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Trophic structure of Lake Tanganyika: carbon flows in the pelagic food web

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Abstract

The sources of carbon for the pelagic fish production in Lake Tanganyika, East Africa, were evaluated in a comprehensive multi-year study. Phytoplankton production was assessed from seasonal *in situ* ^{14}C and simulated *in situ* results, using on-board incubator measurements and knowledge of the vertical distributions of chlorophyll and irradiance. Bacterioplankton production was measured on two cruises with the leucine incorporation method. Zooplankton production was calculated from seasonal population samples, the carbon contents of different developmental stages and growth rates derived from published sources. Fish production estimates were based on hydroacoustic assessment of pelagic fish biomass and data on growth rates obtained from length frequency analyses and checked against daily increment rings of fish otoliths. Estimates for primary production (426–662 g C m^{-2} a^{-1}) were 47–128% higher than previously published values. Bacterioplankton production amounted to about 20% of the primary production. Zooplankton biomass (1 g C m^{-2}) and production (23 g C m^{-2} a^{-1}) were 50% lower than earlier reported, suggesting that the carbon transfer efficiency from phytoplankton to zooplankton was low, in contrast to earlier speculations. Planktivorous fish biomass (0.4 g C m^{-2}) and production (1.4–1.7 g C m^{-2} a^{-1}) likewise indicated a low carbon transfer efficiency from zooplankton into planktivorous fish production. Relatively low transfer efficiencies are not unexpected in a deep tropical lake, because of the generally high metabolic losses due to the high temperatures and presumably high costs of predator avoidance. The total fisheries yield in Lake Tanganyika in the mid-1990s was 0.08–0.14% of pelagic primary production, i.e. within the range of typical values in lakes. Thus, no special mechanisms need be invoked to explain the productivity of fisheries in Lake Tanganyika.

Introduction

Lake Tanganyika in East Africa is known for its productive pelagic fishery, which is reported to yield higher catches per unit area than in most great lakes of the world (Coulter, 1981, 1991; Hecky et al., 1981; Lindqvist & Mikkola, 1989; Hecky, 1991; Roest, 1992). Ultimately, the fish yield is a function of primary production, which in turn depends on solar radiation and external nutrient inputs. The fisheries

yield in lakes usually ranges between 0.02 and 0.2% of primary production (e.g. Morgan et al., 1980), while marine coastal seas often show values an order of magnitude higher (Nixon, 1988). For Lake Tanganyika, a preliminary estimate of 0.45%, resembling those in the marine systems, has been given (Hecky et al., 1981; Hecky, 1984, 1991).

Several hypotheses have been presented to explain the high productivity of the pelagic fishery in Tanganyika (Hecky et al., 1981). Hecky (1991) noted that the food web of Tanganyika has a marine character. As in many productive marine systems, the primary grazer is a diaptomid copepod and the dominant primary planktivores, as well as the piscivores belong to predominantly marine fish families. The phytoplankton and bacterial biomasses are low but the growth rates are high. Organic carbon is not accumulated in the plankton but is channelled into fish biomass and harvested as fish yield. The long geological history of the lake, combined with the special ecological conditions of a deep, continuously warm tropical lake, may have resulted in the evolution of a trophic structure consisting of highly efficient species (Hecky, 1984). As another explanation Hecky et al. (1981) proposed that the flux of dissolved organic matter (DOM) from the anoxic hypolimnion might complement phytoplankton primary production; however, later analyses of available data have not supported this hypothesis (Hecky, 1991).

Earlier assessments of system structure and fish production efficiency were based on fairly limited data. New data have been collected by the FAO/Finnida project 'Research for the Management of the Fisheries on Lake Tanganyika' (LTR) (Mölsä et al., 1999). Rational fisheries management requires good knowledge of the fish production potential. The basic question in the LTR project is whether the present fish catches from Tanganyika are on a sustainable basis and whether or not there are further possibilities to increase the yield by developing the fishery. Total lake-wide catches seem to be increasing (Hanek, 1994; Coenen, 1995; Coenen et al., 1998), but recently, decreasing catches per unit effort both in the Burundi sector in the north and in the Mpulungu (Zambia) waters in the south have aroused concerns about possible overfishing (Roest, 1992; Coenen et al., 1998). On the other hand, there is still considerable local pressure to increase fishing effort to acquire more fish protein. One of the LTR objectives was, therefore, to determine the biological basis of fish production as a basis for management.

In Lake Tanganyika, as in other large and deep clearwater lakes, primary production of phytoplankton is expected to be the major source of energy to higher pelagic trophic levels, including fish. Knowledge of the trophic structure of the lake and the transfer efficiencies in the food chain is of interest for assessing the fishery potential and also for comparison with other lakes. The LTR scientific sampling program covered the major components of the pelagic ecosystem over three years in different parts of the lake. Primary data have been made available in numerous technical documents published by the LTR project; in addition, we present some new data here. Because the analysis of these data still continues, our treatment here is necessarily preliminary. It, nevertheless, provides useful insights about the flow and availability of organic carbon that maintains the pelagic fisheries. This enables a reassessment of the trophic structure of Lake Tanganyika.

Methods and material

Sampling scheme

Physical, chemical and biological components of the pelagic ecosystem of Lake Tanganyika were sampled weekly or fortnightly at three localities (Figure 1) in a comprehensive scientific sampling program from July 1993 to June 1996 (Plisnier et al., 1999); data for the first two years were available for the present account. In addition, representative data were available from 20 lake-wide scientific cruises with the R/V Tanganyika Explorer in 1995–1998.

Solar irradiance

Total irradiance was recorded along with other weather variables at automatic weather stations (land-based in Bujumbura and on a buoy off Mpulungu and Kigoma) (Kotilainen et al., 1995). Irradiance data recorded at Kigoma airport were also available. A LI-COR instrument with a spherical scalar underwater quantum sensor (LI-193SA) and data logger (LI-COR Inc, Lincoln, USA) was used to record the depth attenuation of photosynthetically active radiation (PAR: 400–700 nm). Vertical profiles of *in situ* irradiance were measured during the cruises and during the weekly monitoring at the three field stations.

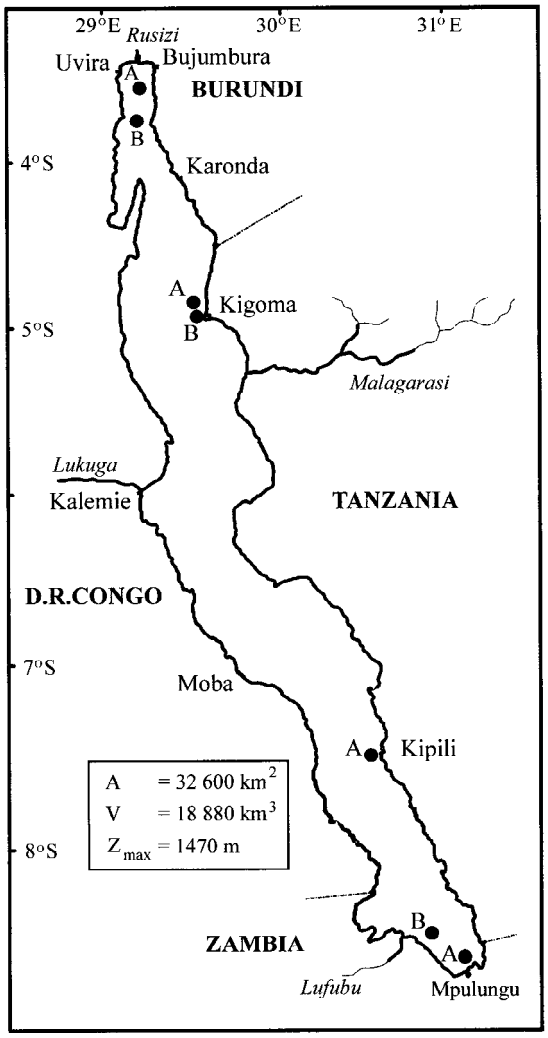

Figure 1. Lake Tanganyika and the locations of the seasonal sampling sites (*A* = weekly sampling sites, B = vertical migration study sites). Lake area (A), volume (*V*) and maximum depth (Z_{max}) are also indicated.

Phytoplankton

In vivo fluorescence of chlorophyll *a* at different depths (down to 100 m) and horizontal positions was measured using a Turner AU-10-005 field fluorometer (with the traditional 10-037 chlorophyll optical kit using F4T5D daylight white lamp, CS-5-60 excitation filter (340–500 nm), CS-2-64 emission filter (>665 nm) and red-sensitive photomultiplier; Salonen & Sarvala, 1994; Sarvala & Salonen, 1995; Salonen et al., 1999). Water samples were taken with a darkened 1-m long Limnos sampler (Limnos Ltd, Finland). Vertical fluorescence profiles at several sites plus numerous additional surface water measurements were made off Bujumbura in April 1994, off Kigoma in April and December 1994 (Salonen & Sarvala, 1994; Sarvala & Salonen, 1995), and throughout the lake in April–May 1995 (Järvinen et al., 1996), October–November 1995, November 1996 (Salonen et al., 1999) and in March–April 1998. Fluorescence readings were calibrated against determinations of extracted chlorophyll *a*. One- or two-litre samples of the same water were filtered on preignited Whatman GF/F glassfibre filters, dried, stored in darkness and extracted in ethanol. Chlorophyll *a* was then determined spectrophotometrically (Salonen & Sarvala 1995; a modified ISO procedure) or using a fluorescence spectrophotometer (Järvinen et al., 1996; Salonen et al., 1999). Vertical series of extracted chlorophyll *a* determinations were also made on two-weekly samples from the permanent field stations off Bujumbura, Kigoma and Mpulungu, starting from August 1995. A biomass estimate for phytoplankton was obtained from the average chlorophyll (0–40 m depth) by assuming a carbon:chlorophyll ratio of 35 (Sarvala et al., 1982).

Phytoplankton primary production was assessed with the whole-water modification of the radiocarbon method (Schindler et al., 1972). Radiolabelled samples and formaldehyde treated controls were incubated *in situ* at different depths in 20-mL glass liquid scintillation vials attached horizontally to a suspending rack (Salonen & Sarvala, 1994). No filtration was applied; the unassimilated radiocarbon was removed through acidification and exchange with air (Niemi et al., 1983). Radioactivities of acid preserved samples were counted with a Wallac Ultrobeta 1200 liquid scintillation counter. Dissolved inorganic carbon (DIC) in water was determined in Finland with a carbon analyser according to Salonen (1981). Because of very high alkalinity (6.7–6.9) and pH (ca. 9; Edmond et al., 1993), the storage of samples did not significantly affect equilibrium concentrations of DIC. Short 3-h incubations around noon plus diel series of 2–3-h successive incubations were done off Kigoma in April and December 1994 (down to 20 m in April and down to 60 m in December) and additional vertical series in September 1994. Further series of seasonal *in situ* measurements with 4-h incubations were made off Bujumbura, Kigoma and Mpulungu between July 1995 and June 1996. These vertically integrated 4-h results were converted to daily values using the ratio between the cumulative daily PAR and the PAR cumulated during the incubation period. Off Bujumbura, 38% of the cumulative daily PAR was received during

the incubation period, and the same value was applied to Kigoma data (at both stations the incubations were started at 7:30 h). Off Mpulungu, the incubations started at 11:00 h and the corresponding percentage was 50%.

During two lake-wide cruises (April–May 1995 and October–November 1995), primary production was also measured in an on-board incubator at different light intensities (25–508 μmol photon m^{-2} s^{-1} PAR) to obtain representative photosynthesis-irradiance (P-I) curves (Järvinen et al., 1996: 8 series; K. Salonen, unpublished: 4 series). During the April–May cruise, phytoplankton samples from 0, 5, 10, and 20 m were combined for the incubations; during the October–November cruise samples from 1, 10, 20, 30 and 40 m depths were incubated separately. Chlorophyll *a* for the incubated samples was estimated from fluorescence readings. Chlorophyll-specific productivity was related to irradiance by fitting the hyperbolic tangent model

$P = P_{max} \tanh(aI/P_{max})$

without a term for photoinhibition (Jassby & Platt, 1976; for an evaluation of production-irradiance models, see Frenette et al., 1993). Fitting was done with the NLIN procedure of SAS computer package. Using this photosynthesis-irradiance relationship, estimates of simulated *in situ* primary production (e.g. Lohrenz et al., 1992) were calculated from irradiance and chlorophyll data. Hourly PAR for each depth was calculated from the annual average of total surface irradiance for that hour, using measured light attenuation coefficients, assuming 5% albedo and taking PAR to be 47% of the total irradiance and using a conversion factor of 1 Wm^{-2} = 4.59 μmol photon m^{-2} s^{-1} between the electromagnetic radiation flux and the photon flux density (Reynolds, 1990). From these irradiance values, chlorophyll-specific productivity was calculated for each depth and hour and daily production values for the whole euphotic water column were obtained by temporal and vertical integration.

Simulated *in situ* primary production was calculated separately for the dry and wet seasons. Dry season calculations were based on the light extinction and chlorophyll measurements and production-irradiance curves obtained during the April–May 1995 cruise, while wet season calculations were based on a higher light extinction coefficient deduced from transparency data, chlorophyll profiles from the cruises in October–November in 1995 and 1996 and production-irradiance curves obtained during the October–November cruise in 1995. For both seasons, calculations were performed with irradiance data from the Bujumbura and Mpulungu weather stations and the results averaged.

Bacterioplankton, community respiration and DOC

Bacterioplankton production was assessed with the leucine incorporation method (Kirchman, 1995) during two cruises (April–May 1995; Järvinen et al., 1996, and October–November 1995). Total respiration of plankton was measured as oxygen consumption off Kigoma in April 1994 (Salonen & Sarvala, 1994), using glass bottles and the Winkler titration method. Dissolved organic carbon (DOC) was determined from two vertical series from 0 to 80 m depth on 30 April and 5 May 1995 at the southern and northern ends of the lake (Järvinen et al., 1996). Carbon was determined by igniting the acidified and dried water samples in sealed glass ampoules and leading the CO_2 produced to the infrared detector of the carbon analyser of Salonen (1979), as described in Järvinen et al. (1996).

Zooplankton

Zooplankton abundance was monitored weekly (fortnightly during the first year) at the three field stations beginning from July 1993 (Kurki et al., 1999a). Three (one in the first year) replicate hauls from 100 m to surface were taken with a 100-μm plankton net of mouth diameter 25 cm. For the only calanoid species (*Tropodiaptomus simplex* (Sars)) and the cyclopoids as a group (consisting of *Mesocyclops aequatorialis aequatorialis* (Kiefer), *Tropocyclops tenellus* (Sars) and *Microcyclops cunningtoni* (Sars)), nauplii, copepodids, adult males and adult females with or without eggs were distinguished. *Limnocnida tanganyicae* Günther medusae, decapod shrimps and fish eggs or larvae were also counted (Kurki et al., 1999b). Nets with mesh sizes of 50 and 100 μm were compared on five occasions in October–November 1993 off Kigoma (Vuorinen & Kurki, 1994) and in 1994 off Bujumbura. Important additional information was obtained from the vertical migration studies (Vuorinen et al., 1999), in which samples were taken at six-week intervals with a transparent 7.4-l tube sampler (Limnos Ltd., Finland) at 20 m depth intervals down to 140 m off Bujumbura and Kigoma and to 220 m off Mpulungu; mesh size was 50 μm.

Individual carbon contents of the main crustacean zooplankton species were determined in Finland with the analyser of Salonen (1979) from two samples preserved in 4% glutaraldehyde (Kigoma, 6 December

1994; southern Burundi waters, April 1995). Preservation in glutaraldehyde should yield carbon values similar to fresh determinations (Salonen & Sarvala, 1985; Kimmerer & McKinnon, 1986). Carbon-length regressions ($\log_e$[carbon] *vs.* $\log_e$[total length including the furcal rami]) were established. Mean carbon values for nauplii and copepodids were derived from these determinations assuming a constant mortality of 21% during each stage. This mortality rate was obtained from the difference between the mean copepodid and naupliar abundances in the vertical migration data. Because cyclopoid species were not distinguished in routine counting, the mean carbon values for cyclopoids were adjusted for the relative abundance of the small species (Kurki et al., 1999a: 45% off Bujumbura, 94% off Kigoma and 14% off Mpulungu). Dry mass-diameter regression for the medusa *Limnocnida* was established from individuals dried in the field on preweighed aluminium foil sheets and weighed later in Finland. The average individual biomass of medusae was obtained with this regression from two sample series covering the 0–100 m water column in April 1998 off Kigoma. Carbon was taken to be 50% of dry mass (Salonen et al., 1976). For the shrimp *Limnocaridina parvula* Calman, an organic dry mass-carapace length regression was constructed from a 0–100 m net sample off Kigoma in April 1998. Mean shrimp biomass was calculated using the carapace measurements in 105 oblique 0–100 m Gulf net samples taken during five lake-wide cruises (Bosma et al., 1998). The same regression was used for all species, because *L. parvula* accounted for >99% of the total shrimp numbers.

Zooplankton production was calculated with the instantaneous growth rate method (Downing & Rigler, 1984; Kimmerer, 1987):

$$P = g \bullet B,$$

where

$g = \log_e (M_{fin}/M_{ini}) / D_i$
B = (numbers) • (individual carbon content)
M_{ini}, m_{fin} = initial and final carbon contents of the stage *i*; D_i = duration of stage *i*)

There is no practical way to work out the average initial and final carbon contents of a developmental stage; the range of observed values would be an overestimate, because it is inflated by variation in individual size. Therefore, approximate *ad hoc* solutions were necessary. The carbon mass of the first naupliar stage was taken as the initial naupliar mass. The mean of the sixth naupliar and the first copepodid stage was used as the final naupliar mass and the initial copepodid mass, and the mean of the fifth copepodid and the adult stage was used as the final copepodid mass. For aggregated developmental stages this routine is more appropriate than the procedure of Irvine & Waya (1999), who used the mean biomasses of successive stages for deriving instantaneous growth rates. Adult female production consisted of egg production which was assessed separately using the numbers of ovigerous females: for instantaneous growth rates the carbon contents of egg-bearing females were related to the initial female mass and the egg development time.

Development times were derived from the literature. For *T. simplex*, we averaged values published for the slightly larger *Tropodiaptomus spectabilis* from South Africa (Hart, 1994) and the similarly-sized *Tropodiaptomus cunningtoni* from Lake Malawi (Irvine & Waya, 1995). For *M. aequatorialis*, we used the recently published values from Lake Malawi (Irvine & Waya, 1995). For the smaller cyclopoid species, we calculated tentative development times from the temperature regressions of *Thermocyclops oblongatus* from Lake Naivasha (Mavuti, 1994). Comparisons with recent LTR rearings of *T. simplex* and *M. aequatorialis* in Kigoma (Hyvönen, 1997) showed reasonable agreement with the adopted values. All development times were adjusted to a temperature of 26 °C, close to the average experienced by Lake Tanganyika copepods during their vertical migrations that expose them daily to almost the maximum seasonal temperature range from 24 to 28 °C (annual average temperatures for the upper 100 m were 25.5, 25.6 and 25.1 °C off Bujumbura, Kigoma and Mpulungu, respectively; Kurki et al., 1999a). Because of the narrow range of possible values, errors owing to the temperature variation remained small.

Fish

Population analyses of pelagic fish (the clupeids *Stolothrissa tanganyicae* Regan, *Limnothrissa miodon* (Boulenger) and the predatory *Lates stappersi* (Boulenger)) were based on weekly catch samples from commercial catches at three main stations and five substations around the lake (Aro & Mannini, 1995). Sampling covered all methods used in the traditional, artisanal and industrial fisheries (lift nets, beach seine and purse seine). Most fishing is done at night as virtually all of these methods rely on light attraction. In the first year of sampling, 429–443 catch samples were taken for each species. Length,

weight, sex and reproductive status were recorded for each fish. Length-frequency analyses (LFA) were applied to derive growth and mortality rates from these data (Mannini et al., 1996). To check the growth information thus obtained, age determinations of the clupeids were also made by counting daily increment rings in the otoliths (Pakkasmaa & Sarvala, 1995; H. Ahonen, unpubl.). Length-specific growth rates were derived from the von Bertalanffy growth curves and converted to weight-specific rates using biomass-length-regressions and, finally, these were combined to average size distributions at each sampling locality to yield daily and annual production rates and production to biomass ratios.

Fish biomass was estimated from five lake-wide hydroacoustic surveys combined with experimental trawling (Szczucka, 1998). Because of high noise levels observed during two cruises, acoustic data from only three cruises (June 1995, November–December 1997, February 1998) could be used for absolute biomass estimation. Additional mortality estimates for each fish species were derived from the combined size distributions in the trawl catches. Biomass proportions of different species were averaged from the results of all five cruises (Mannini, 1998). Total fish production in Tanganyika was obtained using the calculated production to biomass ratios and estimates of fish biomass. Collection of fish catch statistics was done in collaboration with the local fisheries administration of each country (Coenen, 1995; Coenen et al., 1998).

Results

Irradiance

The mean diurnal pattern of total solar irradiance was very similar at the northern and southern ends of the lake, although slightly lower values were recorded before noon in Bujumbura (Figure 2). This may be due to the shading effect of the mountainous terrain or to more frequent clouds in the northern end of the lake. In Bujumbura, the average total irradiance in January–October 1995 was 230 Wm^{-2} (218 Wm^{-2} during the wet season, 232 Wm^{-2} during the dry season); off Mpulungu the average for May–November 1995 was 256 Wm^{-2}. The 1993 annual average of total irradiance at Kigoma airport, some kilometres east of the lake shore, was 206 Wm^{-2}; higher values would be expected on the lake, because clouds tend to be more common over the land in this area.

During the whole-lake cruise in April–May 1995, the measured daytime (7:00–17:00) total irradiance varied between 236–988 (average 554) Wm^{-2} (n = 41). The corresponding long-term averages for the Bujumbura and Mpulungu weather stations in 1995 were 543 and 595 Wm^{-2}, respectively. Average maximum hourly irradiance (PAR) below surface calculated (see below) from the the weather station total radiation (Figure 2) was 1700–1800 μmol photon m^{-2} s^{-1} and the corresponding average for the daytime (7:00–17:00) was about 1160 μmol photon m^{-2} s^{-1}. This compared well with the average daytime irradiance (1192 μmol photon m^{-2} s^{-1}) measured during the April–May 1995 cruise immediately below water surface in six light profiles from three sites covering the whole lake length.

Light extinction coefficients obtained from three vertical profiles off Bujumbura in February–March 1995 ranged from 0.130 to 0.188 m^{-1} and seemed to be inversely related to Secchi depth transparency (11.2–8.5 m). The clearly lower (mean 0.112 m^{-1}, range 0.102–0.117 m^{-1}, n = 6) extinction coefficients obtained from measured irradiance profiles during the April–May 1995 cruise were associated with higher transparency of water (14–16 m), typical for the April–August season. In 1993–1995, the average transparency off Bujumbura and Kigoma was 12.3 m (n = 88). Therefore, the extinction coefficient of 0.15 m^{-1}, roughly corresponding to a Secchi reading of 9.5–10 m, was chosen to represent the wet season, while the value measured during the April–May 1995 cruise (0.112 m^{-1}) was used for the dry season.

Phytoplankton primary production

Fluorescence and chlorophyll profiles showed values approaching 1 mg chl *a* m^{-3} down to 50–60 m depth, in sunny weather a surface depression around noon, and often a maximum in fairly deep water at 30–40 m (Figure 3; Sarvala & Salonen, 1995; Järvinen et al., 1996; Salonen et al., 1999). In connection with local bluegreen blooms, much higher values (tens of mg m^{-3}) were observed immediately below the water surface. Likewise, maximum primary production was usually at the depth of 10–20 m, with measurable production down to 40–50 m (Figure 4). The depth of the euphotic layer, defined as the depth to which 1% of the surface irradiance could penetrate, was also normally between 40 and 50 m throughout the lake in different seasons (Langenberg, 1996). The photic zone was usually deepest off Kigoma, which was the

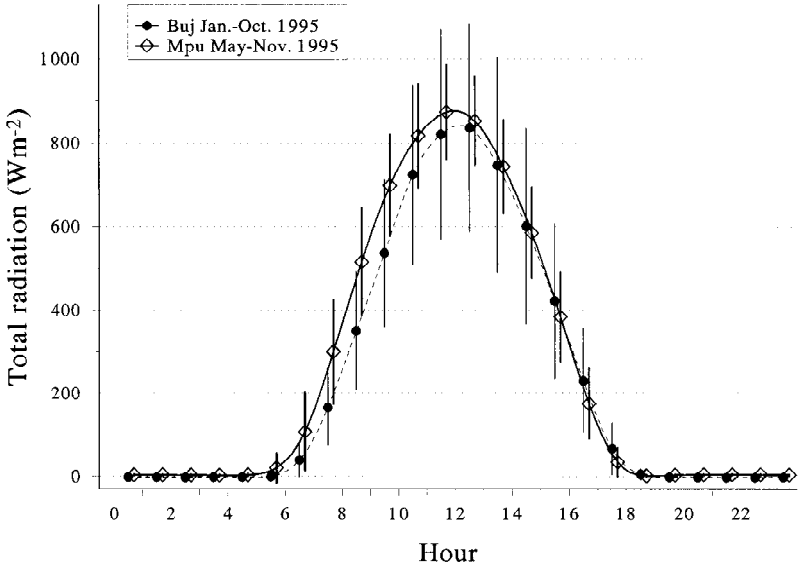

Figure 2. Average daily pattern of total radiation flux (hourly averages; Wm^{-2}) at the automatic weather stations in Bujumbura harbour (Burundi; 13 January – 3 November 1995) and off Mpulungu (Zambia; buoy meteo: 1 May – 28 November 1995). Vertical bars show standard deviations of the hourly averages (time axes slightly displaced for clarity).

only permanent sampling station that represented the conditions in the open central parts of Tanganyika.

During the first cruise in April–May 1995 the average fluorescence in surface water (excluding the midday depression) indicated a mean chlorophyll *a* concentration of 1.4 mg m^{-3} for the whole lake (Salonen et al., 1999). For the uppermost 40 m the fluorescence-derived overall mean value was 0.96 mg m^{-3} (n = 53) and the corresponding mean for extracted chlorophyll *a* was 1.0 mg m^{-3} (n = 27). The vertical profiles measured off Kigoma in April and December 1994 indicated much lower values, with especially pronounced surface depression in April (Figure 3). Vertical profiles from the cruises in October–November 1995 and November 1996 showed higher fluorescence levels and maxima at or close to the surface (Figure 3); the latter series included some surface blooms of bluegreen algae resulting in very high fluorescence values (Salonen et al., 1999). The average chlorophyll in the uppermost 40 m (calculated from fluorescence) was 2.2 mg m^{-3} in October–November 1995 (n = 76) and 2.8 mg m^{-3} in November 1996 (n = 27). Seasonal average values obtained from the first five months of weekly chlorophyll samples from off Bujumbura, Kigoma and Mpulungu were 0.6–1.6 mg extracted chlorophyll *a* m^{-3} (Langenberg, 1996).

Incubator measurements of primary production at different irradiance levels resulted in relatively flat photosynthesis-irradiance curves (Figure 5), showing that the Tanganyika phytoplankton was capable of efficient photosynthesis even at the low irradiance levels occurring at 30–40 m depth. No signs of photoinhibition were observed up to the highest experimental irradiance level of 512 μmol photon m^{-2} s^{-1}. Variability between experiments was high especially for maximum level of production. One of the October–November 1995 experiments (30 m) was omitted because of practically zero production at all irradiances, indicating a technical failure. DIC determinations were consistently 72 mg C l^{-1}. Average primary production assimilation numbers varied from 2.1 mg C (mg chl *a*)$^{-1}$ h^{-1} during the April–May 1995 whole-lake cruise to 3.2 mg C (mg chl *a*)$^{-1}$ h^{-1} during the October–November cruise in 1995. The assimilation number obtained from *in situ* incubations in December 1994 off Kigoma (3.0 mg C (mg chl *a*)$^{-1}$ h^{-1}) was similar to the latter value.

In the incubator experiments in October–November 1995 the chlorophyll-specific productivity *vs.* irradiance curves were practically identical from 1 to 30 m depth, allowing the use of common photosynthetic parameters for these depths (Table 1). Phytoplankton from 40 m showed a steeper photosynthesis-light slope and higher maximum productivity (Figure 5), although the difference was not statistically signific-

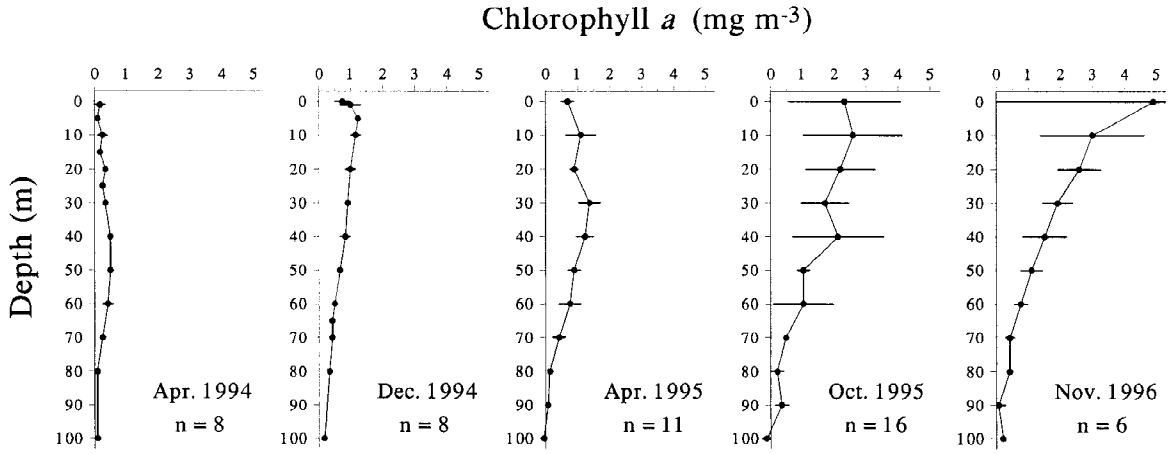

Figure 3. Average vertical profiles of phytoplankton chlorophyll (calculated from fluorescence) off Kigoma in April and December 1994 and during three whole-lake cruises in April–May 1995 (Järvinen et al., 1996), October–November 1995 and November 1996 (horizontal bars show standard deviations; *n* = number of averaged profiles). All profiles taken at different times of day are included.

Table 1. Photosynthetic parameters (photosynthetic efficiency (a) and photosynthetic capacity (P_{max})) for Lake Tanganyika phytoplankton, calculated with the hyperbolic tangent model of the chlorophyll-specific production *vs.* irradiance relationship without a term for photoinhibition (Jassby & Platt, 1976). Data derived from incubation experiments during the cruises in April–May 1995 (samples from different depths combined) and October–November 1995 (depths incubated separately). For the latter cruise, parameters are also given for the combined data of 1–30 m and 1–40 m.

Cruise	Depth (m)	a			P_{max}			*n*
		Mean	Lower CL_{95}	Upper CL_{95}	Mean	Lower CL_{95}	Upper CL_{95}	
Apr.–May	0–40	0.060	0.025	0.095	2.39	1.93	2.85	40
Oct.–Nov.	1	0.045	-0.0001	0.089	3.35	2.26	4.44	12
Oct.–Nov.	10	0.049	0.013	0.086	3.84	2.90	4.78	12
Oct.–Nov.	20	0.048	0.025	0.071	3.56	3.00	4.12	12
Oct.–Nov.	30	0.039	-0.013	0.091	3.46	1.81	5.10	8
Oct.–Nov.	40	0.090	-0.047	0.228	6.38	3.31	9.45	4
Oct.–Nov.	1–30	0.046	0.029	0.062	3.56	3.13	3.98	44
Oct.–Nov.	1–40 (all)	0.046	0.024	0.067	3.52	2.97	4.08	52

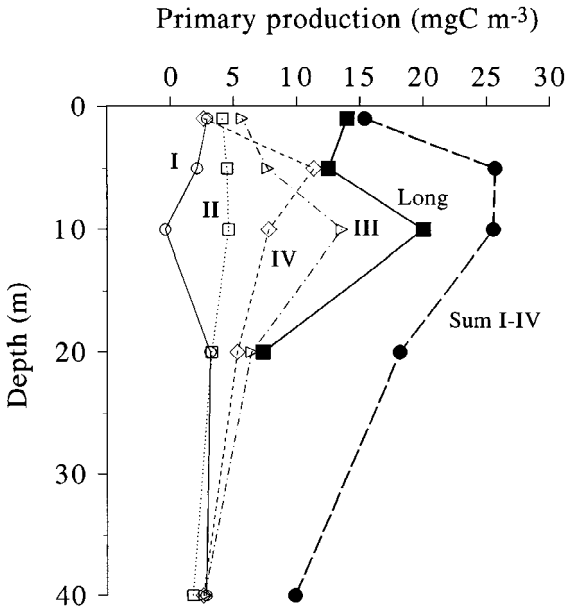

Figure 4. Vertical profiles of phytoplankton primary production measured with the radiocarbon method off Kigoma 2 December 1994 (Sarvala & Salonen, 1995). Results are shown for four successive two-hour incubations (I-IV, between 7:50 and 17:30), their sum (Sum I–IV: black dots), and a whole-day incubation (7:55–17:35; filled squares).

ant. The examination of residuals did not reveal any systematic deviations from the model.

The similar light responses suggest that phytoplankton in the uppermost 30 m had an identical history of light exposure, probably because of only partial mixing within the epilimnion. Indeed, vertical temperature profiles often showed secondary discontinuities at various depths above the major thermocline at 50–70 m (Salonen & Sarvala, 1994; Huttula et al., 1994). At least down to a depth of 5 m, occasionally even down to 9–10 m, the irradiance levels were so high (>500 μmol photons m^{-2} s^{-1}; e.g. Kirk, 1983) that photoinhibition was likely for several h per day; detectable as declining fluorescence values towards the surface in many profiles. Because

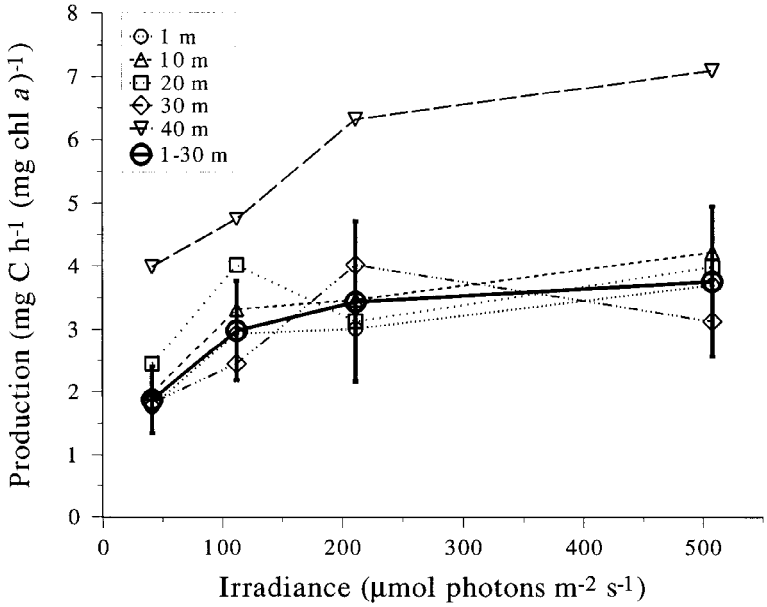

Figure 5. Photosynthesis-irradiance curves for Lake Tanganyika phytoplankton from different depths, obtained from incubator experiments in October 1995. Combined curve for the depths 0–30 m given with standard deviations (vertical bars).

epilimnetic mixing ameliorates deleterious effects of excessive radiation, surface inhibition was ignored in calculating photosynthetic rates, with any inhibition effect incorporated in the measured chlorophyll values. Thus, ignoring photoinhibition, the simulated *in situ* production calculations indicated a photosynthetically saturating light climate for 12 h per day immediately below the surface and for 5–6 h at 15–20 m depth.

In April–May 1995, multiplication of the average assimilation number by the average surface chlorophyll value resulted in an estimate for the overall lake-wide primary production rate of 2.0–2.1 mg C m^{-3} h^{-1}, or, approximately 20–21 mg C m^{-3} d^{-1}. Depth-integrated daily primary production for the uppermost 40 m were 0.80–0.86 g C m^{-2} d^{-1}. In October–November 1995, the corresponding production rate was estimated as 7.0 mg C m^{-3} h^{-1}, resulting in a daily productivity of 2.8 g C m^{-2} d^{-1}. Averaging these estimates yields an annual production of 662 g C m^{-2} a^{-1}.

The average simulated *in situ* production was 1.06 g C m^{-2} d^{-1} for the dry season and 2.49 g C m^{-2} d^{-1} for the wet season. Assuming 6 month duration for both seasons, these values resulted in an annual production estimate of 647 g C m^{-2} a^{-1} for the whole lake.

Third, completely independent estimate for primary production was obtained from the weekly *in situ* radiocarbon measurements done since August 1995 at the three permanent sampling localities in different parts of the lake (Figure 6). The highest values were found off Bujumbura and the lowest off Mpulungu (the mean values (± 95% CL) for the whole measurement period were 2.44±0.71 g C m^{-2} d^{-1} (number of measuring dates = 14), 0.52±0.09 (n = 8) and 0.54±0.38 (n = 7) for Bujumbura, Kigoma and Mpulungu, respectively). An overall average for the whole lake was estimated as 1.2 g C m^{-2} d^{-1} or 426 g C m^{-2} a^{-1}; variability of the *in situ* measurements suggests that the 95% confidence belt of this estimate might be ±35%.

Bacterioplankton production

In the experiments during the first research cruise in April–May 1995 (Järvinen et al., 1996) the rate of leucine uptake varied between 0.0027–0.1292 nM Leu l^{-1} h^{-1}. In terms of bacterial biomass production this rate was equivalent to 0.1–4.9 (average 2.8) mg C m^{-3} d^{-1} (assuming equal rate day and night). This rate was slightly more than 20% of the average phytoplankton primary production (13.6 mg C m^{-3} d^{-1}) measured in two-day experiments during the same cruise. During the second cruise in October 1995, at two sites

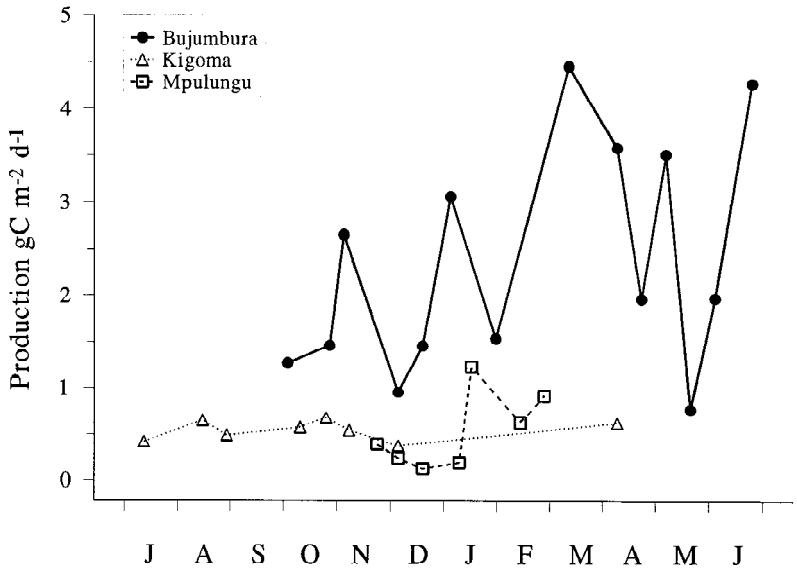

Figure 6. In situ primary production in Lake Tanganyika at the three permanent field sampling stations in 1995–1996. Original results of 4-hour incubations at different depths were converted into daily values using the hourly distribution of irradiance and integrated for the whole euphotic water column.

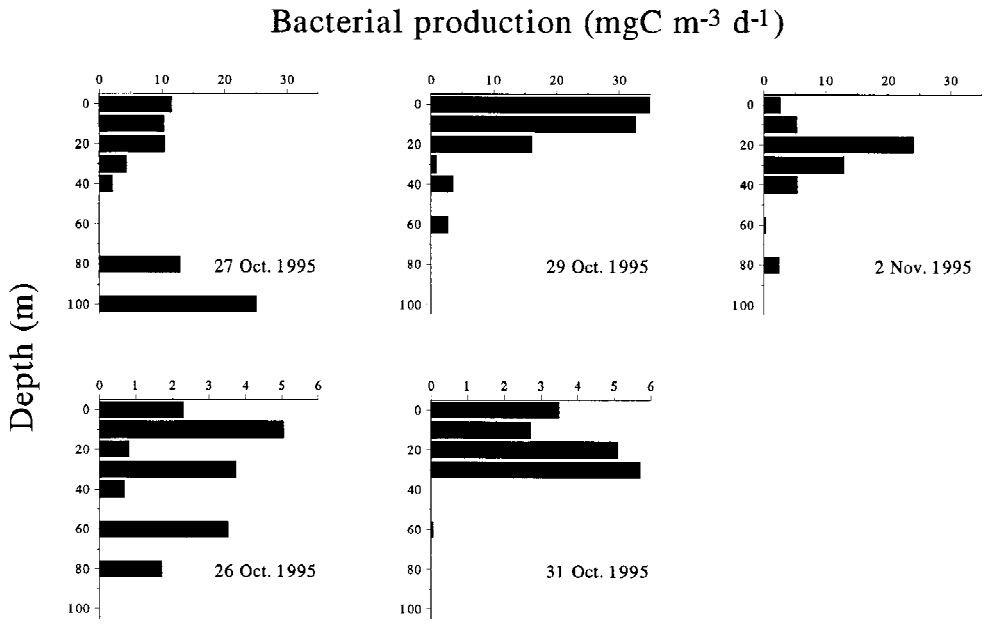

Figure 7. Vertical profiles of bacterial production (mg C m^{-3} d^{-1}; calculated from leucine incorporation) (note different scales) in different parts of Lake Tanganyika in October–November 1995.

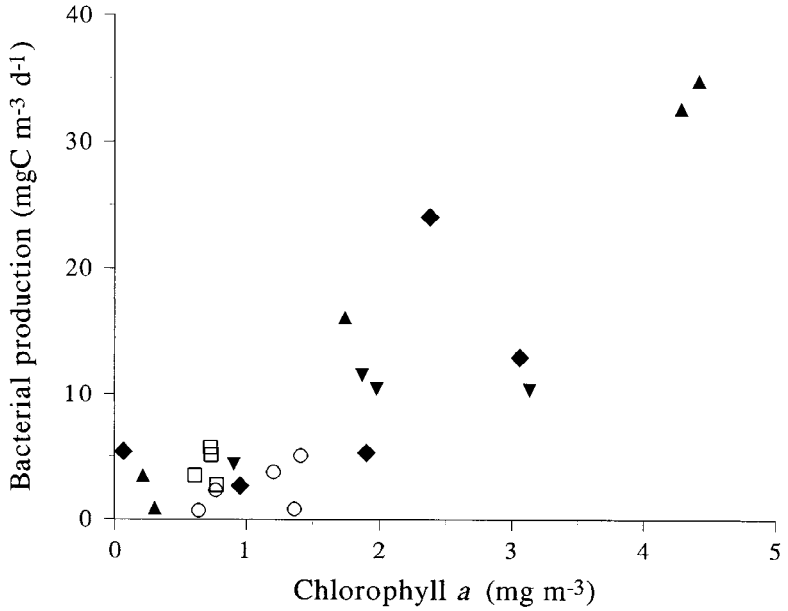

Figure 8. Bacterial production in relation to phytoplankton chlorophyll (calculated from fluorescence) during the cruise in October–November 1995. Different sample series shown with different symbols.

the bacterial production rates were similar to those measured in April–May of the same year, but at three sites much higher values were obtained (Figure 7). Highest values usually occurred in the upper water layers, although at one site the maximum values were recorded below the thermocline; the small number of measurements from the hypolimnion does not allow any firm conclusions as to the potential importance of hypolimnetic bacteria. Bacterial production correlated positively with the chlorophyll *a* concentrations of the same samples ($r^2 = 0.76$, $n = 23$; Figure 8). Consistent with the results from the first cruise, bacterioplankton production was on an average 21% of phytoplankton production estimated from chlorophyll *a* and the average assimilation number.

Table 2. Total body carbon to length regressions [ln$W$ (μg carbon) = ln$a$ + b ln$L$(μm)] for the pelagic copepods of Lake Tanganyika (sample from southern Burundi waters in early May 1995). In regression (1) total length including furcal rami; in regression (2) length without furcal rami. r^2= adjusted coefficient of determination, n= number of carbon determinations, RMS= residual mean square; N= nauplii, C= copepodids, A= adults

			ln a	b	r^2	n	RMS
Tropodiaptomus simplex	C+A	(1)	-17.366	2.6258	0.939	60	0.0441
	C+A	(2)	-16.593	2.5374	0.939	60	0.0439
	N	(1)	-7.058	0.9583	0.645	9	0.0401
Mesocyclops aequatorialis	C+A	(1)	-19.157	2.9280	0.963	26	0.0220
	C+A	(2)	-18.535	2.8683	0.960	26	0.0237
	N	(1)	-8.884	1.2824	0.594	12	0.0615

Zooplankton production

Significant carbon to length regressions were obtained for the three main species of pelagic copepods in Tanganyika from a sample in southern Burundi waters in early May 1995 (Figure 9; equations in Table 2; average carbon values for each developmental stage in Table 3).

The instantaneous growth rates obtained for reproducing females and naupliar stages did not vary much between copepod species (Table 4). Because estimates for the small cyclopoids were the most uncertain, the growth rates of *Mesocyclops* were used for all cyclopoids.

The zooplankton biomass and production estimates calculated from the vertical migration data and from the weekly sampling series (Table 5) were expected to be somewhat different, because of the different sampling sites, mesh sizes and water column depths sampled. The distance between the sites was largest at the southern end of the lake, where the weekly sampling site was only some 10 km from Mpulungu, while the vertical migration study site was more than

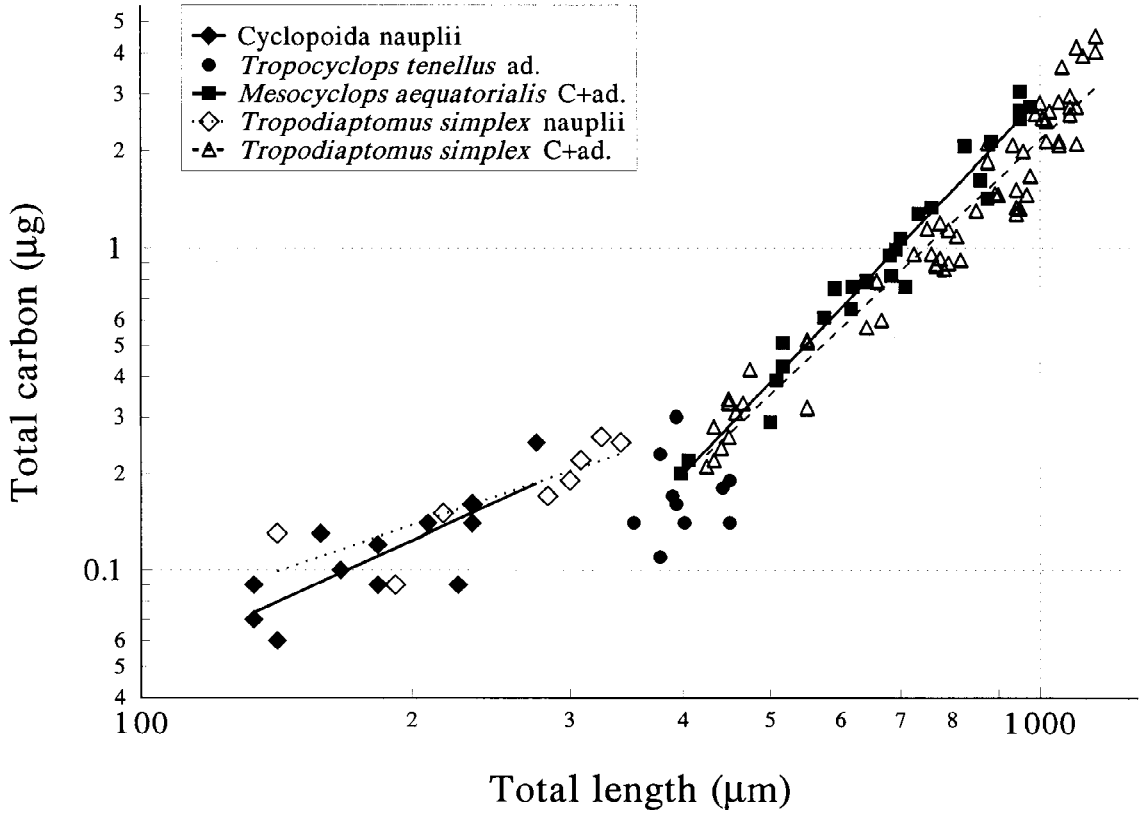

Figure 9. Regressions of individual carbon biomass on total length in the pelagic copepods of Tanganyika, based on a sample from southern Burundi waters in early May 1995.

30 km further north, over deeper water and close to the deep open area of the southernmost basin. Differences between the two Mpulungu data sets thus mainly reflect variation between sites. In contrast, especially off Kigoma both series were expected to represent roughly the same water mass.

Comparative tests with 50-μm and 100-μm net hauls off Bujumbura showed that the 100 μm mesh retained all copepodids and adults and most of the nauplii of *T. simplex*, but that most of the small cyclopoid nauplii passed through. In contrast, the 100-μm net seemed more effective than a 50-μm net in capturing the adult copepods. The Limnos sampler was more effective in catching zooplankton than the vertical 100-μm net hauls: off Kigoma, the average abundances of copepodids and adults obtained from the weekly net hauls were 64% for calanoids, 54% for cyclopoids, of those obtained from the Limnos samples for the 0–100 m water column. For calanoid and cyclopoid nauplii the corresponding percentages were 54% and 3%, respectively.

Off Bujumbura and Kigoma, the volume-specific biomass estimates for *T. simplex* obtained from the vertical migration studies were higher than those from the weekly time series (Table 5). The biomass values for herbivorous copepods were 1.18, 0.88 and 0.36 g C m^{-2} off Bujumbura, Kigoma and Mpulungu, respectively and 0.38, 0.02 and 0.19 g C m^{-2} for predatory copepods. Off Mpulungu, both calanoid and cyclopoid biomass in the weekly series was higher than in the vertical migration series, probably reflecting higher zooplankton abundances in the shallower part of the southern end. For cyclopoids, the large biomass difference between the data sets off Kigoma was caused mainly by the different retention of the cyclopoid nauplii by the 50- and 100-μm meshes. For areal biomass estimates the differences between the data sets became even more pronounced, because notable numbers of zooplankton were found deeper than 100 m.

Production and production-to-biomass estimates obtained from the weekly sampling series were like-

Table 3. Total length and individual carbon biomass (mean ± SD) of the developmental stages of the pelagic copepods in Lake Tanganyika (sample from southern Burundi waters in early May 1995) and total lengths for a sample from Kigoma 6 December 1994. N6 = nauplius 6, C1 = copepodid 1 etc

		Burundi			Kigoma	
	Stage	Total length (μm) B	Total carbon (μg) B	*n* B	Total length (μm) K	*n* K
Tropodiaptomus simplex	egg	150	0.30±0.07	5	109±5	7
	nauplii	260±68	0.18±0.06	9	297±13 (N6)	4
	C1	448±14	0.29±0.06	10	411±16	5
	C2	550±0	0.45±0.11	3	524±8	3
	C3	660±14	0.65±0.12	3	..	-
	C4	776±24	0.99±0.12	12	765	1
	C5 female	946±11	1.50±0.30	6	..	-
	C5 male	905±64	1.49±0.19	3	879±133	2
	ad. female	1061±56	2.95±0.76	20	1085±50	12
	ad. male	943±84	2.01±0.38	5	931±12	3
Mesocyclops aequatorialis	nauplii	190±46	0.12±0.05	12	248±3 (N6)	4
	C1	402±6	0.21±0.01	2	396±7	3
	C2	500±0	0.29±0	1	489±35	6
	C3	514±5	0.44±0.06	3	573±18	5
	C4	600±21	0.69±0.07	4	626±59	2
	C5	695±42	1.01±0.26	4	737±54	6
	ad. female	908±57	2.28±0.50	8	939±48	7
	ad. male	704±20	1.00±0.21	4	704±32	3
Tropocyclops tenellus	ad. female	418±29	0.18±0.06	7	386±10	7
	ad. male	369±14	0.16±0.06	3	336±6	6
	nauplii	..	..	-	156±5(N6)	2

wise biased, because the numbers of nauplii were underestimated. In weekly sampling data for Bujumbura, Kigoma and Mpulungu, the contribution of nauplii to the total calanoid production was 19, 31 and 12%, and to the cyclopoid production 19, 21 and 17%, respectively, while the corresponding figures for the vertical migration data were 65, 27 and 14% (calanoids), and 55, 75 and 43% (cyclopoids).

For both calanoids and cyclopoids, total areal biomass and production estimates were always highest off Bujumbura, while the order of Kigoma and Mpulungu varied between the data sets (Table 5). This variation precludes further comparisons.

T. simplex, cyclopoid nauplii, and copepodids of small cyclopoids were regarded as herbivores, while the copepodids and adults of large cyclopoids were considered carnivores. Thus defined, the production of herbivorous copepods off Bujumbura, Kigoma and Mpulungu was 35.3, 27.3 and 6.5, and the production of predatory cyclopoids was 4.1, 0.3 and 2.1 g C m^{-2} a^{-1}, respectively. The resulting averages for the whole lake were 23.0 and 2.2 g C m^{-2} a^{-1} for the herbivorous and predatory copepods, respectively (Table 8). From these figures, annual P/B ratios for the herbivorous and predatory copepods were estimated to be 28.5 and 11.1 a^{-1}, respectively.

A collection of *Limnocnida* specimens of 2–18 mm in diameter yielded an organic dry mass-diameter regression

$$\log_e(\text{mass [mg AFDM]}) = -5.64 + 2.31 * \log_e(\text{diameter [mm]})$$

(r^2 = 0.95, n = 29). From this regression the average individual mass of *Limnocnida* off Kigoma in April 1998 was 0.061 mg AFDM (n = 629), or 0.03

Table 4. Instantaneous biomass growth rates of the main categories of Lake Tanganyika crustacean zooplankton used in calculating zooplankton production. E = eggs (mean weight and development time refer to an average egg batch, initial and final weights and growth rate to females with developing ovaries); n = nauplii; C = copepodids. For the derivation of different values, see text

	Mean weight (μg C)	Initial weight (μg C)	Final weight (μg C)	Development time (d)	Growth rate (d^{-1})
Tropodiaptomus simplex					
E	1.20	2.10	3.30	1.92	0.235
N	0.15	0.100	0.25	5.5	0.167
C	0.72	0.25	2.10	10.25	0.208
Mesocyclops aequatorialis aequatorialis					
E	0.96	1.36	2.32	2.5	0.214
N	0.098	0.063	0.19	7.0	0.157
C	0.49	0.19	1.36	13.6	0.145
Tropocyclops tenellus					
N	0.050	0.032	0.104	..	..
C	0.132	0.104	0.159	..	..

mg C. Routine zooplankton counting did not include any size classification of the medusae and therefore this average value was used to give a rough indication of the potential role of *Limnocnida* in the pelagic system. Biomass-carapace length regression for the shrimp *Limnocaridina parvula* was

$$\log_e(\text{mass [mg AFDM]}) = -28.205 + 3.828 * \log_e(\text{carapace length [}\mu\text{m]})$$

($r^2 = 0.87$, $n = 49$). The average mass of an individual shrimp derived from the length measurement data of five cruises (105 samples) was 0.059 mg AFDM, or 0.03 mg C.

According to the weekly samples the abundance of shrimps increased from north to south (Kurki et al., 1999b; mean abundances in 1993–1995 off Bujumbura, Kigoma and Mpulungu were 2.8, 6.0 and 11.9 individuals m^{-3} in the 0–100 m water column, respectively), while the abundance of medusae was higher in the north (Kurki et al., 1999b; mean abundances in 1993–1995 off Bujumbura, Kigoma and Mpulungu 79, 25 and 25 individuals m^{-3}, respectively). From these figures approximate average standing biomass estimates off Bujumbura, Kigoma and Mpulungu were 237, 75 and 75 mg C m^{-2}, respectively, for *Limnocnida* and 8, 18 and 36 mg C m^{-2} , respectively, for the shrimps. These values suggest a whole-lake mean biomass of 129 mg C m^{-2} for *Limnocnida* and 21 mg C m^{-2} for the shrimps. Especially the latter value may be an underestimate, because of possible net avoidance and because a considerable part of the shrimp population may also have been deeper than 100 m at the time of routine sampling. Indeed, data from five lake-wide cruises (Bosma et al., 1998), collected with oblique hauls of a Gulf V sampler better suited for catching shrimps, resulted in a biomass estimate of 88 mg C m^{-2}. In the cruise material no consistent regional trends in the abundance of medusae or shrimps were observed along the north-south axis of the lake.

Fish

Growth rates derived from the length frequency analyses (LFA) did not vary much between localities and both clupeid species had similar growth rates (Figures 10–12). Extrapolation of the LFA growth curves to small fish (length < 40–50 mm) normally not present in the catches is arguable, and to reduce the potential bias, the von Bertalanffy growth curves were here forced to go through zero length at zero age. At least for *Limnothrissa* off Bujumbura the LFA results were reasonably consistent with those from the counting of daily otolith increments (Figure 10), but here the lift net catches included high numbers of small fish down to the length of 25 mm. Also off Mpulungu, where even smaller *Limnothrissa* (down to 15 mm length), caught with the beach seines, were incluced in the LFA estimates, the latter were probably reliable even for the

Table 5. Average biomass and annual production of crustacean zooplankton in Lake Tanganyika at the permanent sampling localities in the sampling years 1993–1994 and 1994–1995. Buj = Bujumbura, Kig = Kigoma, Mpu = Mpulungu. Vertical migration study: Limnos tube samples, 50 μm mesh, 0–140 m (Bujumbura and Kigoma) or 0–220 m (Mpulungu); Weekly sampling: vertical net hauls, 100 μm mesh, 0–100 m. P/B_a = annual production to biomass ratio

Vertical migration study 1993–1995

	Biomass (mg C m^{-3})				Biomass (mg C m^{-2})			
	Buj	Kig	Mpu	Whole lake	Buj	Kig	Mpu	Whole lake
Calanoida	5.01	2.86	1.36	3.08	702	400	298	467
Cyclopoida	6.20	3.51	1.15	3.62	868	492	253	537
Copepoda total	11.21	6.37	2.51	6.70	1570	892	552	1004
	Production (g C m^{-2} a^{-1})				P/B_a			
	Buj	Kig	Mpu	Whole lake	Buj	Kig	Mpu	Whole lake
Calanoida	22.6	9.8	4.3	12.2	32.2	24.5	14.4	26.1
Cyclopoida	16.9	17.8	4.3	13.0	19.4	36.1	16.8	24.2
Copepoda total	39.4	27.6	8.6	25.2				

Weekly sampling 1993–1994

	Biomass (mg C m^{-3})				Biomass (mg C m^{-2})			
	Buj	Kig	Mpu	Whole lake	Buj	Kig	Mpu	Whole lake
Calanoida	4.98	2.06	4.44	3.83	498	206	444	383
Cyclopoida	4.02	1.36	2.63	2.67	402	136	263	267
Copepoda total	8.99	3.42	7.07	6.50	899	342	707	650
	Production (g C m^{-2} a^{-1})				P/B_a			
	Buj	Kig	Mpu	Whole lake	Buj	Kig	Mpu	Whole lake
Calanoida	7.1	4.8	5.0	5.6	14.4	23.5	11.4	14.6
Cyclopoida	3.1	2.2	2.9	2.7	7.7	16.1	11.0	10.1
Copepoda total	10.2	7.0	7.9	8.3				

Table 6. Regression of fresh mass on length (mass (g) = a • (total length (mm))^b) for the main pelagic fish species in Lake Tanganyika (from Aro & Mannini, 1995)

	a	b	r^2	n
Stolothrissa tanganicae	4.049×10^{-6}	3.11	0.97	824
Limnothrissa miodon	3.979×10^{-6}	3.13	0.99	1755
Lates stappersi	6.798×10^{-6}	2.99	0.99	452

Table 7. Annual production to biomass ratios (P/B) (data from Mannini et al., 1996) and mortalities (Z; from Mannini et al., 1996) of the main pelagic fish species in different parts of Lake Tanganyika (July 1993 – Dec. 1995; Uvi= Uvira, Buj= Bujumbura, Kar= Karonda, Kig= Kigoma, Kal= Kalemie, Mob= Moba, Kip= Kipili, Mpu= Mpulungu, Surveys= lake-wide trawling cruises 1–5 between June 1995 and February 1998). For details of calculation, see text

		Uvi	Buj	Kar	Kig	Kal	Mob	Kip	Mpu	Surveys
Stolothrissa	P/B	3.00	3.91	3.40	2.41	2.57	3.01	1.94	2.59	3.56
	Z		4.39	6.10	4.79	5.16	5.05	..	..	4.33	4.56
Limnothrissa	P/B	2.28	4.05	2.18	1.30	2.48	..	3.31	4.09	3.36
	Z	..	5.08	..	..	..	..	6.91	4.21	3.13
Lates stappersi	P/B	4.18	4.38	1.33	1.15	..	..	0.92	1.04	1.57
	Z	..	..	..	1.35	..	..	2.33	2.11	1.89

small size groups. For *Stolothrissa*, the length classes < 30 mm were poorly represented in catch samples, making the LFA growth estimates more uncertain. The mass-length regressions of all three species had exponents close to 3.0 (Table 6; Mannini et al., 1996).

Because the growth rates declined steeply with increasing fish size, the production to biomass ratios were dependent on the size-frequency distributions of fish, affected by variable fishing and natural mortalities in each area and by ontogenetic migrations of fish. Very high P/B ratios were obtained for *Lates* off Uvira and Bujumbura, because practically only ju-

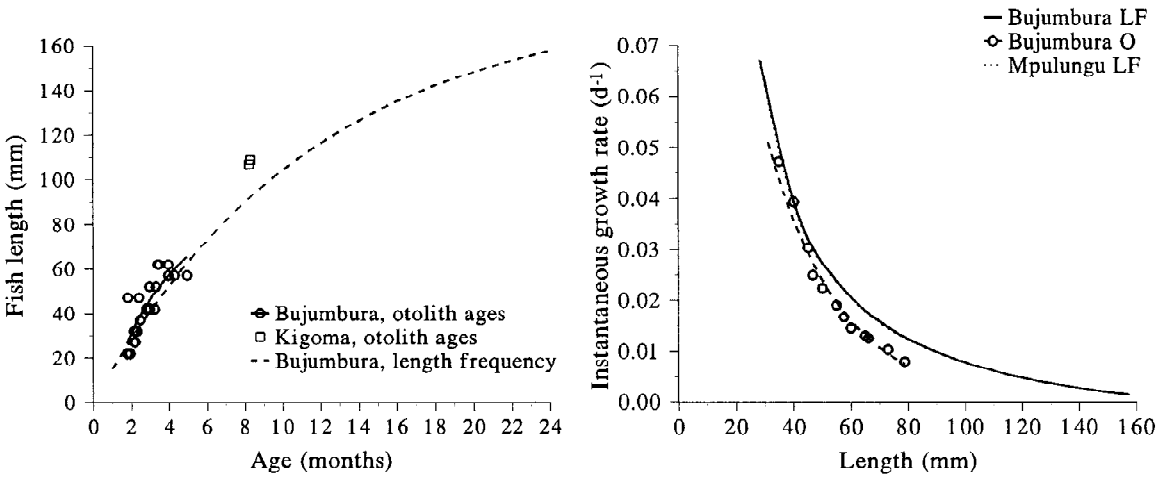

Figure 10. (a) Length growth of *Limnothrissa miodon* off Bujumbura as estimated from the length frequency analyses (Mannini et al., 1996) and from daily otolith increments (Pakkasmaa & Sarvala, 1995). Two otolith-based length-at-age values for larger fish from Kigoma are shown for comparison. (b) Instantaneous length growth rates of *Limnothrissa miodon* off Bujumbura and Mpulungu as estimated from the length frequency analyses (LF; Mannini et al., 1996) and on the basis of daily otolith increments (O; Pakkasmaa & Sarvala, 1995).

Table 8. Annual biomass and production at different trophic levels in Lake Tanganyika. For derivation of values, see text

	Biomass g C m^{-2}	Production g C m^{-2} a^{-1}	%
Phytoplankton	2.4	426–662	100
Bacterioplankton	..	..	20
Herbivorous copepods	0.81	23.0	3.5–5.4
Predatory copepods	0.20	2.2	0.3–0.5
Shrimps	0.09	1.3	0.2–0.3
Limnocnida	0.13	?	?
Fish (clupeids)	0.40	1.4–1.7	0.21–0.40
Fish (*Lates* etc.)	0.18	0.3	0.04–0.08
Fish yield (total)	..	0.5–0.6	0.08–0.14

veniles were caught in these areas. Anomalously low P/B ratios were always linked to a lack of small fish from catch samples (e.g. *Limnothrissa* off Kigoma; Table 7). In *Limnothrissa*, large adult fish occur almost exclusively offshore in the central areas of the lake and are thus underrepresented in the catch samples, while in *Stolothrissa*, the juveniles (length < 30–40 mm) remain offshore and adults tend to move inshore (Mannini et al., 1996; Mannini, 1998). Therefore, the P/B ratios obtained from the size distributions of catch samples were biassed, being too low for *Stolothrissa* and too high for *Limnothrissa* (provided that small fish were well represented as off Bujumbura and Mpulungu). Trawl catches during the lake-wide cruises yielded more representative size distributions, but even they did not include the smallest fish (Mannini et al., 1996). Moreover, owing to the limited number of cruises, these size distributions may still have been influenced by the seasonal cohort succession. In spite of these reservations, P/B ratios based on the combined data from all experimental trawl hauls (Table 7) were considered the most reliable and were chosen for production calculations (Table 8).

In fish populations exhibiting exponential biomass growth, the instantaneous mortality rate equals P/B ratio (Allen, 1971). For all species, the mortality coefficients calculated from the LFA analysis of the commercial catch samples were always higher than the corresponding annual P/B rates (Table 7), but the difference was smaller in the trawl data, especially for *Limnothrissa*. Mortality rates derived from the experimental trawl data (Table 7) were used as P/B ratios to calculate a second estimate of fish production (Table 8).

Hydroacoustic fish biomass estimates for the whole lake were 91 193, 175 681 and 304 463 tonnes in June 1995, November–December 1997 and Febru-

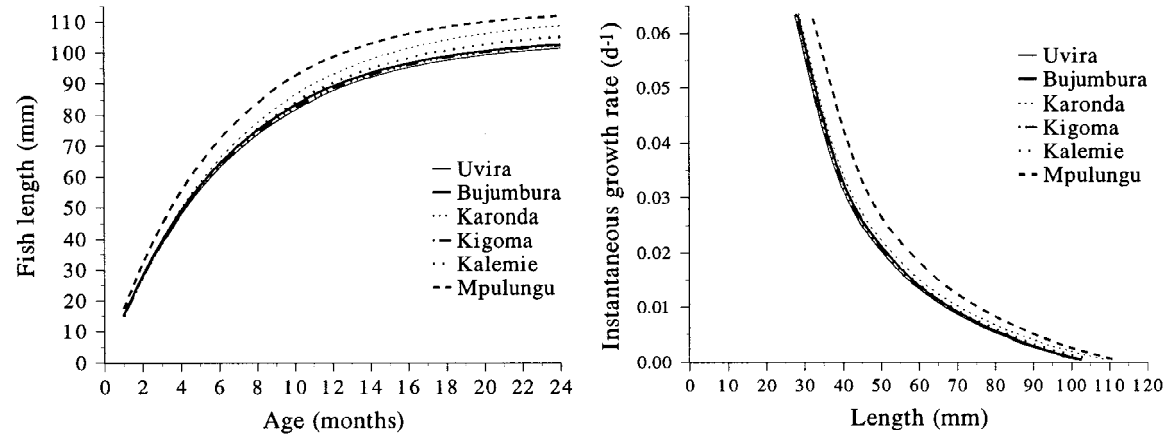

Figure 11. Length growth (left) and instantaneous growth rate relative to length (right) of *Stolothrissa tanganicae* at the main sampling stations. Based on the length frequency analyses by Mannini et al. (1996).

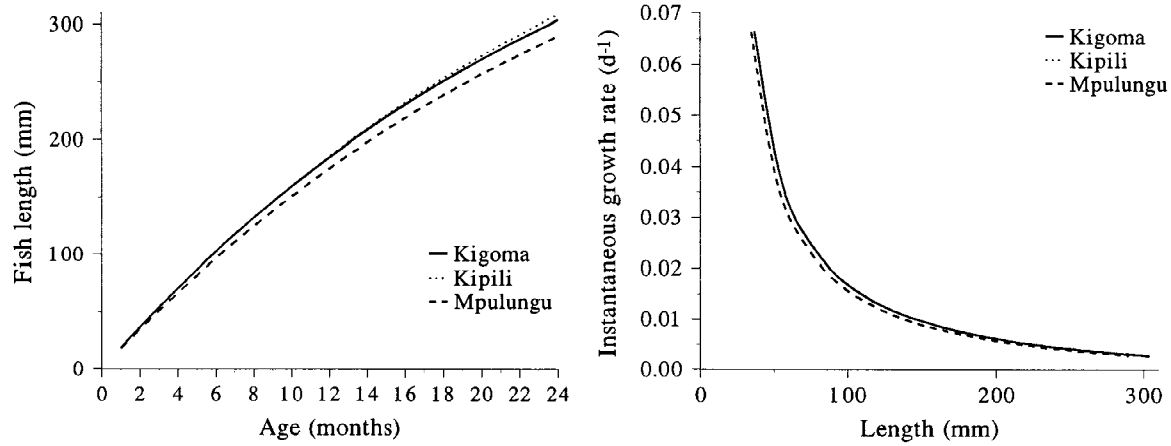

Figure 12. Length growth (left) and instantaneous growth rate relative to length (right) of *Lates stappersi* at three sampling stations. Based on the length frequency analyses by Mannini et al. (1996).

ary 1998, respectively (Szczucka 1998). The observed wide range may reflect seasonal differences, because the catches per haul in experimental trawling were consistent between cruises performed in the same season, i.e. between June 1995 and April 1996, and between November–December 1995 and November–December 1997, respectively (data from Mannini, 1998). The ratio between the acoustic biomass estimate and the mean catch-per-unit-effort in experimental trawling was very similar on all cruises. The overall mean for the hydroacoustic estimates was 190 446 tonnes lake^{-1} (58 kg ha^{-1}) or 0.58 g C m^{-2}. According to the five lake-wide trawling surveys (142 hauls, 4592 kg), the contributions of *Stolothrissa tanganicae*, *Limnothrissa miodon*, *Lates stappersi*, other *Lates* spp. and all other species were 56.7, 12.0, 10.7, 12.7 and 7.9% of total fish biomass, respectively (Mannini, 1998). Using these proportions and the derived P/B ratios, the production of the pelagic clupeids (*Stolothrissa* and *Limnothrissa*) was 1.4–1.7 g C m^{-2} a^{-1} and that of the *Lates* and other mostly piscivorous species 0.3 (0.29–0.34) g C m^{-2} a^{-1}.

DOC determinations and total community respiration

The mean concentration of DOC varied between 2.2 and 2.9 mg C l^{-1}, and was highest close to the surface (Järvinen et al., 1996). The ampoule technique of DOC determination reduced the background 'noise' to low levels (0.2 mg C l^{-1}). Oxygen consumption by

the whole plankton community at 0 and 30 m depth off Kigoma in April 1994 was estimated as 4.3–6.7 mg O_2 m^{-3} h^{-1}. Assuming an RQ of 0.85 (Wetzel, 1983), this corresponds to 1.4–2.1 mg C m^{-3} h^{-1}, or 33–51 mg C m^{-3} d^{-1}. In a 0–50 m water column, representing the fully oxygenated epilimnion, the community respiration would thus be 1.6–2.5 g C m^{-2} d^{-1}. This daily carbon consumption rate is less than 2% of the DOC storage, but it is almost in balance with the phytoplankton primary production estimated for the season, suggesting efficient carbon cycling and steady state conditions within the epilimnion.

Trophic structure and carbon flows in the food web

Our results enable a reassessment of the trophic structure of Lake Tanganyika (Table 8). Trophic level biomass declined steadily from the phytoplankton primary producers through invertebrate consumers to planktivorous fish and piscivorous fish. The medusae seem to be an important component of the system, although their trophic role is enigmatic and they can, at least occasionally, harbour photosynthesizing picoalgae (unpubl. observations). The shrimps seem to be mainly herbivorous (the dominant species *Limnocaridina parvula* feeds on phytoplankton, the larger *Macrobrachium moorei* (Calman) on zooplankton; M. Viherluoto, unpubl.). The production figures indicated fairly low carbon transfer efficiencies between trophic groupings (Table 8), especially from phytoplankton to herbivorous copepods (3.5–5.4%). The ratio of planktivorous fish production to herbivorous copepod production was 6.1–7.4% and the corresponding ratio between the piscivorous and planktivorous fish was 20.0–20.3%. Assuming a production to consumption ratio of 0.25 for invertebrates and 0.10 for fish (Humphreys, 1979), the food requirements of predatory copepods were 8.8 g C m^{-2} a^{-1} and those of planktivorous and piscivorous fish 14–17 and 2.9–3.4 g C m^{-2} a^{-1}, respectively. Thus, deducting the food consumption by predatory copepods from the herbivorous copepod production and adding the production of predatory copepods and shrimps, the food production available for planktivorous fish was 17.7 g C m^{-2} a^{-1}, well matching the calculated food demand of fish. In contrast, the food consumption estimate for *Lates* and other potentially piscivorous fish was higher than prey fish production. However, these fish are not entirely piscivorous: e.g. in *Lates stappersi*, shrimps and copepods comprise >50% of its diet (Mannini, 1998). The total fisheries yield in Lake Tanganyika was in the mid-1990s only 0.08–0.14% of pelagic primary production, i.e., within the range of typical values in lakes. In the whole lake, clupeids accounted for about 65% and the *Lates* species for ca. 30% of total catch (Hanek, 1994), clupeids (mainly *Stolothrissa*) being more dominant in the north and *Lates stappersi* in the south (Coenen et al., 1998).

Discussion

Sources of organic matter: primary production and DOC

Our primary production estimates were 47–128% higher than the values given for Lake Tanganyika by Hecky & Fee (1981). Although the present values still contain uncertainties, they are based on the largest data base so far available from Tanganyika, including satisfactory seasonal coverage at three stations plus three lake-wide surveys. That the *in situ* measurements gave somewhat lower values than the simulated *in situ* procedure may have a methodological origin. The *in situ* incubations at constant depths are likely to result in an exaggerated surface inhibition of photosynthesis by UV radiation. Incubator measurements used in the simulated *in situ* method exclude direct UV effects, but the observed vertical chlorophyll distributions incorporate the natural inhibition effect on freely circulating algal cells. The true level of primary production in Lake Tanganyika may thus be closer to the simulated *in situ* results, i.e. the upper bound of our range of estimates.

Dissolved inorganic carbon determinations were not the reason for different production estimates: the DIC concentration calculated by Hecky & Fee (1981) was 6.4 mm (77 mg C l^{-1}), or very close to our determinations (Hecky & Bugenyi 1992 reported 5.88 mm or 70.6 mg C l^{-1}). However, the primary production estimates of Hecky & Fee (1981) were based on a shallower water column and included only the particulate production, while our results comprised both particulate and dissolved production. Irrespective of whether the so-called dissolved production derives from true algal exudates or is partly a methodological artefact (discussed by e.g. Baines & Pace, 1991), ignoring it may lead to a major underestimation of the total primary production.

Our results for the concentration of DOC were within the ranges given for Tanganyika by Hecky (1991, based on Hecky et al., 1978; around 2–5 mg

l^{-1} or 150–400 μm l^{-1}) and Degens et al. (1971). Our new measurements thus confirmed the relatively low DOC levels in Tanganyika. The much higher and unusually variable DOC values (13.5–43.5 mg C l^{-1} in the epilimnion) reported by Degens and Ittekkot (1983) seem unreliable. Considering the general water quality in the lake, low DOC levels sound realistic, and do not suggest a major role for DOM in the planktonic food web. This conclusion is supported by our preliminary oxygen consumption values that were lower than those given by Hecky et al. (1981: 9.4–13 mg O_2 m^{-3} h^{-1}) and did not require any large additional inputs of organic matter besides phytoplankton production.

Zooplankton biomass and production

The present estimates for zooplankton biomass and production were only half of those earlier given for Lake Tanganyika by Burgis (1984: biomass 2 g C m^{-2}, production 50 g C m^{-2} a^{-1}), but very similar to those reported from Lake Malawi (Irvine & Waya, 1999) and Lake Awasa (Mengestou & Fernando, 1991). Also, our average figures for the whole Lake Tanganyika were not far from the estimates presented by Kurki et al. (1999a: biomass 2.3 g dry mass m^{-2}, production 28 g C m^{-2} a^{-1}), based on the same original abundance data, but derived from literature-based individual biomass and production-to-biomass ratios. Our biomass calculations, in contrast, were based on own carbon determinations and production was calculated by developmental stage using literature-derived but locally checked development times. The resulting P/B ratios (24–26 a^{-1}) did not differ much from those obtained for copepods in Malawi by Irvine & Waya (1999) (31 a^{-1}), or from those used by Burgis (1984) and Kurki et al. (1999a: 23–29 a^{-1}).

The present abundance data had a good temporal coverage with short-interval samples of crustacean zooplankton for two successive years, but regional coverage was low with only three sampling areas. However, data from four lake-wide cruises in June 1995 – April 1996, comprising 7–27 stations, showed no consistent regional differences in zooplankton abundance (Kurki, 1998); the average values were still lower than our figures. Starting from the second sampling year, within-site variation was reduced by taking three replicate vertical hauls on each sampling occasion. The variability between the successive samples from each locality was also reasonably small (Kurki et al., 1999a). However, abundance estimates from the weekly sampling suffer from at least two sources of bias. First, as shown by the vertical migration study (Vuorinen et al., 1999), some of the crustaceans were found below the routine 0–100 m net hauls in the morning when these samples were taken. Second, considerable numbers of cyclopoid nauplii and small copepodids could escape through the 100-μm mesh of the vertical hauls. Both biases could be largely circumvented in the production calculations by utilizing data from the vertical migration study, which used tube sampler and a 50-μm mesh net and in which sampling was extended as deep as copepods were found. Although nauplii may contribute relatively little to the copepod biomass, as found e.g. in Lake Malawi (Irvine & Waya, 1995; Irvine, 1995), their growth is a major part of the total production.

Our values of individual carbon contents for the pelagic copepods were in reasonable correspondence with dry mass values published previously for copepods in African lakes. There was one earlier determination from Lake Tanganyika: Burgis (in Chene 1975) obtained for adult *T. simplex* from Burundi waters a dry mass of 5.7±0.5 μg, and for *M. aequatorialis* a value of 3.3±0.4 μg per individual, corresponding roughly to 2.8 and 1.6 μg carbon, respectively. Regressions for *Thermocyclops* sp. adults from Masundire (1994) gave estimates of 0.15 and 0.11 μg carbon for female and male *T. tenellus*, respectively, which are very close to our values. On the other hand, Masundire's regression for *Tropodiaptomus* sp. adults underestimated the biomass of Lake Tanganyika *T. simplex* (predicted individual carbon values were 1.64 and 1.19 μg for females and males, respectively). Likewise, the equation for Lake Malawi *T. cunningtoni* (Irvine & Waya, 1995, 1999) underestimated the size of the Tanganyikan *Tropodiaptomus* (predicted carbon for females 1.82 μg C). In *M. aequatorialis*, biomass estimates derived from the regressions for this species in Lake Malawi (Irvine & Waya, 1995, 1999) were clearly lower than our observations; this may have been because the exponent in this equation seems unrealistically low. Individual biomass values derived from the general copepod mass-length-regressions (Bottrell et al., 1976) were not far from our observed values. These comparisons show, however, that even estimates derived from the mass-length regressions of closely related or the same species from a different lake may be tens of percents in error compared to the real values. Thus, it is always advisable to obtain at least a few own dry mass or carbon determinations to check the correct levels.

Possible regional or temporal differences in the individual biomasses within the lake could cause additional error in our estimates. However, at least the linear dimensions of different developmental stages of copepods obtained from a sample off Kigoma in December 1994 tallied well with those from the Burundi sample (Table 3). The carbon values obtained for the Burundi sample were therefore used for the whole Tanganyika as the most representative values available.

The individual biomass values used in our calculations differed somewhat from those adopted by Kurki et al. (1999a). For calanoids the difference was minor, but for cyclopoids the values of Kurki et al. (1999a) probably lead to slight overestimates of the biomass, or, if the proportion of the small species among the cyclopoids is large, to great overestimates. Our carbon content values are the most accurate biomass measures available for Lake Tanganyika zooplankton. However, our final biomass estimates remain rough, because the routine counting procedure did not distinguish between different copepodid or naupliar stages, and the large and small cyclopoid species were not differentiated during the first sampling year.

All uncertainties notwithstanding, the close correspondence between the biomass and production figures obtained here and by Kurki et al. (1999a) is encouraging, because it shows that calculations using literature-complemented parameters may result in realistic zooplankton production figures. This was not unexpected, because the major errors in zooplankton production studies derive from the precision of field abundance data. Possible errors owing to stage-specific or length-specific individual biomass differences or to variation in temperature-specific stage durations are generally small compared to the sampling variation of abundance. Therefore, in zooplankton production studies, it is advisable to invest most of the labour in obtaining reliable field estimates of abundance, because accurate abundance estimates will reduce most of the total error variance. Counting should also be done to the finest possible taxonomic and ontogenetic resolution, or size distributions directly measured to enable reliable biomass conversions.

Fish production and yield

The average production-to-biomass ratios of fish derived from our length-frequency analyses (Table 7) were roughly similar to the annual values calculated by Coulter (1981) for *Stolothrissa* in the northernmost part of the lake (3.9 from the graphical Allen curve method and 3.7 from mortality rate, assuming von Bertalanffy type growth). Thus, the intensified fishery seems not to have caused any changes in fish growth. However, growth and mortality estimations using LFA are always somewhat suspect, although our results were in good correspondence with earlier analyses and for *Limnothrissa* were supported by otolith readings (Kimura, 1995; Pakkasmaa & Sarvala, 1995; H. Ahonen, unpubl.). However, for *Stolothrissa*, the otolith studies by Kimura (1995) in southern Tanganyika and by H. Ahonen in central Tanganyika (unpubl.) both indicated faster growth than our LFA analysis. Further work utilizing daily otolith increments is clearly needed to confirm the observed growth patterns of fish.

As anticipated from the growth and longevity characteristics, *Stolothrissa* had the highest and *Lates stappersi* the lowest P/B ratio. However, the difference between *Stolothrissa* and *Limnothrissa* was smaller than expected: while both clupeids had roughly similar growth rates, *Stolothrissa* has a lower maximum size and shorter longevity and should thus have a clearly higher P/B ratio. Indeed, the total mortality deduced from the cruise data was higher and this value may be closer to the true P/B ratio for *Stolothrissa*. In *Limnothrissa* and *Lates stappersi* the P/B ratios and mortality values were satisfactorily consistent, suggesting that they were reliable.

Our fish biomass estimates were lower than previously published values for Lake Tanganyika which show wide variation. Biomass estimates obtained from FAO hydroacoustic surveys in 1973–1976 (Chapman et al., 1978; Coulter, 1991) varied from 211 to 1237 kg ha^{-1}, of which the largest value seems unrealistically high. Roest (1977), using catch samples and acoustic estimates in Burundi waters, ended up at an estimate of 160 kg ha^{-1} for *Stolothrissa* alone. Extrapolating from catch statistics in heavily exploited areas in the north and south, Coulter (1977) estimated the virgin pelagic fish biomass in the north end of Tanganyika at 32–45 kg ha^{-1}, which is only one fourth of the value of Roest (1977). Fish biomass values calculated with the ECOPATH model from a trophic analysis of the pelagic system in the Burundi sector (Moreau et al., 1993) were 63–181 kg ha^{-1} for the planktivorous fish and 37–102 kg ha^{-1} for the piscivorous fish in the early 1980s and the mid-1970s, respectively. Converted to carbon units, the corresponding production estimates were 3.2–7.9 and 0.3–0.7 g C m^{-2} a^{-1}, or higher than our estimates. The P/B ratios applied by

Moreau et al. (1993), based on Moreau et al. (1991), and the fish yield figures used as the starting point for the ECOPATH model were also somewhat higher than ours. Interestingly, according to recent acoustic estimates (Menz et al., 1995), the average pelagic fish biomass in Lake Malawi was 70 kg ha^{-1}, i.e. close to the value adopted here for Tanganyika.

Our fish production estimates can be compared to the realized catch. It is admittedly difficult to obtain reliable catch statistics from a large lake like Tanganyika, where artisanal fisheries take the majority of the catch. However, the recorded total catches from Tanganyika show a clearly increasing trend. Coulter (1977) reported an annual fish yield of 73 000 tonnes in the late 1960s and Roest (1992) estimated 85 000 tonnes for 1987. According to the most recent and probably the most accurate lake-wide statistics produced during the LTR project, the total catch was 167 000 metric tonnes (or 51 kg ha^{-1}) in 1992 (Hanek, 1994; Coenen, 1995), and 196 570 tonnes (60 kg ha^{-1}) in 1995 (Coenen et al., 1998). In 1992, the catch amounted in Burundi waters to 94.5 kg ha^{-1} yr^{-1}, in Zambia to 69, in Tanzania to 60 and in Zaire to 34 kg ha^{-1} yr^{-1} (Hanek, 1994); for 1995 the corresponding figures were 111.5, 53, 40 and 62 kg ha^{-1} yr^{-1}, respectively (Coenen et al., 1998; the Zambian figure came from the year 1994).

Although the present catch figures are the highest so far reported from Lake Tanganyika, they still remain clearly lower than the potential yield levels of 380 000–460 000 tonnes (116–140 kg ha^{-1}) per year postulated in previous papers (e.g. Coulter, 1977). However, the final potential yield estimate of Coulter (1977), 100 kg ha^{-1} yr^{-1}, is close to the present realized yield in Burundi, where the fishing pressure is highest. There, the catches per unit area have in fact decreased since 1967–1971 (Coulter, 1977). During the 1990s, Coenen et al. (1998) recorded declining trends in the catch per unit effort in the industrial fishery in all areas studied and in the lift net fishery in Tanzania. On the other hand, increasing unit catches were noted for apollo units in Burundi where this type of fishery was gradually replacing the industrial fishery. These trends suggest that sustainable catch levels are lower than previously thought. This is also supported by calculations based on the observed zooplankton production, which is lower than previous estimates. Moreover, because the primary production in Tanganyika is mainly dependent on internal nutrient cycling and mixing regimes, productivity in the large central open area may be lower than along the coasts (Ostrovsky et al., 1996). In 1995, the realized catch of the planktivorous fish was in the whole lake 23–28%, and in the most heavily fished Burundi waters 43–52% of the estimated production; for piscivorous fish in the whole lake the catch was 61–73% of the calculated production. These figures suggest that the present fishing pressure in Lake Tanganyika is very high; normally only 20-25% of fish production can be taken as fisheries yield (Houde & Rutherford, 1993).

Carbon flows and the trophic structure

A new view of the trophic structure of Lake Tanganyika is emerging from our data. Our phytoplankton production and carbon biomass figures are higher than the earlier estimates (primary production: Hecky & Fee, 1981; the annual mean phytoplankton biomass reported by Hecky & Kling (1987), extrapolated to a 0–40 m water column, would give ca. 50% lower value than reported here). In contrast, our new zooplankton data indicate lower biomass and production than previously estimated. Thus, contrary to earlier claims (Burgis, 1984; Hecky, 1984, 1991), our data show that, compared to lakes in general (e.g. Pauly & Christensen, 1995), the trophic efficiency between zooplankton and phytoplankton in Lake Tanganyika is low. Likewise, the fish yield seems to be relatively low in comparison with the primary production, as in many other large lakes (Oglesby, 1977; Morgan et al., 1980). According to our estimates, also the fish production in Lake Tanganyika relative to primary production falls within the normal range reported from other lakes (Morgan et al., 1980; Downing et al., 1990). The suggested role of bacterioplankton compares well with the literature (Cole et al., 1988; White et al., 1991).

High carbon transfer efficiency from phytoplankton to zooplankton (17%), suggested by Burgis (1984) for Tanganyika, was strongly dependent on a large correction factor for the filtration efficiency of the coarse plankton nets used, and her zooplankton production estimate may well be inflated. On the other hand, Hecky et al. (1981) obtained an unusually high transfer efficiency from phytoplankton production to fish yield (0.45%). However, the fish yield figure they used (125 kg ha^{-1} a^{-1} or 1.3 g C m^{-2} a^{-1}; Coulter, 1977) represented only the small intensively fished areas in the northern and southern ends of the lake. Both transfer efficiencies were also dependent on the primary production estimate of Hecky & Fee (1981: 290 g C m^{-2} a^{-1}), which may have been an underestimate, as discussed above. For the 1970s, the

ECOPATH analysis of the pelagic system in the Burundi waters (Moreau et al., 1993) likewise suggested very high transfer efficiencies from phytoplankton to zooplankton (25%), to planktivorous fish (2.4%) and to fish yield (0.36%). For the 1980s, the calculated efficiencies were clearly lower (13, 1.1 and 0.2%, respectively), but still higher than our results, especially for the herbivorous zooplankton and fish yield.

It is tempting to speculate that the differences observed between the published values and our new biomass and production estimates for the different trophic groupings might represent real changes in the pelagic ecosystem over the years, owing to e.g. intensified fishing or climatic changes. However, none of the earlier estimates are accurate enough to allow definite conclusions about long-term changes, although at least the phytoplankton chlorophyll concentrations seem to have remained largely similar from the 1970s to the 1990s. We hope that the present monitoring program can be continued for several years to produce a long-term temporal series which are so rare in the tropics.

In fact, low production efficiency of the crustacean zooplankton is not unexpected in a deep, clearwater tropical lake with high epilimnion temperatures. Low efficiency would result from high respiration costs owing to the high temperatures, and/or from the costs of the long vertical migration enforced by the high predation pressure by fish in the clear pelagic waters. Low efficiency of zooplankton production was likewise found in Lake Malawi (Irvine & Waya, 1999), which resembles Tanganyika in many respects. However, similarly low transfer efficiencies have been reported from Lake Michigan (Sprules et al., 1991), which suggests that low efficiency may be a general feature of all deep, oligotrophic lakes. Low phytoplankton densities increase feeding costs and decrease growth rates, tending to diminish the role of cladocerans that are the most productive zooplankton crustaceans. The microbial loop may also have a prominent role in the pelagic food web of oligotrophic systems (Weisse & Stockner, 1993; but see Riemann & Christoffersen, 1993 for opposite view). This leads to inflated respiration costs to the extent that such systems act as net sources of carbon dioxide to the atmosphere (del Giorgio et al., 1996). High dependence of primary production on nutrient regeneration, as in Lake Tanganyika (Hecky, 1991), implicitly suggests low efficiency of carbon transfer through the food web, because nutrients are mainly regenerated by the microzooplankton, which have high respiration rates. Thus, in Lake Tanganyika, the temporally and regionally variable nutrient inputs from the huge hypolimnetic store, through long-range transport via atmosphere and from the land runoff are not only crucial to the absolute levels of production, but, by modulating the role of the microbial loop, they may also affect the efficiency of carbon transfer through the system.

The estimated carbon transfer efficiency from crustacean zooplankton to planktivorous fish was lower than the values reported from Lake Malawi between herbivorous zooplankton and their predators (invertebrates and fish larvae; Allison et al., 1995). Moreover, the efficiency at this step in Tanganyika may be partly affected by the fact that part of the fish production is based on deep-water shrimps which may not have been caught quantitatively with the present sampling scheme. The extremely simple food web structure in the open waters of Tanganyika might enhance fish production: the food chain leading to planktivorous fish production is short. The fishery itself has simplified the food web by decimating piscivorous fish stocks at an early stage of the commercial fishery (Coulter, 1970). On the other hand, a low production efficiency can be expected in a high-temperature environment (Edwards, 1984). In Tanganyika, the upper, almost anoxic layers of hypolimnion may provide zooplankton with a partial refuge from fish predation. This combined with the energetic costs of extensive vertical migrations, necessary in order to avoid piscivorous fish, may lead to a relatively low energetic efficiency of planktivorous fish production. It should be noted that, in spite of the high temperatures, the growth rate of the pelagic clupeids in Tanganyika is in fact low compared with the growth of the specialist planktivorous fish in some cool-temperate northern lakes (e.g. vendace (*Coregonus albula*) in Lake Pyhäjärvi, SW Finland; Sarvala et al., 1994).

We thus conclude that the trophic efficiencies in the pelagic food web of Lake Tanganyika are not unusually high. The crustacean zooplankton production is small, but the recorded fish yields quite normal relative to the measured primary production of pelagic phytoplankton. Thus, as in Lake Pyhäjärvi in southwest Finland (Sarvala et al., 1998), the flourishing fisheries in Lake Tanganyika are not so much based on any exceptional productivity of the system, but on the fact that most of the pelagic production is channelled into a few fish species that have short life cycles and rapid reproduction. Those fish are furthermore easy to catch and thus suitable for an economic fishery.

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