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OF THE FISHERIES ON LAKE  
TANGANYIKA

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EXPERIMENTS ON PHYTOPLANKTON AND BACTERIAL PRODUCTION  
ECOLOGY IN LAKE TANGANYIKA: THE RESULTS FROM THE FIRST  
LAKE-WIDE RESEARCH CRUISE ON R/V TANGANYIKA EXPLORER

by

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FINNISH INTERNATIONAL DEVELOPMENT AGENCY

FOOD AND AGRICULTURE ORGANIZATION  
OF THE UNITED NATIONS

Bujumbura, January 1996

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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 Developmental 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, Zaire 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

The main objectives of the carbon-energy subcomponent of the Lake Tanganyika Research Project 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 planktonic food chains of the lake (Salonen and Sarvala, 1994). The earlier studies of the carbon-energy subcomponent in Lake Tanganyika (Salonen and Sarvala, 1994; Sarvala and Salonen, 1995) were restricted to the areas off Bujumbura and Kigoma. The first lake-wide cruise of *R/V Tanganyika Explorer* on 28 April-5 May 1995 offered an excellent opportunity to take samples from many different sampling stations in the pelagial of the lake, and to test and verify the methodology for the carbon-energy subcomponent. Here we report the results of the studies carried out during the cruise.

## 2. OUTLINES OF THE SUBCOMPONENT DURING THE CRUISE

The main objectives of the carbon-energy subcomponent during the first cruise have been outlined by Sarvala and Salonen (1995). Due to the shorter than planned cruising time, the final objectives were:

- 1) To install, test and run
  - an on-board incubator for the incubations of primary production and bacterial production
  - a Turner Designs 10-AU-005 fluorometer for the determinations of the *in vivo* fluorescence of chlorophyll *a*
  - the applicability of the wet laboratory of the *R/V Tanganyika Explorer* to the hydrobiological studies
- 2) To deliver the chemicals and equipment for the primary production measurements at the stations in Bujumbura (Burundi), Kigoma (Tanzania) and Mpulungu (Zambia)
- 3) To provide lake-wide information on the horizontal and vertical distribution as well as diel changes of algal biomass by means of the measurements of *in vivo* fluorescence of chlorophyll *a*
- 4) To measure primary production of phytoplankton at different illumination levels to work out a relationship between algal photosynthesis and light intensity
- 5) To study the role of nutrients in the regulation of phytoplankton primary production by means of nutrient enrichment experiments and nutrient stoichiometry
- 6) To provide preliminary information on the level of bacterial production at different depths of Lake Tanganyika, and to determine bacterial saturation level for leucine uptake
- 7) To measure the concentrations of dissolved organic carbon (DOC) at different depths of the lake

The training of the local counterparts of the carbon-energy subcomponent was not possible, since all counterparts aboard belonged to the hydrodynamics subcomponent. Instead, the measurements of *in vivo* fluorescence and primary production were carried out together with Mr. V. Langenberg, who could later teach the methods to the counterparts of the subcomponent.

### **3. MATERIAL AND METHODS**

#### **3.1. Horizontal variation of chlorophyll a**

Surface water samples for the determination of the horizontal distribution of the *in vivo* fluorescence of chlorophyll a were frequently taken from the vessel's stern with a darkened 2-L plastic sampler, and measured immediately with a Turner Designs 10-AU-005 fluorometer. Due to mixing of the surface water by the propeller of the vessel, the results represent the upper few metres of the water column. Fluorescence was measured at all hours of the day to find out possible differences in the concentrations of chlorophyll a between the light and dark periods of the day. Solar radiation data was provided by the meteo station of the vessel (see Huttula and Nieminen, 1995). The settings of the fluorometer were as follows: LOW (AUTO) (RAW) TIME CONST 10 (SEC).

#### **3.2. Vertical distribution of chlorophyll a**

Vertical distribution of the *in vivo* fluorescence of chlorophyll a was determined during the longer stops (Table 1). Altogether 12 vertical profiles of *in vivo* fluorescence were measured with a Turner designs 10-AU-005 fluorometer from the surface to the depth of 100 or 120 meters at 10 metre intervals. Samples were taken with a darkened 1 m long Limnos sampler. At six sampling stations, two litres of water were also filtered (pre-ignited Whatman GF/F glassfiber filters) for later determinations of chlorophyll a in Finland. This made it possible to produce a relationship between the *in vivo* fluorescence and the concentrations of chlorophyll a. The chlorophyll filters were dried in a desiccator and stored in darkness in small plastic bags in the cold room (2-6 °C) of the vessel. In Finland, four pieces of known area were punched from each filter, extracted in 7 ml of 96 % ethanol and determined for the concentration of chlorophyll a with a Hitachi F-4000 Fluorescence Spectrophotometer. Temperature stratification was obtained from the CTD measurements carried out by the hydrodynamics subcomponent during the cruise (Huttula and Nieminen, 1995).

#### **3.3. Primary production of phytoplankton**

Primary production of phytoplankton was measured with the radiocarbon method according to Salonen and Sarvala (1995). The time-schedule of the cruise did not allow any *in situ* incubations of primary production at different depths of the lake. Instead, primary production was measured from composite samples (samples from the depths of 0, 5, 10 and 20 m pooled together) taken with a darkened Limnos sampler into a 15 L darkened polyethylene container. Samples were incubated at five different light intensities with the on-board incubator in the wet laboratory of

the vessel. This allowed later estimations of light saturation of algal photosynthesis, i.e. the production of the PI curve. Light intensities inside the incubator were adjusted to 25, 41, 112, 211 and 508  $\mu\text{E m}^{-2} \text{s}^{-1}$  with neutral density screens. Water temperature was kept constant (29-30 °C) inside the incubator with a continuous through-flow of filtered lake water, and it was slightly warmer than the surface water temperature of the lake (27-27.5 °C).

Table 1. Vertical sampling stations and the time of sampling during the cruise.

<i>Date</i>	<i>Time</i>	<i>Sampling station</i>	<i>Latitude (S)</i>	<i>Longitude (E)</i>
28 April 1995	17:03-17:48	S4	03°58.00'	29°21.00'
	20:59-21:33	S7	04°20.39'	29°32.12'
30 April 1995	13:45-14:55	Mpulungu buoy	05°00.73'	29°33.04'
	23:38-00:03	S123	08°20.00'	30°59.00'
2 May 1995	6:46-7:49	Mpulungu buoy new position	08°32.16'	30°52.11'
	10:23-11:30	Mpulungu buoy new position	08°32.16'	30°52.11'
	16:02-17:29			
	22:57-23:38	S103	07°29.00'	30°31.00'
3 May 1995	9:46-10:52	S62	06°11.00'	29°40.00'
	15:31-16:20	S61	06°11.00'	29°29.30'
	20:56-21:38	S21	05°10.00'	29°25.00'
5 May 1995	5:58-7:01	S11	04°19.88'	29°15.00'

One 20 mL glass liquid scintillation vial for each illumination level was filled with sample water. In addition, two vials were filled for the determination of dark fixation of dissolved inorganic carbon (DIC). After this, 100  $\mu\text{L}$  (0.11 MBq [3  $\mu\text{Ci}$ ]) of radiocarbon solution ( $\text{Na}_2^{14}\text{CO}_3$ ) was added to each vial. The vials for the dark fixation of DIC were wrapped in aluminium foil. All vials were placed in the incubator. Incubation time was four hours and it was terminated by 1 mL of conc. formaldehyde. After this, the vials were mixed properly and subsamples of 6 mL were pipetted into 20 mL plastic scintillation vials. One drop of orthophosphoric ( $\text{H}_3\text{PO}_4$ ) acid was added to the vials to remove excess radiolabelled DIC. The samples were transported this way to Finland, where remaining traces of inorganic radiocarbon were removed from the water by an exchange with atmospheric  $\text{CO}_2$  during two days. After this, 9 mL of Wallac HiSafe 3 Scintillation Fluor was added to the vials, and mixed thoroughly. The radioactivity was measured with the Wallac 1409 Liquid Scintillation Counter.

Dissolved inorganic carbon (DIC) in water was determined in Finland from unpreserved samples with a carbon analyser (Salonen, 1981). The high pH and alkalinity of the Lake Tanganyika water make the proportion of free CO<sub>2</sub> low, wherefore the rather long storage time did not affect markedly the results of DIC. The concentrations of DIC were very similar in all experiments, averaging 72.4 mg L<sup>-1</sup> (range 71.4-72.8 mg L<sup>-1</sup>). The final results of primary production were calculated from the measured radioactivity and DIC. The dark fixation of DIC was subtracted from the results.

### **3.4. Nutrient contents of zooplankton and total particulate nutrient ratios**

Total particulate nutrient (C, N, P) ratios were obtained from the pre-ignited Whatman GF/F glass fiber filters prepared for chlorophyll a determinations. Four pieces of known area were punched from the filters, and total particulate carbon was analysed with a high temperature combustion method (Salonen, 1979). Total particulate nitrogen and phosphorus were determined from the rest of the filter using the standard wet oxidation method. Nutrient contents of zooplankton were determined from the sample taken with a 50 µm mesh net from the depth of 120 m to the surface in the northern basin of the lake (station S11) on 5 May 1995. The sample was screened through 100, 500 and 1000 µm mesh nets to separate different size fractions of zooplankton. The zooplankton fraction of 50-100 µm represented mainly nauplii of the copepods, 100-500 µm the copepods *Tropocyclops* and *Mesocyclops*, 500-1000 µm the calanoid copepod *Tropodiptomus* and >1000 µm mainly medusae, shrimps and large copepods. The different size fractions of zooplankton were scraped into clean glass scintillation vials, dried in a desiccator, and transported to Finland for later analyses of nutrient (N, P) contents.

### **3.5. Bacterial production**

Bacterial production was measured three times with the leucine incorporation method (Simon and Azam, 1989) from the depths of 0, 10, 40 and 80 m. Duplicate samples of 5 mL in 20 mL glass scintillation vials, wrapped in aluminium foil, were incubated in the on-board incubator for 1 h with 100 nM of L-[U-<sup>14</sup>C]leucine (specific activity 11.7 GBq mmol<sup>-1</sup>). Samples treated with 200 µL of formaldehyde served as blanks. Incubation was terminated by the addition of 200 µL of conc. formaldehyde. In Finland, 0.5 mL of ice-cold 50 % trichloroacetic acid (TCA) was added to formalin fixed samples. Precipitated proteins were filtered onto 0.2 µm Sartorius cellulose nitrate filters, and rinsed twice with 5 mL of ice-cold 5 % TCA. The filters were dissolved in 0.2 mL of ethylene glycolmonomethylether. After addition of the scintillation cocktail (Optiphase Hisafe 3), the filters were stored for 24 h at room temperature. Then the radioactivity of the filters was counted with a Wallac 1409 Liquid Scintillation Counter. A kinetic approach (e.g. Looij and Riemann, 1993) with six different concentrations (10, 25, 50, 75, 100, 200 nM) of <sup>14</sup>C-leucine was carried out once on 5 May 1995 to determine the concentration dependent incorporation of leucine in Lake Tanganyika. Leucine incorporation by bacterial cells (mol L-

1 h<sup>-1</sup>) was converted to biomass production (g C L<sup>-1</sup> h<sup>-1</sup>) by means of "the theoretical approach" (Kirchman, 1993). Except for isotope dilution (ID), which was estimated to be 1 by the kinetic approach (chapter 4.5), the best current estimates of the parameters were used (Simon and Azam, 1989; Kirchman, 1993).

### 3.6. Nutrient enrichment experiments on algal and bacterial production

Three nutrient enrichment experiments were carried out simultaneously with other measurements of primary production to detect possible nutrient limitation of primary production of phytoplankton in Lake Tanganyika (Table 2). Nutrient additions were fresh autoclaved stock solutions of KHPO<sub>4</sub>, NH<sub>4</sub>Cl and D+glucose (C<sub>6</sub>H<sub>12</sub>O<sub>6</sub>). Sample water for experiment II (2-4 May 1995) was collected from the southern basin of the lake (Mpulungu buoy, latitude 08°32.16'S). In experiments I (30 April - 2 May 1995) and III (3-5 May 1995), sample water was collected from the northern (latitude 05°00.73'S) and the central (S27, latitude 06°11.00'S) basin, respectively.

Table 2. Nutrient additions in the nutrient enrichment experiments.

<i>Treatment</i>	<i>PO<sub>4</sub>-P</i> <i>µg L<sup>-1</sup></i>	<i>NH<sub>4</sub>-N</i> <i>µg L<sup>-1</sup></i>	<i>D+-glucose-C</i> <i>µg L<sup>-1</sup></i>
Control	0	0	0
P	25	0	0
N	0	175	0
C	0	0	250
PNC	25	175	250

The samples were taken from the depths of 0, 5, 10 and 20 m with a 1-m long darkened Limnos sampler into a darkened 15 L polyethylene container. Two 20 mL glass liquid scintillation vials for each treatment were filled with water. Dark fixation of DIC was not determined. After filling, the vials were kept in darkness to avoid photodamage of phytoplankton. When filling was completed, nutrients were added to the vials. Then a 100 µL (0.11 MBq [3 µCi]) of radiocarbon solution (Na<sub>2</sub><sup>14</sup>CO<sub>3</sub>) was added to each vial. Samples were incubated for 2 d in the on-board incubator in the wet laboratory of the vessel. In experiments I and II, light intensity inside the incubator was adjusted to 211 µE m<sup>-2</sup> s<sup>-1</sup> with neutral density screening. In experiment III we used higher illumination (511 µE m<sup>-2</sup> s<sup>-1</sup>). Incubation was terminated by 1 mL of conc. formaldehyde, and the samples were treated as described in chapter 3.3. During the incubations, water temperature inside the on-field incubator was a little warmer (29-30 °C) than in the surface of the lake (27-27.5 °C). There was no visible microbial growth on the walls of the sample vials during the experiments. With some exceptions (Experiment I: control and PNC treatment;

Experiment II: PNC treatment), primary production in the duplicate vials was very similar.

Effects of nutrient enrichment on bacterial production were studied once on 3 May 1995 using similar treatments as for the primary production (Table 2). Samples for bacterial production were taken from the depth of 10 m and treated according to chapter 3.5.

### **3.7. Dissolved organic carbon**

Vertical distribution of dissolved organic carbon (DOC) was measured from the depths of 0, 20, 40 and 80 m on 30 April and 5 May 1995. Samples were taken with a darkened 1 m long Limnos sampler into pre-ignited 25 mL glass-stoppered bottles. Samples were stored unpreserved in darkness in the cold room of the vessel, and transported to Finland for the determination of DOC. DOC was determined using two different methods. In the first method, the concentrations of DOC were measured from the acidified samples with a high temperature combustion method with a carbon analyser (Salonen, 1979). In the second method, 1 mL of sample water was pipetted into pre-ignited 2 mL glass ampoules. Samples were acidified to pH < 5.0, and dried at 80 °C to remove dissolved inorganic carbon. After this, the ampoules were closed under constant flow of oxygen gas. Then the ampoules were ignited in the oven at a temperature of 450 °C overnight to oxidize all organic material inside the closed ampoules. After cooling, the ampoule was opened by breaking the neck, and CO<sub>2</sub> produced during oxidation was lead to the infrared detector of the carbon analyser for the determination of CO<sub>2</sub>.

## **4. RESULTS**

### **4.1. Horizontal distribution of chlorophyll a**

Lowest values of the relative fluorescence were found in daylight (Fig. 1). The decrease of *in vivo* fluorescence during the light period was, however, less pronounced than expected. Correspondingly, correlation between the surface water fluorescence and solar radiation at the time of the *in vivo* fluorescence measurement was weak ( $r^2 = 0.052$ ,  $N = 98$ ). The horizontal variation of *in vivo* fluorescence was too large to make areal comparisons between the different basins of the lake.

### **4.2. Vertical distribution of chlorophyll a**

In most of the vertical profiles, *in vivo* fluorescence peaked at a depth of 30-40 m or even deeper (Fig. 2). The values of fluorescence and chlorophyll a decreased during the course of the day, indicating harmful effects of light on algae. The depth maxima of *in vivo* fluorescence varied both in the north and south basins of the lake, and usually were closely related to the depth of the thermocline (data not shown).

Chlorophyll a usually had a very similar vertical distribution to *in vivo* fluorescence (Fig. 3). Accordingly, the

correlation ( $r^2 = 0.634$ ) between the two parameters was significant (Fig. 4). The colour of the chlorophyll filters varied with the sampling depth, indicating differences in the algal/bacterial assemblages. In the upper 20 metres, the filters were usually green, from the depth of 30 to 70 m of brownish/pinkish colour and deeper in the water column, again green.

#### 4.3. Primary production of phytoplankton and the PI curve

After four hours incubation, fixed radioactivity of the samples was low (125-841 dpm). Dark fixation of DIC was almost at the same level (98-146 dpm) in all experiments, and depending on the illumination contributed, 14-92 % of the total counts. Primary production of phytoplankton (dark fixation of DIC subtracted) was low and varied from 0.10 to 6.90 mg C m<sup>-3</sup> h<sup>-1</sup> (mean 2.44 mg C m<sup>-3</sup> h<sup>-1</sup>, N = 40). Accordingly, the mean photosynthetic rate (i.e. mg C fixed per mg chlorophyll per hour) was 2.66 mg C (mg Chla h)<sup>-1</sup>, when average values of *in vivo* fluorescence of chlorophyll a at the depths 0-20 m were separately calculated for each treatment according to the regression equation in the figure 4. Highest primary production and photosynthetic rate were measured in experiments III and IV, carried out near the Mpulungu meteo buoy in the southern basin of the lake in the morning and before noon on 2 May 1995, respectively (Fig. 5). In experiment V, carried out later in the same day, primary production was 50-60 % lower. Similarly, on 3 May, primary production was higher in experiment VI (S62), carried out in the morning than in experiment VII (S61), which was conducted in the afternoon. Altogether, although the experiments with low primary production at all illumination levels had the lowest *in vivo* fluorescence at the beginning of the experiment (Fig. 5), the photosynthetic rate in these experiments was also lower (0.14-3.27 mg C (mg Chla h)<sup>-1</sup>) than in experiments II, III and IV (1.93-7.76 mg C (mg Chla h)<sup>-1</sup>). In general, primary production of phytoplankton decreased only slightly with decreasing illumination, which resulted in a flat PI curve (Fig. 6).

#### 4.4. Primary production in nutrient enrichment experiments

Primary production of phytoplankton varied between 20-144 mg C m<sup>-3</sup> (2 d)<sup>-1</sup> in the different treatments. In all experiments, primary production was strongly stimulated by a combined addition of P, N and C (Fig. 7). Phosphorus enrichment also stimulated primary production, but less than PNC treatment. In contrast, the addition of nitrogen resulted in smaller primary production in experiments II and III than in the untreated controls. The very high stimulation of primary production by the PNC treatment in experiment II was probably erroneous, since one vial of the PNC treatment had exceptionally high dpm values. Without the replicate value, the PNC treatment of experiment II increased primary production as much as in the other experiments. The particulate nutrient ratios indicated no severe single limitation by P or N at the beginning of experiments I and III (Fig. 7).

#### 4.5. Bacterial production

The dpm values of the duplicate vials differed 1-47 % (mean 19 %), and in the formaldehyde killed blanks usually less than 25 %. On 5 May 1995, bacterial production at the depths of 0 and 80 m is based on a single determination of radioactivity, since the very high values of the replicate were discarded. The results from the depth of 40 m from the same day had to be discarded due to exceptionally high and variable dpm values.

The rate of leucine incorporation varied between 0.0027-0.1292 nM Leu L<sup>-1</sup> h<sup>-1</sup> in the experiments. In terms of bacterial biomass production, it was equivalent to 0.1-4.9 µg C L<sup>-1</sup> d<sup>-1</sup>. In the first measurement on 30 April 1995, bacterial production was highest at the depth of 10 m (Fig. 8), which coincided with a distinct chlorophyll peak (Figs. 2 & 3). Bacterial production was also high at the 40 m depth, but decreased to almost zero at the 80 m depth. In the second measurement on 3 May 1995, bacterial production was highest in the upper 10 m of the epilimnion and decreased again to almost zero at the 80 m depth. In the third measurement on 5 May 1995, highest bacterial production occurred at the 80 m depth. However, the reliability of the results of the third experiment is poor due to analytical difficulties. Correlation between the bacterial production and algal biomass was weak ( $r^2 < 0.300$ ) if experiment III was included in the calculations. Without the third experiment, the correlation between the bacterial production and the *in vivo* fluorescence ( $r^2 = 0.808$ ) or chlorophyll a ( $r^2 = 0.814$ ) was significant ( $p < 0.005$ ).

All nutrient additions increased bacterial production in comparison to the control (Fig. 9). The highest increase in the bacterial production (37 %) resulted after the combined addition of P, N and glucose. Incubation time of the nutrient enrichment experiment was one hour, and it is probable that the differences between the treatments would have been greater if the nutrient additions had been carried out some hours before the start of the incubation of bacterial production.

A kinetic approach resulted in a hyperbolic saturation curve (Fig. 10). However, the curve was quite linear at the concentrations of 10 to 100 nM leucine. According to the curve, additions of 100 nM leucine seemed to saturate the incorporation rate resulting in an isotope dilution factor of 1.

#### 4.6. Particulate nutrients and nutrient stoichiometry

The levels of particulate C, N, and P correlated strongly with chlorophyll a (Figs. 11-13), suggesting that most of the particulate nutrients were bound into algal biomass. Accordingly, particulate nutrients correlated well with each other (Figs. 14-16). Also, the vertical distributions of the particulate organic carbon (Fig. 17), particulate nitrogen (Fig. 18) and particulate phosphorus (Fig. 19) resembled the vertical distribution of chlorophyll (Fig. 3). The highest particulate nutrient values were found at the depth of 0-20 m on 28 April - 2 May, and deeper (30-50 m) on 3-5 May 1995.

The ratio of particulate organic carbon to chlorophyll a (POC:Chla) varied between 90-427 (by mass) at the depth of 0-50 m, and except in the morning on 2 May 1995, it steeply increased to 109-1720 at the depth of 60-100 m (Fig. 20). In the northern part of the lake, the POC:Chla ratio peaked at the depth of 80 m both on 28 April and 5 May 1995. This was due to low concentrations of chlorophyll a (Fig. 3) at the 80 m depth, since POC levels were not exceptionally high (Fig. 17).

The carbon to nitrogen (C:N) ratio varied around 5-13 (by mass), with a rather even vertical distribution (Fig. 21). The carbon to phosphorus (C:P) ratio usually varied between 50 and 100 (by mass) (Fig. 22). The particulate nitrogen to phosphorus (N:P) ratio varied around 10 (by mass) with slightly higher values deeper in the water column (Fig. 23). The average epilimnetic (0-100 m) atomic C:N:P ratio was 180.0:20.8:1. For the productive layer (0-40 m) the C:N:P ratio was 168.3:19.1:1. The atomic C:N:P ratio for non-algal organic material, based on the calculated intercept values of the figures 11-13 and on the assumption of linear correlation, was 191:25:1 (74:11:1, by mass).

In the zooplankton, most of the particulate material was in the size fraction of 500-1000  $\mu\text{m}$ , representing the calanoid copepod *Tropodiaptomus* sp. Particulate organic nitrogen to phosphorus ratio (PON:POP) of zooplankton was less than 6 (by mass) in all size fractions (Fig. 24). The low PON:POP ratio of zooplankton may partly be due to a loss of nitrogen ( $\text{NH}_4$ ) from the samples, since the desiccator was ineffective in drying the size-fractionated zooplankton samples, which were more or less in a state of decay in Finland.

#### **4.7. Dissolved organic carbon**

The high and poorly defined background (0.5-1  $\text{mg C L}^{-1}$ ) of the high combustion method prohibits its application for samples with a low concentration of DOC. In the ampoule technique, the background was lower (0.2  $\text{mg C L}^{-1}$ ). The mean concentration of DOC varied between 2.2-2.9  $\text{mg C L}^{-1}$  in the water column, and was highest near the surface of the lake (Fig. 25).

#### **4.8. The applicability of the wet laboratory to the hydrobiological studies**

The wet laboratory of the vessel was suitable for hydrobiological studies. During the first cruise there was no ventilation inside the laboratory, which occasionally increased the room temperature up to 40 °C degrees. This caused some extra stress to the equipment and researchers as well. The on-field incubator proved to be useful in the incubations of primary and bacterial production. The water temperature inside the incubator was very constant despite the fluctuations in room temperature. The through-flow system was on all the time during the cruise (altogether 8 days). Except for some sedimented litter and small microbial growth during the last days of the cruise, the walls of the incubator were clean, permitting the penetration of light from the light source.

In the forthcoming cruises, a refrigerator is needed in the wet laboratory for the storage of chemical and biological samples. Exchange of air could be easily arranged by a ventilator. This is of importance, because some determinations require hazardous chemicals, which otherwise persist too long inside the laboratory.

## 5. DISCUSSION

### 5.1. Photoinhibition of algae

The results of this study agree with our earlier findings (Salonen and Sarvala, 1994; Sarvala and Salonen, 1995) that epilimnetic concentration of chlorophyll decreases during the bright hours in Lake Tanganyika. This can be related to pigment bleaching and other damage of algal cells (e.g. Häder, 1995).

The decrease of epilimnetic chlorophyll could be seen in the vertical profiles of *in vivo* fluorescence taken at different times of the day, but not so clearly from the horizontal samples taken from the stern of the vessel. The observed horizontal distributions of chlorophyll suggested large variations in algal biomass, which is not unexpected in large lakes. *In vivo* fluorescence of chlorophyll may be used as a complementary tool to take this variation into account in deriving whole lake estimates from local phytoplankton measurements. It is therefore important to continue the measurements of *in vivo* fluorescence of upper epilimnetic water during the cruises. However, there are some technical problems. First, it seems that manual sampling does not permit sufficiently frequent measurements of horizontal fluorescence, particularly if other determinations are carried out, which usually is the case. Second, the continuous and automated measurement of the *in vivo* fluorescence of chlorophyll may prove to be difficult since the pumping of lake water through the fluorometer is difficult to organize in the wet laboratory of the vessel, particularly while sailing. Third, the distance between the wet laboratory and the meteorological station of the vessel, where the data can be logged, is several metres. However, this problem can be easily solved with a long cable, but it may also need one extra serial port to the meteorological station of the dry laboratory. Another possibility is to have a portable pc for data-logging in the wet laboratory.

The weak correlation between the surface water *in vivo* fluorescence and solar radiation at the time of the fluorescence measurement may be explained by time delay. It is probable that *in vivo* fluorescence is more related to light conditions an hour/some hours before the determination of fluorescence.

In most of the vertical profiles, the *in vivo* fluorescence peaked at a depth of 30-40 m or deeper, which agreed with the earlier results of the vertical distribution of algae in Lake Tanganyika (Salonen and Sarvala, 1994, Sarvala and Salonen, 1995). The decrease of the *in vivo* fluorescence of chlorophyll could be observed deep in the epilimnion during the light period. This downward spread of the chlorophyll decrease may be explained

by vertical mixing of the epilimnetic waters. The chlorophyll maxima often occurred at the depth of the thermocline. The moderately high daily and areal variation of the depth of the thermocline, as indicated by the CTD-data of the hydrodynamic subcomponent, could partly explain differences in the vertical distribution of chlorophyll peaks in the water column.

Chlorophyll a usually had a very similar vertical distribution to *in vivo* fluorescence. It is important to continue the simultaneous measurements of *in vivo* fluorescence and chlorophyll a during the cruises and at other times to acquire even a more representative fit between the parameters.

## 5.2. Photosynthesis and light relationships

Already the illumination levels of  $>100 \mu\text{E m}^{-2} \text{s}^{-1}$  seemed to saturate algal photosynthesis in most of the on-field incubator experiments. This is somewhat surprising, particularly since the intensity of light required to saturate algal photosynthesis should increase with higher water temperature (e.g. Wetzel, 1983). On the other hand, the highest illumination level used in our study ( $508 \mu\text{E m}^{-2} \text{s}^{-1}$ ) had no deleterious effects on primary production. Light intensities exceeding ca.  $500 \mu\text{E m}^{-2} \text{s}^{-1}$  are known to be harmful to phytoplankton (e.g. Kirk, 1983). Whatever the reason, the small differences in the algal photosynthesis at different light intensities resulted in a very flat PI curve with high variation between the treatments. One explanation for the variation was the ambient chlorophyll concentration of the sample water. Secondly, the experiments were carried out at different parts of the lake, and algal communities may have been different. This can be important since algal groups have different adaptation capabilities in a changing light climate (Wetzel, 1983). Third, the measurements of primary production were based on a single determination per each illumination level without duplicates, which increased the risk of erroneous results.

The light saturated photosynthesis generally increases much higher in algae grown under high light intensities (Wetzel, 1983). In this study, primary production in samples collected during high illumination was not necessarily higher at high light intensities. The highest primary productivity was observed in the experiments carried out in the southern part of the lake, which may indicate differences between the trophic state of the basins. In the forthcoming cruises, it is important to carry out more experiments on interactions between photosynthesis and light intensity. Instead of one determination per light level there should be at least replicate vials for each light intensity.

## 5.3. Bacterial production

The level of bacterial production in Lake Tanganyika ( $0.1\text{-}4.9 \mu\text{g C L}^{-1} \text{d}^{-1}$ ) was within the range of results from other freshwater and marine environments ( $0.4\text{-}153 \mu\text{g C L}^{-1} \text{d}^{-1}$ ; Cole *et al.*, 1988;  $0.5\text{-}302 \mu\text{g C L}^{-1} \text{d}^{-1}$ ; White *et al.*, 1991). As in other freshwaters (White *et al.*, 1991), bacterial production correlated well with algal biomass. According to the preliminary calculations, bacterial production accounted for about 25 % of pelagic primary production in Lake Tanganyika, which is also the

case in many other aquatic environments (Cole *et al.*, 1988). Our measurements of bacterial production were restricted to the upper 80 m of the lake, but since bacterial production often increases in the anoxic layers of the water column, it is important to study bacterial production in the deeper (>100 m) anoxic parts of the water column in Lake Tanganyika. Furthermore, in the forthcoming cruises bacterial production should also be measured from the oxic-anoxic boundary layer, where bacterial activity can be high.

According to the kinetic approach, an addition of 100 nM of leucine seemed to be enough to overcome the isotope dilution effect. The concentration of leucine in the water may fluctuate seasonally (e.g. van Looij and Riemann, 1993), and therefore more isotope dilution studies are needed.

#### **5.4. Nutrient limitation of plankton**

Particulate nutrient composition ratios measured during the cruise suggest no severe single nutrient limitation of plankton by P or N. The average atomic C:P ratios of 168 and 180 for the productive layer (0-40 m) and also for the whole epilimnion (0-100 m), respectively, suggested moderate P limitation of phytoplankton (Healey and Hendzel, 1980), while the average N:P ratios (19 and 21, by atoms) indicated P sufficiency. The average C:N ratios measured off Kigoma in the rainy season in November-December 1994 have indicated moderate N limitation (Sarvala and Salonen, 1995), which could also be found in the samples collected in April-May 1995. Further work on particulate nutrient ratios in Tanganyika clearly seems to be worthwhile. It is also important to study the N:P ratios of different zooplankton species to determine the possible role of zooplankton in the nutrient limitation of primary production (e.g. Hessen and Andersen, 1992).

In all nutrient enrichment experiments, the primary production of phytoplankton was stimulated by additions of phosphorus. This indicated that P was the nutrient most potentially limiting phytoplankton primary production in the upper epilimnion (0-20 m) of Lake Tanganyika in April-May 1995. The results were in agreement with the moderately high particulate C:P ratios. The particulate nutrient ratios from November-December 1994 also suggested possible P limitation of phytoplankton in the lake (Sarvala and Salonen 1995). In any case, the strong stimulation of primary production by the combined additions of N and P (PNC treatment) suggests that no severe single N or P limitation existed in the lake. According to these preliminary experiments it appears that plankton in Tanganyika experience a restricted, but approximately balanced nutrient supply as also suggested by Edmond *et al.* (1993) and Hecky *et al.* (1993).

#### **5.5. Dissolved organic carbon**

The determination of DOC by means of the ampoule technique proved successful. In this method the background was small. The concentrations of DOC found in this study agree well with previous measurements carried out in Lake Tanganyika (Degens *et al.*, 1971; Hecky *et al.*, 1978). In any case, we need more measurements of the vertical distribution of DOC in Lake Tanganyika, particularly from the deeper parts of the water column. Already our present results support the conclusion of Hecky (1991) that primary production of phytoplankton is the main source of energy for the secondary production in Lake Tanganyika.

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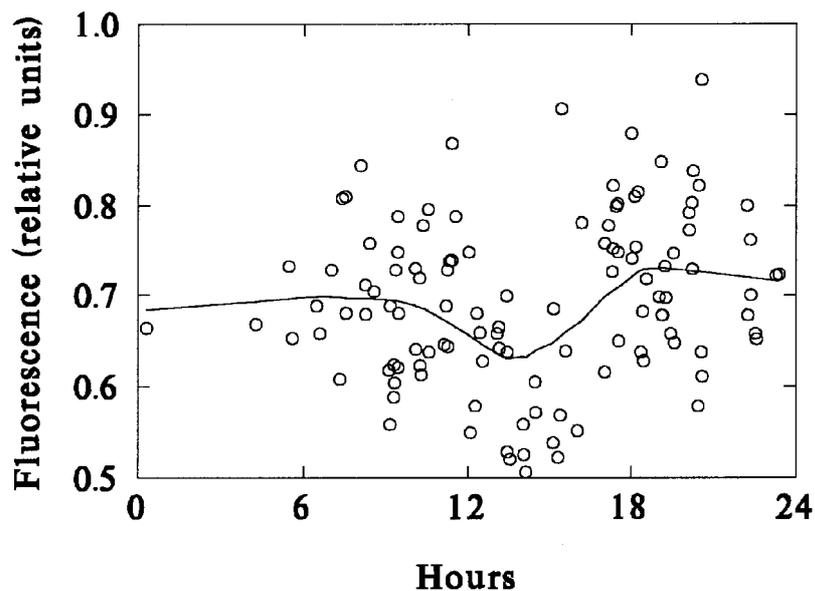


Fig. 1. *In vivo* fluorescence of chlorophyll *a* in the surface water of Lake Tanganyika at different times of the day on 28 April - 5 May 1995. Lowess scatterplot smoothing.

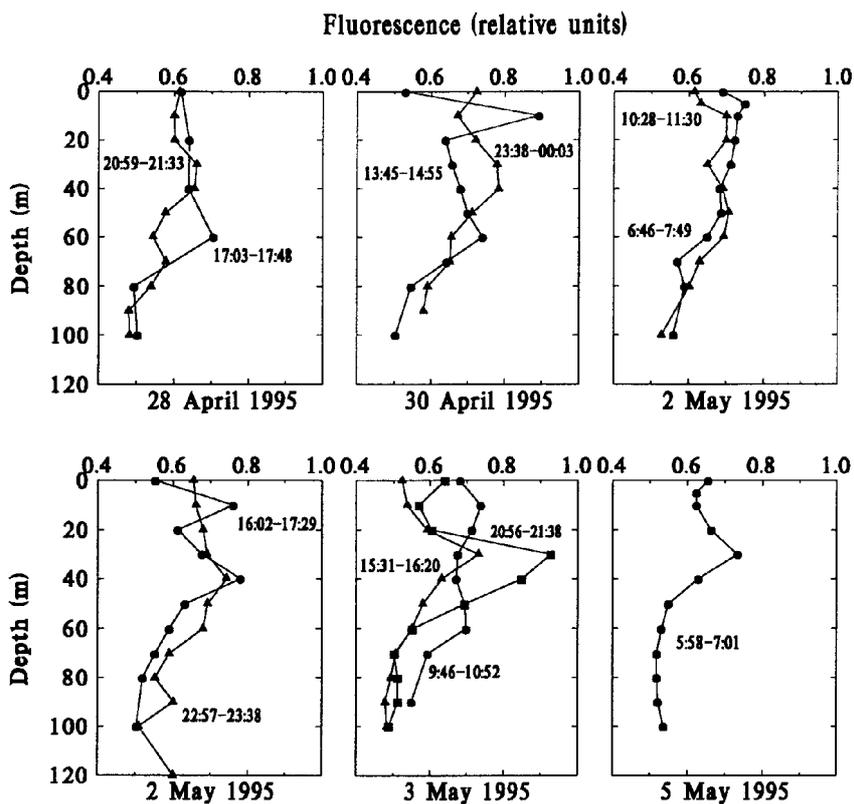


Fig. 2. Vertical distribution of *in vivo* fluorescence of chlorophyll *a* in Lake Tanganyika on 28 April - 5 May 1995.

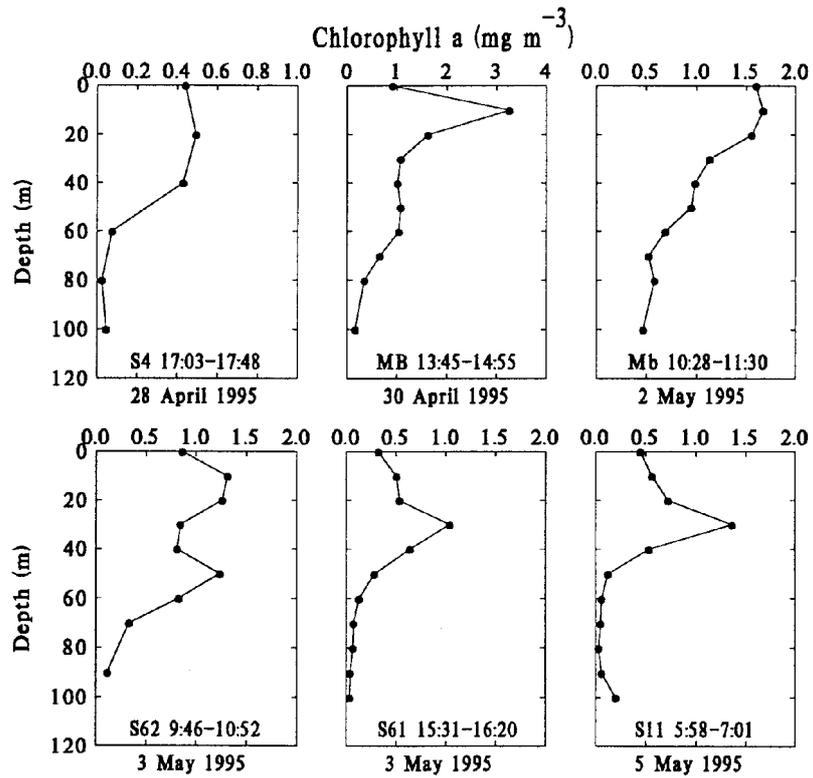


Fig. 3. Vertical distribution of chlorophyll *a* in Lake Tanganyika on 28 April - 5 May 1995. MB = Mpulungu buoy, Mb = Mpulungu buoy, new position. Note the differences in the x-axis.

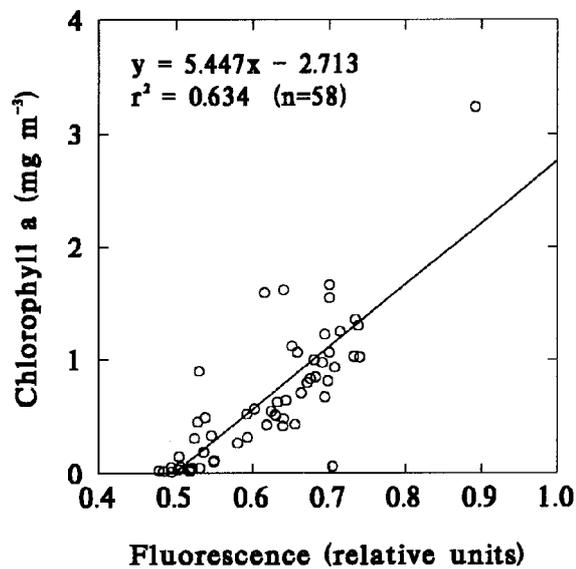


Fig. 4. A relationship between chlorophyll *a* and *in vivo* fluorescence of chlorophyll *a* in Lake Tanganyika on 28 April - 5 May 1995. Data from all sampling stations and depths.

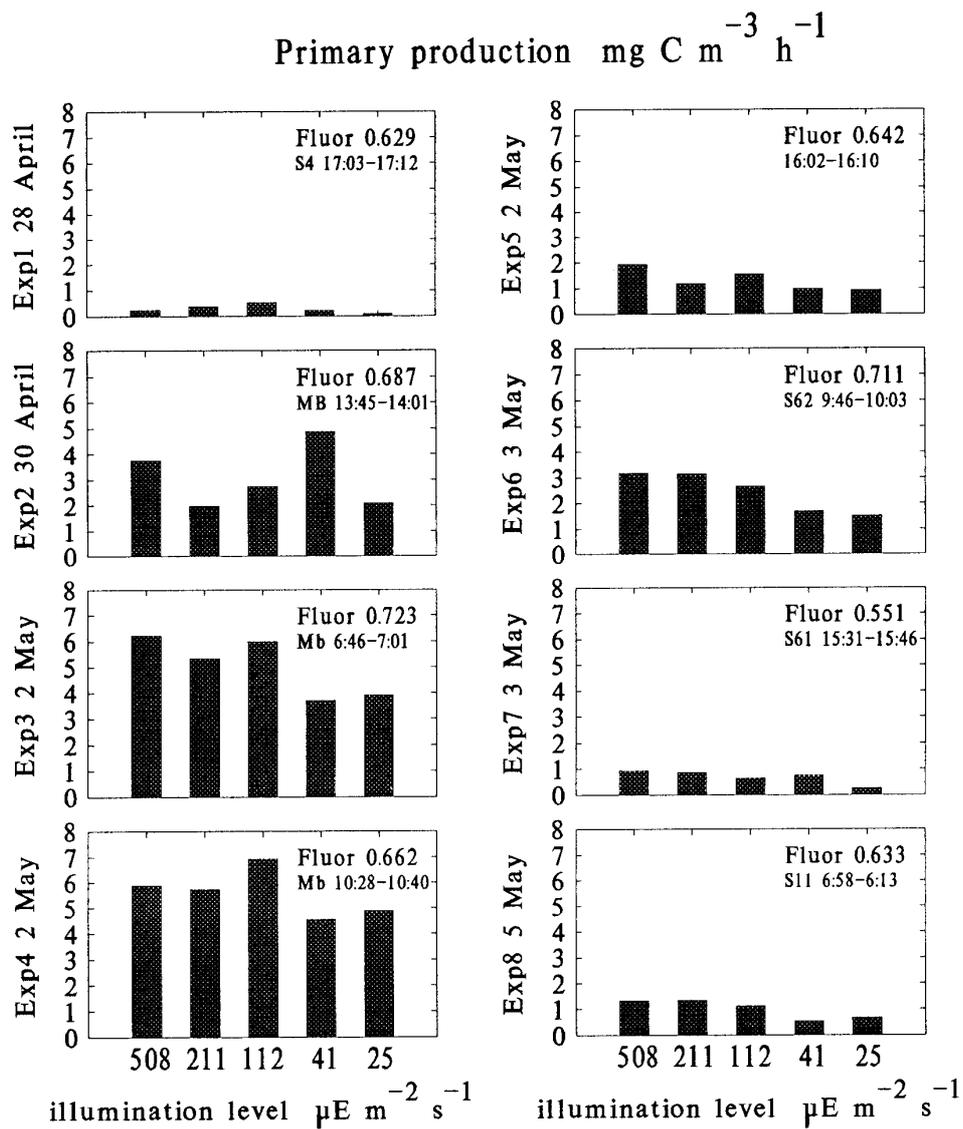


Fig. 5. Primary production of phytoplankton at different illumination levels in Lake Tanganyika on 28 April - 5 May 1995. Ambient values of *in vivo* fluorescence of chlorophyll *a* at the beginning of the experiments, and the sampling time and station in the upper right corner of the panels. MB = Mpulungu buoy, Mb = Mpulungu buoy, new position.

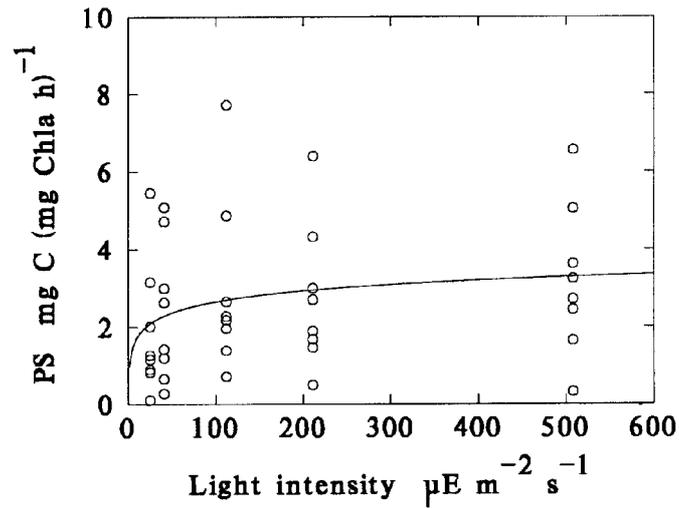


Fig. 6. A relationship between algal photosynthesis and light intensity in Lake Tanganyika on 28 April - 5 May 1995. Data from all experiments (see Fig. 5). Logarithmic smoothing.

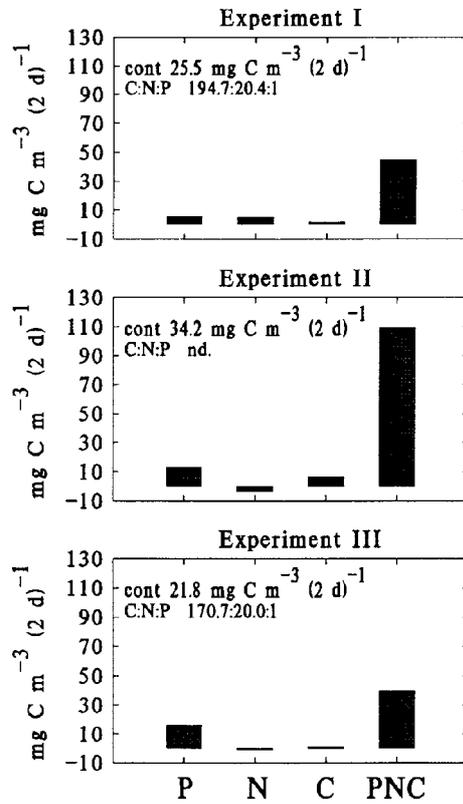


Fig. 7. Effects of nutrient enrichment on algal photosynthesis in Lake Tanganyika water (0-20 m), and the total particulate nutrient ratio (C:N:P, by atoms) of the sample water at the beginning of the experiment. Primary production of the control vials (cont) subtracted from the results. nd. = not determined, P = PO<sub>4</sub>, N = NH<sub>4</sub>, C = D+glucose, PNC = a combined addition of PO<sub>4</sub>, NH<sub>4</sub> and D+glucose.

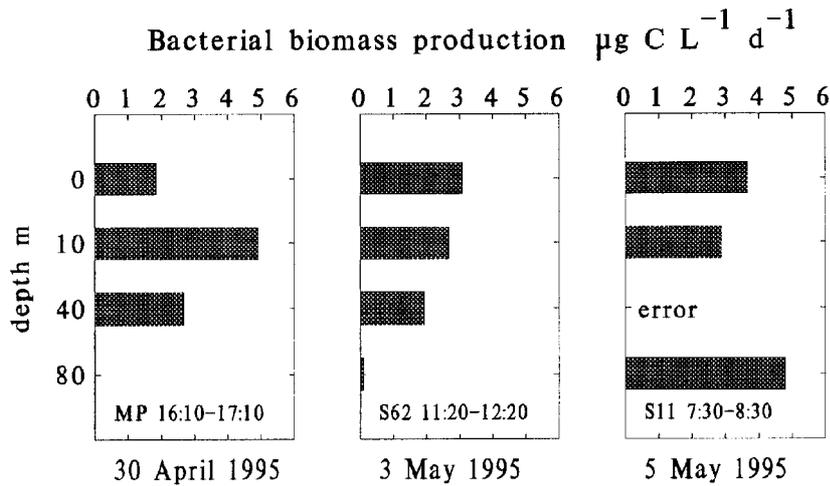


Fig. 8. Vertical distribution of bacterial production in Lake Tanganyika. The sampling station and the time of incubation at a lower part of the panels. MP = Mpulungu buoy.

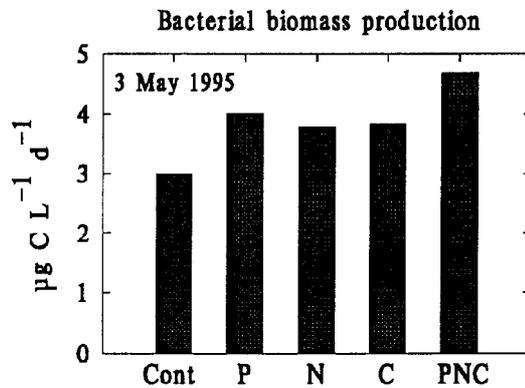


Fig. 9. Effects of nutrient enrichment on bacterial production in Lake Tanganyika on 3 May 1995. Cont = untreated control, P =  $\text{PO}_4$ , N =  $\text{NH}_4$ , C = D+glucose, PNC = a combined addition of  $\text{PO}_4$ ,  $\text{NH}_4$  and D+glucose.

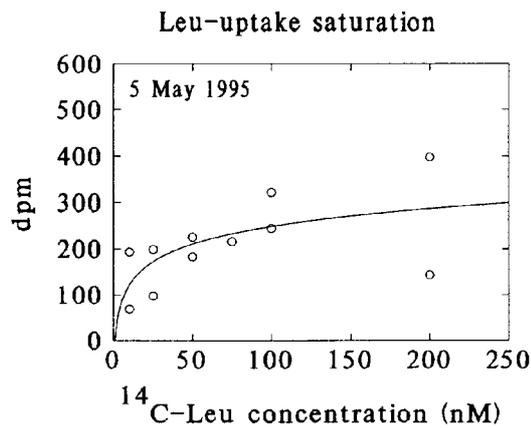


Fig. 10. Saturation of bacterial leucine uptake in Lake Tanganyika on 5 May 1995. Logarithmic smoothing.

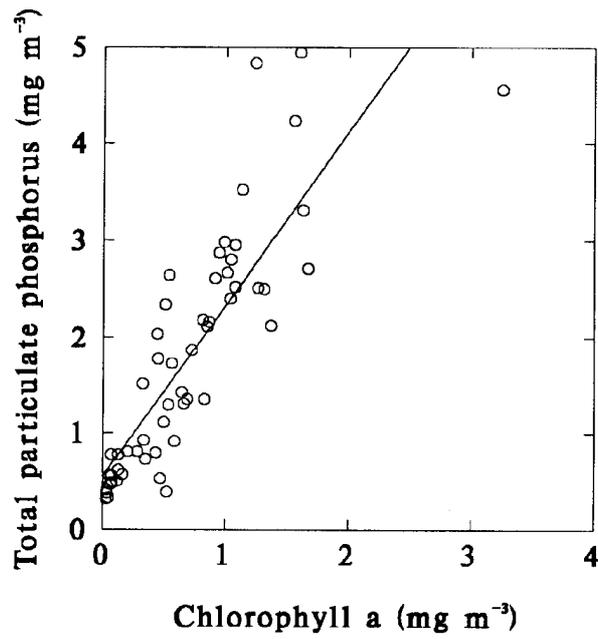


Fig. 11. A relationship between total particulate phosphorus and chlorophyll *a* in Lake Tanganyika on 28 April - 5 May 1995. Data from all sampling stations and depths.

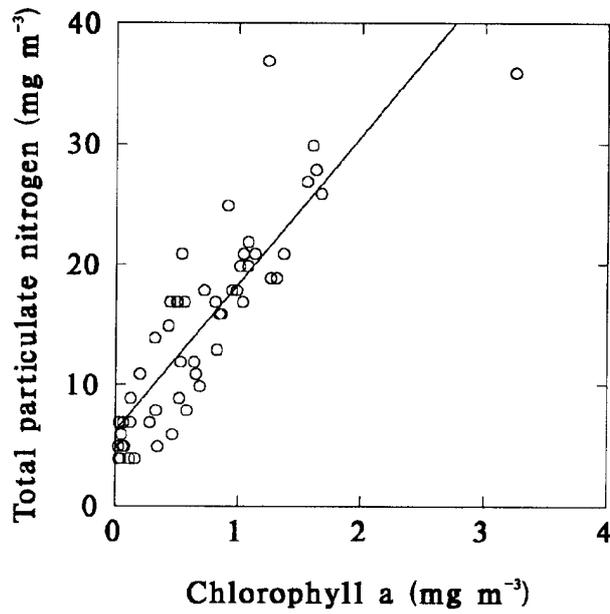


Fig. 12. A relationship between total particulate nitrogen and chlorophyll *a* in Lake Tanganyika on 28 April - 5 May 1995. Data from all sampling stations and depths.

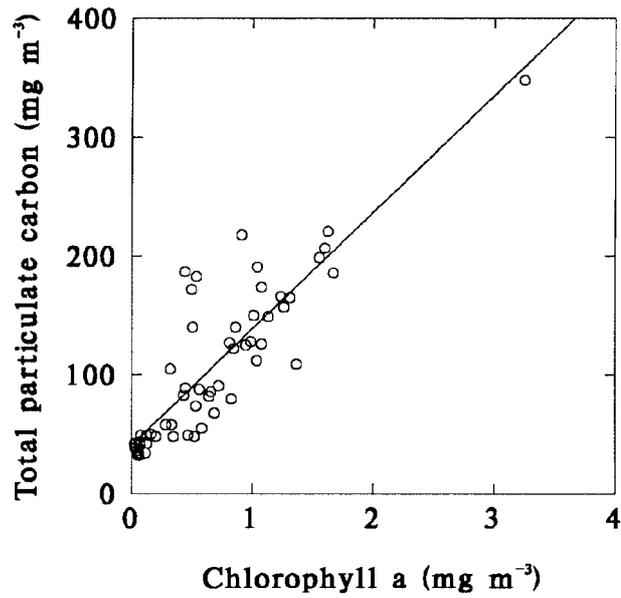


Fig. 13. A relationship between total particulate carbon and chlorophyll *a* in Lake Tanganyika on 28 April - 5 May 1995. Data from all sampling stations and depths.

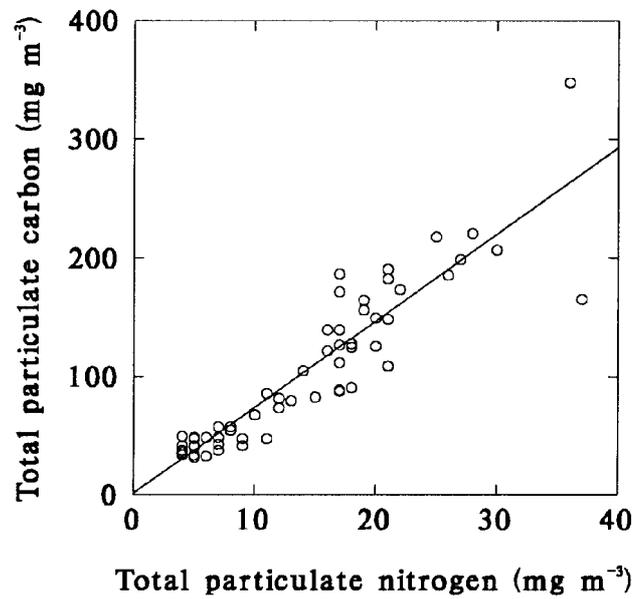


Fig. 14. A relationship between total particulate carbon and nitrogen in Lake Tanganyika on 28 April - 5 May 1995. Data from all sampling stations and depths.

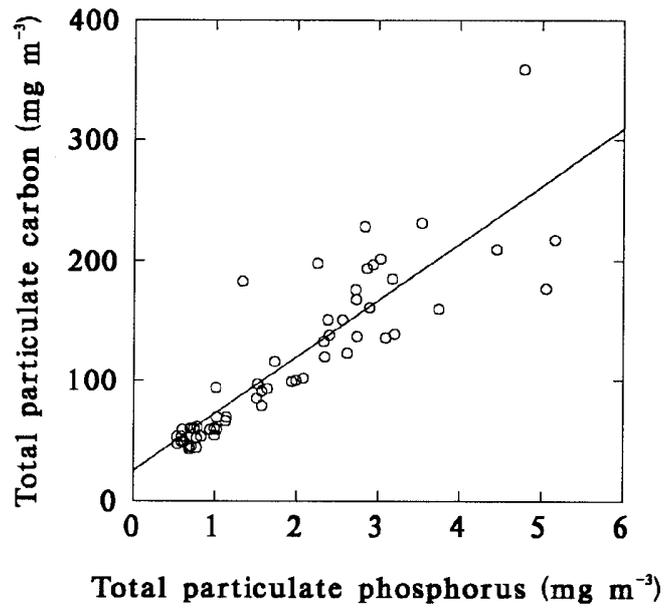


Fig. 15. A relationship between total particulate carbon and phosphorus in Lake Tanganyika on 28 April - 5 May 1995. Data from all sampling stations and depths.

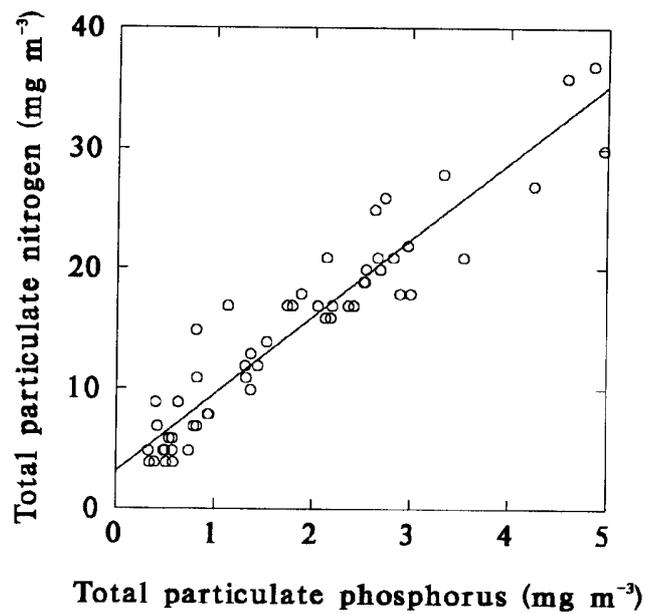


Fig. 16. A relationship between total particulate nitrogen and phosphorus in Lake Tanganyika on 28 April - 5 May 1995. Data from all sampling stations and depths.

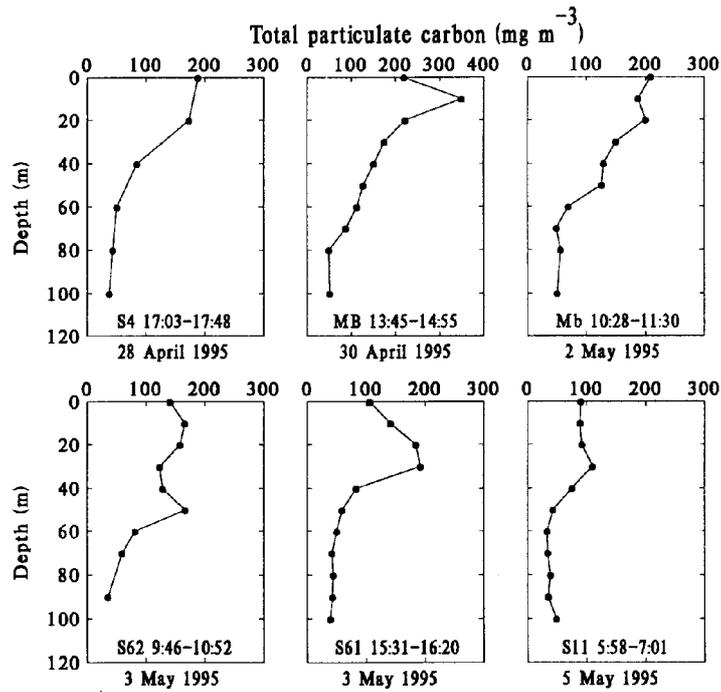


Fig. 17. Vertical distribution of total particulate carbon at different sampling stations in Lake Tanganyika on 28 April - 5 May 1995. MB = Mpulungu buoy, Mb = Mpulungu buoy, new position. Note the differences in the x-axis.

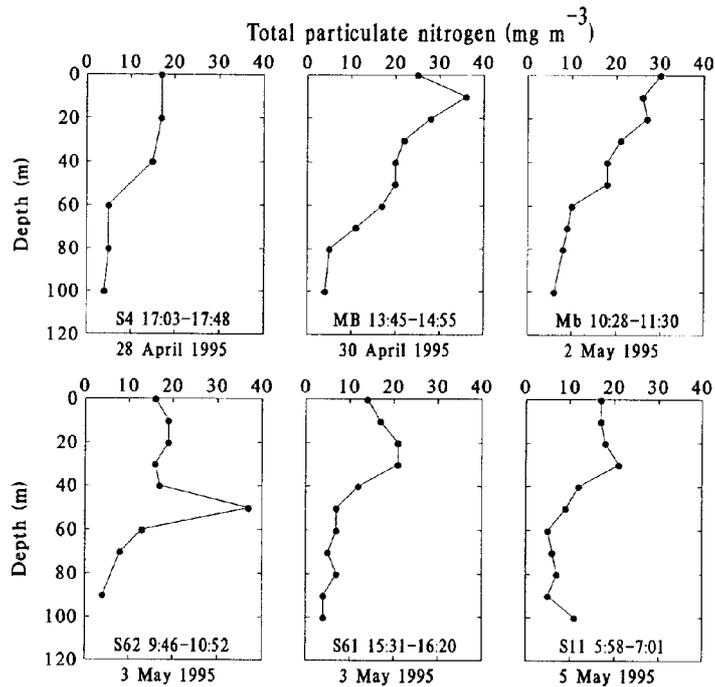


Fig. 18. Vertical distribution of total particulate nitrogen at different sampling stations in Lake Tanganyika on 28 April - 5 May 1995. MB = Mpulungu buoy, Mb = Mpulungu buoy, new position.

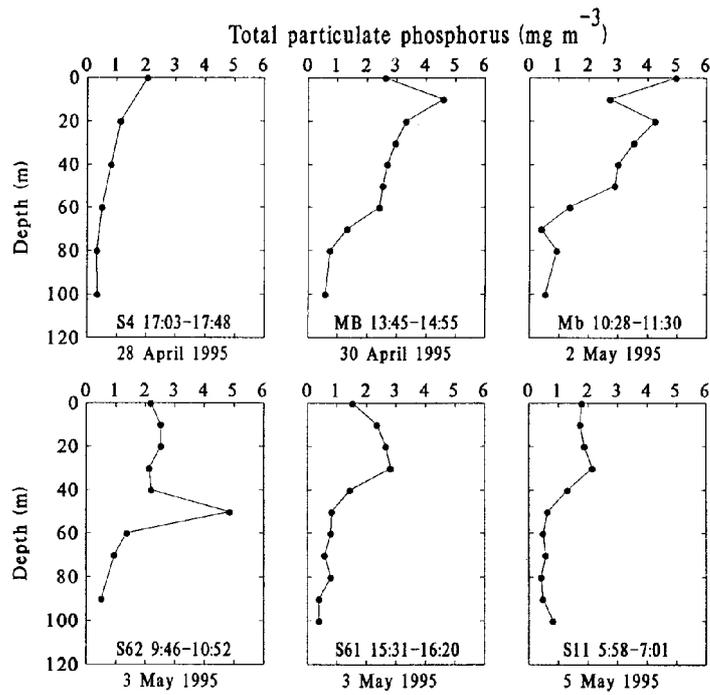


Fig. 19. Vertical distribution of total particulate phosphorus at different sampling stations in Lake Tanganyika on 28 April - 5 May 1995. MB = Mpulungu buoy, Mb = Mpulungu buoy, new position.

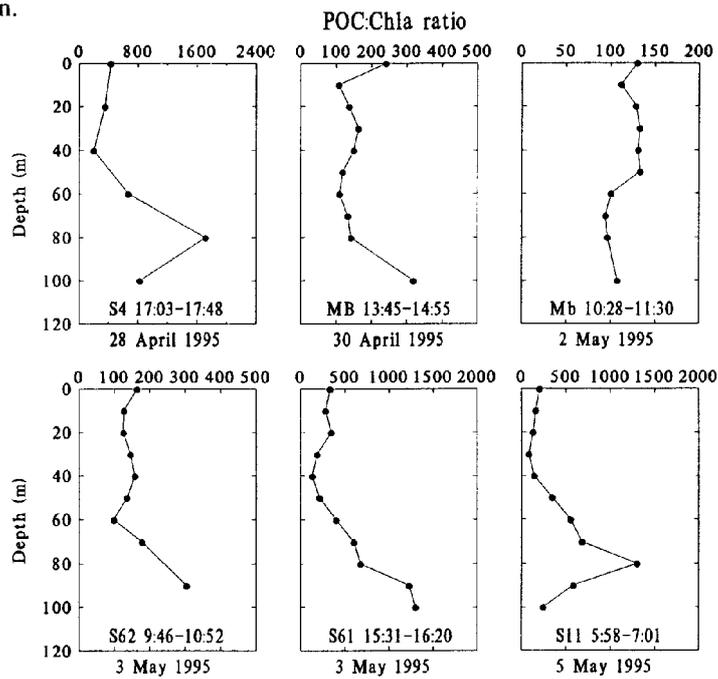


Fig. 20. Vertical distribution of the total particulate carbon to chlorophyll *a* ratio (POC:Chla) at different sampling stations in Lake Tanganyika on 28 April - 5 May 1995. MB = Mpulungu buoy, Mb = Mpulungu buoy, new position. Note the differences in the x-axis.

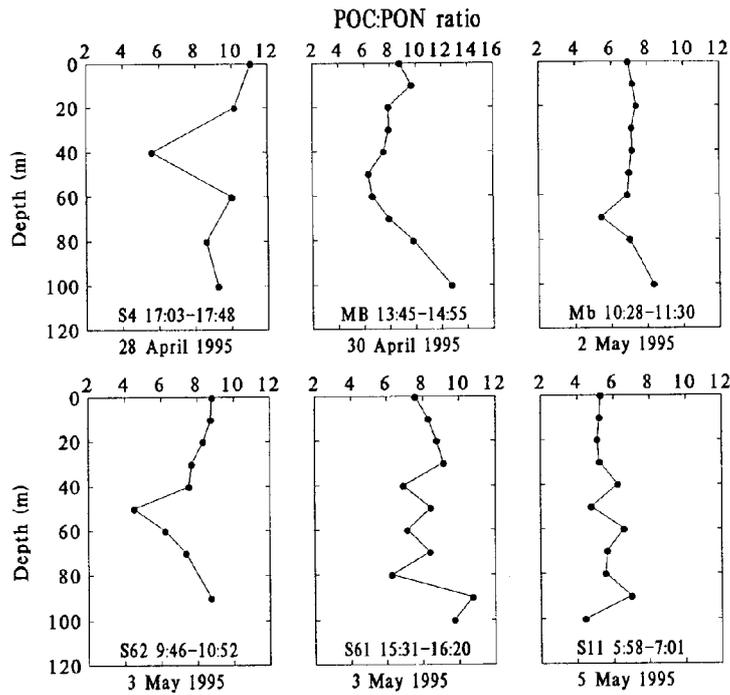


Fig. 21. Vertical distribution of the total particulate carbon to nitrogen ratio (POC:PON) at different sampling stations in Lake Tanganyika on 28 April - 5 May 1995. MB = Mpulungu buoy, Mb = Mpulungu buoy, new position. Note the differences in the x-axis.

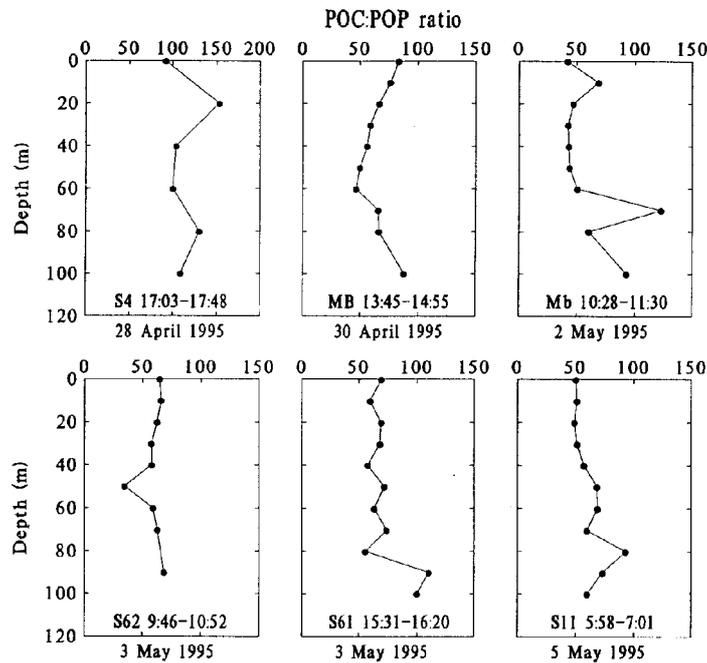


Fig. 22. Vertical distribution of the total particulate carbon to phosphorus ratio (POC:POP) at different sampling stations in Lake Tanganyika on 28 April - 5 May 1995. MB = Mpulungu buoy, Mb = Mpulungu buoy, new position. Note the differences in the x-axis.

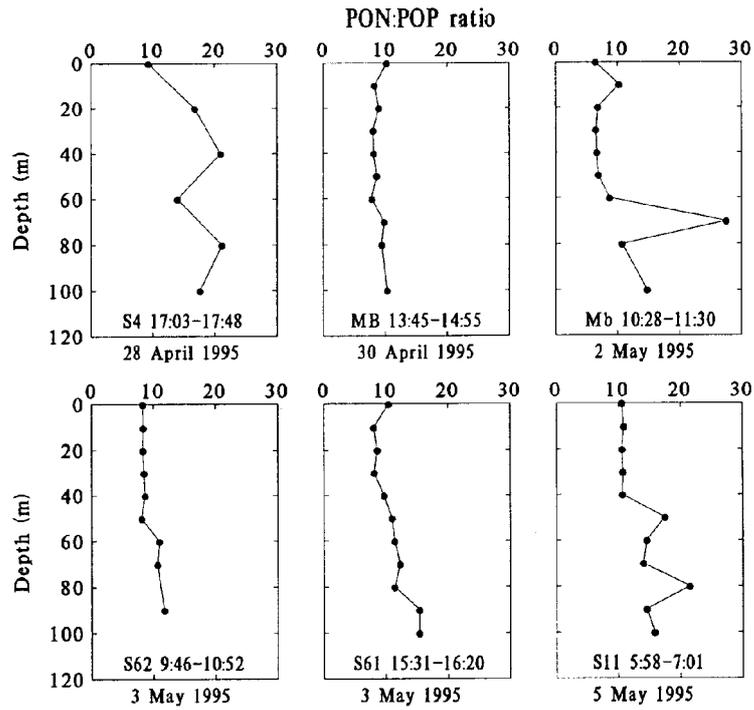


Fig. 23. Vertical distribution of the total particulate nitrogen to phosphorus ratio (PON:POP) at different sampling stations in Lake Tanganyika on 28 April - 5 May 1995. MB = Mpulungu buoy, Mb = Mpulungu buoy, new position.

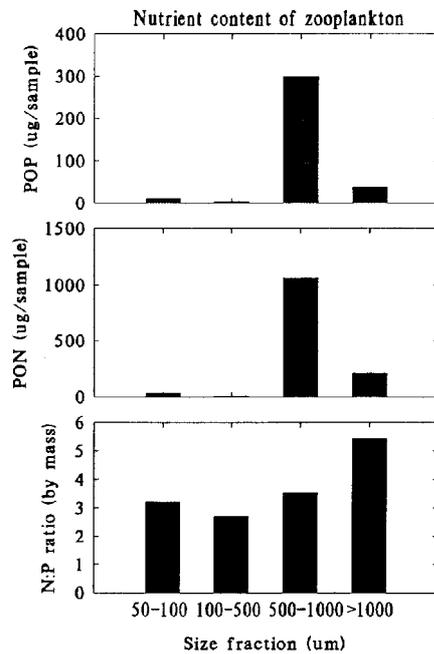


Fig. 24. Nutrient contents and the total particulate nitrogen to phosphorus ratio (N:P, by mass) of different size fractions of zooplankton at the depth of 0-120 m in Lake Tanganyika on 5 May 1995.

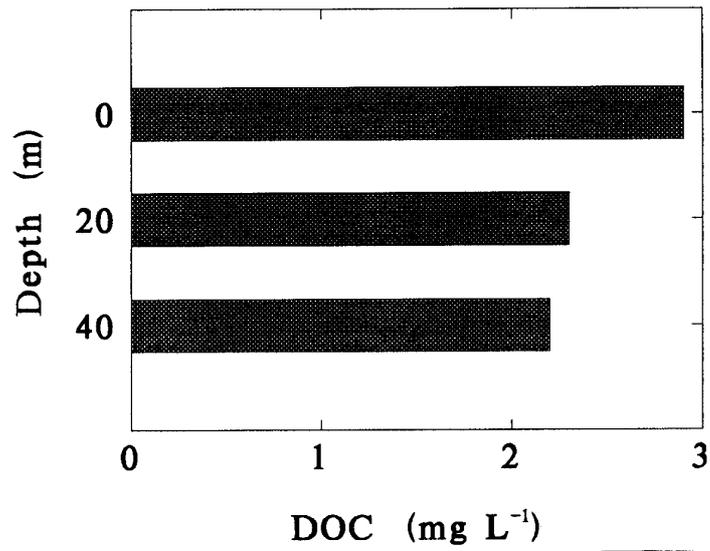


Fig. 25. Average concentrations of dissolved organic carbon (DOC) at the different depths of Lake Tanganyika on 30 April - 5 May 1995.

APPENDIX 1. Fluorometer readings in Lake Tanganyika on 28 April-5 May 1995.  
H = surface water sample from the stern of the vessel.

Date	Time	Depth	Fluor	Date	Time	Depth	Fluor
28 April	11.25	H	0.646	29 April	18.12	H	0.812
	12.45	H	0.661		18.24	H	0.817
	13.42	H	0.701		18.42	H	0.684
	15.45	H	0.908		19.54	H	0.749
	16.18	H	0.783		19.57	H	0.650
	17.03	0	0.618	30 April	06.68	H	0.660
	17.12	20	0.640		07.00	H	0.730
	17.25	40	0.639		07.31	H	0.610
	17.27	60	0.704		07.39	H	0.810
	17.39	80	0.494		07.51	H	0.812
	17.48	100	0.503		07.53	H	0.682
	18.35	H	0.640		08.07	H	0.846
	19.28	H	0.699		08.24	H	0.713
	20.21	H	0.805		08.40	H	0.760
	20.23	H	0.731		08.54	H	0.706
	20.59	0	0.613	09.10	H	0.620	
	21.02	10	0.600	09.15	H	0.690	
	21.03	20	0.601	09.35	H	0.730	
	21.05	30	0.660	09.43	H	0.790	
	21.08	40	0.654	10.09	H	0.643	
	21.09	50	0.577	10.23	H	0.721	
	21.14	60	0.544	10.35	H	0.780	
	21.16	70	0.578	10.54	H	0.798	
21.22	80	0.539	10.57	H	0.640		
21.28	90	0.480	11.21	H	0.690		
21.33	100	0.482	11.41	H	0.870		
22.34	H	0.764	11.54	H	0.790		
23.38	H	0.725	12.04	H	0.750		
29 April	12.27	H	0.580	12.33	H	0.682	
	13.15	H	0.644	12.54	H	0.630	
	13.45	H	0.640	13.13	H	0.667	
	14.03	H	0.560	13.45	0	0.530	
	14.06	H	0.527	13.54	10	0.892	
	14.49	H	0.573	14.01	20	0.640	
	15.14	H	0.687	14.07	30	0.658	
	15.59	H	0.641	14.12	40	0.680	
	17.02	H	0.760	14.20	50	0.700	
	17.16	H	0.780	14.25	60	0.740	
17.34	H	0.824	14.38	70	0.643		
17.50	H	0.804	14.45	80	0.546		
18.00	H	0.881	14.54	100	0.504		

APPENDIX I. (continued).

<b>Date</b>	<b>Time</b>	<b>Depth</b>	<b>Fluor</b>	<b>Date</b>	<b>Time</b>	<b>Depth</b>	<b>Fluor</b>	
30 April	17.51	H	0.750	2 May	11.31	100	0.528	
	17.54	H	0.652		12.09	H	0.551	
	18.16	H	0.756		13.08	H	0.660	
	19.09	H	0.850		13.55	H	0.522	
	19.12	H	0.680		14.13	H	0.508	
	19.14	H	0.680		14.47	H	0.607	
	20.11	H	0.794		15.39	H	0.570	
	20.26	H	0.840		16.02	0	0.553	
	20.47	H	0.824			10	0.760	
	20.56	H	0.940			20	0.612	
	22.22	H	0.812			30	0.677	
	22.25	H	0.680			40	0.780	
	22.36	H	0.702			50	0.632	
	23.28	0	0.724			60	0.590	
	23.32	10	0.673			70	0.552	
	23.34	20	0.722			80	0.520	
	23.38	30	0.780			16.29	100	0.503
	23.40	40	0.784			17.30	H	0.728
	23.43	50	0.712			17.43	H	0.801
	23.47	60	0.656			18.02	H	0.743
	23.51	70	0.652			19.02	H	0.700
	23.58	80	0.591			19.23	H	0.734
	2 May	06.46	0		0.690	20.12	H	0.775
06.51		5	0.750	22.57	0	0.654		
06.55		10	0.730		10	0.660		
07.01		20	0.723		20	0.680		
07.06		30	0.712		30	0.690		
07.12		40	0.683		40	0.742		
07.19		50	0.687		50	0.692		
07.25		60	0.650		60	0.680		
07.34		70	0.571		70	0.590		
07.42		80	0.590		80	0.553		
07.47		100	0.560		90	0.601		
08.25		H	0.681		100	0.510		
10.28		0	0.615		23.38	120	0.601	
10.32		5	0.632	3 May	00.30	H	0.666	
10.36		10	0.700		09.46	0	0.682	
10.40		20	0.700		09.46	10	0.738	
10.49		40	0.691		10.03	20	0.714	
10.57		50	0.707		10.07	30	0.675	
11.00		60	0.694		10.20	40	0.671	
11.06		70	0.630		10.26	50	0.694	
11.13	80	0.602	10.31		60	0.698		

APPENDIX 1. (continued).

<b>Date</b>	<b>Time</b>	<b>Depth</b>	<b>Fluor</b>	<b>Date</b>	<b>Time</b>	<b>Depth</b>	<b>Fluor</b>
3 May	10.40	70	0.592	3 May	21.32	90	0.512
	10.52	90	0.549		21.38	100	0.488
	15.13	H	0.540		22.53	H	0.660
	15.31	0	0.524	5 May	04.25	H	0.67
	15.37	10	0.538		05.45	H	0.734
	15.46	20	0.592		05.58	0	0.655
	15.55	30	0.732		06.04	5	0.624
	15.52	40	0.632		06.08	10	0.624
	16.01	50	0.580		06.13	20	0.663
	15.58	60	0.550		06.19	30	0.734
	16.08	70	0.506		06.25	40	0.629
	16.13	80	0.494		06.28	50	0.549
	16.18	90	0.478		06.38	60	0.531
	16.20	100	0.484		06.44	70	0.518
	18.45	H	0.630		06.47	80	0.518
	18.55	H	0.720		06.58	90	0.521
	19.44	H	0.660	07.01	100	0.536	
	20.44	H	0.580	09.14	H	0.560	
	20.56	0	0.640	09.27	H	0.590	
	21.00	10	0.570	09.29	H	0.626	
	21.02	20	0.605	09.32	H	0.606	
	21.05	30	0.928	09.43	H	0.750	
	21.09	40	0.850	09.44	H	0.623	
21.14	50	0.694	10.07	H	0.732		
21.18	60	0.553	10.24	H	0.625		
21.22	70	0.503	11.13	H	0.648		
21.28	80	0.512					

APPENDIX 2. The concentrations of chlorophyll  $\alpha$ , total particulate carbon (POC), nitrogen (PON) and phosphorus (POP) in Lake Tanganyika on 28 April-5 May 1995.

Date	Time	Depth <i>m</i>	Chl-a <i>mg m<sup>-3</sup></i>	POC <i>mg m<sup>-3</sup></i>	PON <i>mg m<sup>-3</sup></i>	POP <i>mg m<sup>-3</sup></i>
28 April	17.03	0	0.44	188	17	2.1
	17.12	20	0.50	173	17	1.1
	17.25	40	0.43	84	15	0.8
	17.27	60	0.08	50	5	0.5
	17.40	80	0.03	43	5	0.3
	17.48	100	0.05	37	4	0.3
30 April	13.45	0	0.91	219	25	2.6
	13.54	10	3.25	349	36	4.6
	14.01	20	1.63	222	28	3.3
	14.07	30	1.08	175	22	3.0
	14.12	40	1.01	151	20	2.7
	14.20	50	1.08	127	20	2.5
	14.25	60	1.04	113	17	2.4
	14.38	70	0.66	87	11	1.3
	14.45	80	0.35	49	5	0.7
	14.55	100	0.16	51	4	0.6
2 May	10.28	0	1.60	208	30	5.0
	10.36	10	1.67	187	26	2.7
	10.40	20	1.56	200	27	4.3
	10.45	30	1.13	150	21	3.5
	10.50	40	0.99	129	18	3.0
	10.55	50	0.95	126	18	2.9
	11.00	60	0.69	69	10	1.4
	11.06	70	0.52	49	9	0.4
	11.13	80	0.58	56	8	0.9
	11.30	100	0.47	50	6	0.5
3 May	09.46	0	0.86	141	16	2.2
	09.46	10	1.31	166	19	2.5
	10.03	20	1.26	158	19	2.5
	10.07	30	0.85	123	16	2.1
	10.20	40	0.81	128	17	2.2
	10.26	50	1.24	167	37	4.9
	10.32	60	0.83	81	13	1.4
	10.40	70	0.33	59	8	0.9
	10.52	90	0.12	35	4	0.5
	3 May	15.31	0	0.32	106	14
15.37		10	0.51	141	17	2.4
15.46		20	0.54	184	21	2.7
15.54		30	1.04	192	21	2.8
15.52		40	0.64	83	12	1.4

APPENDIX 2. (continued).

<b>Date</b>	<b>Time</b>	<b>Depth</b> <i>m</i>	<b>Chl-a</b> <i>mg m<sup>-3</sup></i>	<b>POC</b> <i>mg m<sup>-3</sup></i>	<b>PON</b> <i>mg m<sup>-3</sup></i>	<b>POP</b> <i>mg m<sup>-3</sup></i>
3 May	16.01	50	0.28	59	7	0.8
	15.58	60	0.13	50	7	0.8
	16.08	70	0.07	42	5	0.6
	16.13	80	0.07	44	7	0.8
	16.18	90	0.04	43	4	0.4
	16.20	100	0.03	39	4	0.4
	5 May	05.58	0	0.45	90	17
06.08		10	0.56	89	17	1.7
06.13		20	0.72	92	18	1.9
06.19		30	1.37	110	21	2.1
06.25		40	0.53	75	12	1.3
06.28		50	0.13	43	9	0.6
06.38		60	0.06	33	5	0.5
06.44		70	0.05	34	6	0.6
06.48		80	0.03	39	7	0.4
06.58		90	0.06	35	5	0.5
07.01		100	0.20	49	11	0.8