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OF THE FISHERIES ON LAKE TANGANYIKA

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SOURCES OF ENERGY FOR SECONDARY PRODUCTION IN LAKE TANGANYIKA
OBJECTIVES, APPROACHES AND INITIAL EXPERIENCES

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 of 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 the Governments concerned.

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1. INTRODUCTION

Rational fisheries management requires a good knowledge of the fish production potential. Ultimately, the fish yield is a function of primary production, which in turn depends on solar radiation and nutrient inputs from the drainage area. The fisheries yield in lakes usually ranges between 0.02 - 0.2 % of primary production (e.g. Morgan et al. 1980). For Lake Tanganyika, a preliminary estimate of about 0.4 % has been given in the literature (Hecky 1984, 1991). To explain this unusually high productivity, Hecky and Fee (1981) speculated that the long geological history of the lake has allowed evolution of communities consisting of highly efficient species. As another explanation they proposed that the flux of dissolved organic matter (DOM) from the anoxic hypolimnion may complement phytoplankton primary production.

In Lake Tanganyika, as in other deep clearwater lakes, primary production of phytoplankton is expected to be the major source of energy to higher pelagic trophic levels, including fish. The present estimates of primary production in Tanganyika are based on extrapolations from very limited data. So far, no studies have extended over a seasonal cycle. Only two series of measurements exist, from April-May and October 1975 (Hecky and Fee 1981), made under artificial light with water sampled from the surface down to the depth of 25 m, and even these surveys suffered from technical problems. Although the measurements covered the whole length of the lake, their temporal and vertical coverage was thus inadequate. Further, due to methodological difficulties, the proportion of dissolved (exuded) production, which may be of the order of 50 % in oligotrophic waters, could not be quantified (Hecky and Fee, 1981). Irrespective of whether the dissolved production derives from true algal exudates or is leaked from damaged cells, ignoring it may lead to a major underestimation of the total primary production. Therefore, in order to assess the potential productivity of Lake Tanganyika, new measurements of phytoplankton primary production with reliable methods and with good horizontal, vertical and temporal coverage are necessary.

Dissolved organic carbon (DOC) levels given for Tanganyika by Hecky (1991, based on Hecky *et al.*, 1978) were around 2-5 mg L^{-1} (150-400 µM L^{-1}), and values given by Degens *et al.*, 1971 were within the same range. Considering the general water quality in Tanganyika, such DOC levels sound realistic, and do not suggest a major role for DOM in the planktonic food web. In contrast, much higher DOC values were reported by Degens and Ittekkot (1983), but they seem to be too high for such a clear-water lake as Tanganyika. The latter results also showed unrealistically high variability, suggesting problems with the measurements. Therefore, the importance of DOM clearly deserves new studies with more modern methods.

One of the LTR objectives is to determine the biological basis of fish production in Lake Tanganyika. Therefore, we are complementing the ongoing scientific sampling programme with a new sub—component on the carbon cycling in the lake. This sub—

component aims to quantify the main sources of organic carbon available for secondary production in the food chain maintaining the pelagic fisheries.

2. OUTLINES OF THE SUB-COMPONENT

The objectives of the proposed programme are: (1) to obtain a more reliable estimate for phytoplankton primary production; and (2) to evaluate the importance of DOM for planktonic food chains.

The estimate of primary production will be improved by collecting more complete data than is available from earlier studies. This includes the following aspects: (1) sampling will be regular and cover the whole year; (2) regular measurements will be made at three stations in different parts of the lake; (3) the spatial coverage will be complemented with supporting data on chlorophyll contents of water from: (i) samples taken while cruising to the regular monitoring stations; (ii) remote sensing (if technically possible); and (iii) later lake-wide surveys using the research vessel *R/V Tanganyika Explorer;* and (4) Close attention will be given to primary production in the smallest size fractions (picoplankton, also dissolved production). Methodological aspects require initial testing at local conditions.

Mineralization of organic matter is an important measure for the evaluation of energy and carbon balance in Lake Tanganyika, and it will be measured routinely along with primary production. The seasonal course of dissolved and particulate carbon will be determined to reveal the sources of organic matter for decomposition. Along with these, bacterial and protozoan populations and their growth will be evaluated. As has recently become evident in oceanographic research, appropriate methodology is critical for the correct determination of the low DOM concentrations found in clear waters (Sharp *et al.*, 1993). Therefore, also this part of programme requires experimentation and testing of techniques, prior to launching a routine sample processing procedure.

Although the main focus of attention is on the carbon cycling in the plankton of Tanganyika, biomass samples collected for that purpose will also be used for the determination of major nutrients. Nutrient ratios, in particular, may prove to be important tools in explaining trophic relationships and seasonal dynamics in the lake (e.g. Elser and Hassett, 1994).

3. TENTATIVE TIME SCHEDULE

The proposed programme is progressive and consists of successive stages. The first visit in April 1994 was introductory and allowed for adaptation of planned procedures to local laboratory and field conditions, including the chemical and biological properties of Lake Tanganyika. After this stage,

the procedures chosen will be introduced to the local project staff, and basic routines can be established and described in a field manual. The second visit (in December 1994) will start a series of more far reaching experiments which will illustrate various aspects of trophic relationships in plankton. The results of these experiments will also be used to develop the routine programme, running continuously in the field. Detailed manuals will be prepared and appropriate training provided for each procedure to be used by the local counterpart staff.

TABLE 1. Schedule for 1994 and 1995.

Time	Duration	Purpose
April 1994	2 weeks	Procedural tests by Salonen and Sarvala (consultancy). Demonstration to local staff of elementary procedures for the determination of primary production (radiocarbon method) and mineralization of organic matter (plankton community oxygen consumption)
December 1994	2 weeks	Methodological experiments by Salonen and Sarvala (consultancy: bacterial and protozoan production; light mineralization of DOM). Training of local staff.
January 1995	12 months	Routine measurements of primary production and mineralization of organic matter by local staff (starting time depends on the availability of necessary equipment).
March 1995		Evaluation of results from the first measurement period (by Salonen and Sarvala).

4. TENTATIVE STUDY PROCEDURES

4.1 Phytoplankton primary production

Purpose: To estimate how much autotrophic production is available for consumers.

Time schedule: Twice a month at three stations (off Bujumbura, Kigoma and Mpulungu) starting January 1995 and continuing until the end of the project's scientific sampling programme.

Method: Radiocarbon method with acidification and bubbling as well as/or with filtration (routine measurement). *In situ* or 'simulated' *in situ* method with incubation in a water bath on the deck of the research vessel or in the shore laboratory under a series of neutral light filters (methods to be decided after the introductory visit in April 1994 and further experiments). The radioactivity is counted in Finland using a liquid

scintillation counter. The results are calculated by multiplying the measured primary production by the ratio between daily total radiation and the total radiation measured during the time of the experiment. Dissolved inorganic carbon concentration is calculated from pH and alkalinity.

Tests:
- the effect of incubation time
- optimum radioactivity of stock solution
- possibility to evaporate samples to dryness in plastic liquid scintillation vials before sending to Finland for counting
- possibility of replacing harmful formaldehyde with Lugol's solution
— size fractionation of primary production
— methods to remove inorganic radiocarbon from water (in Finland before April 1994)
— importance of time delays in the treatment of samples under tropical conditions before filtration

4.2 Mineralization of organic matter

Purpose: To obtain an estimate of the mineralization of organic matter in water (excluding larger zooplankton)

Time schedule: Twice a month at three stations (off Bujumbura, Kigoma and Mpulungu) starting in January 1995 and continuing until the end of the project's scientific sampling programme.

Method: Biological respiration will be measured in darkness as oxygen consumption in the lake or at natural temperature in an incubator together with primary production bottles (routine measurement).

Description: To be specified after field experiments in April and December 1994.

Tests:
- possible abiotic mineralization by light in quartz bottles (allowing UV-penetration)
— diel time course of mineralization

4.3 Growth rates of bacteria and protozoa

Purpose: To assess the importance of bacteria and protozoa in the planktonic food web

Time schedule: starting in 1995, in connection with biological cruises with *R/V Tanganyika Explorer.*

Method: Production of bacteria by leucine uptake, and production of bacteria and protozoa by microscopic method.

Description: To be specified after field experiments in December 1994.

4.4 Biomass determinations

Purpose: To obtain an estimate of food quality and quantity available for consumers.

Time schedule: Twice a month at three stations (off Bujumbura, Kigoma and Mpulungu) starting in December 1994 and continuing until the end of the project's scientific sampling programme. Routine collection from the samples taken for primary production measurement; occasionally also from deeper water samples in connection with other limnological sampling.

Methods: (1) Particulate organic carbon is measured by high temperature combustion from circles cut from glass fibre filters. P and N are measured from similar filters after persulphate oxidation. (These measurements are also needed for zooplankton species.) Alternatively P can be determined after oxidation at 450°C and dissolution in acid, and N by high temperature combustion. N and P determinations may be made in local laboratories (wet oxidation) and C is analysed in Finland. Further specification of procedures after field experiments in December 1994;

(2) Phytoplankton biomass is estimated by counting species with an inverted microscope (possibly as a consultancy: 1 month for one year);

(3) Bacterioplankton biomass is estimated after staining on 0.2 µm black Nuclepore membranes. The cell number counts and measurements are made with an epifluorescence microscope and an image analyzer in Finland (consultancy by Salonen);

(4) Chlorophyll *a* is measured after filtration on glass fibre filters and extraction in ethanol of circles cut from the filter. A separate manual should be prepared following the principles of the international standard for chlorophyll measurements (ISO 10260—1992(E))

Tests:
- comparison of Whatman GF/C and GF/F filters for the determination of POC and chlorophyll.

4.5 DOC

Purpose: To estimate the importance of DOM as a potential food resource for plankton.

Time schedule: Twice a month at three stations (off Bujumbura, Kigoma and Mpulungu) starting in December 1994 and continuing until the end of the project's scientific sampling programme.

Method: High temperature combustion of dried acid water sample and infrared detection of carbon dioxide.

Description: Samples are regularly taken from the primary production samples. In addition to this, once a month, samples are also taken from 50, 100 m and sometimes even deeper, simultaneously, as water will be taken for other purposes.

Because of low concentrations, determination of DOC is sensitive to the uncertainties in blank values, which cannot be absolutely sure in the absence of absolutely carbonless water. To avoid most of the problems caused by water, an evaporation/high temperature combustion technique is used. However, with the drying method, one must be very careful to avoid contamination from the absorption of atmospheric organic matter. Ten mL of sample are taken into a preignited glass ampoule and heated to dryness at 60°C. The ampoule is then closed with a stopper or by melting the glass neck. In the latter case, flame combustion gases are kept out by $C0_2$-free oxygen which also fills the dry ampoule. The closed ampoule is baked at 450°C overnight. Carbon dioxide in the ampoule is measured with an infrared carbon analyzer. Sample preparation to dry state will be made at Tanganyika and final determination is made in Finland. Further specification of procedures will be made after field experiments in December 1994.

Tests:
- all steps in the method need rigorous testing in Finland before

field tests at Tanganyika
- comparison with high temperature liquid determination
- preservation in phosphoric acid (pH ca. 2).

4.6 Accessory measurements

Solar radiation: Values for the total or (preferably) photosynthetically active radiation (PAR) need to be measured both continuously at the weather stations and on the boat during the field incubations. Information on radiation conditions will enable the calculation of daily primary production estimates from the short—term experiments as well as the extrapolation of these estimates to intervening dates. Measurements of light penetration into water would also help generalizations from the primary production measurements. Spectral distribution of light at different depths should also be measured, with special reference to ultraviolet wavelengths.

4.7 Materials needed

Each field station will require:
- stainless steel filtration funnel 47 mm (for chlorophyll determinations);
— vacuum pump;
— vacuum bottle;
- filtration manifold 8 x 25 mm (for primary production measurements, if filtration were needed);
- Nuclepore filters 0.2 µm; 500 pcs (for primary production measurements, if filtration were needed);
- glass-fibre filters (for concentrating chlorophyll; e.g. Whatman GF/C or GF/F);
— spectrometer for chlorophyll measurements: for use in the visible range up to 750 nm, with a resolution of 1 nm, preferably a bandwidth of 2 nm or less, sensitivity less than or equal to 0.001 absorbance units and with optical cells of path length between 1 cm and 5 cm; to make possible the determination of oxygen through detection of iodine, the spectrometer should

also cover the UV range down to at least 287.5 nm;
— on board incubation chamber (will be required on the research vessel);
- piston burette for oxygen titration (not needed if iodine is measured spectrophotometrical ly);
— borosilicate glass bottles with ground glass stopper, volume ca. 100 mL; 50 pcs;
- bacteria/phytoplankton plastic sample bottles, 100 mL; 100 pcs/yr;
- plastic liquid scintillation vials 1000 pcs;
— glass liquid scintillation vials 200 pcs;
— glassware and chemicals for oxygen determinations with the Winkler technique;
- preservation liquids (Lugol's solution, formaldehyde);
- phosphoric acid;
— radiocarbon solution;
- a 40 µL dosing pipette (e.g. Finnpipette) for the injection of radiocarbon stock solution;
- buoy with suspending device for incubating samples in the lake;
- 10 mL glass ampoules for DOC analyses;
— an integrating total irradiance measuring system; alternatively
a device measuring irradiance in the visible light area (also necessary on the *R/V Tanganyika Explorer).*

5. METHODOLOGICAL EXPERIMENTS AT LAKE TANGANYIKA

5.1 General

In order to find out the optimum procedures for primary production measurement, with the assistance of local LTR personnel, we made some preliminary experiments at lake Tanganyika in April 1994. Firstly, we tested whether *in vivo* fluorescence of chlorophyll measured by a field fluorometer could be applied as a rapid supplementary measurement to extend the spatial coverage of primary productivity data. Secondly, we experimented with the radiocarbon method, in order to find a procedure most appropriate for routine determination of primary production at lake Tanganyika.

5.2 Methods

Vertical and horizontal distribution of phytoplankton was estimated indirectly from the *in vivo* fluorescence of chlorophyll *a* using a Turner 10-AU field fluorometer operated by a 12 V battery. Water samples for the measurement were taken with a Limnos sampler. Sampler contents were drained through the fluorometer by connecting the sampler's draining tube to the black inlet tube of the fluorometer. Fluorescence values were recorded during the throughf low of water after the reading had stabilized. Temperatures at each depth were read from the water sampler's mercury thermometer. The locations on the lake were determined with GPS.

Primary production was measured with the radiocarbon method.

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, 40 µL (1.2 kBq) of radiocarbon solution ($Na_2{}^{14}C0_3$) was added to 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 floating freely in the lake for the time of incubation. The vertical distribution of primary production was measured in a 3—hour incubation around noon at the depths of 1, 2, 5, 10 and 20 m. In a diel time series, we used short successive 2—3—hour incubations starting at sunrise and ending almost at sunset, and, in addition, one long incubation was equal in length to the sum of the short-term experiments. After the incubation, vials were wrapped in aluminium foil and transported to the laboratory. In one time series experiment, however, the subsampling and filtration steps were made on the deck of the vessel.

In the field laboratory, 10 mL of mixed water was filtered through a 0.2 µm Nuclepore filter which was then placed in an empty plastic liquid scintillation vial. Another subsample (6 mL) was pipetted directly into a vial and acidified to pH < 2 with phosphoric acid. Later in Finland, the 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, opened liquid scintillation vials were kept 10 mm under the fuming of strong hydrochloric acid. After these treatments, 6 mL of Wallac HiSafe 3 scintillation fluor was added to each vial and mixed thoroughly. The radioactivity was measured with Wallac Ultrobeta 1200 liquid scintillation counter.

Dissolved inorganic carbon (DIC) in water was determined in Finland with a carbon analyser according to Salonen (1981). Long storage time and pressure changes during the flight do not significantly affect DIC results of Tanganyika, because the high pH and alkalinity make the proportion of free CO_2 in DIG very low.

The final results of primary production were calculated from the measured radioactivity and DIC. The dark results were subtracted from the light ones.

The respiration of plankton was determined as oxygen consumption in darkened glass bottles with ground glass stoppers.

5.3 Results

In vivo fluorescence

Horizontal series of measurements from nearshore areas towards the open lake were made at the depths of 1, 10 and 20 m.

The differences between different locations were sometimes large (Figs. 1-3). This suggests uneven horizontal distribution of phytoplankton which is not unexpected in large lakes. However, because of the rapid diel changes in surface fluorescence (see below), part of this variation may have been due to time lags between measurements.

Vertical temperature profiles suggested that the epilimnion extended down to about 60 m, although there was a minor secondary thermocline between 20 and 40 m (Fig. 4). During daytime, the maximum values of fluorescence were always observed deep in the epilimnion, at the 40 - 60 m depth zone (Figs. 5-8). In the upper epilimnion fluorescence decreased markedly during the course of the day. A detailed diel sampling showed that early in the morning the *in vivo* fluorescence of chlorophyll *a* was rather uniform throughout the mixed layer down to 60 m (Fig. 9). After sunrise, the fluorescence started to decrease in the whole epilimnion, and near the surface it ultimately became undetectable.

Although the results consistently indicated a decrease of fluorescence in the water column during the day, this observation might have been caused by replacement of water masses at the sampling site. Such a possibility was supported by the observed horizontal differences of *in vivo* fluorescence. To exclude this alternative ca. 10 L water was taken in a large open plastic container on the deck of the research vessel and the temporal development of fluorescence in this confined water mass was followed. The results showed a rapid decrease of fluorescence (Fig. 10) being thus in full agreement with simultaneous *in situ* measurements (Fig. 9). Thus the decrease of fluorescence was evidently caused by excessive solar radiation.

Phytoplankton primary production

Contrary to earlier results, the acidification and bubbling method yielded useful results with no sign of problems from abiotic binding of inorganic radiocarbon. The measured primary production during three hours around noon was very low (Fig.ll) The vertical distributions of particulate and total (particulate + dissolved) primary production were rather similar, but near the surface, the proportion of the dissolved fraction may have been larger. In the 0-20 m water column the proportion of dissolved primary production was fairly high, ca. Fifty percent of the total production.

The diel time series experiment revealed several times higher production rates in early morning hours than later during the day (Fig. 12). The decrease during the day was more dramatic at 1 m than at 5 m, probably reflecting stronger inhibition of photosynthesis near the surface. The sum of the short time incubation results at 1 m was similar to that obtained from the long incubation covering the whole day, while at 5 m the sum was ca. 3 times higher. This difference may be explained, if the inhibition near the surface was so strong that most of the primary production took place during the early hours of the day both in the 2-h and whole day incubations. This agrees well with the time course of *in vivo* fluorescence (Figs. 9—10) and

suggests strong light inhibition near the surface.

Respiration of plankton

Preliminary experiments indicated that it is possible to determine respiration of plankton with 24-h incubation in the pelagial of Tanganyika. Only two series of determinations were made (TABLE 2) so that they do not allow conclusive comparisons with primary production, but the results showed an order of magnitude higher respiration than primary production. However, due to the probable great importance of early morning hours in photosynthesis (Fig. 12), our primary production estimates (Fig. 11) may be markedly too small.

TABLE 2. Respiration of plankton off Kigoma 13 April 1994 (24-h incubations in darkened bottles at *in situ* temperature).

Depth	Oxygen consumption mg 0_2 L^{-1} h^{-1}	SD % of mean	n
1 m	0.0067	6	4
30 m	0.0043	13	5

Because the oxygen consumption is calculated as a small difference between two relatively large values, the results are sensitive to any random or systematic variation. Therefore, we preliminarily studied how the accuracy of the oxygen determination, based on spectrophotometric detection of iodine (Duval *et al.*, 1974) compares with that of the conventional thiosulphate titration, using starch indicator for endpoint detection (TABLE 3). The precision of the spectrophotometric method was comparable to the thiosulphate titration, but the spectrophotometric method is more rapid and less demanding.

TABLE 3. The precision of oxygen determination in Tanganyika water with different methods. CV = coefficient of variation (100 * standard deviation/mean); n = number of replicates.

	CV%	n
Routine Winkler titration with starch		
	0.06	4
	0.07	4
	0.21	5
	0.08	5
Spectrophotometric determination		
	0.07	5
	0.08	7

5.4 Discussion

The adverse effects of strong solar radiation on primary production have been well documented (e.g. Vincent and Roy 1993). Surface inhibition of primary production is a typical feature of results from *in situ* bottle assays at fixed depths. However, at least to a large extent, this may be a methodological artefact, because in nature, the algal cells circulate freely in the epilimnion and experience variable irradiance levels within a short time period, and are therefore not damaged by the high radiation close to the surface. Similar pronounced surface inhibition of phytoplankton in the natural water column, as found in our study, was reported earlier from Lake Titicaca (Vincent *et al*., 1984), a tropical high mountain lake. In Titicaca, near surface thermoclines form each day and retain phytoplankton under extreme irradiances. This bright light exposure results in strongly depressed chlorophyll fluorescence and photosynthesis. During each afternoon, the phytoplankton are redistributed by wind—induced mixing, and full recovery is accomplished soon after nightfall. In Lake Titicaca, photoinhibition apparently operates by reversible inactivation of photosystem II reaction centers; it is not only UV-radiation but also excessive visible light which is responsible for the damage to photosynthetic structures(Vincent et *al*., 1984). Thus, although the diel mixing cycles are slightly different in Tanganyika and Titicaca, observations on the surface inhibition of phytoplankton are quite similar. The rapidity and depth penetration of the chlorophyll depression in Tanganyika probably result from the high transparency of water, closeness to the equator and moderate altitude (773 in a.s.l.) of the lake.

Judging by the high transparency values during our experiments in April, phytoplankton biomasses were probably close to their annual minimum. Nevertheless, the fluorescence measurements proved to be sensitive enough to yield valuable information on Tanganyika’s phytoplankton. This method would be particularly useful on the research vessel, where the data collection can be easily automated using the vessel’s computer system. However, due to the generally low level and strong diel variation of near—surface fluorescence, horizontal distributions of phytoplankton cannot be easily secured by pumping surface water through a fluorometer during cruising, vertical profiles are also needed. These can be obtained either by taking discrete water samples or by pumping through a tube which is gradually lowered to 100 m depth. In both cases a pressure sensor for the identification of sampling depth would improve the quality of the results.

Our results have significant consequences for the procedures to be adopted in the carbon-energy subcomponent of LTR. The minima of the *in vivo* fluorescence of chlorophyll and primary production near the surface and their diel decrease during the light period probably reflect strong photoinhibition of phytoplankton. The dynamic nature of these processes highly complicates the measurement of phytoplankton primary production. Light intensity is an important factor for primary production, and the existence of photoinhibition further emphasizes its importance. Therefore, continuous light measurements are

essential for the determination of daily primary production. Because harmful ultraviolet—B radiation may penetrate unexpectedly deep in clear waters (e.g. Gleason and Wellington 1993, Herndl *et al*., 1993), it would be advisable to also determine the spectral properties of underwater light.

The primary production measurements must clearly be extended to deeper water than expected. Hecky (1991) calculated from light extinction measurements that the average depth of the euphotic zone in Tanganyika would be only 28 m. However, our observation of the maximum production at 20 m suggests that much deeper water should be sampled. Judging by the vertical distribution and diel periodicity of photosynthesis, it seems likely that the published figures for primary production in Tanganyika are underestimates (cf. Rivkin and Putt 1987).

Our results have also significant implications for the satellite limnology subcomponent. Because the surface water layers of Tanganyika seem to be typically poor in chlorophyll (fluorescence) from late morning to late afternoon, and the situation may change very rapidly, it seems unlikely that satellite remote sensing of chlorophyll could be successful in the daytime, when the surface water chlorophyll levels are simply not representative of the whole water column. However, early morning satellite pictures might give more reliable estimates of chlorophyll, because during night mixing processes equalize the chlorophyll levels in the uppermost tens of metres (epilimnion). In any case, the rapid changes of the *in vivo* fluorescence make the ground calibration extremely difficult. The Pelagic Fisheries Assessment Project at Lake Malawi also had difficulties in remote sensing of chlorophyll and they decided to use satellite data only to map the surface temperatures of Lake Malawi (Dr. G. Patterson, pers. com.).

Although phytoplankton biomass and production in April are expected to be close to their annual minima in Tanganyika (Hecky, 1991), the radiocarbon method of measuring primary production was successful. Moreover, in spite of earlier difficulties (Hecky and Fee, 1981), the acidification and bubbling technique seemed to work properly. This greatly improves the possibilities to assess phytoplankton primary production of Lake Tanganyika. The advantages of the acidification and bubbling method are:

1) Because filtration is not needed, the determination has low material and labour requirements and is perfectly suited to working in the field at any site;

2) The incubations can be stopped by e.g. formaldehyde immediately after taking bottles out of water. This makes the handling of samples convenient and it may also improve the quality of the results under tropical conditions;

3) The unlimited storage time of preserved samples allows final determination of radioactivities in Finland. Thus, investments in expensive laboratory instruments, like liquid scintillation counter, are not compulsory.

Our results for the oxygen consumption by the whole plankton community at 1 and 30 m depths off Kigoma in April 1994 were not far from the values given earlier by Hecky *et al.*, 1981 (9.4-13 mg 0_2 m^{-3} h^{-1}). These values are high compared to known primary production, but, as noted above, the latter estimates may turn out to be too low. It seems possible to measure the plankton community's respiration in Tanganyika by the oxygen consumption method.

6. FURTHER DEVELOPMENT OF THE SUB-COMPONENT

Determination of *in vivo* fluorescence and primary production and a few experiments gave a good idea about the general conditions at Tanganyika. From these results, it will be possible to develop an optimum procedure for the determination of phytoplankton primary production in this lake. However, the dynamic nature of chlorophyll and primary production in Tanganyika make the determination exceptionally difficult and still necessitate some further methodological experiments before starting routine measurements.

On the basis of work accomplished so far, it seems clear that *in situ* determinations of primary production might yield the most realistic results. With the *in situ* approach, the light quality experienced by phytoplankton in each vial is very close to the natural situation at each depth. Thus, we can avoid the possibility of an unnaturally high proportion of UV-B radiation at lower light levels, which is a disadvantage of the alternative 'simulated' *in situ* (incubator) techniques, applying various screens to obtain different illuminations (hard glass is partially pervious to UV-B radiation). The main problem with the *in situ* measurements is how to take into account the distinct diel differences so that the determinations could be performed routinely at the three main field stations of the Lake Tanganyika Research Project. Ultimately, photosynthesis-irradiance relationships of phytoplankton together with the daily course and vertical attenuation of solar radiation need to be known for each site and date to obtain reliable whole-day estimates of primary production. If it were possible to mimic the spectral properties of natural underwater light, an incubator method may be a good solution for use on the *R/V Tanganyika Explorer* (cf. Harrison *et al.*, 1985, Lohrenz *et al.*, 1992).

The vertical series of the determination of primary production should be extended much deeper than 20 m. In further tests, the vertical series should cover the water column down to 80 m and it should also include diel time series determinations at different depths. To find possibilities of extrapolating the results of determinations over varying conditions under a diel cycle, such experiments should also include the determinations of light intensity and *in vivo* fluorescence of chlorophyll *a.*

The strong effect of light on *in vivo* fluorescence and primary production suggests that precautions are necessary in the handling of primary production samples to shelter phytoplankton from exposure to direct sunlight. Therefore, the

water sampler should be coated with black plastic tape and all operations on board the vessel should happen in the shade.

As most of the necessary equipment for the determination of phytoplankton primary production already exists at Kigoma, some experiments could be realised by the local staff. Over deep water (> 100 m) they could arrange the following determinations:

(1) detailed depth profile of primary production. This should include the depths of 1, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 60, 70 and 80 m. If needed, more series could be made according to the results. This experiment would help to decide at which depths primary production should be determined. The incubations should start in early morning and last for two or three hours; and

(2)diel time series of primary production.

Series of successive 2 h incubations starting at sunrise and ending at sunset should be made at the depths of 1, 5, 10, 20 and 40 m. In addition, one long time experiment is needed, which is equal in length to the sum of 2—hour incubations. These determinations would help to plan an incubation procedure which would best take into account the surface inhibition of primary production.

After these experiments, it will be possible to complete the field manual for routine primary production measurements at the three main LTR stations. Then measurements can be performed by the local staff in connection with the limnological sampling schedule.

The determination of respiration using the Winkler titration method is demanding, because the results are obtained as a small difference between two titration results. Spectrophotometric quantification of the colour of iodine in the oxygen method is an attractive alternative at Tanganyika, where water colour is very low and thus does not bias the measurement. However, the prerequisite for this modification is the availability of a UV-Visible spectrophotometer. If such instruments could be provided at the field stations of Lake Tanganyika Research, the local staff could easily perform the respiration measurements in connection with the routine limnological sampling and primary production measurements. To check the reliability of the spectrophotometric method, more experimentation is needed during the consultancy in December 1994. Then it will be possible to establish the final procedure for routine use.

Other more detailed experiments should be made on a consultancy basis starting in December 1994. These would include the use of field fluorometer and light intensity measurements in trying to correlate primary production and in vivo fluorescence over a diel cycle. Another important aspect would be to study the size distribution of phytoplankton. It would be particularly interesting to get an idea about the possible role of picoplankton. The size distribution of phytoplankton primary production would yield essential information for the nutrition studies of zooplankton. Simple cultures of original and

manipulated plankton communities would reveal information about the role of bacteria and microbial loop. In these, the effect of UV-B radiation could be also assessed. It would be possible to use a spectroradiometer (from Finland) to estimate the level of UV-B radiation at Tanganyika.

In conclusion, the routine measurements of chlorophyll *a,* primary production and community respiration at the three main sampling stations can be merged into the limnological sampling schedule with a little extra effort. The material requirements are likewise modest.

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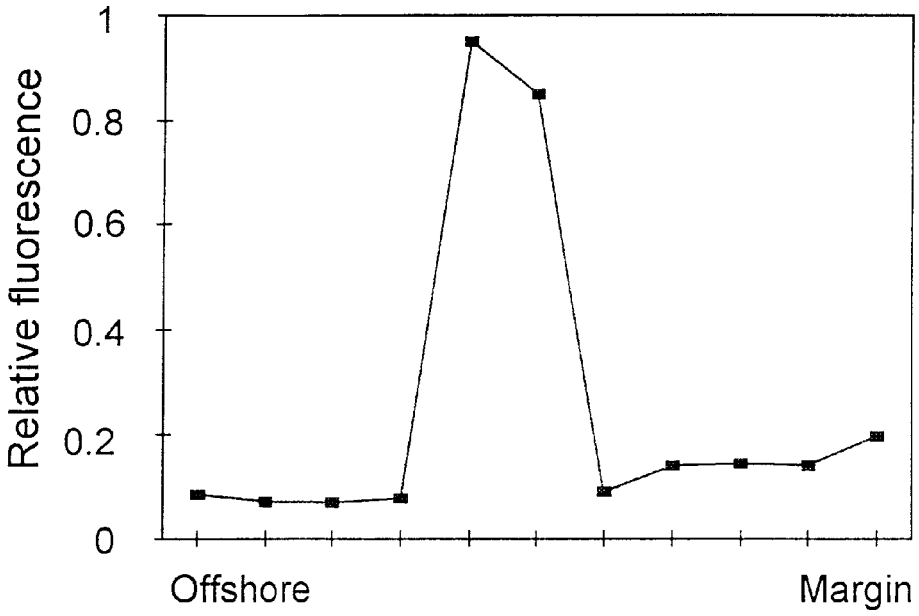

Fig. 1. Horizontal distribution of *in vivo* fluorescence at 1 m off Bujumbura 9 April 1994 in late afternoon.

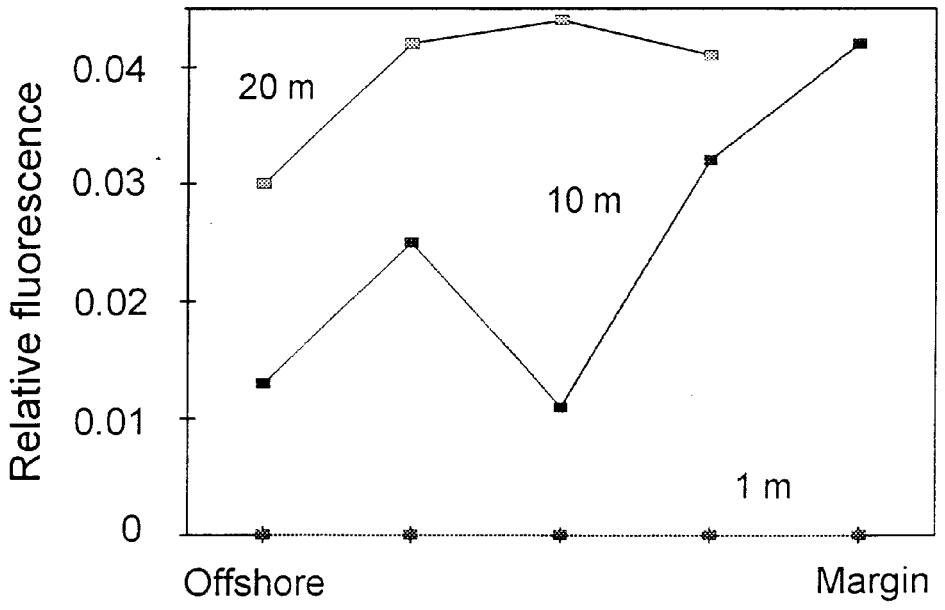

Fig. 2. Horizontal distribution of *in vivo* fluorescence off Kigoma 11 April 1994 at 13.10-14.10.

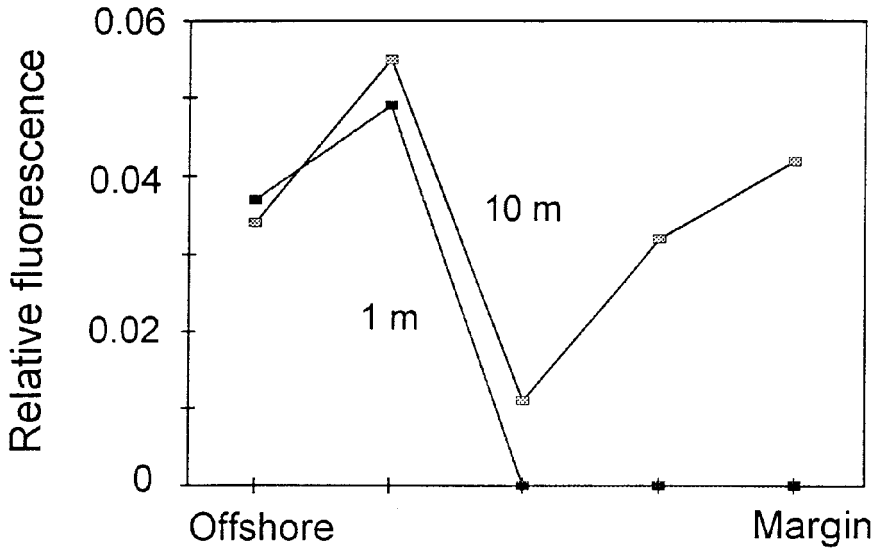

Fig. 3. Horizontal distribution of *in vivo* fluorescence off Kigoma 12 April 1994 at 13.45-14.15.

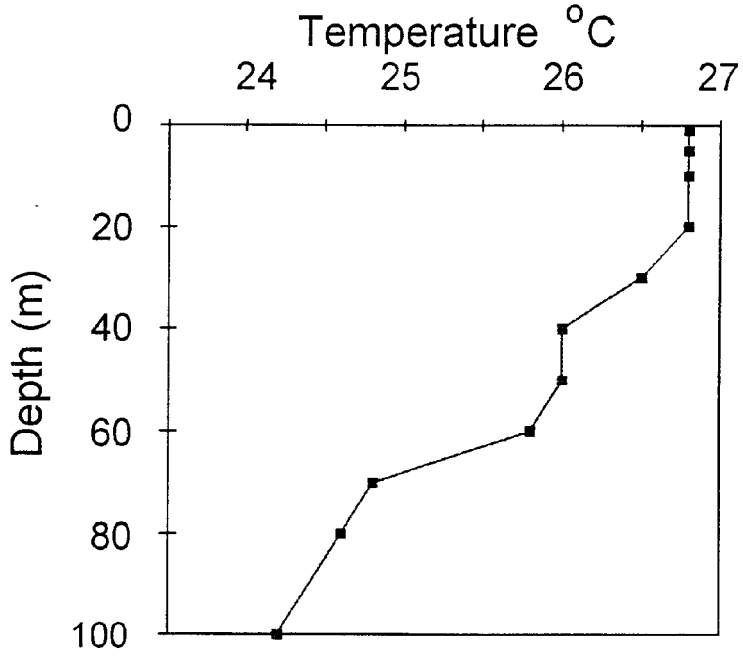

Fig. 4. Vertical distribution of temperature off Kigoma 14 April 1994 at 16.20.

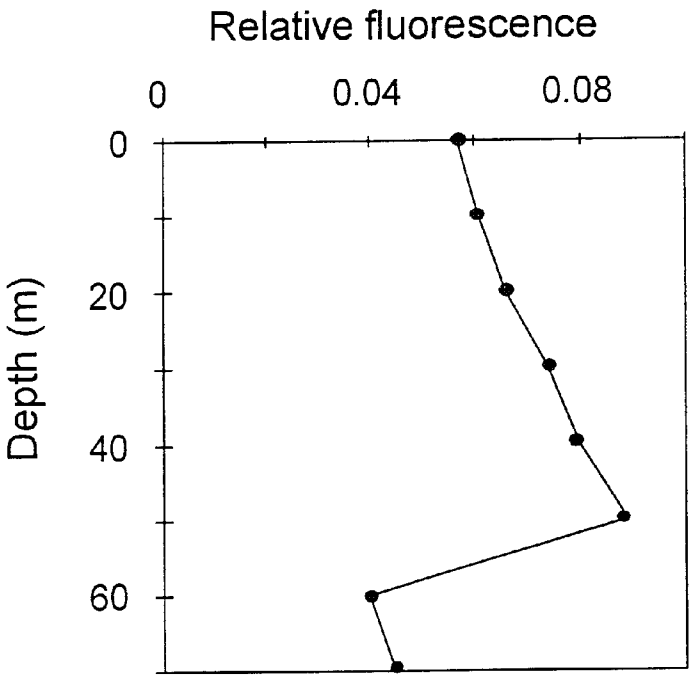

Fig. 5. Vertical distribution of *in vivo* fluorescence off Bujumbura 9 April 1994 at 15.00.

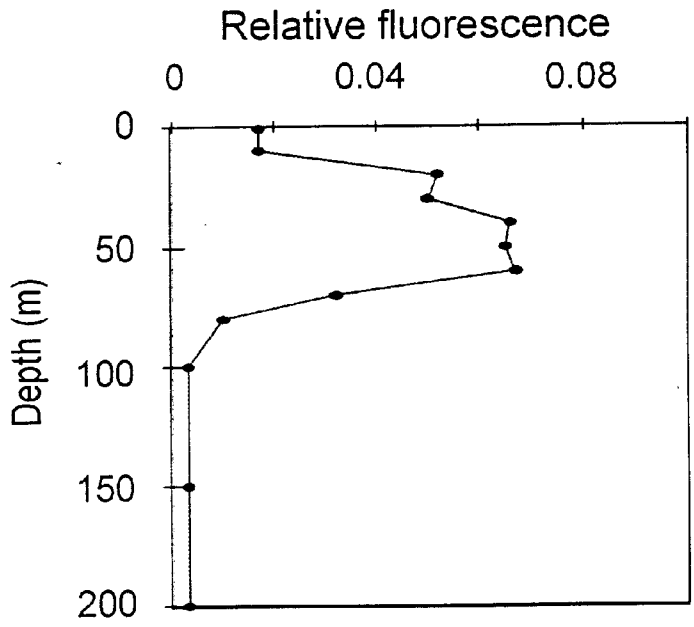

Fig. 6. Vertical distribution of *in vivo* fluorescence off Kigoma 11 April 1994.

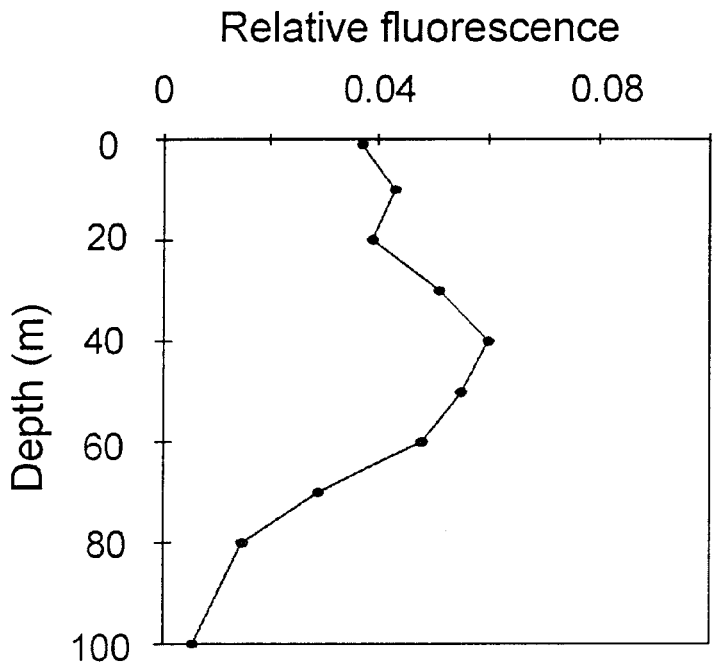

Fig. 7. Vertical distribution of *in vivo* fluorescence off Kigoma 13 April 1994 at 16.00.

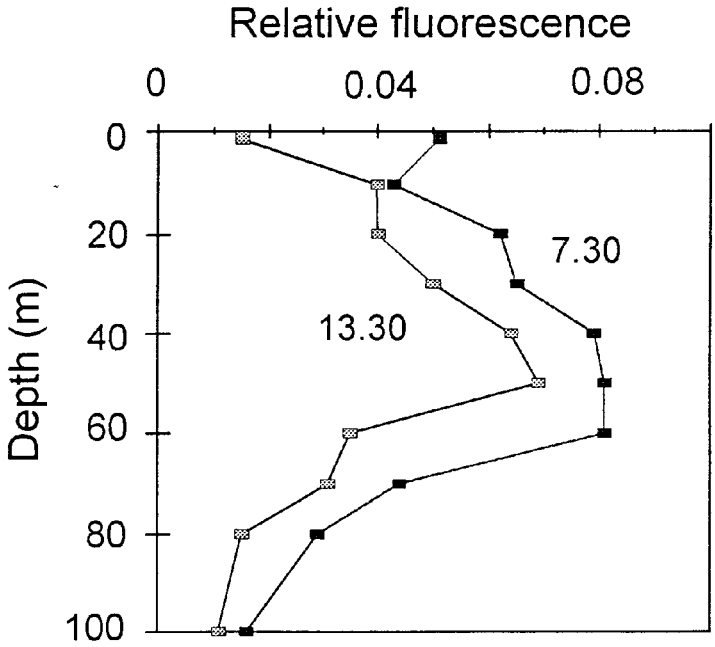

Fig. 8. Vertical distribution of *in vivo* fluorescence off Kigoma 12 April 1994.

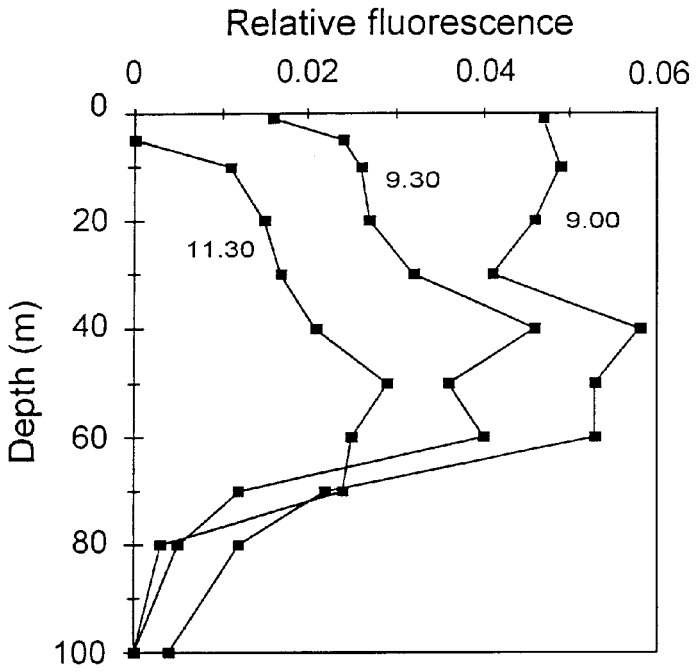

Fig. 9. Vertical distribution of *in vivo* fluorescence at different times of day off Kigoma 14 April 1994.

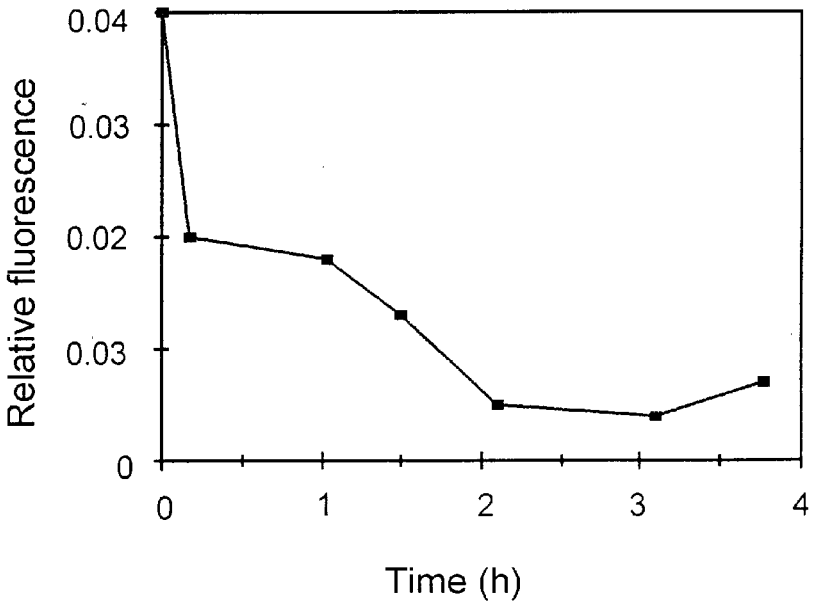

Fig. 10. Decrease of *in vivo* fluorescence of water from 1 m depth off Kigoma in an open container kept under sunshine on the deck of the research vessel from 8.30 on 14 April 1994.

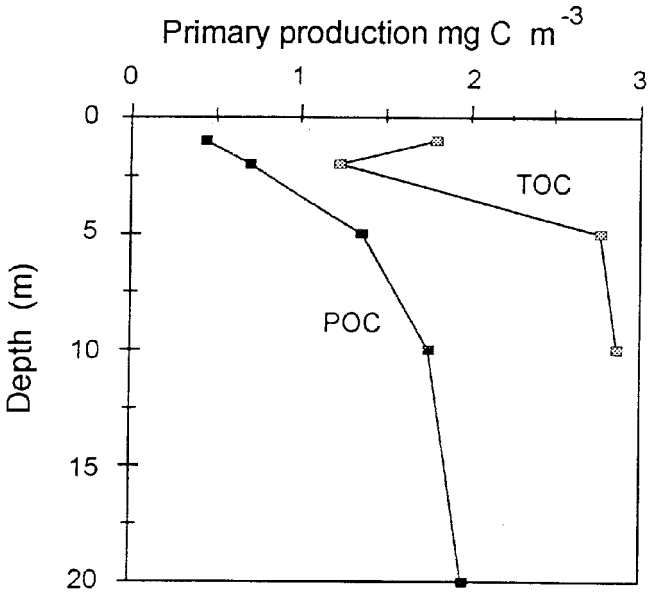

Fig. 11. Vertical distribution of primary production of phytoplankton during 3 hours (10.00 - 13.00) off Kigoma 14 April 1994. POC - particulate organic carbon production; TOC - total organic carbon production.

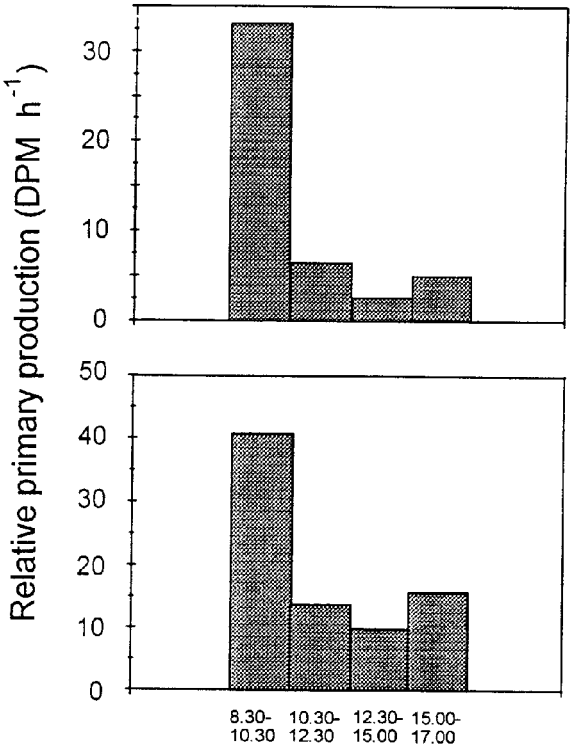

Fig. 12. Diel distribution of primary production in samples taken with ca. 2 h intervals on 14 April 1994 from two depths off Kigoma.

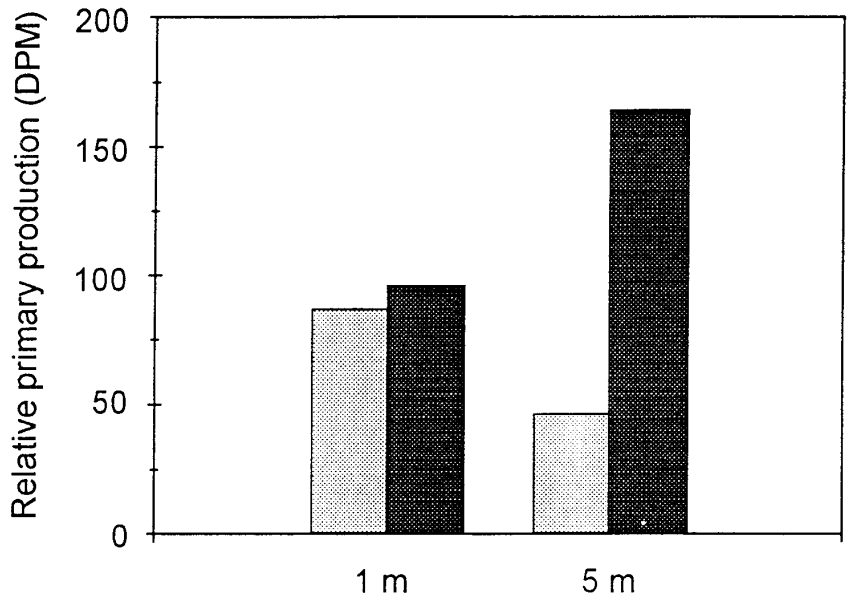

Fig. 13. Comparison between the primary productivities measured in whole-day incubations started in the morning and those obtained as a sum of short incubations (Fig. 12).