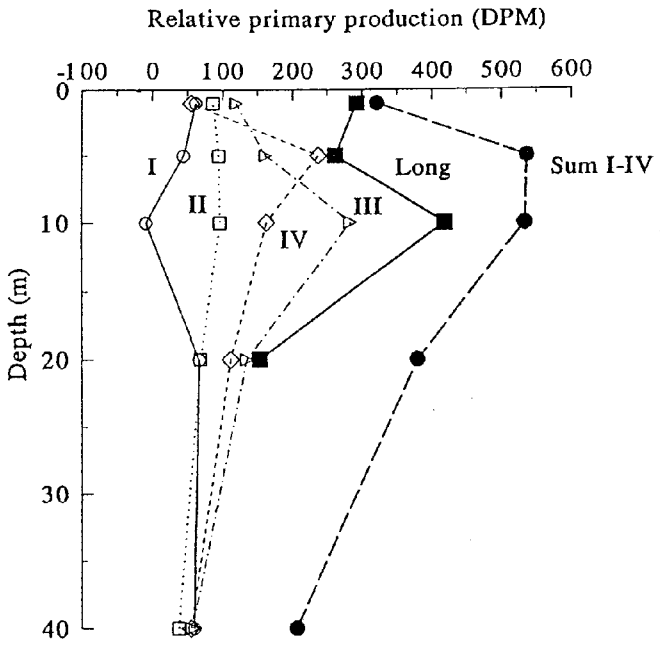

Fig. 7. Diel course of the vertical distribution of relative primary production (in net dpm units) off Kigoma 2 Dec. 1994. Results are shown for four successive two-hour incubations (I–IV, between 7.50 and 17.30), their sum (black dots), and a whole-day incubation (7.55 - 17.35; filled squares).

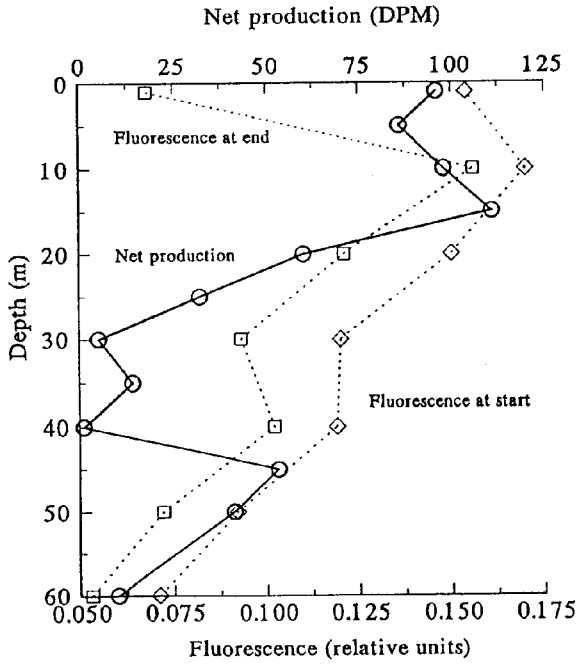

Fig. 8. Vertical distribution of relative primary production (in net dpm units) off Kigoma 7 Dec. 1994. Relative fluorescence values in the beginning and at the end of the two-hour incubation are also given.

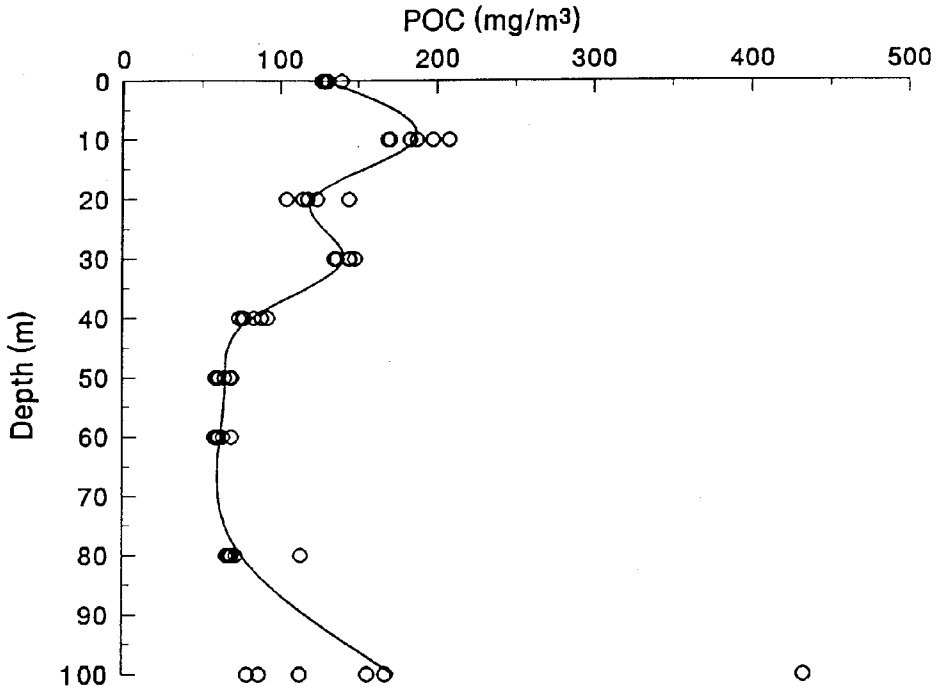

Fig. 9. Vertical distribution of particulate organic carbon off Kigoma 5 Dec. 1994. Values are shown for six replicates from two parallel filtered samples at each depth. The curve is based on cubic spline smoothing.

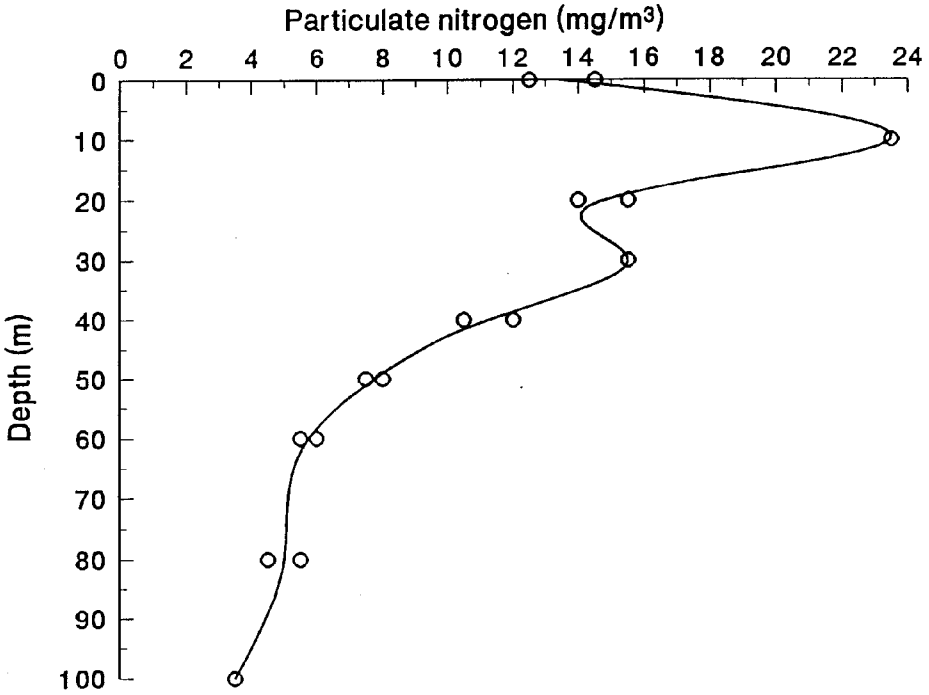

Fig. 10. Vertical distribution of particulate nitrogen off Kigoma 5 Dec. 1994. Values are shown for two parallel filtered samples at each depth. The curve is based on cubic spline smoothing.

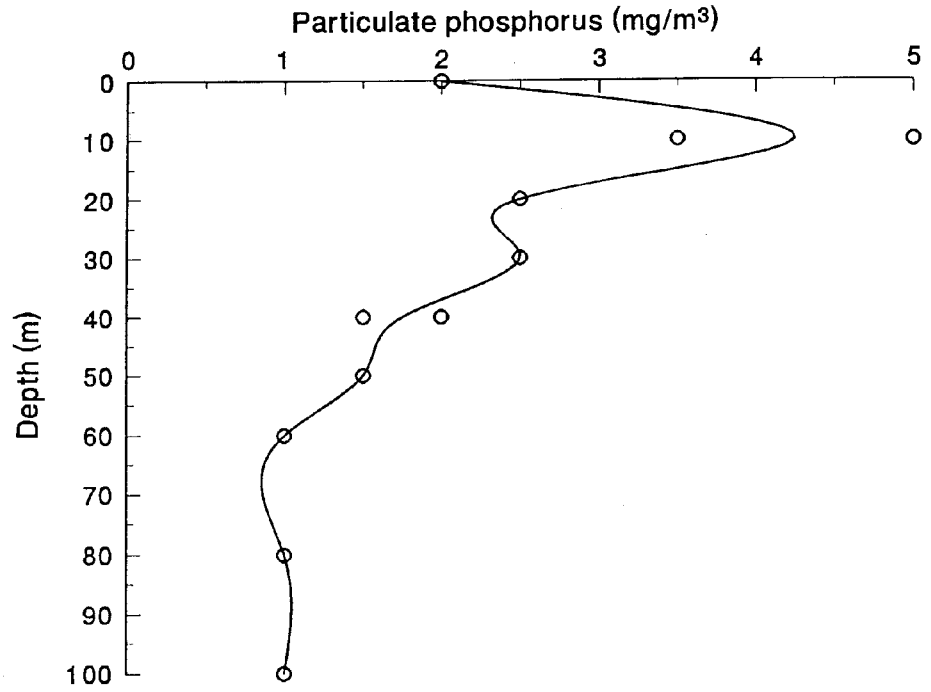

Fig. 11. Vertical distribution of particulate phosphorus off Kigoma 5 Dec. 1994. Values are shown for two parallel filtered samples at each depth. The curve is based on cubic spline smoothing.

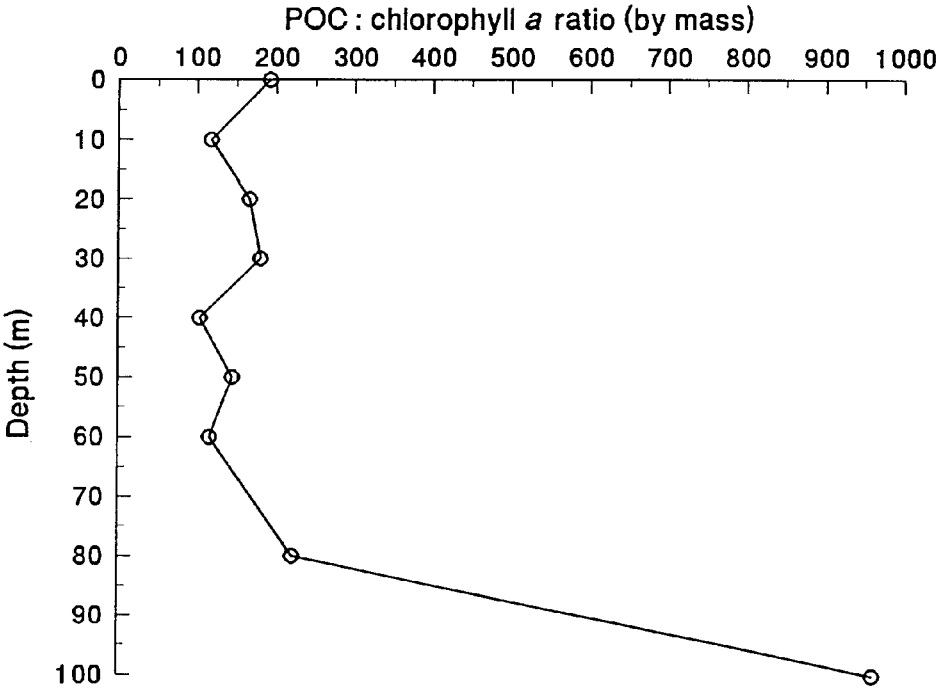

Fig. 12. Vertical distribution of the particulate organic carbon *vs.* chlorophyll *a* ratio (by mass) off Kigoma 5 Dec. 1994. Average values are shown for each depth.

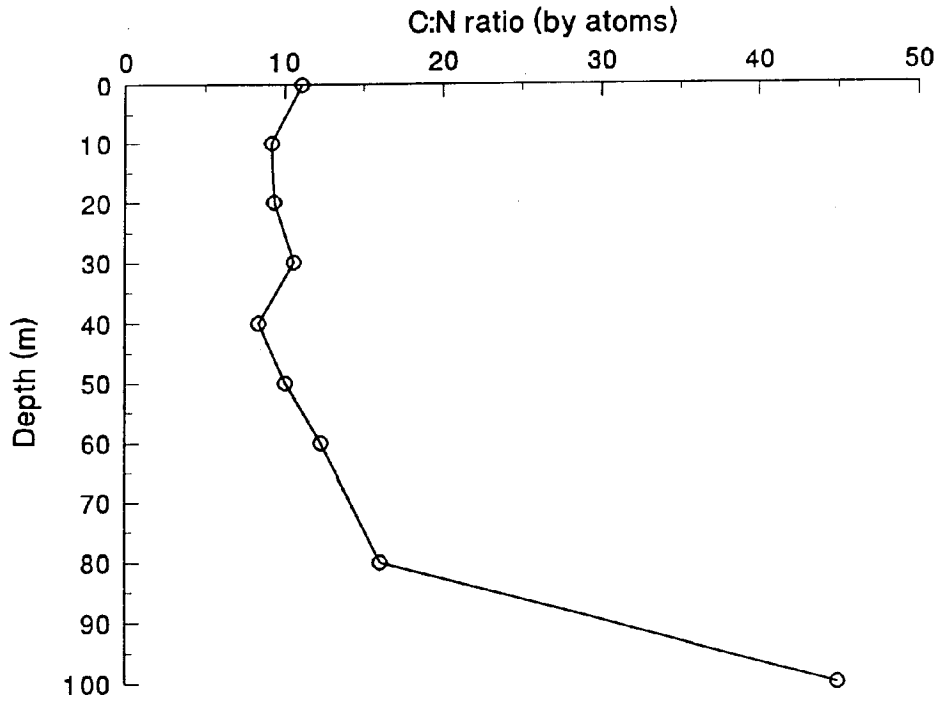

Fig. 13. Vertical distribution of the particulate C:N ratio (by atoms) off Kigoma 5 Dec. 1994. Average values are shown for each depth.

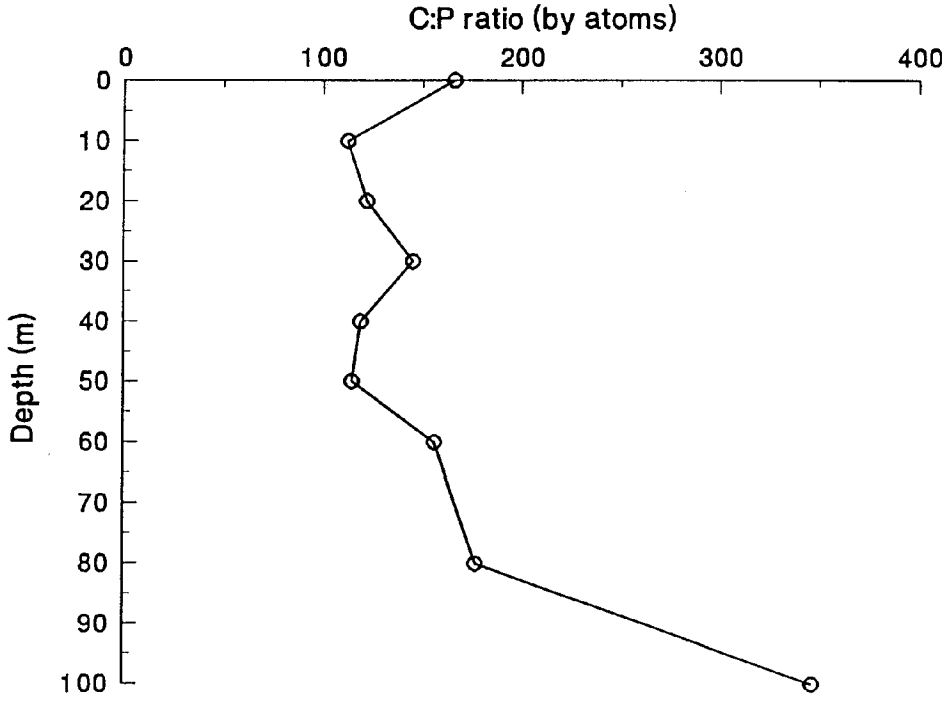

Fig. 14. Vertical distribution of the particulate C:P ratio (by atoms) off Kigoma 5 Dec. 1994. Average values are shown for each depth.

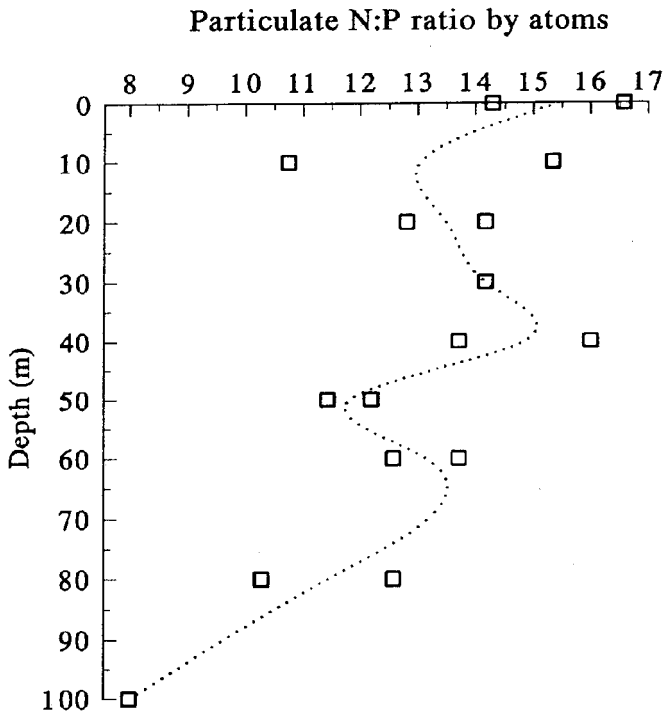

Fig. 15. Vertical distribution of the particulate N:P ratio (by atoms) off Kigoma 5 Dec. 1994. At each depth, both measurements were made from subsamples of the same filter.

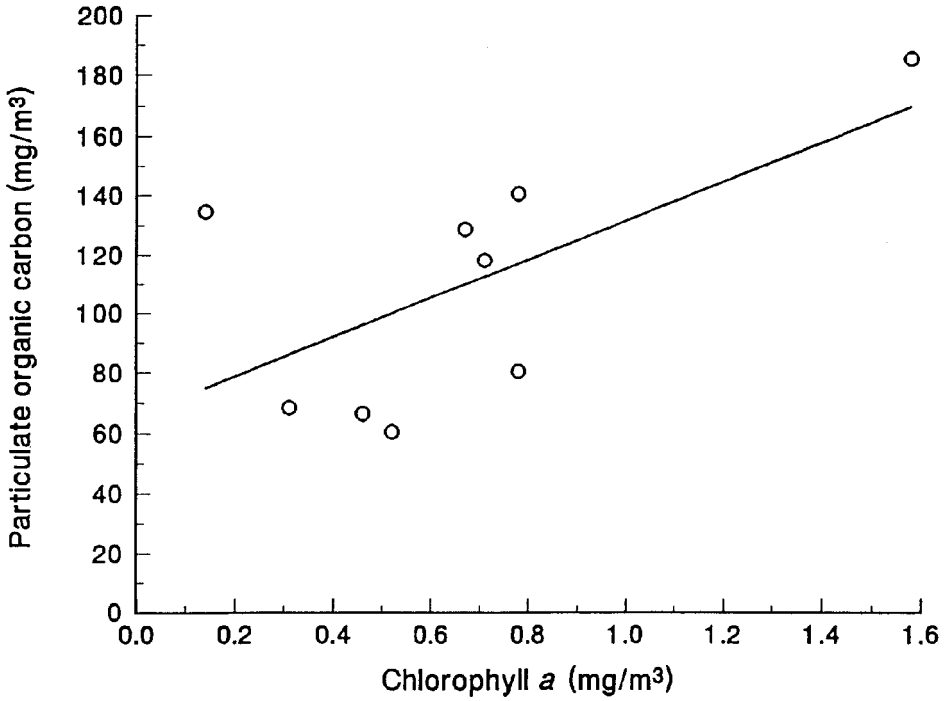

Fig. 16. Relationship between the particulate organic carbon and extracted chlorophyll off Kigoma 5 Dec. 1994. Average values for each depth were used.

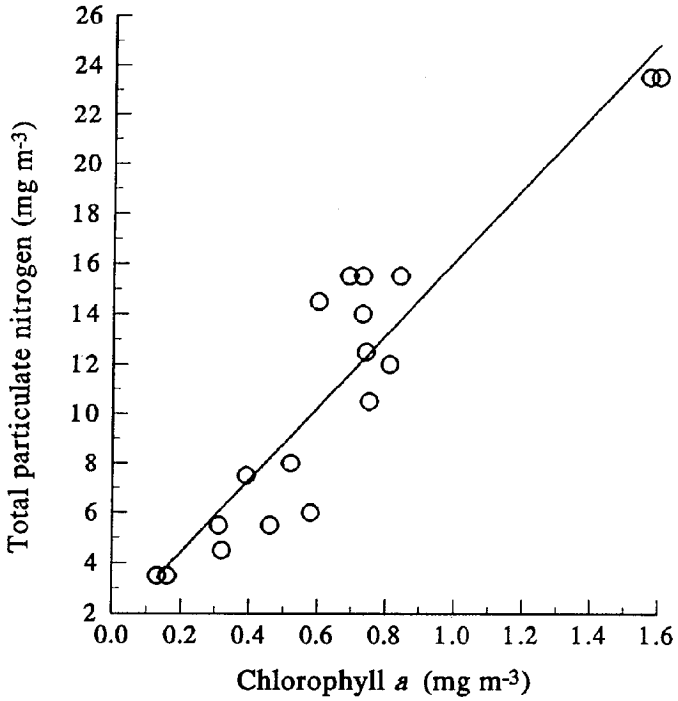

Fig. 17. Relationship between the particulate nitrogen and extracted chlorophyll off Kigoma 5 Dec. 1994. At each depth, both measurements were made from subsamples of the same filter.

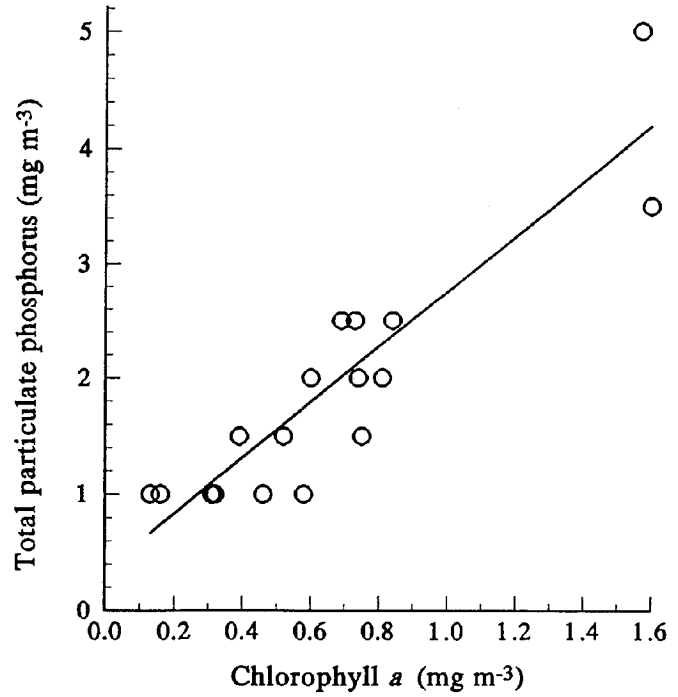

Fig. 18. Relationship between the particulate phosphorus and extracted chlorophyll off Kigoma 5 Dec. 1994. At each depth, both measurements were made from subsamples of the same filter.

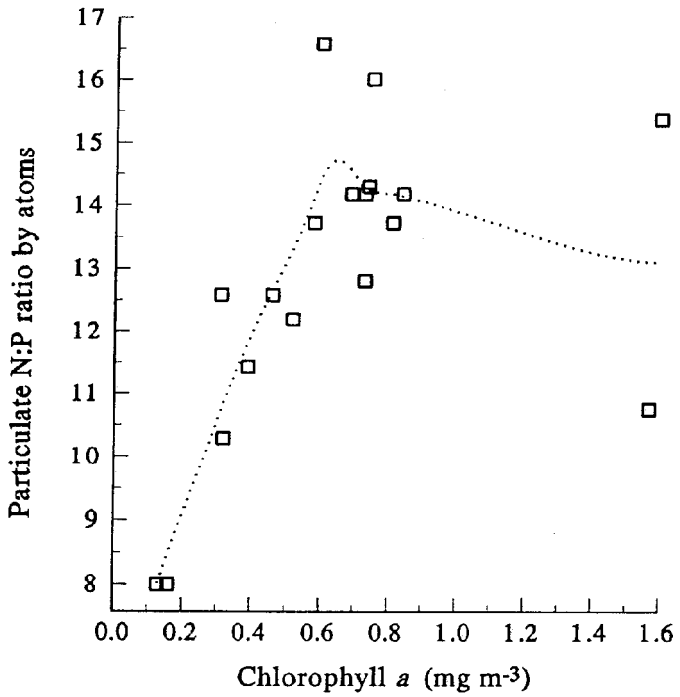

Fig. 19. Relationship between the particulate nitrogen to phosphorus ratio and the extracted chlorophyll off Kigoma 5 Dec. 1994. At each depth, all measurements were made from subsamples of the same filter.

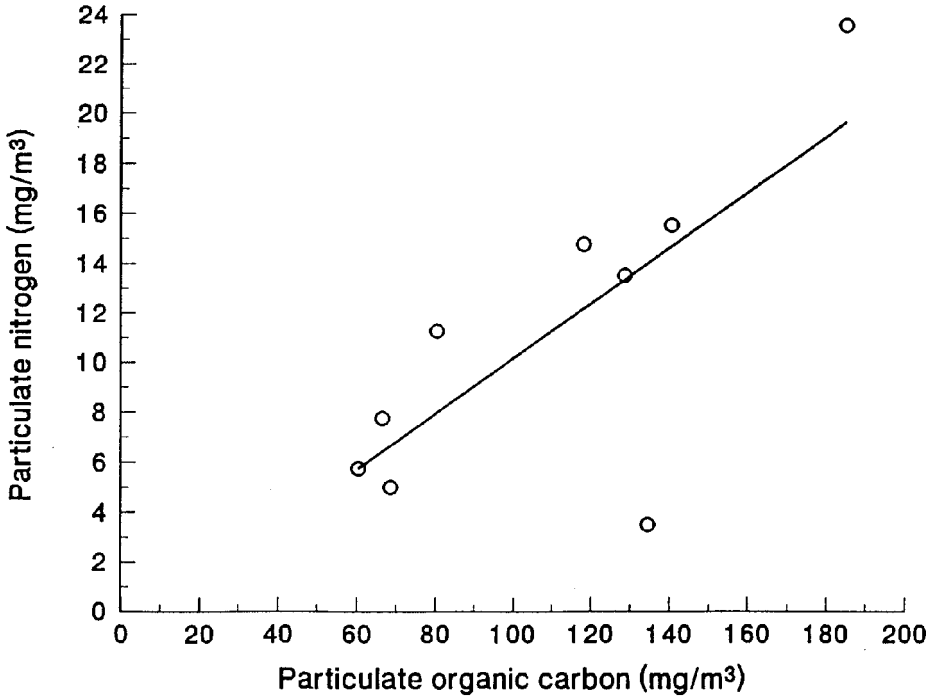

Fig. 20. Relationship between the particulate nitrogen and particulate organic carbon off Kigoma 5 Dec. 1994. Average values are shown for each depth.

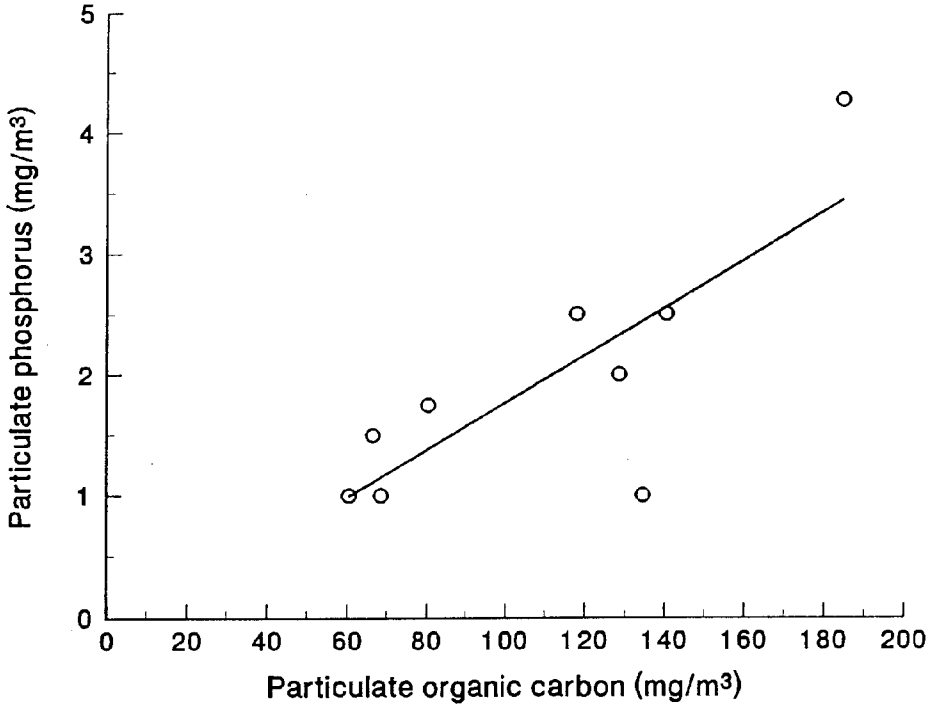

Fig. 21. Relationship between the particulate phosphorus and particulate organic carbon off Kigoma 5 Dec. 1994. Average values are shown for each depth.

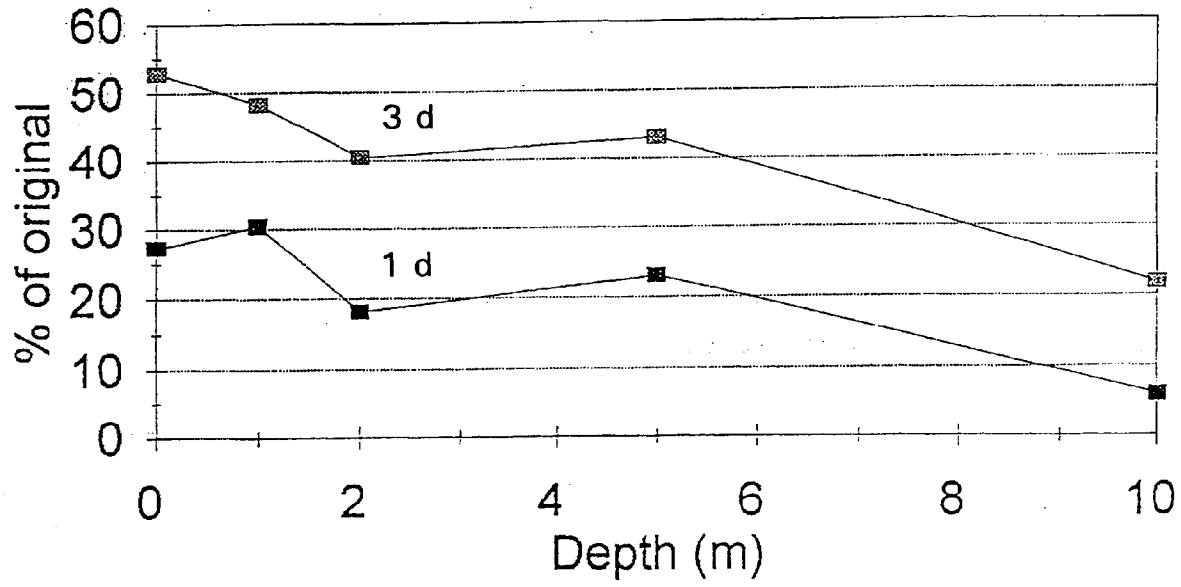

Fig. 22. Decrease of colour in fulvic acid preparations incubated in quartz glass tubes in natural light for 1 or 3 days at different depths off Kigoma 4–7 Dec. 1994.

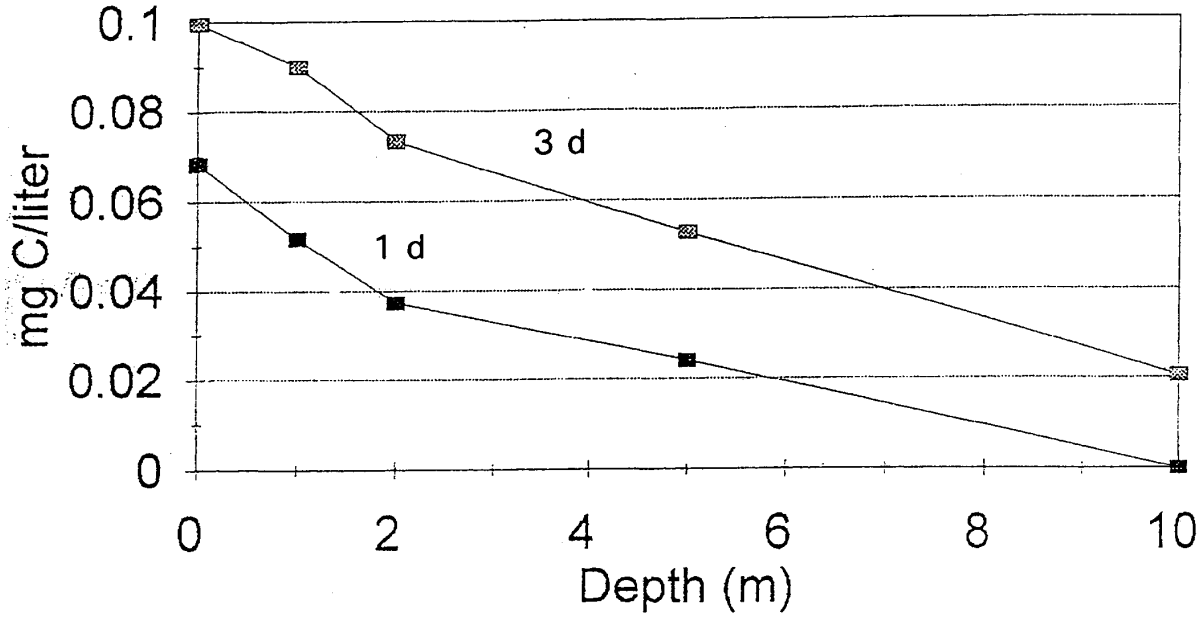

Fig. 23. Volatile organic carbon formation in fulvic acid preparations incubated in quartz glass tubes in natural light for 1 or 3 days at different depths off Kigoma 4–7 Dec. 1994.

Appendix

Fluorometer readings off Kigoma on 2 December 1994.

	Time periods			
Depth	*8.00-8.55*		*14.05-14.48*	*16.02-16.18*
0	0.093	0.109	0.075	0.062
1	..		0.077	..
10 0.105	0.117		0.105	
20 0.103	0.097		0.084	
30 0.118	0.109		0.105	
40 0.086	0.083		0.079	
50 0.078	0.063			
65 0.058	0.041			
80 0.051	0.030			

Fluorometer readings on 5 December 1994 off Kigoma.

	Time periods		
Depth	*10.23–11.29*		
0	0.098		
10	0.130		
20	0.128		
30	0.093		
40	0.098		
50	0.074	surface	0.067
60	0.061		
80	0.043		
100	0.025 unstable		

and after returning to the starting location

0	0.053		
10	0.141		

Weather clear in the morning, after 12 o'clock clouds and finally rain.

Fluorometer readings off Kigoma on 7 December 1994.

	Time periods			
Depth	*7.40-7.53*	*9.10-9.55*		*11.13-11.42*
0	0.160	..		0.080
1	0.148	0.170	0.138	0.068
5	0.146	..		..
10	0.140	0.170		0.156
20	..	0.150		0.121
30	..	0.120		0.093
40	..	0.119		0.102
50	..	0.092		0.072
60	..	0.071		0.053
70	..	0.052		..
80	..	0.047		..

Weather was clear and sunny. The previous day was cloudy with abundant rain.