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RESULTS OF THE LTR'S 20th MULTI-DISCIPLINARY CRUISE

by

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(eds.)

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PREFACE

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

LTR's objective is 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, Democratic Republic of Congo, Tanzania, and Zambia).

Particular attention is 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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INTRODUCTION

The last survey of the LTR Project was conducted from March 10 through April 17, 1998, finishing just one week before the end of the three year long charter agreement and return of the *R/V Tanganyika Explorer* to her owners. The survey and related sampling and laboratory work was aiming not only at multidisciplinary issues in limnology, fish biology and fishery but was undertaken by an exceptionally large group of Finnish scientists and students, 21 people in all. Fourteen students took part in this study tour funded partly by their home universities, the Finnish Ministry of Foreign Affairs and partly by the LTR project. The implementation of the exercise was possible only with the assistance of the project personnel, particularly Mr. D. Chitamwebwa and his colleagues in Kigoma, and onboard the *Explorer*. To run such an extensive group of people and a great set of various research topics required also logistic support from the Lake Tanganyika Biodiversity Project (LTBP) which is greatly appreciated.

The objectives of fourteen short-term mini surveys were planned first to provide new insights on the production and nutrient metabolism of phytoplankton and picocyanobacteria communities and on the role and function of medusae and shrimps in the pelagic food chain. Novel investigations were made on endosymbiotic algae of medusae and their phosphorus turn-over in the laboratory experiments on the *Explorer*. The studies of shrimp feeding were made to complement the earlier findings of their importance in the lake's trophic structure. The advanced limnological studies took now the benefit of the intensive measurements of currents and vertical mixing made simultaneously with ADCP, workhorses and STD device during the cruises.

Second group of the themes dealt with the feeding biology of clupeid larvae, a target that was paid less attention to during the project, and fish growth as analysed from otolith readings. And thirdly, fish freshness and quality in the consumers' preference and biochemical composition point of view were measured in fish self caught with the trawl net and sampled on fish markets. In this connection the analytical methods were adjusted to fit into the tropical environment, often in insufficient laboratory conditions. Finally, to cover the entire chain from hydrophysical events through to the fishermen's society, an interview study on fishermen's earnings and attitudes was conducted in Kigoma region.

The field work that took up to six weeks gave the participants an excellent opportunity to develop their skills in the field and laboratory. One week main cruise headed towards the south from Kigoma and it was completed with shorter trips and diel sampling in the middle part of the lake. The study plans were followed in such details as possible but several improvisations and modifications became necessary due to various unforeseen surprises in the

working conditions, irregular electricity supply and lack of equipment that were stuck in Dar es Salaam or even before that on the way to Tanzania. The intensive study period was most educational for all whom this was the first trip to Africa and developing countries in general. Though a bit rough, the implementation of every topic became to successful solution although hardly anybody believed this was going to be possible, especially during an El Niño reinforced rainy season.

It is difficult to describe all the feelings and experiences the team had while working through day-and-night on board, sleeping under the clear sky on the deck, joining the fishermen on their fishing trips, etc. The Nile perch were too clever to hit our lures, but we were lucky in catching nice batches of sardines for the samples and food. To work with the fishermen or salesmen on the markets was an unforgettable experience. Young people created several friendships in town and saw interesting views and animals in surrounding villages.

We as the supervisors of the study tour, LTR 20th Survey, are more than happy in supplying this summary of the study reports. The results complete our picture of the lake ecology and post-harvest sector of the fishery. Also they indicate there are ever growing possibilities to find new areas of further studies on Lake Tanganyika, and worth of stressing, the group of new researchers have now laid ground for their future collaboration with the counterpart colleagues at the Lake.

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DIEL VERTICAL MIGRATION OF PLANKTONIC SHRIMPS, JELLYFISH AND COPEPODS IN LAKE TANGANYIKA

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INTRODUCTION

The pelagic crustacean zooplankton community in Lake Tanganyika is extremely simple. Three copepod species *Tropodiaptomus simplex, Mesocyclops aequatorialis* and *Tropocyclops tenellus* dominate the pelagic zooplankton community in numbers and biomass (Coulter 1991; Dumont 1994). Endemic decapod species (*Limnocardinia*) and the freshwater jellyfish *Limnocnida tanganyicae* are also an important part of the pelagic zooplankton. Van Meel (1954) found zooplankton throughout the oxygenated water column down to 200 m in Lake Tanganyika, but most of them seemed to concentrate above 40 m especially at nights. Coulter (1991) used echo-sounding technique to study the dusk upward migration of pelagic fish in Lake Tanganyika. He also noticed a rising diffuse trace below the typical fish school traces which may represent a rising layer of zooplankton. These early observations of diel vertical migration (DVM) were verified by Vuorinen et al. (1999).

It is generally agreed that the ultimate reasons of DVM at zooplankton are linked to food and avoidance of predation (Zaret & Suffern 1976). Around this core light intensity provides a triggering and timing mechanism for DVM (Haney 1988, Hutchinson 1967). In the most common type of DVM zooplankton escapes visual predators (fish) into deep water with dim light and returns to the food rich epilimnion to feed only for night.

Detailed knowledge about the vertical distribution and DVM of pelagic zooplankton would contribute to the understanding of trophic interactions between pelagic zooplankton and fish. In this study the existing results of the DVM of copepods in Lake Tanganyika were completed by introducing new information on jellyfish and shrimps of which the latter is very important in the diet of fish.

METHODS

Zooplankton samples were collected between 31.3.–15.4.1998 from the northern part of Lake Tanganyika near Kigoma. Zooplankton samples were taken from the surface to 100 m with closing plankton nets as 10 m high hauls at midnight and at midday. Two conical closing nets with different mesh sizes were used simultaneously. A 500 µm (0.8 m mouth diameter) net was used to collect jellyfish and shrimps and a 50 µm (0.25 m mouth diameter) net was used to collect mesozooplankton. It took about one hour to complete each set of vertical samples. The samples were preserved in 4 % (final concentration) formaldehyde. Later the dense

zooplankton samples were divided with Huntsman Marine Laboratory Beaker method (HMLB) (Van Guelpen et al. 1982). Zooplankton species in the subsamples were determined and counted using a grooved disc under a preparation microscope (Hakala 1971). The movements of the jellyfish were also observed visually by a scuba-diver.

RESULTS

During the whole sampling period the vertical temperature profile remained quite constant (Fig 1) and there were also no marked diel differences between day and night. The depth of epilimnion was ca. 30 m. Within the thermocline oxygen concentration declined towards deeper water from ca. 6 mg l^{-1} in the epilimnion to only 1 mg l^{-1} at 100 m (Fig 1).

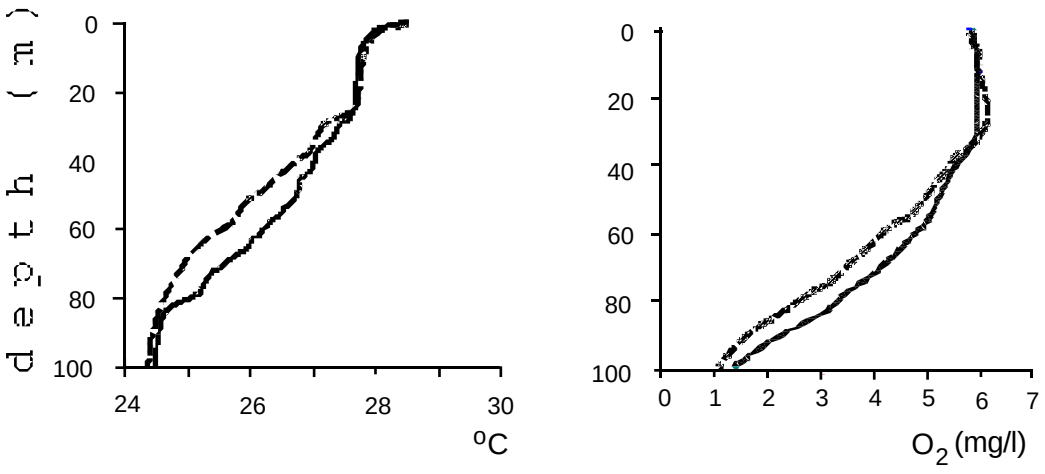

Fig. 1. Vertical distributions of temperature and oxygen on 14. April 98 at 4 pm (solid line) and on 1.4.98 at 12 am (broken line) in Lake Tanganyika off Kigoma.

Seven invertebrate species were identified and counted in the samples. *Limnocnida tanganyicae*, *Limnocardinia parvula*, *Tropocyclops tenellus* and *Tropodiaptomus simplex* were the most abundant species (Table 1). A cyclopoid *Mesocyclops aequatorialis* was rather scarce. During the nights the freshwater jellyfish *Limnocnida tanganyicae* occurred in swarms near the surface. Most jellyfish were only 1–2 mm in diameter. At all depths larger individuals (diameter up to 6 mm) were rare. The shrimps *Limnocardinia spinipes* and *Pallasea morei* were so infrequent that the results of the three decapod species were pooled. The naupliar stages of *Tropodiaptomus simplex* and *Tropocyclops tenellus* were quite common above 50 m. The eggs and juveniles of fish (Nile perch *Lates* sp. and clupeids *Stolothrissa tanganyicae* and *Limnothrissa miodon*) occurred only occasionally in the samples.

Table 1. Mean (n = 4) abundances of different zooplankton taxa.

	ind. m^{-2}
Tropodiaptomus simplex	1269
Tropocyclops tenellus	285
Mesocyclops aequatorialis	788
Limnocnida tanganyicae	1500
T. simplex nauplii	67
Cyclopoida nauplii	228
shrimps	889

The DVM behaviour of pelagic invertebrates in Lake Tanganyika varied from remarkable migration of some species throughout the whole epilimnion to nonexisting or so small that it could not be detected with the applied sampling resolution. At midnight the shrimps were found near the surface and during the night they descended deeper reaching ca. 80 m at noon (Fig. 2). Thus the diel amplitude of their DVM was ca. 60 m. The DVM of *Tropodiaptomus simplex* was very similar to that of the shrimps. However, their amplitude of DVM was somewhat smaller (ca. 50 m). *Mesocyclops aequatorialis* migrated like *T. simplex* but the amplitude of its DVM was only ca. 20 m. Most of the population of the jellyfish *Limnocnida tanganyicae* was situated in the water column > 50 m both at day and night with ca. 10 m amplitude of DVM (Fig. 2). Although the amplitude was low and hence somewhat uncertain, the descent of jellyfish from the upper 10-20 m water column for daytime was consistently verified by scuba diving. *Tropocyclops tenellus* copepods and *Tropodiaptomus simplex* nauplii did not seem to migrate within the vertical resolution used in this study. The eggs and larvae of *Lates* sp. and the clupeids were so infrequent in the samples that no DVM patterns could be recognised.

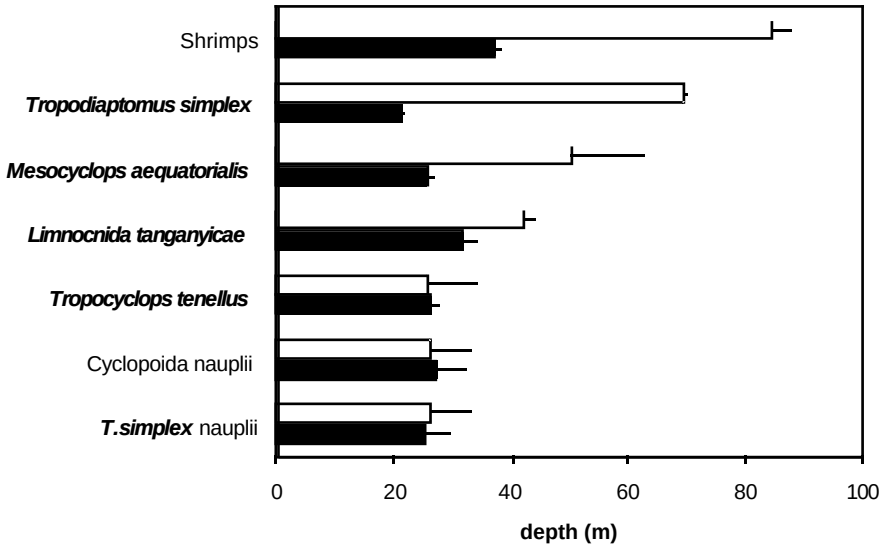

Fig.2. The mean depths (range shown by narrow bars) of different zooplankton populations in Lake Tanganyika at noon (black bars) and at midnight (white bars) in two series of samples taken 1. and 14. April 1998.

DISCUSSION

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The observed high diel amplitude of DVM of *Tropodiaptomus simplex* is in agreement with the results found by Vuorinen et al. (1999) who studied the DVM of copepods in Lake Tanganyika monthly during both the dry and wet seasons. Similar to our results they demonstrated less extensive DVM of cyclopoids although they did not differentiate between different species of which *Tropocyclops tenellus* did not seem to migrate during the present study and although the vertical resolution of their sampling approach was 20 m vs. 10 m in the present study. Possibly the results of the present study represent conditions where the amplitude of migration was lowest. However, a general agreement between these short-term results with the long term ones of Vuorinen et al. (1999) can be anticipated, because the seasonal differences in Lake Tanganyika are small.

Vuorinen et al.(1999) found that egg-carrying female copepods exhibited the most pronounced DVM and in this study the amplitude of the DVM of invertebrates in Lake Tanganyika also seemed to correlate positively with animal size. These findings fit with the present conception that the risk being seen and eaten by predators is one of the ultimate reasons of DVM. In an East African reservoir Cahora Bassa Gliwicz (1986) found that predation by the visually hunting *Limnothrissa miodon* seemed to be the most important factor responsible for mortality in all crustacean populations. Similarly in Lake Tanganyika the small clupeids *Limnothrissa miodon* and *Stolothrissa tanganyicae* are abundant (Coulter 1991) and responsible for most of the consumption of pelagic invertebrates. Lake Tanganyika is nearly 10 times more transparent than Cahora Bassa (Heckey & Fee 1981, Gliwicz 1986) and thus the depth of the minimum light intensity that allows clupeids to see their prey is expected to be much higher and to lead into more pronounced DVM.

All vertically migrating copepod species and shrimps in Lake Tanganyika are eaten by the clupeids (Marlier 1957, Chèné 1975) and their populations have been shown to be under a top-down control (Coulter 1991). Thus the high amplitude of DVM of shrimps and the copepods *Tropodiaptomus simplex* and *Mesocyclops aequatorialis* can be explained as an adaptation to a strong predation pressure from clupeids. The latter also migrate vertically either to cope with zooplankton DVM or/and to escape predation by Nile perch (*Lates* spp.) (Poll 1953, Coulter 1961, Begg 1976). Although shrimps are the preferred food of the clupeids, they seldomly occur in densities which could be the primary food source for clupeids (Coulter 1991). Adult copepods are always more abundant than shrimps and comprise an important proportion in the diet of adult clupeid fish. Within the sampling resolution nonmigrating *Tropocyclops tenellus* and copepod nauplii occupied more or less to the same depth zone as phytoplankton both at day and night. Due to their small

size nauplii are not preferred food source for the adult clupeids, but they may be eaten by juvenile fish (Chèné 1975). The low predation pressure may partly explain the lack of distinct DVM on *T. tenellus* and nauplii. Small zooplankton also have a low capacity to migrate long distances and hence the amplitude of their DVM is likely smaller than that of the larger zooplankton (Hutchinson 1967). The results of Vuorinen et al. (1999) suggest that at least in the neighbourhood of the surface nauplii probably have some DVM. Further, if *T. tenellus* and copepod nauplii are significantly consumed by predators, they may also migrate vertically. To prove the DVM of nauplii sampling with higher depth resolution is required. The apparent lack of DVM of *Limnocnida tanganyicae* might be explained by the fact that it has no predators. However, the visible migration of few large jellyfish near the surface was masked in the results by the abundance of small animals and by too coarse vertical sampling resolution.

The solar ultraviolet radiation has been found damaging to zooplankton (Williamson & Zagarese 1994) and thus as suggested by Vuorinen et al. (1999) during daytime the harmful UV-radiation could explain the low numbers of zooplankton in the first 10 m in Lake Tanganyika. The bottle samples of Vuorinen et al. (1999) representing the very surface conditions better than our 0-10 m water column net hauls showed very clearly that at noon, surface water of Lake Tanganyika was often almost devoid of animals. Direct measurements of light penetration of Lake Tanganyika have shown that UV-B-radiation can penetrate several meters into the lake (Salonen et al. (1999). Finally, the experimental results of Tarvainen (1999) verified that the intensity of UV-B-radiation in the uppermost water layers is lethal to jellyfish and can hence alone explain the disappearance of this species from the uppermost water layers for daytime. Thus there is convincing evidence that UV-radiation forms an upper limit to the daytime occurrence of zooplankton.

At the lower end of DVM of invertebrates in Lake Tanganyika the oxycline forms a barrier to migrating invertebrates. Low oxygen concentration may also allow zooplankton to escape clupeid predation as the fish do not seem to enter depths where oxygen concentration is less than 2 mg l^{-1} (Coulter 1991). In Lake Tanganyika shrimps and *Tropodiaptomus simplex* may utilise migration to weakly oxygenated water to avoid predation. The hypothesis that vertical migration to deeper water layers provide metabolic advantage to zooplankton has been rejected in temperate lakes, but in tropical lakes it is not realistic at all, because the difference in water temperature between epi- and hypolimnion remains very small.

With the possible exception of jellyfish and larger shrimps, phytoplankton is the main food of migrating invertebrates in Lake Tanganyika. Phytoplankton is rather uniformly distributed in the epilimnion (Hecky et al. 1978, Nuottajärvi 1999; Salonen et al. 1999), but sometimes clear metalimnetic maximum at 30-50 m is also found (Nuottajärvi

1999; Salonen et al. 1999). Because the depth of 1 % surface light intensity during the wet season was ca. 40 m (Salonen et al. 1999), the feeding range of the clupeids is very deep and their predation efficiency on zooplankton can be high. Thus to optimise between adequate feeding and tolerable mortality, particularly larger invertebrates are obliged to follow distinct DVM. Predation is one of the most important factors of natural selection in plankton communities being responsible for the adaptations in size, transparency, morphology, cyclomorphosis, motility and migration behaviour of animal (Post & McQueen 1987). Only zooplankton capable to adopt an effective overall predation avoidance mechanism can survive in the pelagial of clear water Lake Tanganyika. The capability of planktonic invertebrate species to adopt enough efficient adaptations for adequate feeding and avoidance of predation under the conditions of Lake Tanganyika probably has formulated the species assemblage of its invertebrate plankton. Copepods as rather fast swimmers have been able to fit their behaviour within these constraints. Instead, the absence of cladocerans may be explained by their lower motility compared to copepods. Altogether, the low diversity of pelagic crustacean zooplankton in Lake Tanganyika is probably a symptom of extreme conditions. If the conditions are really so difficult, they must also be costly which should inevitably be also reflected in the production efficiency of Lake Tanganyika zooplankton.

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TURNOVER OF PHOSPHORUS IN THE PELAGIAL OF LAKE TANGANYIKA

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INTRODUCTION

In temperate lakes phosphorus has been identified as a factor that most often limits the growth and production of phytoplankton (Schindler 1977; Kalff & Knoechel 1978). Most of phosphorus occurs as particulate organic phosphorus (POP) in organisms and detritus. Orthophosphate (PO_4) is believed to be the most available form of phosphorus to phytoplankton (Wetzel 1983; Goldman & Horne 1978; Nalewajko & Lean 1980). However, in many studies it has been documented that ambient phosphate uptake in the aquatic environments is dominated by very small organisms (Berman 1985; Friebele et al. 1978; Lehman & Sandgren 1982; Schindler et al. 1979; Lean & White 1983; Rai & Jacobsen 1990). Currie & Kalff (1984) indicated that in phosphorus limited environment bacterioplankton is responsible for virtually all the uptake of orthophosphate. Instead, when the concentration of PO_4 increases, a higher proportion is taken up into larger size fractions (Schindler et al. 1979; Lean & White 1983; Lean 1984).

In the meromictic Lake Tanganyika most of the nutrients reside in the anoxic monimolimnion and they are distributed to mixolimnion and trophogenic zone by diffusion and vertical mixing processes. Vertical mixing is most intense during the dry season (May-August) when strong southern trade winds cause upwelling at the southern end of the lake. During the wet season (September-April) the thermal stratification is strongest and the thermocline at the level nearer to the surface effectively restricts nutrients to diffuse to upper layers (Coulter 1991). According to Hecky et al. (1991) ca. 90% of phosphate input comes through vertical mixing from anoxic water layers. Because of the intense denitrification and other heterotrophic microbial processes in the metalimnion, the oxic-anoxic boundary is a sink for all forms of fixed nitrogen. This causes low (generally less than 8:1) atomic N:P-ratio in dissolved inorganic nutrients in the metalimnion (Rudd 1980). Thus wind-driven upwelling, while a source of phosphate, provides little accompanying fixed nitrogen. Edmond et al. (1993) conclude that production is nitrogen limited and must depend, to a substantial degree, upon fixation in the lake itself and upon inputs from rainfall and runoff. Shortage of nitrogen probably limits the production particularly during the dry season. During the wet season rainfall and runoff bring along nitrogen and rainfall may be rich in nitrogen because of thunderstorms in the atmosphere.

In this study I determined turnover times of phosphorus in the plankton of Lake Tanganyika at the end of the wet season. I also concentrated on the interesting question of

the partition phosphate uptake between different micro-organisms.

MATERIAL AND METHODS

The uptake of dissolved orthophosphate in water was studied using radioactive $^{33}PO_4$ for the determination of its turnover time. Phosphorus uptake experiments were carried out off Kigoma in the northern part of Lake Tanganyika in the spring 1998. Sampling was done on board R/V Tanganyika Explorer, where all the experiments were also accomplished. Samples were taken from different depths using a black Limnos-sampler. Water was drained to 500 ml bottles covered with black cloth bags to protect them from sunlight. In the laboratory 10 ml subsamples were taken from each bottle to 20 ml glass vials. Then 5 ml of $^{33}PO_4$ solution was introduced and vials were placed in an incubator with a lake water through-flow to keep temperature same as in the lake. One control bottle with 0.5 ml of 40% formaldehyde was included in each series before the addition of $^{33}PO_4$. After 8, 16 and 32 min 1 ml subsample from each glass vial was filtered through 0.2 :m pore size polycarbonate filter. To determine the proportions of incorporated $^{33}PO_4$ in different size fractions, 1 ml of water from each vial was also filtered through 0.2, 0.6 and 2.0 :m filters.

The filters were put into plastic scintillation vials and amended with 2 ml water and 3 ml scintillation liquid (Wallac Hi Safe 3). Radioactivities were determined with a portable liquid scintillation counter (Hidex Triathler). Two 1 ml subsamples were also taken from each vial to plastic scintillation vials to determine the total amount of added $^{33}PO_4$ -radioactivity. These samples were treated as described above except that only 1 ml of water was added together with 3 ml of scintillation liquid. Uptake rate constants for phosphate were calculated from plots of ln % $^{33}PO_4$ in the 0.2 :m filtrate against time. Only the results with the degree of explanation of the regression higher than 0.95 were taken into account. Turnover times were calculated as reciprocals of the rate constants.

From the same 0-60 m samples as taken for phosphate uptake experiments 100 ml subsamples were taken six times for the determination of soluble reactive phosphorus (SRP) which is an estimate of PO_4-phosphorus. SRP samples were filtered and frozen at -20^{o}C until determination with an AKEA autoanalyser according to Murphy and Riley (1962).

Some experiments with nutrient additions were also made to find out whether they would influence turnover times of phosphorus. The experiments were performed as described above with few exceptions. Three parallel 10 ml subsamples were taken from one depth, usually 20 m, and before additions nitrogen (N-NO_3) was added to one sample and nitrogen and iron to the other. The final concentration of nitrogen was 200 mg m^{-3} in both samples. No additions were introduced to the third sample.

RESULTS

During the study period the stratification of temperature in Lake Tanganyika was rather shallow (Fig. 1).. Below ca. 20 m the surface temperature of ca. 28 ^{o}C declined steadily to 24.8 ^{o}C at 70 m. Thus most of the illuminated zone was within the thermocline.

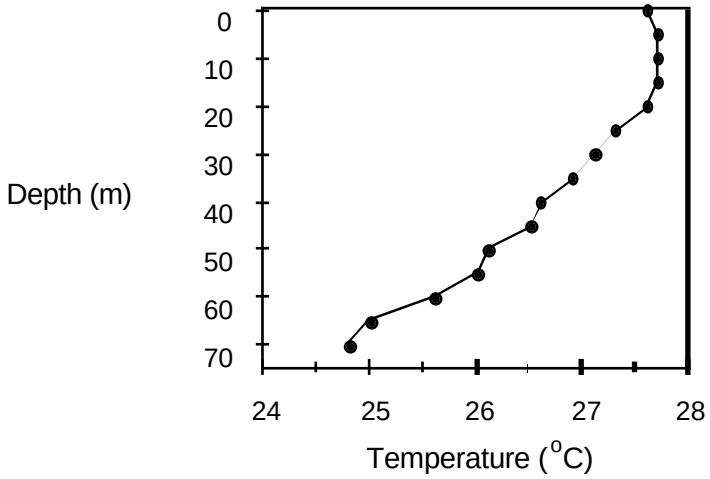

Fig. 1
Temperature at different depths off Kigoma (S 4 ^{o} 52.50 ‘, E 29 ^{o} 34.15 ‘) 28.3.1998
at 6:12 am .

The concentration of phosphate phosphorus was determined six times (26.3., 28.3., 9.4., 12.4., 13.4. and 14.4.). Its concentration was always below the limit of detection (<5 mg P m^{-3}) except at 60 m, where the concentration was ca. 8 mg m^{-3}. Although the number of phosphorus turnover time determinations was small, it seems that they were shortest, generally < 30 min, between the depths of 10-20 m (Table 1). Neither the addition of nitrogen nor nitrogen and iron caused any marked changes in the turnover times of phosphorus at any depth (Table 2).

Table 1. Turnover times of phosphorus at different depths and times of day off Kigoma in March - April 1998.

Depth	Time of day							
	7:00	9:30	14:30	14:45	15:00	17:26	21:40	2:00
0m	22					56	79	14
10 m	20	35		11		19	7	11
20 m	24	16	33			19	8	10
			28					
30 m	93	34		33	45	21		

Table 2.Turnover times of phosphorus at different depths with and without nutrient additions off Kigoma in the spring 1998. NO_3 - nitrogen added, NO_3+Fe - nitrogen and iron added.

Depth	Amendment	Time of day		
		15:30	18:00	19:00
0 m	None	44		
	NO_3	64		
	NO_3+Fe	53		
10 m	None	15		
	NO_3	12		
	NO_3+Fe	12		
20 m	None	14	29	26
	NO_3	12	27	33
	NO_3+Fe	8	26	26

Between the surface and the most productive depths (10-30 m) of Lake Tanganyika, the smallest size fractions (bacteria and picoplankton) were responsible for almost 50 % of the uptake of phosphate (Fig. 2). Phytoplankton larger than 2.0 µm in diameter incorporated only less than 10 % of the added $^{33}PO_4$ except at 30 m where they took ca. 12 %. There were no marked vertical differences in the partitioning of phosphate uptake between different sized organisms.

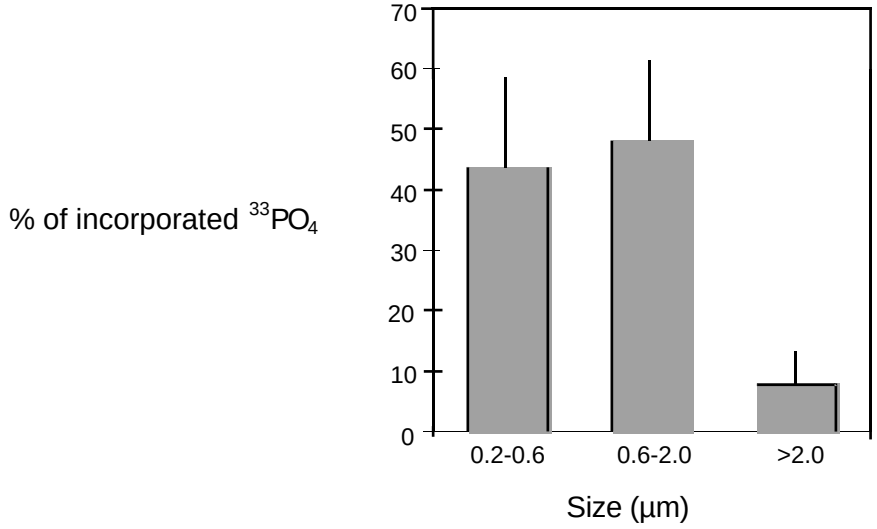

Fig. 2. Incorporation (mean±SE; n=48) of $^{33}PO_4$ in different size fractions of plankton in 0, 10, 20 and 30 m off Kigoma in March - April 1998.

DISCUSSION

Similar to many other oligotrophic lakes (Berman 1985; Friebele et al. 1978; Lehman & Sandgren 1982; Schindler et al. 1979; Lean & White 1983; Rai & Jacobsen 1990; Currie & Kalff 1984) in Lake Tanganyika, the smallest bacterial sized organisms were responsible for most uptake of phosphate (Fig. 2). The 0.2-2.0 µm size fraction is rich in picocyanobacteria which mostly passed 0.6 µm Nuclepore filter (Nuottajärvi 1999). Thus it was impossible to differentiate

between the phosphate uptakes of bacteria and picocyanobacteria. It may be speculated that due to their small size picocyanobacteria are particularly competitive in nutrient uptake and this may explain their high density in Lake Tanganyika. At the end of the wet season off Kigoma, the role of larger phytoplankton in phosphate uptake was minor although their importance in primary production was high (Nuottajärvi 1999). Thus they must take most of their phosphorus from other sources (dissolved organic phosphorus) than inorganic phosphate or their phosphate replenishment is based on random microscale patches of higher nutrient concentrations.

Short turnover times of phosphorus are generally attributed to the shortage of dissolved phosphate or to an abundant phytoplankton (Rigler 1956, 1968; Lean & Nalewajko 1976; Levine & Schindler 1980). Long turnover times are associated with scarcity of biota or physical conditions inappropriate for growth (Rigler 1964, 1966), phosphorus sufficiency (Lean & Nalewajko 1979) or growth limitation caused by shortage of some other nutrient. The short turnover times and undetectable concentrations of phosphate phosphorus off Kigoma in the spring 1998 probably indicate a shortage of phosphorus. In agreement with this, nutrient addition experiments also indicated no notable changes in the turnover time of phosphorus after the additions of nitrogen or nitrogen and iron.

The observed situation represents the conditions at the end of the wet season, when nutrient input from deeper water is most restricted. Due to heavy rains in the spring 1998 the surface level of Lake Tanganyika was higher than for many years. Nutrient input in huge masses of water flowing from the catchment area have probably had remarkable effect on the nutrient input to the epilimnion of Lake Tanganyika, but unfortunately there is no information of the inorganic nutrient concentrations in the major inflowing rivers. Due to the extreme conditions in early 1998 the nutrient limitation situation may thus have been exceptional.

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EFFECT OF UV-RADIATION ON THE VERTICAL DISTRIBUTION OF JELLYFISH *Limnocnida tanganicae*

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INTRODUCTION

There are only few species of jellyfish (Cnidaria) in inland waters and their ecology has been little studied (Dumont 1994). In Lake Tanganyika the jellyfish, *Limnocnida tanganyicae,* is a significant component of plankton (e.g. Sarvala et al. 1999), but its trophic role is still uncertain. Beadle (1974) observed that it followed the vertical migration of zooplankton which may indicate trophic relationship. Vertical migration is quite common for jellyfish (Pages & Gili 1992). Further, Dumont (1994) has suggested that *L. tanganyicae* consumes pelagic eggs of freshwater clupeids.

In clear water lakes, such as Lake Tanganyika, solar ultraviolet (UV) radiation can markedly affect zooplankton (Williamson & Zagarese 1994). Due to the shorter light path for sunlight in tropical environments the ambient level of solar UV radiation is very high (Madronich 1994) and this is further emphasised by the elevation (ca. 770 m above the sea level) of the lake. UV-radiation is harmful to living organisms and particularly its shortest wavelengths (UV-B, 280-330 nm) are hazardous (Molina & Rowland 1974).

The purpose of this study was to evaluate the effect of UV radiation on the vertical distribution and diel migration of *L. tanganyicae*.

METHODS

The study was performed on board R/V Tanganyika Explorer between 10th of March and 19th of April 1998. The samples were mainly taken off Kigoma. To minimise the damage due to mechanical interference, jellyfish were collected by diving generally at night from ca. 0-2 m water column into small tubes with a 300 µm mesh plankton net at the other end. When animal was caught in the tube, the other end was closed with a stopper and the animal was taken in water to the laboratory and released to experimental bottles.

Vertical samples of jellyfish were taken at midnight and at noon with a 500 µm closing net (mouth diameter 80 cm) as 10 m vertical hauls down to the depth of 100 m. Temperature was measured with a CTD.

The UV-light experiments were done on the roof of R/V Tanganyika Explorer. Generally 13 animals were placed in 2 l quartz bottles which were put in the water bath of an open white plastic polystyrene incubator. Water temperature was kept similar to the lake by pumping water from the lake

through the incubator. One bottle was exposed to direct sunlight, and another one was kept under an UV-protected polyethylene film. Animals in the dark bottle were used as controls. During the experiment (starting at 11:45) spectral sunlight radiation was measured at 15 min intervals with Macam SR 591 spectroradiometer.

The number of alive animals in the light bottles was counted every 10 minutes. In the dark bottle counting was made after the experiment. Animals which showed no pulsating activity were considered dead. For practical reasons animals kept under the UV-screen were counted only once during the course of the experiment. Then the bottle was taken to a black cotton bag and transported to the laboratory to be able to inspect the condition of animals without exposing them to solar UV radiation. The experiment was finished when all animals had died in the bottle kept in the water bath under direct sunlight. After that dead jellyfish in the other bottles were also counted.

RESULTS

In clear water Lake Tanganyika, UV-B radiation penetrated rather deep into water. 1 % of surface UV-B radiation was found at the depth of ca. 5 m. (Fig. 1). Thus the UV-B affected zone covered roughly 15 % of the depth of the epilimnion.

The vertical closing net samples showed that most jellyfish were very small with a mean bell diameter of 1.5 mm. In the whole oxic water column, the size structure of the population seemed homogeneous. The only exception was that at night large jellyfish were concentrated nearer to the surface (Fig. 2). This suggests that at least large individuals migrated vertically. Diel vertical migration was also found in the distributions of the numbers of *L. tanganyicae* (for more details see Juvonen 1999). The most pronounced vertical migration of jellyfish was restricted in the uppermost water layers which are under the influence of UV-radiation.

During the UV-exposure experiment cumulative UV-B radiation (280-330 nm) increased almost linearly with time indicating that light conditions during the experiment were stable (Fig. 3). The UV screen removed effectively radiation < 350 nm, but at the same time it also reduced radiation within visible light wavelengths by ca. 30 % (Fig. 4). UV radiation proved to be hazardous to jellyfish. Under direct sunlight all jellyfish died within 75 min. Under the UV screen only 2 animals died within the same time interval and animals in the dark bottle all animals remained alive to the end of the experiment (Fig. 5).

DISCUSSION

Solar UV-radiation has damaging effects on water invertebrates (Hurtubise & Havel 1998) and it was also shown lethal to the *Limnocnida tanganyicae*. Although the results seem clear they do not yet supply quantitative characterisation of the effects of UV-light on *L. tanganyicae*. Accumulation of damage was likely underestimated, because the cellular death of animals is unlikely instantaneous. Longer term tests at lower UV-radiation level would be necessary for the more precise determination of critical levels and doses of UV-B. In spite of this limitation the results show that within at least 3 m from the surface jellyfish can experience lethal daily dose of UV-B. Consequently *L. tanganyicae* must avoid too high daytime UV-radiation and is forced to migrate downwards for day. Thus UV-radiation is an important factor affecting the vertical distribution of jellyfish and its diel migration in Lake Tanganyika.The diel vertical migration of jellyfish was not striking but still clear in Lake Tanganyika (Juvonen 1999). The increased concentration of large individuals near the surface at night might be due to different behaviour of different size animals or it might reflect higher swimming speed, and thus higher potential migration amplitude, of large animals. The reasons for the ascent of jellyfish at night still remain obscure, but its daytime descent is evidently caused by UV-radiation.

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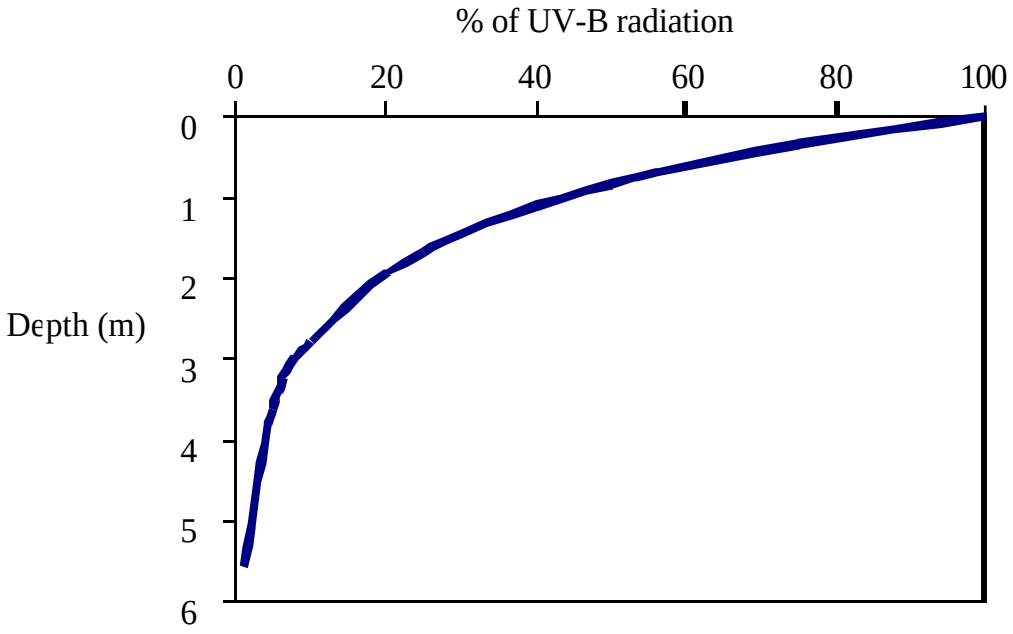

Fig. 1. Relative attenuation of surface UV-B radiation in the water column of Lake Tanganyika off Kigoma Bay in 7th April 1998.

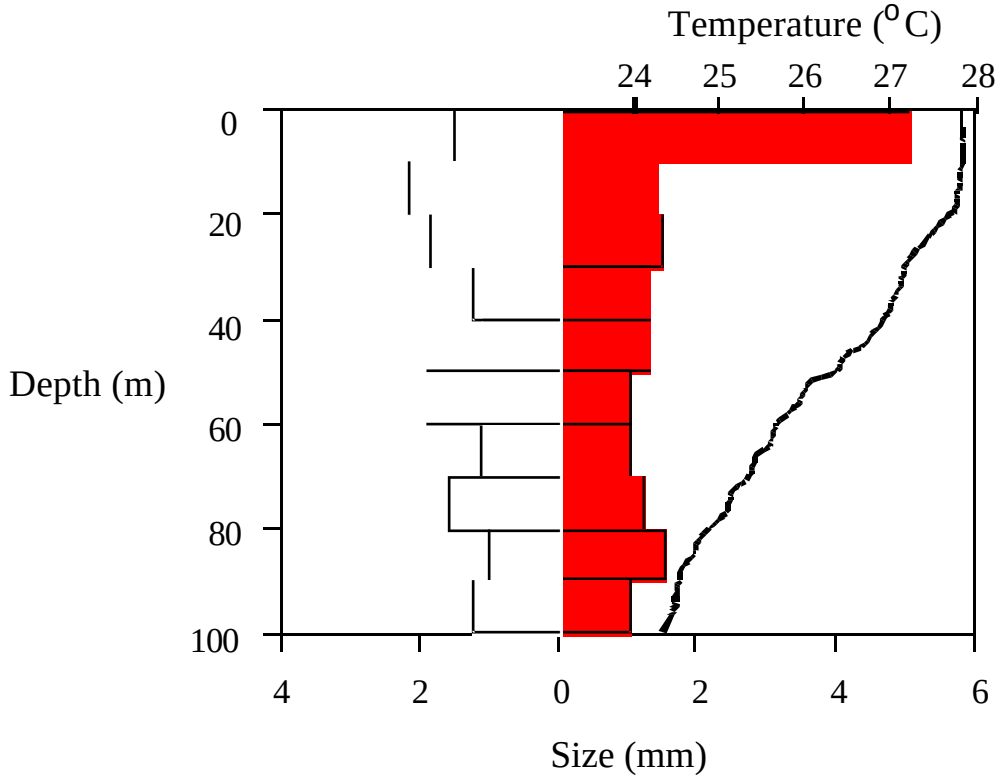

Fig. 2. Vertical distribution of water temperature and the mean diameter of jellyfish at noon and at midnight.

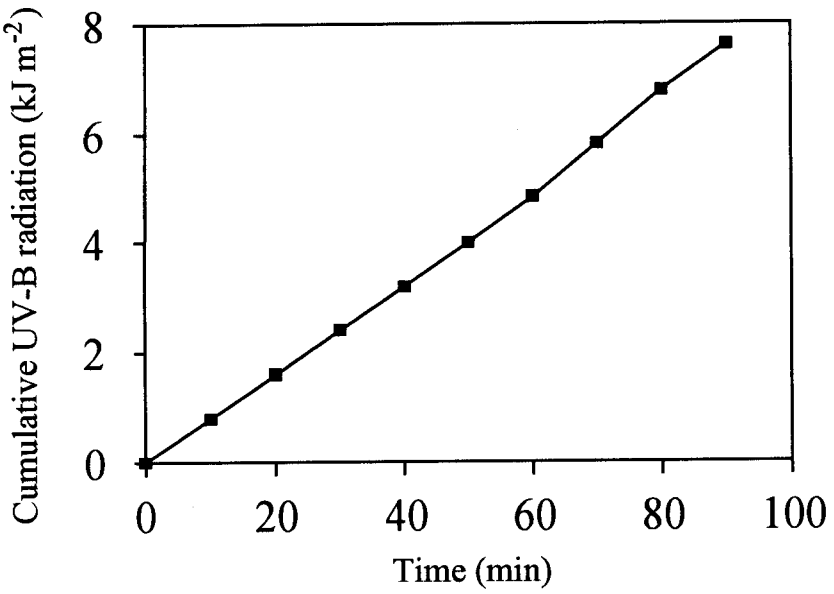

Fig. 3. Cumulative UV-B radiation during the UV-exposure experiment.

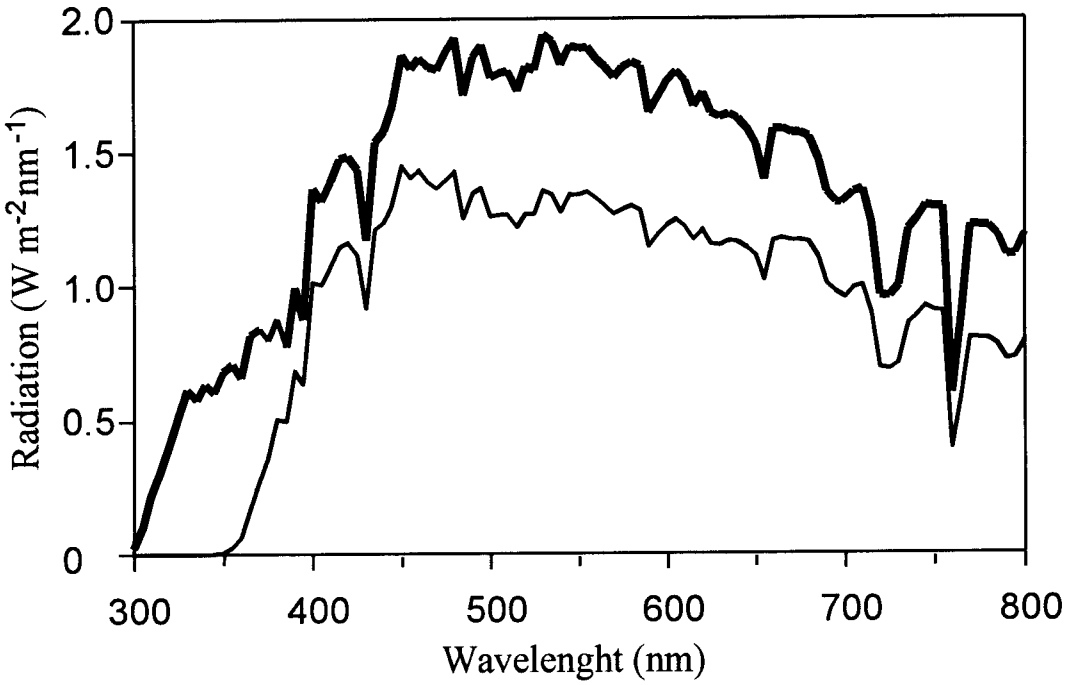

Fig.4. Sunlight spectrum during the UV-exposure experiment. Dark line - in direct sunlight; Thin line - under polyethylene UV screen.

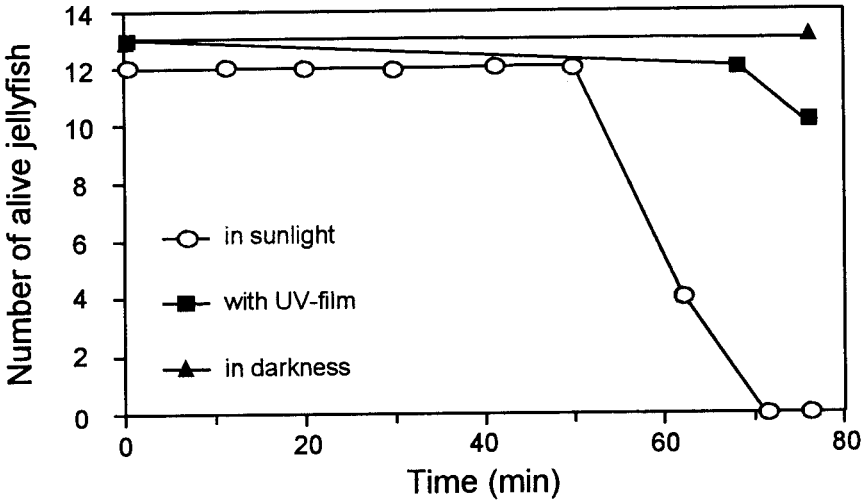

Fig. 5. Survival of *Limnocnida tanganyicae* in quartz bottles under direct exposure to sunlight, UV-screened sunlight and in darkness.

PICOCYANOBACTERIA - AN IMPORTANT COMPONENT IN THE PLANKTON OF LAKE TANGANYIKA

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INTRODUCTION

The existence of phototrophic picoplankton in both marine and fresh waters was discovered in the late 1970s (Paerl 1977) and since then their distribution was found to be global (Stockner 1988). They have also been found in very oligotrophic environments in marine pelagial and large lakes and their proportion in primary production can exceed 90% (Stockner 1988). Picophytoplankton include cyanobacteria and eucaryotic algae. Due to their role in microbial food webs they were originally believed to have a key role in the energy transfer in lakes (Caron et al. 1985).

It has been suggested that picoplankton populations are mainly controlled by grazing (Liu 1997). The possible predators are heterotrophic and mixotrophic flagellates, rotifers, ciliates, cladocerans and copepods (Stockner 1988). Heterotrophic flagellates appear to be the main grazers on algal picoplankton in both marine and freshwater ecosystems (Stockner 1988). Ciliates on the other hand seem to graze on algal picoplankton mostly in marine waters (Sherr et al. 1986). Some freshwater rotifers are also efficient grazers on algal picoplankton, especially in oligotrophic lakes (Stockner 1988). Freshwater copepods and cladocerans have been recorded to ingest picocyanobacteria but according to several observations they seem unable to digest the picocyanobacteria (Stockner and Antia 1986). In addition to grazing, picoplanktonic populations can be affected by viral lysis and intensive solar irradiance (Cottrell & Suttle 1995).

The research on picoplankton in tropical lakes has been scarce. The purpose of this study was to collect basic information of the abundant population of picoplankton in Lake Tanganyika.

MATERIALS AND METHODS

The samples were mainly taken at two different sites i.e. off Kigoma and off Malagarasi River delta. The samples were taken with 10 m intervals down to the depth of 50 - 100 m with a black 1 m long Limnos sampler. In the laboratory 5 ml subsamples of lake water were filtered through a black 0,2µm Millipore polycarbonate filter. The filter was placed on a glass slide, a drop of immersion oil was dropped on it and a cover glass was placed on the filter. Picophytoplankton preparations were counted immediately or after freezing at ca. -18 ^{o}C. The counting was made using green and blue excited autofluorescence with a

Nikon Optiphot epifluorescence microscope (magnification ca. 1250 x). Picocyanobacteria have procaryotic cellular structure and their chromatophores contain phycoerythrin or phycocyanin (Stockner 1988). Under green excitation light phycoerythrin produces orange autofluorescence. Under blue excitation chlorophyll a of eucaryotic cells produces red autofluorescence. The number of cells was counted in 20 randomly chosen fields on each filter. The proportions of picoplankton in different size fractions were determined similarly by filtering samples also through 0.6, 0.8 and 1.0 µm filters.

The proportions of different phytoplankton size classes in primary production of Lake Tanganyika were determined by size fractionating samples incubated in water labelled with inorganic radiocarbon. $NaH^{14}C$ solution was added into water samples which were then incubated under 535 µE m^{-2} s^{-1} light intensity and at lake temperature for 8 h. After the incubation, 10 ml of water was filtered through 0.2, 0.6, 1, 5 and 10 µm pore size transparent Millipore polycarbonate filters. The radioactivity on the filters were assessed with a Hidex Triathler portable liquid scintillation counter. Light saturation curves of photosynthesis in different size fractions were also measured as above in the incubator. In this experiment, the samples were taken from the depths of 0, 10, 20, 30 and 40 m and were incubated at 5 light intensities in the incubator.

RESULTS

The vast majority of picophytoplankton fluoresced brightly under the green excitation light, but almost no emission was found under the blue excitation. Thus the bulk of picoplankton algae were evidently cyanobacteria. They were present in very high densities (10^5 - 10^6 cells ml^{-1}) generally down to ca. 50 m. The maximum density was most often observed at 30 - 40 m depth (Fig. 1) where there is still enough light for photosynthesis but not too much harmful UV -radiation (Tarvainen 1999). The vertical distributions and densities of picocyanobacteria remained rather similar throughout the diel cycle.

Off Kigoma and off Malagarasi delta the numerical proportions of picoplankton size classes in 0 - 60 m water column were quite different from each other (Fig. 2). Off Kigoma the smallest, 0.2 - 0.6 µm, size class was clearly dominating in the uppermost 0 - 30 m water column while in deeper water larger cells became more abundant. Off Malagarasi delta there was also a deep-water minimum, but its depth was much shallower (30 m). In deeper water the proportion of the smaller cells increased again. Although the minimum proportions of the 0.2 - 0.6 µm size fraction were observed at remarkably different depths, in both cases these depths represented approximately similar light climate. Off Kigoma the secchi depth was ca. 13 m, but off Malagarasi it was only ca. 6 m due to the turbidity brought by the river.

The size fractionation results of phytoplankton production indicated only little primary production in the size class of 0.6 - 1.0 :m and therefore the results are shown only for three size classes. Only ca. 20 % of primary production in 0-40 m water column was due to 0.2-0.6 :m picoplankton. At all depths phytoplankton larger than 5 :m in diameter was most productive (Fig. 3) so that more than half of primary production was due to cells larger than picoplankton. In this small data no marked vertical differences were found in the proportions of primary production in different size fractions.

The combined results of the light saturation experiments for 0-40 m water column showed that primary production of total phytoplankton was ca. three times higher than that of the 0,2 - 1 :m fraction (Fig. 4). Thus, in agreement with the other size fractionation results, primary production of algae > 1 :m in diameter was dominating over picocyanobacteria. The light saturation curves of both total phytoplankton and cyanobacterial size fraction were similar indicating saturation at ca. 100 :E m^{-2} s^{-1}. Because the measured primary production in the > 1 :m size fraction was so much higher than in the 0,2 - 1 :m fraction, it means that light saturations of picophytoplankton and larger phytoplankton were similar.

DISCUSSION

The observed picoplankton densities in Lake Tanganyika were among the highest reported in the literature, but according to the size fractionation results their size was extremely small - of the same order as that of bacteria. Hence the proportion of picocyanobacteria in the total biomass of phytoplankton was much smaller than that indicated by their density. Although the growth rate of small phytoplankton cells can be considerably higher than that of large ones, the size fractionation results of phytoplankton primary production showed that off Kigoma at least at the end of the wet season, picocyanobacteria were responsible only for the minority of phytoplankton primary production. The absence of diel differences in the density of picocyanobacteria in the vertical profiles also did not indicate high production or their cell division cycle was not synchronized with time.

The highest abundance of picocyanobacteria in the upper metalimnion was fully consistent with the vertical maximum of phycoerythrin *in vivo* autofluorescence (Salonen et al. 1999). The decreasing trend in their density from the thermocline to the surface probably partly reflects the high intensity of UV-radiation in the uppermost water layers of Lake Tanganyika (Tarvainen 1999). During the wet season the inhibition of algae by UV-radiation is likely most pronounced, because then the depth of stratification is shallowest and periodic daytime temporary stratifications may trap algae near to the surface and they are exposed to prolonged high intensities of harmful UV-radiation. Besides harmful effects of UV-radiation the metalimnetic maximum of

picocyanobacteria is probably affected by increased nutrient availability towards deeper water. The decrease of cell density below ca. 50 m is likely due to decreased light intensity. Surprisingly many cyanobacteria were also found in very deep water, sometimes down to 100 m which is much deeper than 1 % light level occurring around 40 m (Salonen et al. 1999).

Although not quantitatively dominating in primary production the earlier unknown picocyanobacteria in Lake Tanganyika comprise a characteristic and significant part of its phytoplankton at all seasons (Salonen, unpubl.). Picocyanobacteria are likely utilized by protozoans, but their final trophic status in the food web of Lake Tanganyika still awaits verification.

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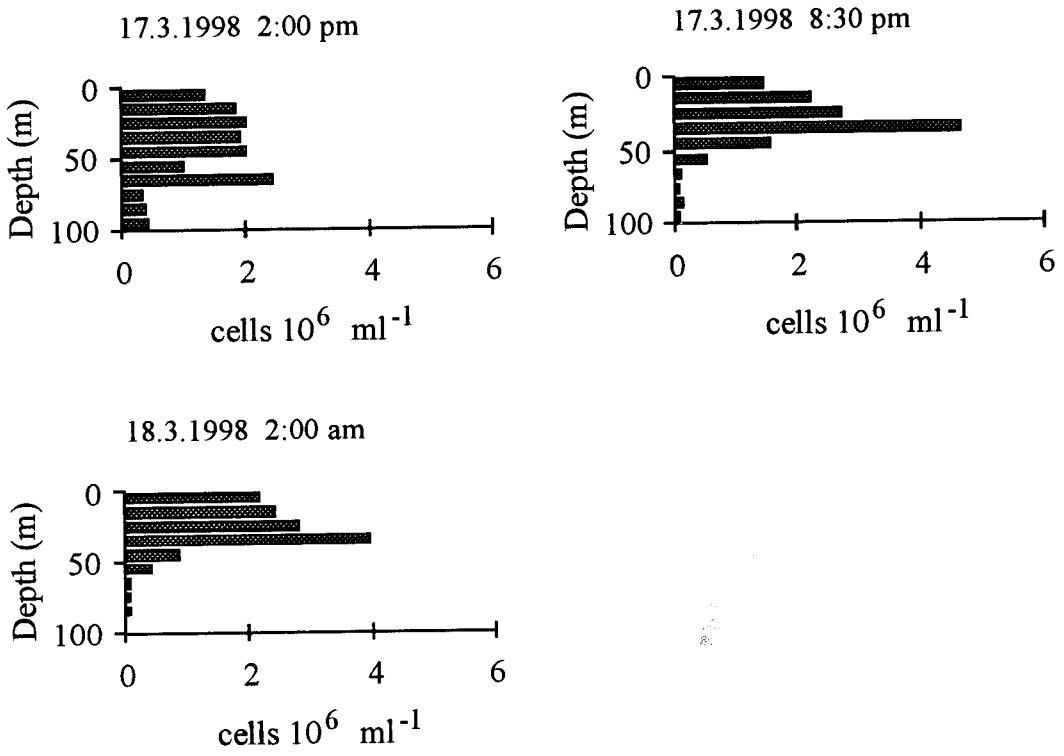

Figure 1. Examples of the vertical distributions of picocyanobacteria off Kigoma at different times of a day in March 1998.

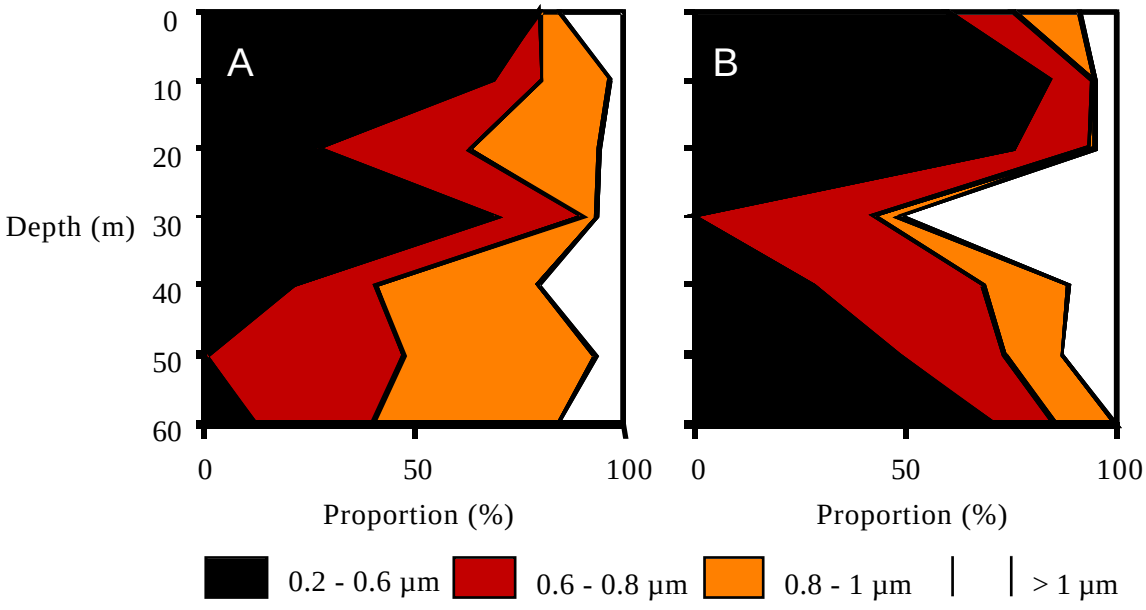

Figure 2. The proportions of picoplankton size classes at different depths off Kigoma (A) and off Malagarasi delta (B) in March 1998.

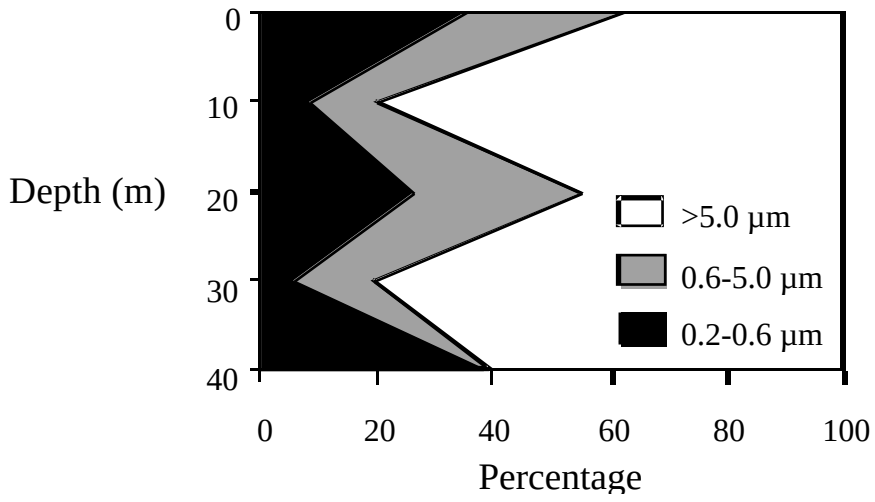

Figure 3. Size fractionation of primary production; the percent proportions of the production of different fractions at different depths off Kigoma.

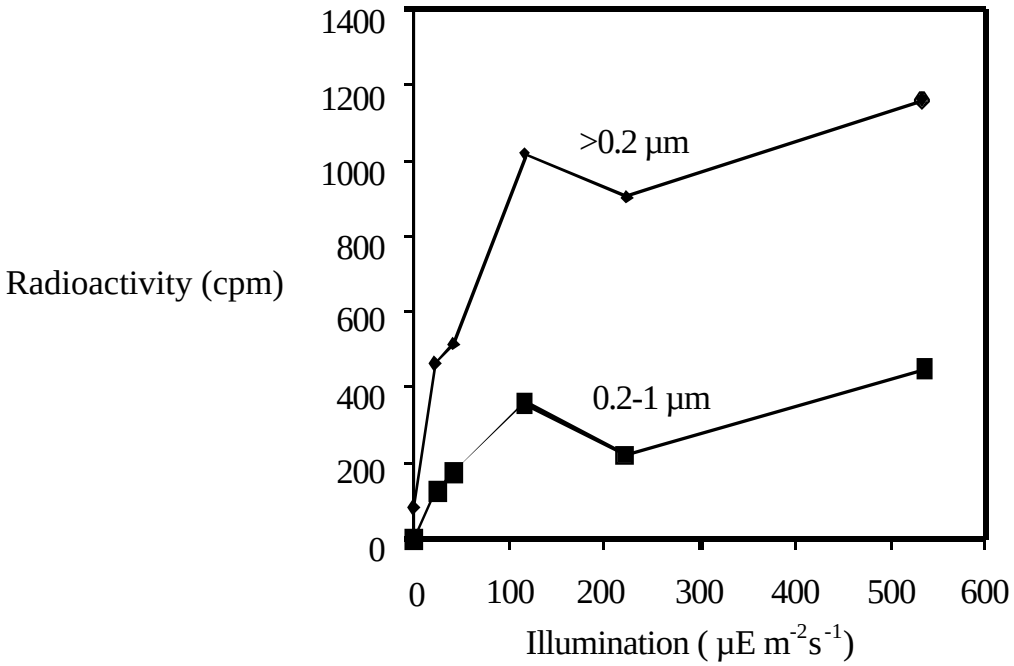

Figure 4. Mean light saturation of primary production in the 0-40 m water column off Kigoma in March 1998.

GROWTH OF THE CLUPEIDS *Limnothrissa miodon* AND *Stolothrissa tanganicae* ESTIMATED BY OTOLITH MICROSTRUCTURE ANALYSIS

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INTRODUCTION

Information on the population dynamics of fish is important in the study and management of fisheries. Knowledge of growth, mortality and reproduction rates and recruitment patterns coupled with data on catches and biomass enable the calculation of turnover rates of target fish species and the making of proper management plans to obtain optimal yields in a sustainable way. Closed areas, closed seasons, restrictions concerning the sizes of fish that may be landed or the type of gear used as well as setting of quotas are examples of management practices applied (Bagenal,1978).

Fisheries in Lake Tanganyika are largely based on the pelagic clupeids *Limnothrissa miodon* and *Stolothrissa tanganicae*. These fisheries are very productive and provide a significant protein source for the people in the Tanganyika area (Coulter 1991). Clupeids form most of the commercial catch together with the centropomid *Lates stappersiii*. At present, it does not seem likely that the clupeids were overexploited lake-wide. However, there might be excessive local pressures on stocks in the northern and southern parts of the lake. During their life cycle, the species shift habitats in different ways, which makes them differently vulnerable to various fishing gears at successive life stages. The growing human population and the increasing fishing effort, especially towards young life stages, may lead to over fishing and declining stocks if no management practices are implemented in the future (Mannini, 1998).

The growth of *L. miodon* and *S .tanganicae* has been mainly studied by length-frequency analyses (Aro & Mannini 1995). In addition, there have been some attempts at ageing fish by counting daily increments on otoliths (Kimura 1995; Pakkasmaa 1996). The length-frequency method used in growth studies might give biased results with tropical species because the cohorts overlap due to the weak seasonality and extended breeding periods. The formation of daily increments has not been validated for these species. However, since environmental conditions in Lake Tanganyika are optimal for diel periodicity of growth and the increments observed are similar to those in many other validated clupeids (Kimura 1995), the assumption of daily increment formation is well founded.

The purpose of the present study was to compare the growth rates of *L.miodon* and *S.tanganicae* in two different habitats in the North Tanzanian part of the lake by otolith microstructure analysis. In addition to increment number, other properties of otoliths, such as otolith weight (Pawson 1991; Fletcher 1991) and otolith shape (Smith 1992) can provide information on fish growth. Otoliths tend to gain weight, length and width along

with increasing increment number (Reznick et al. 1989; Huuskonen & Karjalainen 1993). These traits and otolith thickness were also measured from *L. miodon* and *S. tanganicae* otoliths in order to evaluate their applicability in working out growth differences between species and areas. An overview of the preliminary results will be given in the present paper, and more detailed analysis of data will be published later.

MATERIALS AND METHODS

Sampling

Samples were collected during March-April 1998 off Kigoma (4°54 53-4°59 67 S; 29° 31 28- 29° 41 35 E), off Malagarasi river delta (5° 00 82-5° 21 60 S; 29° 42 60-29° 44 89 E) and from southern Lake Tanganyika (7° 38 49-7° 41 55 S; 30° 30 48-30° 31 52 E). Size compositions of both species in each area are presented in Table 1. Larvae under 17 mm in total length (TL) were caught with a Gulf sampler by a method described by Karjalainen and Markkanen (1999) and juveniles and adults with a trawl.

Table 1. Composition of samples and measurements of traits from each sampling area

	Delta of Malagarasi		Kigoma		South Tanganyika	
L.miodon						
	N	Range	N	Range	N	Range
Total length (mm)	159	36-125	76	4-16 and 77-108	72	12-26
Weight (g)	33	0,6-10,2	34	0,0057-0,0082 and 3,1-8,3	8	0,0095-0,02760
Age (days)	10	63-578	54	6-41 and 188-432	49	29-63
Otolith weight (µg)	101	76,7-1283,1	42	374-956,7	16	3,8-19,3
Otolith length (mm)	77	0,8-2,83	45	0,03-0,2 and 1,77-2,1	50	0,15-0,53
Otolith width (mm)	89	0,5-1,35	26	0,01-0,1 and 0,80-1,05	50	0,13-0,37
Otlith thickness (mm)	25	0,09-0,23	10	0,15-0,23	3	0,02-0,03
S.tanganicae						
Total length (mm)	123	38-88	108	5-15 and 76-96	5	21-25
Weight (g)	28	0,63-4,66	55	0,0035-0,0040 and 2,7-6,3	-	-
Age (days)	72	65-237	70	5-32 and 162-268	5	43-67
Otolith weight (µg)	69	79,3-521,	45	272,7-569,6	2	14,3-24,9
Otolith length (mm)	64	0,81-1,9	58	0,03-0,23 and 1,65-2,00	3	0,40-0,48
Otolith width (mm)	70	0,50-0,7	62	0,03-0,22 and 0,70-1,00	3	0,32-0,35
Otolith thickness (mm)	10	0,09-0,14	7	0,12-0,19	-	-

Sample preservation and field measurements

Larvae under 30 mm TL were preserved in 90 % ethanol and juveniles and adults were frozen. Fish over 20 mm TL were measured to the nearest mm and weighed to the nearest 0.1 g and sexed when possible in the field. The sagittal otoliths were removed under a dissecting microscope, washed in water and stored and dried in paper bags or Eppendorff tubes and delivered to the University of Turku. Larvae under 20 mm were delivered to Turku in ethanol.

Otolith preparations and measurements

One of the two sagittal otoliths was randomly chosen for the analysis. The number of otoliths measured for each trait is presented in Table 1. The larval otoliths were removed under a dissecting microscope with 50 x magnification. The larva was placed on an glass slide, covered by glycerol and measured to the nearest mm. Some specimens were also weighed. The sagittal otoliths were then removed with dissecting and microstift needles (Secor et al. 1992).

Some otoliths were weighed with a Cahn- microbalance to the nearest 0.1 µg. Then the otoliths were mounted on a glass slide using Euparal as a mounting medium (Pakkasmaa 1996), sulcus side of the otolith down (Secor et al. 1992, Huuskonen & Karjalainen 1993) and covered with a coverslip. When necessary to enhance transparency, the otoliths of *S. tanganicae* over 75 mm TL and those of *L. miodon* over 90 mm TL were ground with a 1200 grit size abrasive paper on both sides. For this purpose the otolith was glued on a slide with Loctite 424 instant glue, the sulcus side of the otolith up. Then the otolith was ground and polished with carborundum powder to the midplane, left in an oven at 100°C for 8-12 hours or for some days at room temperature. The otolith was detached of the slide with forceps and 70 % ethanol and turned around for grinding and polishing until the increments were visible by using Euparal as a clearing medium (Secor et al. 1992).

The assumed daily increments were counted under Olympus compound microscope at a magnification of 400-1000 x. TV screen was used to facilitate counting. The increments were counted along rostrum where they were most easily distinguishable, except at the marginal end, or along postrostrum, where the increments were thinner but the marginal end was less aberrant (Kimura 1991b). Increments on each otolith were counted 2-4 times. The otoliths of *S.tanganicae* were more difficult to count than those of *L.miodon*. Some otoliths were excluded from the analysis as impossible to count.

Otolith length and width were measured with an ocular micrometer under Olympus compound microscope with a magnification depending on the size of the otolith. Otoliths were prepared for thickness measurements first by glueing the otolith on a slide and then breaking it along sulcus. Thickness was measured with an ocular micrometer at 100x magnification under a dissecting microscope.

RESULTS

Growth in length was fastest when the fish were young, declining along with larger size and older age (Fig. 1). In length classes over approximately 70 mm TL, *S.tanganicae* grew slightly faster than *L. miodon*. At 80 mm of TL, *L.miodon* had ca. 220 and *S.tanganicae* ca.190 increments. *S.tanganicae* seemed to grow somewhat faster off Kigoma than off the delta of Malagarasi.

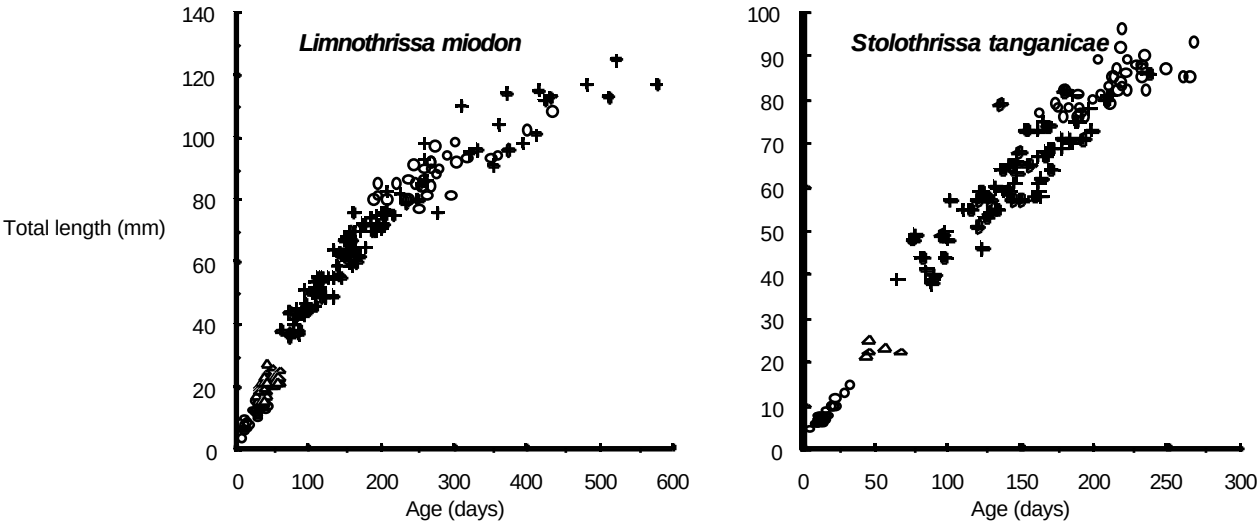

Figure 1. Age-length relationship of *L.miodon* and *S.tanganicae*. Symbols denote areas (O = off Kigoma,+ = off the delta of Malagarasi and ?= southern L. Tanganyika).

Growth in weight was very slow until the fish were about 20-40 mm TL (Fig. 2). Weight increased along with length and age. *L.miodon* seemed to gain weight more rapidly relative to total fish length than *S.tanganicae*.

Gain of weight of otoliths accelerated along with increasing TL of a fish and was linear with age after the fish had passed the larval stage. Prior to that otolith weight gain was very slow. In samples from off the delta of Malagarasi, otoliths of both species seemed to be heavier relative to TL of a fish than off Kigoma. Otoliths of *L.miodon* seemed to be heavier and thicker relative to TL of a fish than those of *S. tanganicae.*

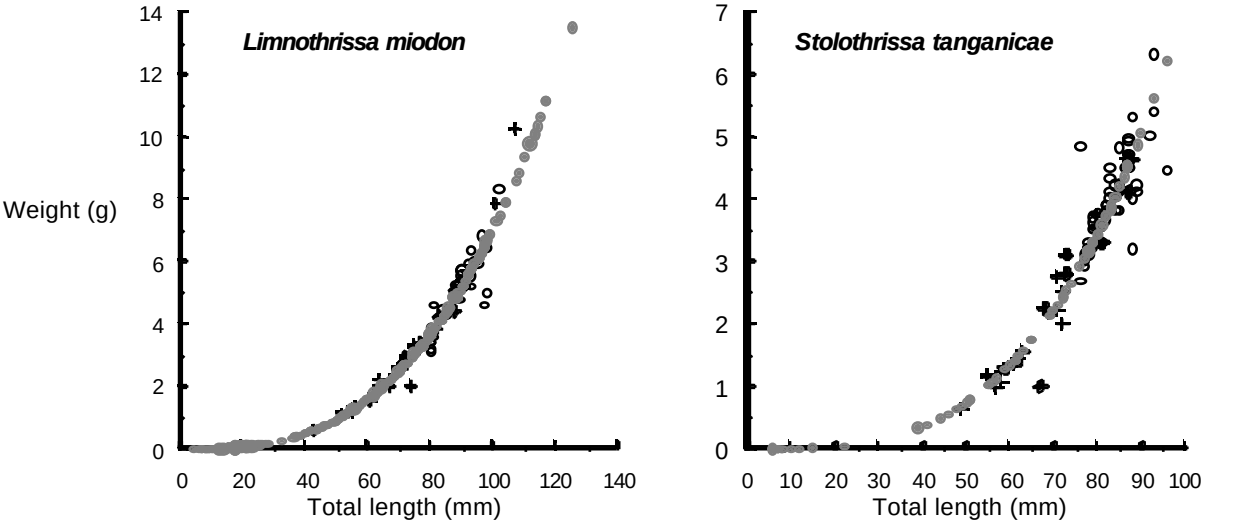

Figure 2. Length-weight relationship of *L.miodon* and *S.tanganicae*. Symbols denote areas (O = Kigoma, += delta of Malagarasi and ?=South L.Tangayika). Small dots indicate predicted weights at length obtained from the equation *W=a*length**b*, where W indicates predicted weight and *a* and *b* are regression coefficients of *logWeight=loga+b*logTotal length*.

Growth in length and width of otoliths of both species was curvilinear relative to TL of a fish and the otoliths of both species were round in shape in larval fish. Otoliths of *L.miodon* were wider relative to TL of a fish than those of *S.tanganicae.*

DISCUSSION

The present study suggested differences in growth rates between *L.miodon* and *S.tanganicae* and also spatial growth rate differences within the species. *S.tanganicae* had lighter, narrower and thinner otoliths and less increments relative to total length than *L.miodon*. Instead, *L.miodon* gained weight faster than *S.tanganicae* relative to total length of a fish. Within both species, specimens from Kigoma seemed to have grown faster than specimens from off the delta of Malagarasi.

Primary production in the pelagial of Lake Tanganyika is not very high, and availability of food may be a limiting factor for fish growth. There are possibly spatial differences in plankton abundance. In their length-frequency analyses, Aro and Mannini (1995) obtained slightly more variable growth rates for *S.tanganicae* than for *L.miodon*. Growth rates of *S. tanganicae* were slower off Kigoma than in the northern end of the lake off Bujumbura and Uvira or in the southern end of the lake off Mpulungu. Indications of spatial differences of growth rates within both species were also obtained by Pakkasmaa (1996) by counting the increments indirectly and by measuring otolith width and length.

The present study suggests that growth rates of the clupeids were higher off Kigoma than off the delta of Malagarasi.This was somewhat unexpected, because the delta of Malagarasi is rich in nutrients, especially so at the time of the sampling when abundant rains had lasted for several months. However, the water in this area was very turbid compared to the Kigoma area and this may have caused difficulties for the visual feeding of fish.

Adult growth rates seemed to differ between species, *S.tanganicae* growing faster than *L.miodon*, while such differences were not found in larval fish. In both species, the length growth of larvae was rapid. As commonly found for many fish species (Campana and Neilson 1985), the growth rates of the length and width of otoliths relative to the length of a fish were curvilinear in larval fish.

CONCLUSIONS

The clupeids of Lake Tanganyika seem to grow at different rates in various parts of the lake. Sampling that would cover the whole lake at the same time would reveal the growth patterns of different areas more clearly. Especially *S.tanganicae* seems to show spatial variation in growth rates. Also validation of the daily otolith increment formation in controlled conditions would help the counting of the increments and specifying between-species differences.

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DIEL PATTERN OF FEEDING INTENSITY OF LARVAE OF THE PELAGIC CLUPEIDS *Stolothrissa tanganicae* AND *Limnothrissa miodon* IN LAKE TANGANYIKA

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INTRODUCTION

Lake Tanganyika is an especially large rift lake, situated in East Africa near the equator (3° - 9° S). The four countries that share the lake are Tanzania, Burundi, D.R.Congo (Zaïre) and Zambia. The lake is 650 km long, mean width being 50 km, and the mean and maximum depths are 570 m and 1470 m, respectively. It contains one-fifth of the world's free fresh water. The lake is considered to be meromictic and oligotrophic (Coulter, 1991).

The fisheries of Lake Tanganyika are of great importance to the surrounding population of several millions because other sources of animal protein are scarce in the area. The fisheries are mainly based on two pelagic clupeids *Stolothrissa tanganicae* and *Limnothrissa miodon* and four predatory Nile perch species (*Lates* spp.). Of these the clupeids are the most important source of animal protein (Roest, 1992).

Published data suggest that Lake Tanganyika has exceptionally high fish production in relation to primary production. Hecky and Fee (1981) argued that the annual catches of the areas exploited were 5 to 10 times higher than could be expected on the basis of primary production. Hecky (1984) explained that this was due to extremely efficient function of the trophic structure.

Evolution has led to very specific relationships between the pelagic clupeids and zooplankton in Lake Tanganyika. The amounts of nutrients control primary production both spatially and temporally, and zooplankton feeds mainly on phytoplankton. Clupeids prey on a few zooplankton species present in the pelagial. The abundance, fecundity and condition of clupeids of Lake Tanganyika are influenced by the abundance of cyclopoid copepods and one calanoid copepod (*Tropodiaptomus simplex*). In general pelagic fish are dependent on the population biology of zooplankton.

Although the trophic hierarchy among the pelagic fish is a simple one, the diets show considerable overlap. Both clupeids feed on many of the same prey items where they occupy the same habitats, but competition is evidently minimized in several ways. *Limnothrissa* spends its larval stage inshore and moves further from shore from about 40 mm length, while *Stolothrissa* is mostly pelagic but spends some time inshore from about 35 mm length to about 50 mm. However, where the basin sides are very steep, e.g. near

Kigoma, populations presumably mix freely. In the pelagial *Limnothrissa* utilizes components, e.g. insects, not taken by *Stolothrissa*. Niche overlap is reduced also by different timing of reproductive peaks. Finally, *Stolothrissa* seems to be more specialized in offshore environment and is always found there in higher numbers (Coulter, 1991).

Another intensively studied aspect in Lake Tanganyika is the flow of energy between different components of food chain. It has been thought that the most intensively exploited areas have a carbon transfer efficiency from primary production to fish production as high as the most efficient marine fisheries. The trophic structure in the pelagic zone is simple in terms of species numbers and trophic levels. Growth rates of plankton and clupeids are high, and efficient grazing at different trophic levels keeps the total plankton biomass generally low. Carbon accumulates as fish rather than as phytoplankton biomass (Coulter, 1991).

However, recent more comprehensive data (Sarvala et al. 1999) show that phytoplankton production is higher than formerly thought, zooplankton production and biomass are lower and grazing efficiency low, not exceptionally high. Thus the efficiency of fish production is not high in relation to primary production. In fact, it is within the normal limits. The low efficiency of zooplankton production is not surprising in deep, clear, warm and oligotrophic tropical lake when one takes into account the high costs of respiration and the vertical migrations to avoid the predation. The seemingly efficient transfer of carbon from zooplankton to fish may be due to lacking information on the significance of shrimps in the diet of the fish. On the other hand, although the extremely simple and short trophic structure leading to fish enhances fish production, it is rather expected that such a deep, warm lake has low efficiency of fish production. The fish can prey only during relatively short time daily because zooplankton migrates vertically to avoid predation. Zooplankton presumably hide to the almost anoxic upper layers of hypolimnion where fish can not manage. This leads to lower ecological efficiency. It may be that the flourishing fishery is not based on any exceptionally efficient part of system but the fact that most of the pelagic production is channelled to a few short-lived species of fish which have rapid reproduction.

In connection with the 20th multidisciplinary cruise of R/V Tanganyika Explorer, the diel patterns of the feeding intensity of the larvae of *Stolothrissa tanganicae* and *Limnothrissa miodon* were observed and compared. The aim was to gain more information about the ecology of these two pelagic clupeids. For one thing it was needed from an evolutionary perspective to define more precisely the niche overlap in their feeding behavior and for another to learn more about the specific events behind the observed general energy flow processes.

MATERIAL AND METHODS

In March-April 1998, a research expedition to Lake Tanganyika was carried out by the Universities of Kuopio, Jyväskylä and Turku. It was closely connected with the international Lake Tanganyika Research Project (LTR; Research for the Management of the Fisheries on Lake Tanganyika), financed mainly by the Finnish International Development Agency (FINNIDA), and executed by FAO.

Sampling was carried out in the eastern side of Lake Tanganyika outside the town of Kigoma (Tanzania), where basin sides are steep and the littoral zone narrow. The sampling apparatus used was a Gulf-V -sampler and it was towed behind the research vessel R/V Tanganyika Explorer, a 26 m long, 450 hp stern trawler.

Sampling was conducted on 17 - 31 March 1998 and it took place on several occasions during twenty-four hours cycle, concentrating most frequently at dusk, midnight and dawn. One sampling haul took about 25 minutes and it included five different depths between the surface and about 100 meters depth.

The larvae caught were preserved in 70% ethanol immediately after sampling to halt postcapture digestion (Emmet et al. 1982). Digestion is extremely fast at tropical temperatures and must be stopped fast to conserve prey items in gut. The identification of fish species, observation of fullness of alimentary canal, and length measurements were conducted with preparation microscope in laboratory conditions. If clearly < 50% of the length of the gut (measured from the end) contained food, the category of the fullness was "empty" (or 0 in some figures). In that case the feeding had stopped for a good while ago. If from about 50% to 75% of the length contained food, the category was "average" (or 1), and if over 75% of the length contained food the category was "full" (or 2), and the fish was supposedly caught when it was feeding.

In statistical analysis the CATMOD procedure and Maximum Likelihood Ratio (ML) of SAS were used to find out the differences of gut fullness between species and between length classes at different points of time, and differences in overall fullness at different points of time. Length distributions were surveyed with Mann Whitney U and Chi-Square -tests.

In analysis, two species (*Limnothrissa* and *Stolothrissa*), two length classes (< 8 mm and ≥ 8 mm), three categories of fullness (0-2) and three points of time depending on original sampling hours (dusk, dawn and "day or night"; 18h00-19h50, 6h20-7h00 and 7h20-17h20 or 0h00-0h50, respectively) were used.

RESULTS

Almost all *Limnothrissa* measured for this study were over 8 mm, whereas *Stolothrissa* were divided quite evenly between both length classes: *Limnothrissa* had greater average length than *Stolothrissa*, 11.3 mm and 7.7 mm, respectively (Fig. 1). The length distribution of *Stolothrissa* differed significantly from normal distribution ($p < 0.001$, chi-square = 66.2, Fig. 1) while that of *Limnothrissa* did not (p = n.s., Fig. 1). The length distributions differed significantly from each other ($p < 0.001$, Z = -6.75, Mann-Whitney).

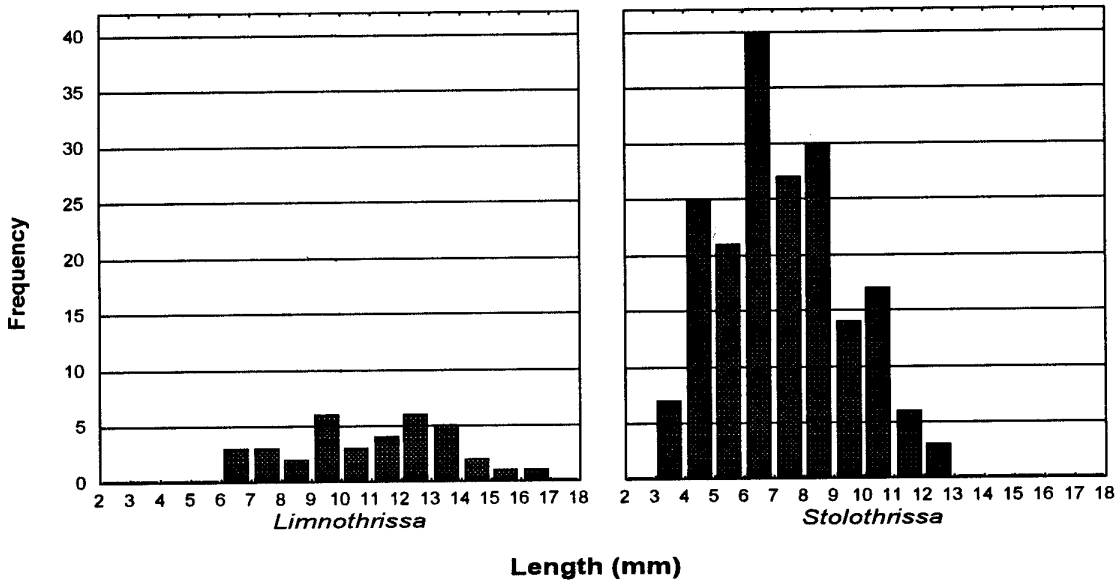

Fig. 1. Length distribution of *Limnothrissa miodon* (mean = 11.3 mm) and *Stolothrissa tanganicae* (mean = 7.7 mm).

The gut fullness was recorded in connection with the laborious and time consuming observation of prey items in the guts (see Markkanen & Karjalainen 1999). Thus the total amount of specimens investigated was quite modest: 36 for *Limnothrissa* and 190 for *Stolothrissa*.

There were differences in overall gut fullness between dusk, dawn and "day or night" ($p = 0.036$, d.f. = 4, chi-square = 10.27, CATMOD, Fig. 2). Feeding occurs not only during the main feeding hours at dusk and dawn as expected, but there is also some feeding at other times: 5 out of 24 (21 %) specimens caught at night and 13 out of 55 (24 %) specimens caught at daytime had some food in the gut (Figs. 2, 5 and 6). Only about 40 % of specimens caught at dusk and dawn had food in the gut (Fig. 2). The difference in fullness between species at different hours was almost significant ($p = 0.057$, d.f. = 5, chi-square = 10.71, CATMOD, Fig. 3). When species were analysed separately, there were differences in gut fullness of *Limnothrissa* between the three points of time ($p = 0.006$, d.f. = 4, chi-square = 14.38, CATMOD, Fig. 3). The feeding was most intense at dusk (Fig. 3). *Stolothrissa* showed significant connection between gut fullness and different

points of time (p = 0.014, d.f. = 8, chi-square = 19.141, ML, Fig. 3) and it was observed from the frequency table that the feeding was most intense at dusk and dawn (Fig. 3).

Surprisingly, it seems that *Limnothrissa* is the more efficient predator in the pelagial outside Kigoma at day, night and dusk. At daytime 50% of *Limnothrissa* and only 10% of *Stolothrissa* had notable amounts of food in the gut, and at night 25% and 20%, respectively (Figs. 5 and 6). Coulter (1991) states that feeding of adult *Stolothrissa* takes place at dusk, usually 18h00 to 19h00. In my study the fullest guts of larval *Stolothrissa* were also found at those hours, but most of larval *Limnothrissa* seemed to feed intensively over a longer period starting at about 17h00 and stopping before 20h00. Intense feeding of both species started again at dawn and decreased towards daylight. The exact starting point of the feeding could not be determined because no specimens with food items only in the anterior part of the gut were found.

Length class was not a statistically decisive factor in determining gut fullness at different hours (p = n.s., CATMOD, Fig. 4).

Phases of the moon timed so that the moonlight did not affect the feeding behaviour at night.

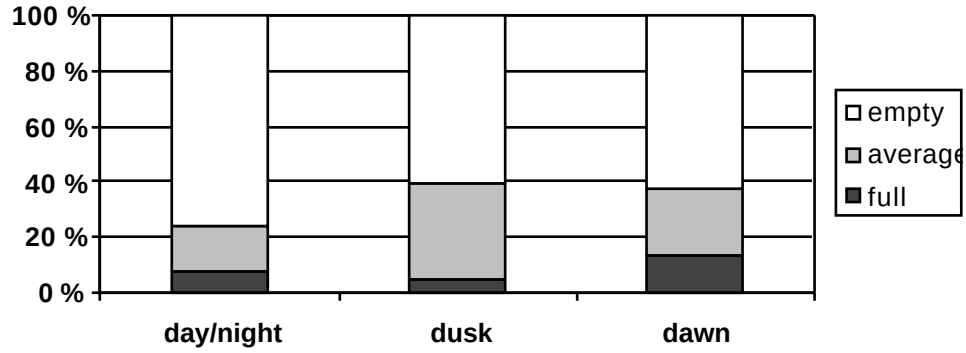

Fig. 2. Gut fullness of larvae at different hours.

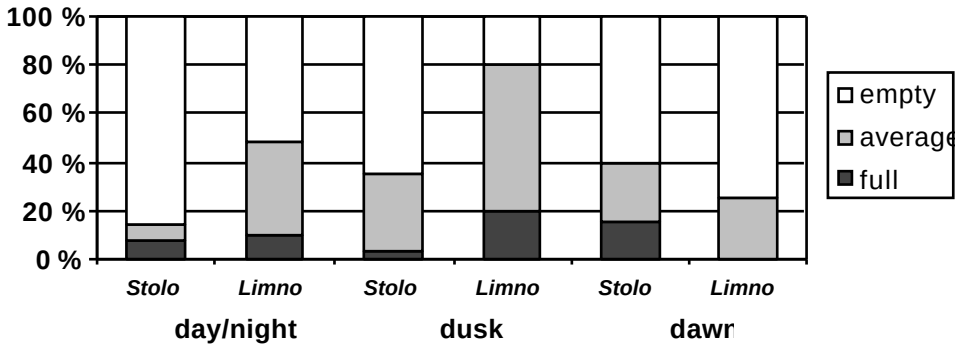

Fig. 3. Gut fullness of larvae of both species at different hours.

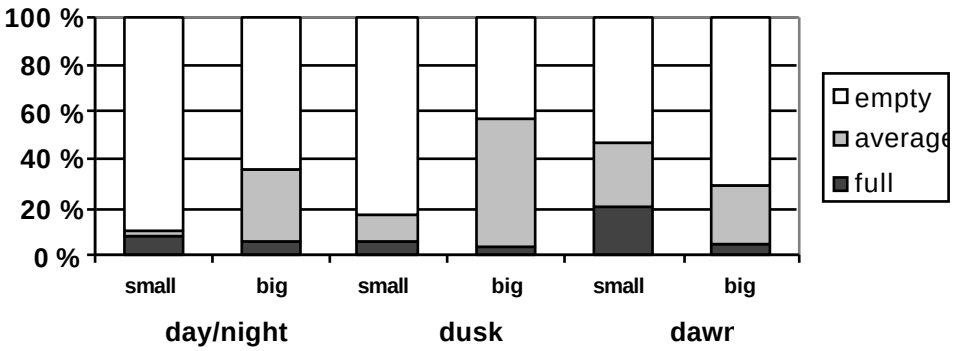

Fig. 4. Gut fullness of larvae of both length classes (< 8 mm and ≥ 8 mm) at different hours.

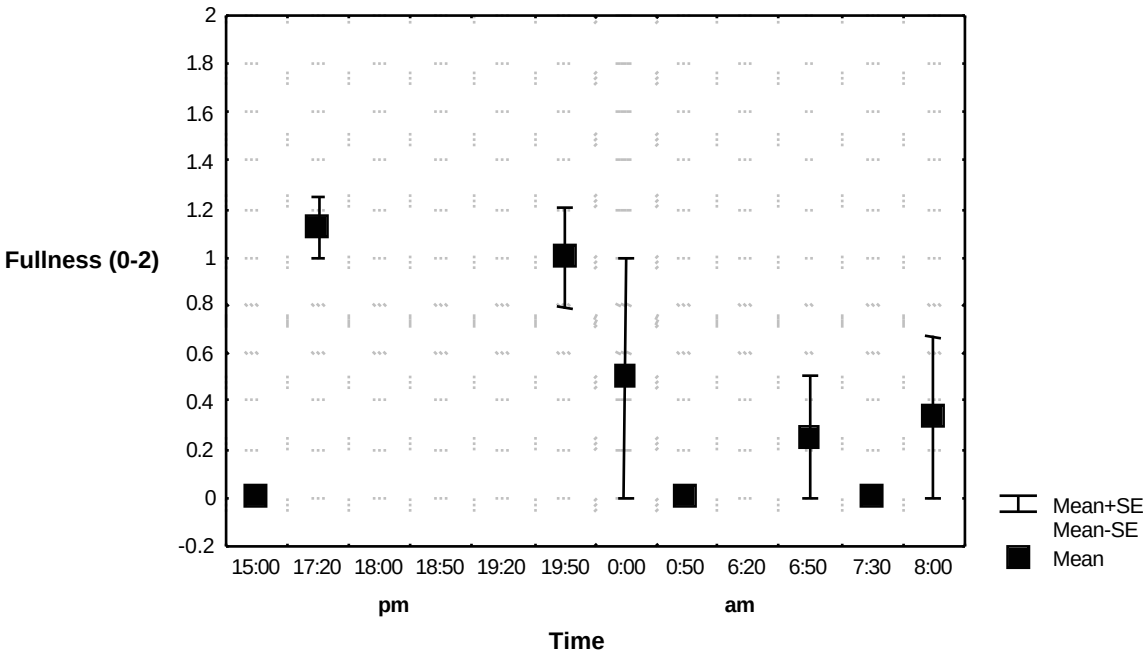

Fig. 5. Mean gut fullness of *Limnothrissa* at original sampling hours.

DISCUSSION

In my study the main feeding hours concentrated at dusk and dawn as earlier observed in adult clupeids, but also 21 % of specimens caught at night and 24 % caught at daytime had notable amounts of food in the gut. This does not agree with the general observation on adult clupeids of Blaxter & Holliday (1963) who argue that clupeids stop feeding at night. Also Chèné (1975) showed that adult clupeids of Lake Tanganyika ate mainly at dusk and the fullness of the stomach decreased towards dawn as the food was digested, but he did not sample at dawn. In Lake Tanganyika, the diurnal feeding patterns of clupeids are

related to their own vertical migrations and to those of their zooplankton prey. Clupeids follow the diurnal zooplankton migration (Poll 1953) and avoid also their visual predators, but they are not argued to feed at daytime. At daytime zooplankton migrate to almost anoxic upper layers of hypolimnion to avoid predation in light. At night the clupeids can also stay in the surface layer because there is not enough light for their

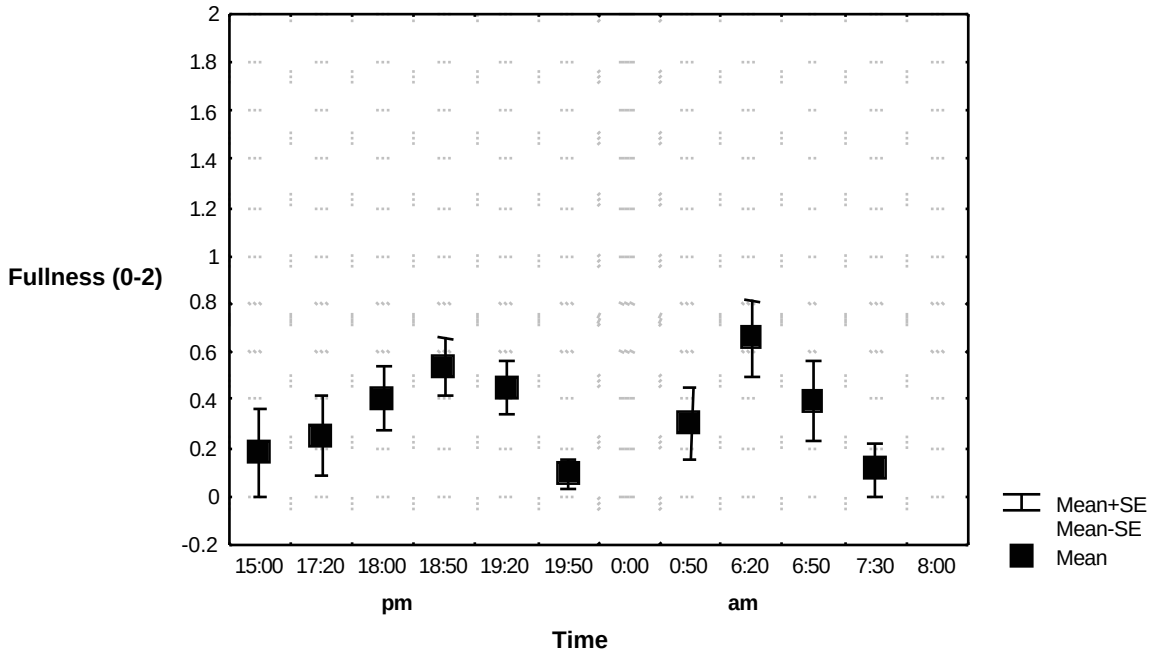

Fig. 6. Mean gut fullness of *Stolothrissa* at original sampling hours.

visual predators (e.g. Coulter, 1991). The vertical migration causes energetic costs and leads to lower efficiency of energy intake. The feeding at nighttime as observed in this study can be explained by Chene's (1975) suggestion that the feeding of clupeids depends at least partly upon filtration. Chèné reached this conclusion on the basis of unselectivity of prey items, characteristics of *Stolothrissa* gill-rakers and small size of certain cyclopoids taken as food by adult clupeids. Feeding at daytime may be also based on filtration, or, if the downward migration follows the zooplankton at the right light conditions depending on the position of sun of that moment, the feeding may also be active, based on vision. The fact that not a single specimen which had just started feeding was found also supports continuous feeding habits, at least among most specimens.

Only 40% of specimens had considerable amount of food in the gut even during the main feeding hours, dusk and dawn. Considering the energetic costs mentioned above and that the tropical fishes are generally supposed to grow fast and have rapid metabolism at high temperatures, preying

seems quite unefficient. If the preying of larval clupeids is as ineffective at the main feeding hours (of adults) as it seems, it is clear that the feeding hours must be extended to gain enough energy. Later in adult stage preying may be more effective because of faster moving abilities. On the other hand, recent growth data show that relative to the high temperature, the clupeids of Lake Tanganyika do not grow very fast (e.g. Sarvala et al. 1999).

Competition between *Limnothrissa* and *Stolothrissa* is minimized in several ways. Temporal and spatial segregation occur; for example, their reproduction peaks differ which decreases the probability of mass occurrences of young of both species at the same time. In addition, *Limnothrissa* has a less specialized diet because it spends its larval stage inshore in littoral, where the prey items are more diversified. However, in Kigoma, where our sampling was conducted, the basin sides are very steep and both species presumably mix freely in the pelagial and thus niche overlap is considerable. In my study the proportion of *Limnothrissa* in the catch was so modest (36/226 specimens, i.e. 16%) that it seems that in Kigoma only partial competition occurs (see also Markkanen & Karjalainen 1999), but at least at ”day or night” and dusk *Limnothrissa* surprisingly seems to win the battle for food, although *Stolothrissa* should be the more specialized of these species to life in the pelagial (Figs. 3, 5 and 6).

No statistical differences in gut fullness at different hours between length classes were observed, although simultaneous studies about food item selection of larval *Limnothrissa* and *Stolothrissa* (see Karjalainen & Markkanen 1999) showed different preferences between length classes.

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VERTICAL AND HORIZONTAL DISTRIBUTION OF HETEROTROPHIC BACTERIA IN LAKE TANGANYIKA

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INTRODUCTION

During past decades heterotrophic bacteria and other micro-organisms have been recognized as important parts of the pelagic food web both in marine and freshwater environments (e.g. Azam et al. 1983; Sherr & Sherr 1988). Traditionally, heterotrophic bacteria were regarded as a remineralisers recycling nutrients to primary producers. More recently it has been found that in resource-limited systems bacteria are in fact competing with phytoplankton for nutrients (Bratbak & Thingstad 1985; Currie 1990). Rothhaupt (1992) demonstrated in P-limited experiments that algae were able to grow only when protozoans reduced bacterial numbers and made bacterial phosphorus available to phytoplankton. The ability of bacteria to compete successfully for nutrients with phytoplankton may be due to the larger surface to volume ratio of small bacteria (Bratbak & Thingstad 1985). Cole et al. (1988) showed that bacterial production was closely related to primary production. Bacteria utilize dissolved and particulate organic carbon and convert it to bacterial biomass, relying on carbon sources which otherwise might be lost to the food web (Sherr & Sherr 1988). Dissolved organic carbon is mainly produced by phytoplankton (Brock & Clyne 1984) but also via the feeding process of zooplankton (Lampert 1978), allochthonous input (Robarts & Ashton 1988) and phytoplankton cell lysis (Cole et al. 1984). Bacterial production can be 20 - 60 % of primary production both in freshwater and saltwater ecosystems (Cole et al. 1988). Especially in highly humic lakes where primary production of phytoplankton is low, heterotrophic processes can dominate in plankton. In such environments, bacteria seem to be an important link between allochthonous dissolved organic matter and higher trophic levels (Salonen et al. 1992).

Bacterial production increases with eutrophication (Pace & Cole 1996). Billen et al. (1990) discovered that bacterial biomass was proportional to the richness of the environment. They assumed that bacterial production was proportional to the flux of organic matter available for the bacteria. Some studies also indicate that bacterial growth is more P-limited than C-limited (e.g. Coveney & Wetzel 1992; Morris & Lewis 1992). Currie (1990) suggested that during stable environmental conditions bacterial growth is not strongly P-limited and competition between phytoplankton and bacteria is replaced by mutualism.

Besides nutrient and carbon supply also grazing pressure is an important mechanism controlling bacterial

production. This top-down control is considered to be more effective in eutrophic than in oligotrophic environments (Berninger et al. 1993). Pace et al. (1990) could demonstrate that the fate of bacterial production in Upton Lake depended on planktonic community structure. Heterotrophic nanoflagellates (HNF) were primary consumers of bacterial production in winter and fall and *Daphnia galeata* at other times. Several studies have demonstrated that HNF are effective grazers on bacteria and are able to limit bacterial growth and biomass (e.g. Bloem & Bär-Gilissen 1989; Kuuppo-Leinikki 1990; Weisse 1990). HNF grazing on bacteria is size-selective and flagellates prefer larger bacteria (Chrzanowski & Simek 1990). They are able to control bacterial production by removing dividing cells (Sherr et al. 1992). Also *Daphnia* species have been found to be able to limit bacterial production and biomass (e.g. Christoffersen et al. 1993). *Daphnia* have been called key-species because they are able to diminish the energy flow going through the microbial food web and to use bacterial production directly. Also ciliates affect bacteria, the bacterivorous ciliates through grazing, and other species indirectly through grazing on various bacterivorous protozoans (Epstein et al. 1992).

Viruses are also suggested to be an important part of microbial food web, causing cell lysis and losses in bacterial populations (Bratbak et al. 1990). Bergh et al. (1989) found many times higher amounts of viruses than reported in previous studies in natural aquatic environments.

In spite of increasing interest in the functioning of the microbial food web and the role of bacteria in it, the knowledge of natural bacterial species composition and its relation to environmental factors is still scarce (Riemann & Christoferssen 1993). Höfle (1992) demonstrated that the structure of the whole microbial community was affected by nutrients. It responded rapidly to changes in nutrient supply but was rather inert to massive introduction of allochthonous bacteria.

The aim of the present study was to widen our knowledge about the occurrence of heterotrophic bacteria in Lake Tanganyika and to correlate their abundance with abiotic and biotic environmental factors. The bacterial abundances in Tanganyika had been studied occasionally in the LTR project. In April-May 1995 and in November 1996, bacterial production was about 20 % of primary production and there was a positive correlation between bacterial production and phytoplankton production (Sarvala et al. 1999). The multidisciplinary 20th cruise with R/V Tanganyika Explorer in March 1998 offered an opportunity to complement the previous data with numerous samples from the late phase of the rainy season.

MATERIAL AND METHODS

This study was carried out during four cruises with R/V Tanganyika Explorer. Water samples were taken between 21-31 March 1998 from 14 sites at different times of day from surface to 60 m (80 m in the southern basin; Table 1). The uppermost sample was taken from 1 m.

Slides for the microscopic counting of bacteria were prepared immediately after sampling.. Samples of lake water were stained with DAPI (Porter and Feig 1980) for 5 min and were then filtered through 0.2-µm black Nuclepore filters. Filters were mounted on slides with immersion oil and the slides were stored in a refrigerator. The bacteria were counted within one day of sampling with an epifluorescence microscope.

Table 1. The dates and times of sampling at different locations.

Sample Location	Southern basin	Utinta	Utinta transect	Mahale	Ujiji	Kigoma	Malagarasi
Date	21 Mar	23 Mar	24 Mar	25 Mar	26 Mar	27 Mar 30 Mar	31 Mar
Sampling time	10:00am 03:00pm 08:30pm	- 06:30pm 11:00pm	08:30am 12:15am 03:00pm	09:55am 04:45pm -	08:30am - -	10:00am 06:30pm -	- - 08:00pm

RESULTS

The vertical distribution of bacteria varied between areas (Fig. 1). The abundance of bacteria was between 1. 6* 106 - 1.2*108 cells ml-1. Except for some occasional samples, the highest abundances were observed at the surface. In one series taken from the southern basin (at time 10:00am), the highest values were exceptionally at 80 m depth. From Utinta area samples were taken in early and late evening, and in both samples the highest abundances were at the surface. In the Utinta transect, in the morning and evening the highest values were at the surface, but at noon the surface sample was impoverished and highest abundance was at 10 m. In Mahale area the highest values were again at the surface. The lowest bacterial abundances were found in Ujiji area, but highest values were again at the surface. In Kigoma area the samples were taken on two different days. In the first sample, bacterial abundances were quite similar in the whole water column, but in the second sample there were large differences in abundance between the surface and deeper water layers. Also off Malagarasi bacterial values were highest at the surface.

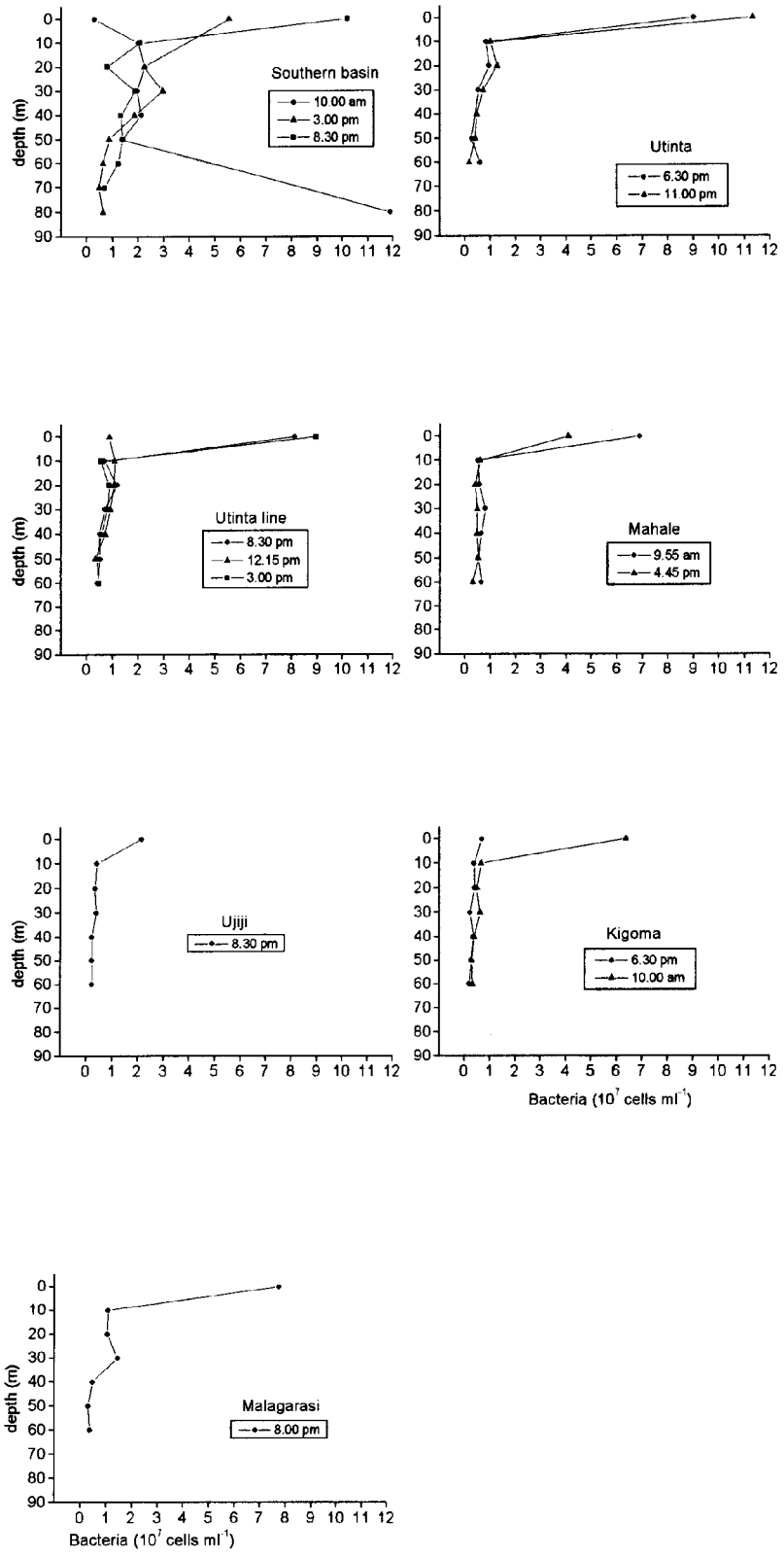

Fig. 1. Vertical profiles of bacterial abundance in different areas of Lake Tanganyika on 21-31 March 1998.

DISCUSSION

In earlier LTR studies on the vertical distribution of bacteria in Lake Tanganyika, the abundances varied from 0.38-3.09* 10^6 cells ml^{-1} and the highest bacterial numbers were at about 20 m depth (K. Salonen, pers. comm.). In the present study, the maximum bacterial abundances (1.6* 10^6 - 1.2*10^8 cells ml^{-1}) were very high compared to the previous LTR study or to literature values (0.14-1.4 * 10^6 cells ml^{-1}; Coulter 1991). Earlier studies suggested highest bacterial abundances in the south basin, and this was the case also in the present study. It may be worth noting that in the present study the very high values were restricted to the surface samples.

The observation of the highest bacterial abundances at the surface was unexpected. At the very surface the bacteria are exposed to strong solar radiation which might damage their cells. However, the so-called surface samples were taken from about 1 m depth, relieving them from the strongest UV light. In simultaneous samples the phytoplankton peak was always deeper in the water column (K. Vuorio, pers. comm.), which makes it even more difficult to explain the bacterial distribution. Some speculations are still possible. The concentration of dissolved organic carbon (DOC) in Lake Tanganyika is quite low, but the highest concentrations have been found near the surface (Järvinen et al. 1996). At the surface, UV-light can cause photochemical reactions splitting larger organic molecules to smaller ones (Kieber et al. 1990). The smaller compounds are more available to bacteria (Strome & Miller 1978), and this might explain high bacterial values at the surface.

The concentration of DOC has been suggested to increase in the south due to upwelling which brings DOC from deeper water to epilimnion (Coulter 1991). Indeed, in the present study bacterial abundances in the uppermost water layers were highest in the southern basin and in the Utinta area. Although phytoplankton is the main carbon source for secondary production, also allochthonous input of DOC might explain bacterial abundances at the surface, especially in the Malagarasi area where the river water brings organic matter to the lake. It should also be noted that as a consequence of major floods in Jan.-Feb. 1998, unusually much macroscopic organic material was floating all over Lake Tanganyika still in March, which probably increased the availability of DOC in the surface water. The situation was thus quite different from the conditions prevailing during the long dry period when the previous bacterial studies of LTR were made.

One reason for the elevated bacterial counts in surface samples might be contamination from the vessel. To check this possibility, control samples were taken in front of the vessel when it was slowly moving forward. This was done once off Kigoma and once off Ujiji. In the Kigoma sample, numbers of bacteria did not differ from other surface samples taken

from the same area, but in the Ujiji sample bacterial abundances were considerably lower than in a sample taken from the immobile vessel, being quite similar to samples taken from deeper water in the area. More numerous tests should have been done to eliminate the possibility of contamination by the vessel.

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THE FOOD UTILISATION AND DIEL FEEDING PATTERN OF SHRIMPS (ATYIDAE AND PALAEMONIDAE) IN LAKE TANGANYIKA

Maiju Viherluoto

INTRODUCTION

The high fish yield and its correct utilisation in African lakes is very important to local people. In East Africa, almost half of the total human consumption of animal protein is obtained from fish. In Lake Tanganyika, efficient fishing started in the 1950s and since then there have been clear changes in the fishstock. Some species have almost disappeared. Now there are six abundant fish species in the lake: the planktivores *Stolothrissa tanganicae* and *Limnothrissa miodon* and four predatory fishes from the genus *Lates* (Coulter 1991). Because of the growing human population, the need for fishing is not decreasing with the decrease of fish yield and fish species, and it is important to know what supports the fish production.

Basically, fish production is based on the amount of phytoplankton which regulates the growth of all species on the higher trophic levels. Between phytoplankton and fish, the energy flows through zooplankton, which makes the zooplankton important for fish production (Kurki et al. 1999b). Also the predatory fishes, which generally feed on other fishes, need zooplankton in their juvenile stages because zooplankton has a better energy content than phytoplankton (Koli et al. 1988; Post & McQueen 1994). Fernando (1994) has shown that the timing of fish reproduction depends on the abundance of zooplankton because the plankton species of different size are the most important food for juvenile fishes. The density of planktivores is in direct correlation with the abundance of zooplankton (Hanek & Craig 1995).

Zooplankton may also regulate primary production. The numbers of grazers have to be sufficient to regulate the density of phytoplankton crop in relation to the nutrition level of the lake (Moreau et al. 1993). The consumers at the next trophic level, the fish, are very abundant and they regulate the production, age and size distribution of zooplankters (Coulter 1991). The distribution of different zooplankton groups varies between different areas of Lake Tanganyika and the distribution depends probably on different patterns of mixing due to seasonal winds (Kurki et al. 1999a,b) and on the intensity of predation. In the southern parts of the lake the most abundant species are calanoid copepods (Copepoda: Calanoida) and shrimps (Atyidae: *Limnocaridina*, Palaemonidae: *Macrobrachium (Palaemon)*) and in the northern parts cyclopoid copepods (Copepoda: Cyclopoida) and jellyfish (Cnidaria: *Limnocnida*) (Craig 1997; Kurki et al. 1999a).

The fishes prefer different groups of zooplankton in their diet. In the southern parts of the lake the most abundant fish species is *Lates stappersii* and in the

northern parts the planktivorous fishes. Shrimps have been found in the stomachs of *Lates stappersii* and *Stolothrissa tanganicae*. The abundance of shrimps in the diet depends on the area and the time of the year (Rufli & Chapman 1975; Kurki et al. 1999a). Near Kigoma (northern part of the lake) shrimps were found in the stomachs of fishes almost every month and in the south constantly every month (Kurki et al. 1999a). Shrimps become available for fishes because of their vertical migration between surface and deeper water. They migrate downwards through water column to escape visual predation in daytime and return upwards at night to feed in the surface layers where food is more abundant (Coulter 1991). Shrimps are a good source of energy for the fishes because of their big body size (up to 1-2 cm) compared to zooplankton (Narita 1987). Shrimps constitute only 2 % of the total numbers in zooplankton samples in the lake but their relative biomass is much higher (Coulter 1991). The uneven distribution of fish species in the lake may be related to the uneven distribution of different zooplankton groups (Hanek & Craig 1995). Because zooplankton and, especially in the south, shrimps compose a big proportion of the diet of fishes (Sona 1989; Kurki et al. 1999a) it is important to study also the diet of shrimps and the diel periodicity of their feeding. Research on the food resource utilisation and feeding time gives good information of the efficiency of energy flow from zooplankton to higher trophic levels.

The main aim of this study was to find out what the different species of shrimps eat. In addition, the diurnal timing of feeding was studied. Comparisons were also made between the stomach contents of shrimps from different parts of the lake (northern, middle and southern part).

MATERIALS AND METHODS

The shrimp samples were taken from three places in different parts of Lake Tanganyika. The first samples were taken from the middle of the lake outside of the delta of the river Malagarasi, the second samples from the northern part of the lake, Kigoma sub-basin, and the third samples from the southern part of the lake, Moba sub-basin. The samples were taken from the research vessel Tanganyika Explorer between 11 and 24 March 1998 with the Gulf-sampler (Kelso & Rutherford 1996). Samples were taken at different times of the day, in daylight, at dusk, at night and at dawn. The sampler was hauled about 25 minutes behind the vessel at a speed of three knots at different depths so that as many shrimps as possible were caught irrespective of their possible vertical migration.

The shrimps were identified to the species level and their body length was measured (from the base of compound eyes to the tip of telson) to the nearest millimetre (as in Mashiko et al. 1991). The stomach was dissected and opened in a water drop on a glass slide. For abundant species, six stomachs were opened from each sample. For species of which few individuals were found in the samples, all stomachs were

opened. Altogether 101 stomachs were investigated for the three species using a research microscope (magnification of 100-320). The stomach contents (both phytoplankton cells and zooplankton pieces) were identified to the lowest possible taxonomic level.

RESULTS

Three species of shrimps were found in the samples. The most abundant species in all three sampling areas was *Limnocaridina parvula,* numerous individuals of which were found in every sample. The other two species, *Limnocaridina spinipes* and *Macrobrachium moorei*, were not present in every sample. *M. moorei* was more abundant in the southern part of the lake than in the middle or northern parts. The individuals of the two species of genus *Limnocaridina* were much smaller in length than *Macrobrachium* shrimps (3-6 mm, 6-22 mm, respectively) (Fig. 1).

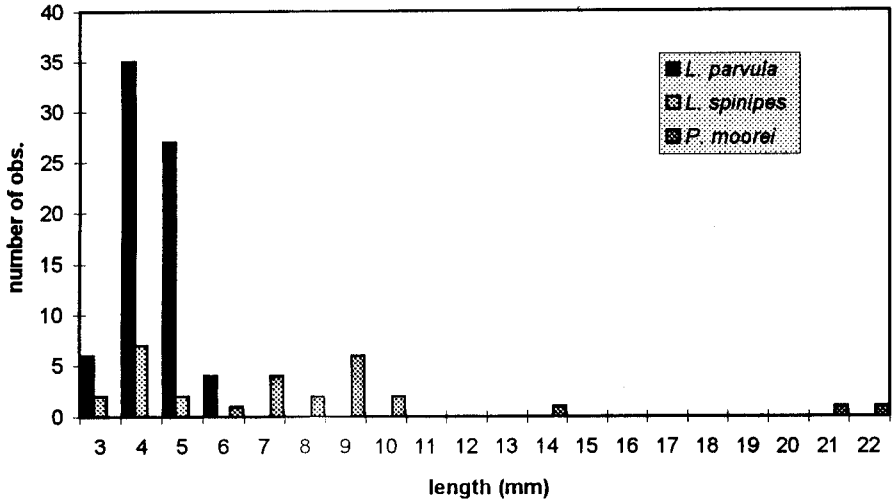

Fig. 1. The length distribution of the three shrimp species found in Lake Tanganyika.

The timing of feeding and the stomach contents

The samples were taken at four different times of the day. In the daytime when the sunlight was very strong, the stomachs of shrimps were empty. At other times when the light conditions were low, at dusk, at night and at dawn, the stomachs and guts clearly contained eaten food. So the stomach content analyses were all based on the dusk/night/dawn samples.

The diet analyses were based on 72 stomachs from *Limnocaridina parvula* and on 11 stomachs from *Limnocaridina spinipes*. The diet of these two *Limnocaridina* species consisted only of phytoplankton. The main component of the diet in both species was diatoms (>65 %). Other groups which were found were blue-green algae and dinoflagellates (Fig. 2).

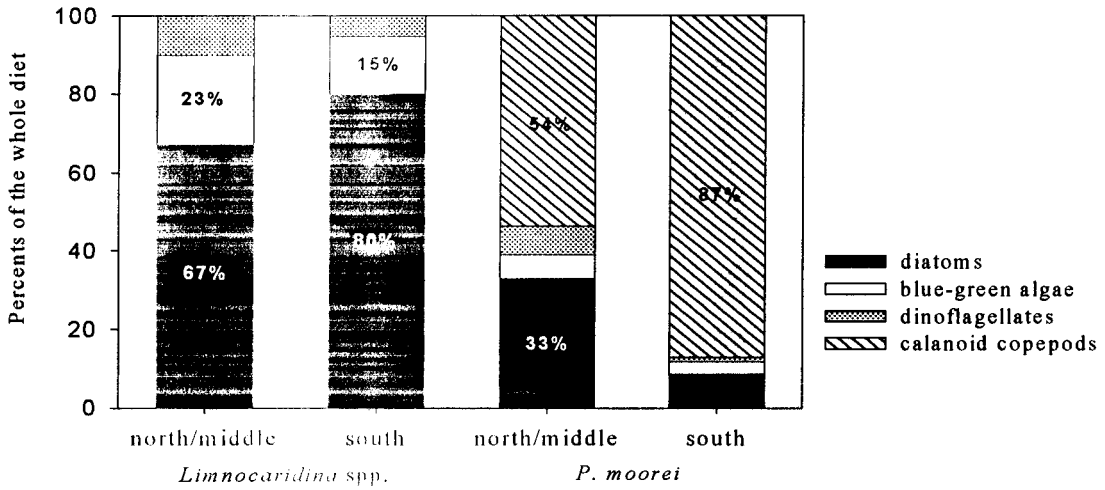

Fig.2. Stomach contents of *Limnocarudina* spp. *and Macrobrachium moorei* in different parts of Lake Tanganyika. Contents are average values of all stomachs in every category. Percentages represent particles found in the stomachs. North and middle-part stomachs are put together because they were similar, and also stomachs of both *Limnocaridina* species are put together.

The diet analyses from *Macrobrachium moorei* are based on 18 stomachs. *M. moorei* ate both zooplankton and phytoplankton. Zooplankton parts in the stomachs were all from calanoid copepods. In a few stomachs the copepods had remained whole but most often the recognition was based on antennas, pieces of legs and furca. Phytoplankton cells belonged to diatoms, blue-green algae and dinoflagellates. Diatoms constituted the main part of phytoplankton diet also *M. moorei* (Fig. 20. Other phytoplankton groups were not found in every stomach but only occasionally. The diets of *Limnocaridina* spp. and *M. moorei* differed from each other. Significant differences were found between the amount of diatoms and copepods (Mann-Whitney U-test $z=-2.92167$, $p<0.001$, N= 101, respectively). In the analyses two *Limnocaridina* species were put together because their diets were similar. There were no major differences between the diets of shrimps taken at dusk, at night or at dawn.

Diet in different parts of the Lake

The diets of *Limnocarida* species did not significantly differ from each other between the three different parts of the Lake Tanganyika. At all three locations both species fed mainly on the diatoms, and blue-green algae and dinoflagellates were found in the stomachs infrequently. The diet of *M. moorei* was clearly different in the southern part of the lake from the diet in the middle or northern parts. In the south, stomachs consisted almost only of calanoid copepods and also some diatom frustules were found. In the middle part and in the north, diets were similar, consisting of calanoid copepods and phytoplankton cells in equal amounts. Significant differences were found only in the

amount of dinoflagellates between south and north samples (Tukey's HSD test for unequal N, $p<0.05$, N=18).

DISCUSSION

Diel feeding

The shrimps in Lake Tanganyika seem to be feeding only from dusk till dawn, i.e. when the light is dim enough. This feeding rhythm is probably related to vertical migration. In Lake Tanganyika it has been noticed that besides zooplankton also shrimps migrate vertically (Coulter 1991). The migration depends on the light level in the water column. In the evening when the sun goes down shrimps swim towards surface to feed and in the morning when the sun rises they swim downwards to deeper waters, probably to escape visual predation. The vertical migration is an important factor influencing the feeding patterns of macrozooplankton. This has been noticed widely for example in the Baltic (Rudstam et al. 1992) and in Lake Michigan (Bowers & Vanderploeg 1982). Also in the tropics, vertical migration of prawns has been observed (Moreira & Odinetz 1993). The surface waters offer shrimps larger food supply than the deeper parts of water column. Phytoplankton biomass is restricted to the upper 60 meters of water. This part of the water column is too bright for shrimps except after dusk when the light level decreases and it is safer for shrimps to swim and ascend. Shrimps migrate vertically to avoid predation and to get where the food is most abundant.

The two genera of shrimps in the lake fed predominantly on different food items. This cannot be explained on variations in food supply because all three species were present in all parts of the lake. The main reason is probably the size difference of the species. *Limnocaridina* species are just a few millimetres long whereas *M. moorei* individuals may be even 2 centimetres long. Small shrimps may not be able to catch zooplankton and therefore mainly feed on phytoplankton cells which are not escaping the approaching shrimps. Also *M. moorei* ate phytoplankton but in almost every stomach also parts of copepods were found. Smallest *M. moorei* individuals were 6 to 7 millimetres long, or as long as the biggest individuals of the *Limnocaridina* species. We may ask why similar size *M. moorei* and *Limnocaridina* spp. eat different kinds of food? This size can be the threshold size of shrimps. In mysids (Mysidacea), which correspond closely in size with the present shrimp species, the threshold size at which they start to eat zooplankton is at a length of from 5 to 7 millimetres. Below that size the main food is phytoplankton (Viherluoto et al., in prep.). If this is the case with shrimps of the Lake Tanganyika, too, then it can be that some small individuals of *M. moorei* eat only phytoplankton and some others eat both zooplankton and phytoplankton. As to their size, the largest individuals of *Limnocaridina* species would be able to feed on zooplankton, but they did not. They were herbivores and *M. moorei* was an omnivore despite of the sizes of individual shrimps.

As an obligate herbivore, *Limnocaridina* may affect phytoplankton communities, especially because *Limnocaridina parvula* is very common in the lake. *M. moorei* might influence both phytoplankton and zooplankton communities. In the southern parts of the lake, the dominating species in zooplankton community are calanoid copepods. This is probably the reason why calanoid copepods are the main part of the diet of *M. moorei.* They are both most abundant in the same areas of the lake. Copepods are the only larger zooplankters available for the shrimps because in Lake Tanganyika there are no cladocerans (Coulter 1991) and other species are much smaller in size.

Shrimps are a part of the diet of at least two fish species (*Lates stappersii* and *Stolothrissa tanganicae*) (Rufli & Chapman 1975; Kurki et al. 1999a). *Limnocaridina* shrimps are smaller and their energy value for fish can be lower than that of *M. moorei,* because *Limnocaridina* feed only on phytoplankton which is nutritionally worse quality food than zooplankton (Adare & Lasenby 1994). In the southern part of the lake *M. moorei* is more abundant than in other areas. There their effect on fish populations is more pronounced and their abundance might affect fish densities.

Interestingly, shrimps resemble mysids (Mysidacea) and krill (Euphausiacea) in their trophic position in the ecosystem. Mysids and krill eat both phytoplankton and zooplankton regulating densities of plankton communities and on the other hand they are important prey for many fish species (Mauchline 1980). Tropical freshwater lakes lack both groups. Krill are oceanic species and mysids are found in the tropics only in brackish lagoons (Dumont et al. 1994). In Lake Tanganyika endemic shrimps fill this same niche when competitive groups are absent.

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SPATIAL DISTRIBUTION OF PHYTOPLANKTON, CHLOROPHYLL *A* AND TOTAL PARTICULATE NITROGEN AND PHOSPHORUS IN LAKE TANGANYIKA

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INTRODUCTION

Lake Tanganyika is meromictic and oligotrophic. Because the residence time of water is long and the reserves of nutrients are in the deep waters, the productivity should be mostly dependent on internal nutrient loading. Deep waters can be important sources of phosphorus, but rainfall, riverine inputs and *in situ* biological nitrogen fixation are considered to be possible sources of nitrogen. The pelagic food web resembles those of marine systems (Coulter 1991). Phytoplankton biomass is low but the growth rate is high (Hecky & Fee 1981) and organic carbon is accumulated as fish yield. Lake Tanganyika is known to have a productive pelagic fishery (Sarvala et al. 1999).

Phytoplankton are the major primary producers in many aquatic systems and are an important food source for consumers (Reynolds 1984). The most important factors regulating phytoplankton community dynamics are light, temperature, water column mixing, nutrients, organic substances and grazing. Light and temperature are quite constant in tropical lakes, and nutrients are generally considered to limit algal productivity (Coulter 1991). In temperate lakes phosphorus (P) is considered to be the limiting nutrient (Reynolds 1984), while in the tropics nitrogen (N) has been suggested as the nutrient most likely to limit algal growth (Coulter 1991). However, conditions in lakes vary widely both spatially and temporally, and there can be deficiency as well as sufficiency in both macronutrients (Reynolds 1984). In large lakes with long residence times, the particulate nutrient composition ratios reflect the general availability of N and P for growth and the ratios of particulate nutrients may be the simplest and most comparable way of defining nutrient status of phytoplankton (Hecky et al. 1993).

Only a few studies have previously examined the phytoplankton community structure in Lake Tanganyika (e.g. Hecky & Kling 1987; Cocquyt et al. 1991), and the earliest ones were mainly descriptive (West 1907 and Van Meel 1954 cit. Coulter 1991). In this study, phytoplankton was studied together with chlorophyll *a* (chl *a*) concentration and total particulate nutrients (N and P) to get more accurate information about the distribution of phytoplankton in Lake Tanganyika. The emphasis of the paper is in the spatial distribution, whereas the vertical distribution will be discussed elsewhere. The vertical and horizontal distribution of *in vivo* fluorescence is presented by Salonen et. al. (1999) and the nutrient limitation of phytoplankton is also discussed more closely in Järvinen et. al. (1999).

MATERIAL AND METHODS

The study was carried out during cruises onboard R/V Tanganyika Explorer between 3 March and 1 April 1998, during the wet season. Samples from 23 study locations (Fig. 1) were taken from the surface to the depth of 60 m at 10 m intervals with a darkened 1 m long tube sampler (diameter 10 cm, Limnos Ltd, Finland).

The phytoplankton samples (100 ml) were preserved immediately with 0.25 ml acid Lugol's solution. Phytoplankton samples were counted with an inverted light microscope (Olympus IMT-2) using standard Utermöhl technique (Utermöhl 1958). For phytoplankton counts, 50 ml of each sample was allowed to settle. Phytoplankton were identified to species level whenever possible.

For chl *a* determinations, two litres of water were filtered (filtration area 13.20 cm^2) through Whatman GF/C or GF/F glassfibre filters. The filters were stored at –20 °C in a freezer, dried at 60 C to constant weight, and stored in darkness. The laboratory work was completed at Lammi Biological Station, University of Helsinki. In the laboratory, four pieces of 0.84 cm^2 were punched from each filter for the determination of chl *a*. From the filters, chl *a* was extracted in 7 ml of 96 % ethanol using 75 ?C water bath for 5 min (Keskitalo & Salonen 1994). Chl *a* was determined with a HITACHI F-4000 Fluorescence spectrophotometer (emission at 671 nm and excitation at 435 nm), calibrated against pure chl *a*. The remaining part of each filter was used for N and P determinations using a wet oxidation method (Koroleff 1983).

The water transparency was measured as Secchi depth during daytime sampling. Vertical temperature profiles were measured at some study locations with CTD. Water currents were registed at several locations with ADCP.

RESULTS

Altogether 204 taxa were identified; including 38 taxa of Cyanobactetria, 4 taxa of Cryptophyceae, 4 taxa of Dinophyceae, 32 taxa of Diatomophyceae and 89 taxa of Chlorophyceae. Most of the identified species seemed to be cosmopolitan. The most abundant cyanobacterial species, *Chroococcus* cf. *mipitanensis* (Wolosz.) Geitler and *Anabaena* sp., were found most commonly in the southern part of the lake. Chlorophytes, *Kirchneriella* cf. *mayori* (G.S. West) Kom.-Legn. in Kom., *Lagerheimia subsalsa* Lemm. and *Monoraphidium*

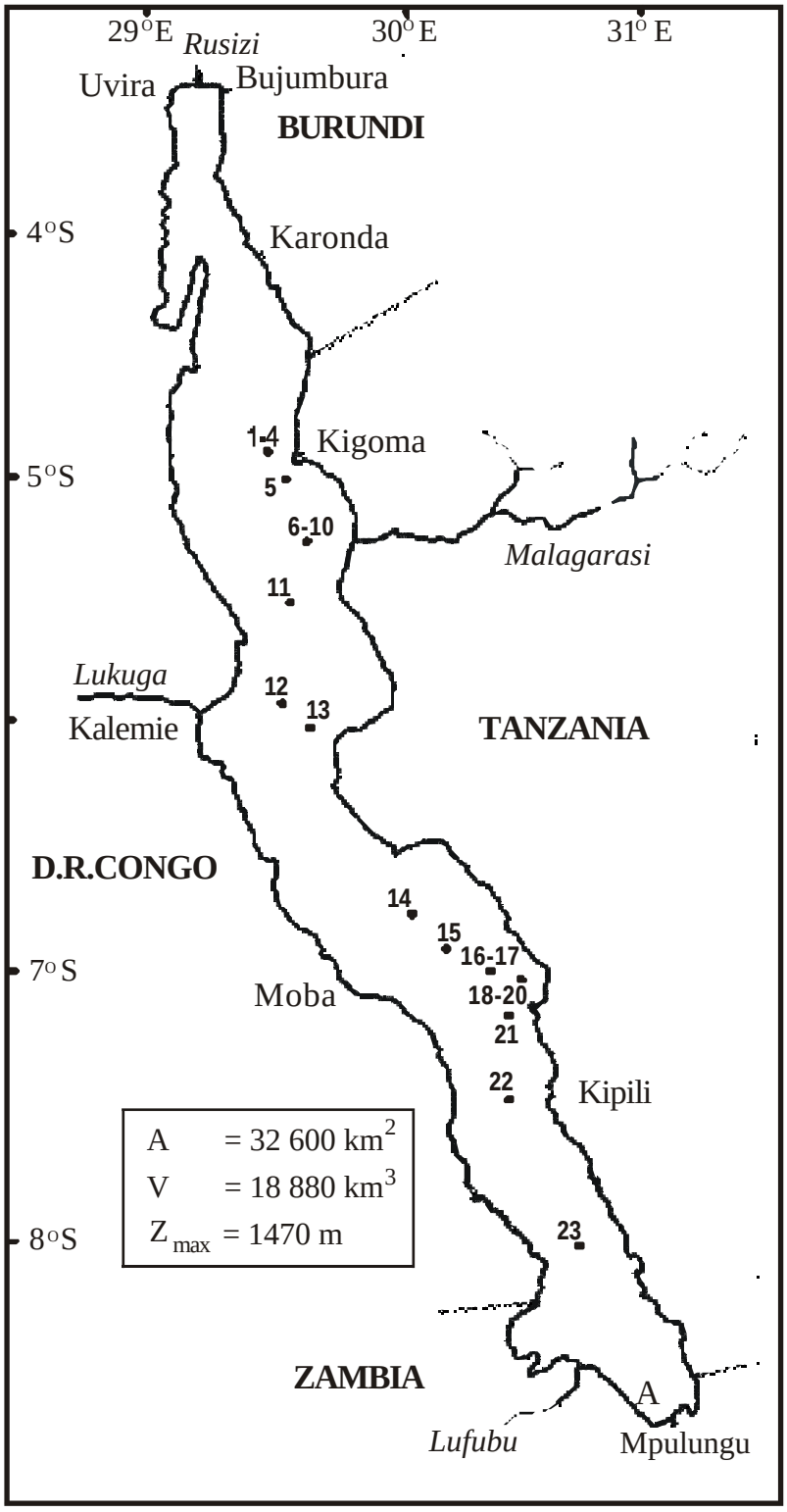

Fig. 1. Study locations in Lake Tanganyika in March 1998.

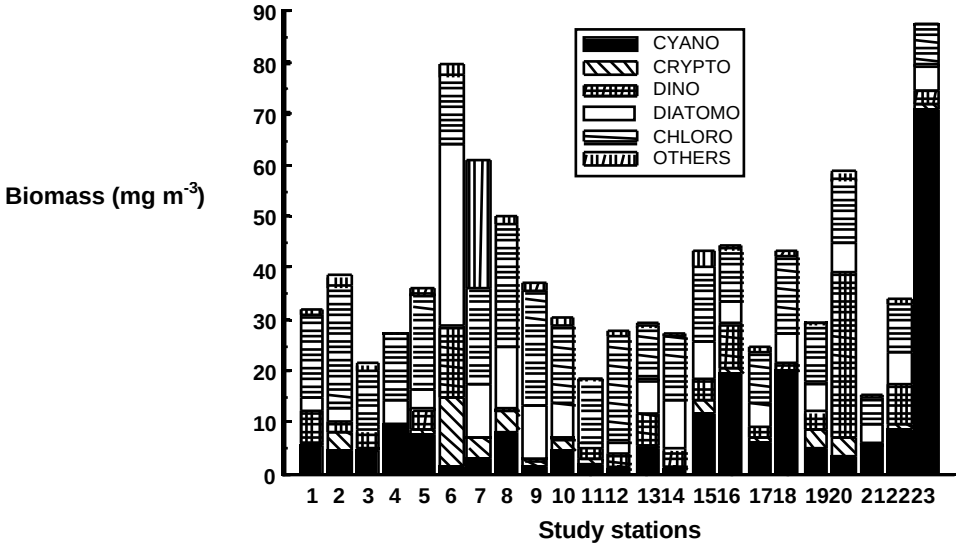

Fig. 2. Average phytoplankton biomass at the study locations in Lake Tanganyika from 11 March to 31 March 1998 (CYANO = cyanobacteria, CRYPTO = cryptophytes, DINO = dinophytes, DIATOMO = diatoms, CHLORO = chlorophytes and OTHERS = other phytoplankton groups).

minutum (Naeg.) Kom.-Legn. were present in almost every sample. The most common diatoms were *Achnanthes* spp., *Nitzschia* spp. and *Nitzschia actinastrioides* (Lemm.) van Goor. Cyanobacteria and chlorophytes dominated the upper part of the water column (10-30 m), while diatoms and dinophytes were found most abundantly in deeper water layers (40-60 m).

Total phytoplankton biomass in the whole lake (Fig. 2) varied between 16.0 and 87.6 mg m^{-3} wet mass. The biomass maximum was found in the southernmost part of the lake (study location 23). The whole lake total biomass average was 39.1 mg m^{-3} (s.d. = 18.2, n = 23). Both horizontal and vertical distribution of algal biomass varied between study locations. The total phytoplankton biomass maximum was most commonly at 10 or 20 m depth. The waters off Malagarasi made an exception and the maximum was near the surface. The water was very clear (Fig. 3) and the visibility varied between 11 and 16 m, except off Malagarasi where the water transparency was the poorest measured (3 m). The surface temperature was rather high, about 28 ?C and the thermocline was steeper towards the northern end of the lake. The horizontal currents often flowed in opposite direction in water layers above and below about 30 m depth.

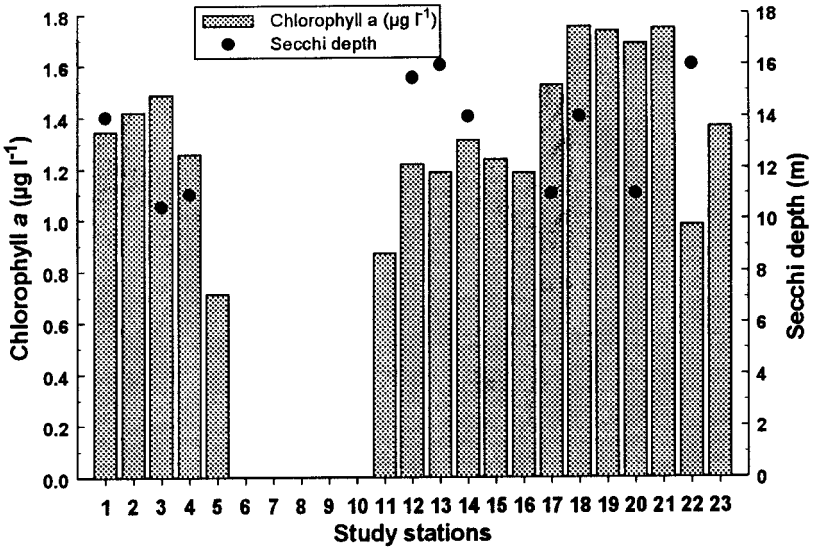

Fig. 3. Distribution of chlorophyll *a* mean concentrations (µg l^{-1}) and Secchi depth between study locations in Lake Tanganyika from 17 March to 31 March 1998.

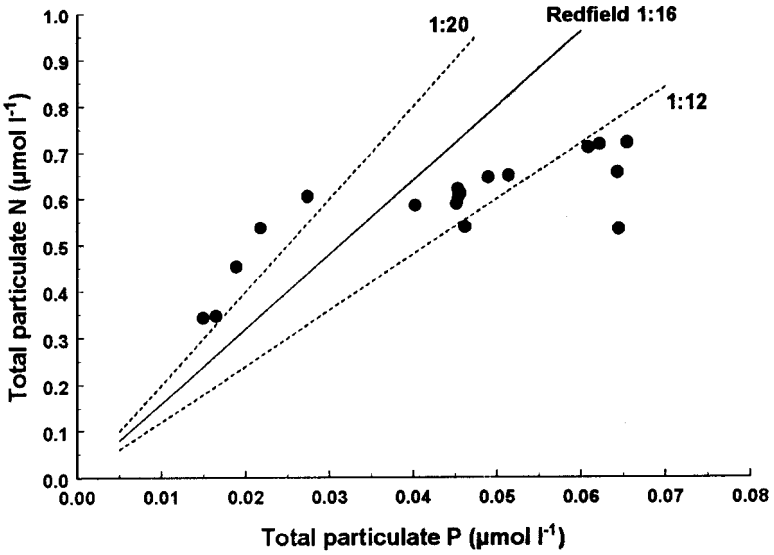

Fig. 4. The ratio of the average total particulate nitrogen to total particulate phosphorus by study locations compared to the Redfield ratio in Lake Tanganyika from 17 March to 31 March 1998.

The mean concentration of chl *a* varied from 0.87 to 1.75 µg l^{-1}, (Fig. 3), the whole lake average was 1.36 µg l^{-1} (s.d. = 0.27, n = 23). The maximum of chl *a* concentration was most commonly found from 30 to 50 m depth. The total particulate nitrogen (Fig. 4) varied between 0.356 and 0.720 µmol l^{-1} (x = 0.591, s.d. = 0.099, n = 18). The minimum value of total particulate phosphorus (Fig. 4) was 0.016 and maximum 0.065 µmol l^{-1} (x = 0.045, s.d. 0.018, n = 18). The ratio of N to P (Fig. 4) varied between 8 and 25 by mass (x = 15, s.d. = 6, n = 18). The whole lake average of N to P ratio (by mass) was quite close to the Redfield radio and the ratios

determined earlier by Edmond et al. (1993) and Järvinen et. al. (1999). The ratio indicated that 13 of the locations were N limited and five of them were P limited. Chl *a* showed clear correlation with N and P, and also N to P ratio.

DISCUSSION

The total phytoplankton biomass was low in comparison to previous studies (Hecky & Kling 1981; Cocquyt et al. 1991), although the lowest biomasses were detected during the wet season also in those studies. Similar seasonal pattern was found in polymictic, eutrophic Lake Xolotlán in Nicaragua, were the biomass decreased during the rainy period because of decreased wind and less turbulence which allowed less buoyant species to sink into deeper water layers (Coulter 1991; Edmond et al. 1993 and Erikson 1997). As usual in wet seasons, similar climatological conditions with low wind velocity and low water turbulence also prevailed in Lake Tanganyika during the present study. High water transparency also indicated low phytoplankton biomasses. The phytoplankton species composition seemed to be quite similar to the studies of Hecky & Kling (1987), although the number of species now identified was almost double the previous numbers.

Neither the phytoplankton species composition, total phytoplankton biomass, chl *a* nor the N and P concentrations and N to P ratio did not show any clear spatial pattern. The ratio between phytoplankton biomass and chl *a* concentration indicated the influence of photoadaptation and photoinhibition on the chl *a* concentrations of phytoplankton species (Salonen et al. 1999). Differences in temperature gradients showed dissimilarities in water column mixing between study locations, which might have had an influence on the horizontal distribution of phytoplankton. Also the horizontal currents flowing into opposite directions may have affected the phytoplankton biomass and species composition.

The particulate nutrients have been measured only once before (Sarvala & Salonen 1995; Järvinen et al. 1999). The whole-lake mean of N to P ratio (by mass) was, however near the Redfield radio and the variation of the ratio disagreed with the idea of tropical freshwaters being N-limited (Edmond et al. 1993). The lake seemed to be P limited when the P concentration was lowest and N limited when the P concentration was higher. The phytoplankton biomass and chlorophyll *a* concentration varied between study locations mainly because of variability in P concentration.

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FOOD SELECTION AND LARVAL DISTRIBUTION OF *Stolothrissa tanganicae* AND *Limnothrissa miodon* IN THE PELAGIAL ZONE OF LAKE TANGANYIKA

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1. INTRODUCTION

Lake Tanganyika has a rich and diverse fish fauna, which is often divided in two categories: cichlids and non-cichlids. Highest diversity of species occurs in the littoral zone, while economically important pelagic fish stocks consist mainly of six species, which all are non-cichlids. Most important target species of the commercial and artisanal fishing are two clupeids, *Stolothrissa tanganicae* and *Limnothrissa miodon*, and one of the native Nile perch species, *Lates stappersii* (Coulter 1991). Three other Nile perch species, *L. angustifrons, L. mariae* and *L. microlepis* are caught in smaller numbers.

The clupeids, *Stolothrissa tanganicae* and *Limnothrissa miodon*, have different life strategies. *S. tanganicae* spawns in the pelagic zone, where it also spends its larval stage. After reaching the length of 35 mm *S. tanganicae* migrates to the littoral (Coulter 1991, Mannini *et al.* 1996). Later when 50 mm long, *S. tanganicae* returns back to the pelagial. *Limnothrissa miodon* in turn grows its first year in the littoral and migrates to open waters at the length of 40 mm (Coulter 1991).

Stolothrissa tanganicae is supposed to be more specialized into planktivorous feeding than *Limnothrissa miodon* (Matthes 1967) and to use pelagic zooplankton as its primary prey. At the beginning of the exogenous feeding it is said to feed mainly on phytoplankton (Coulter 1991). *L. miodon* on the other hand can use a broader variety of prey species, so it can benefit from spending the larval stage in the littoral zone, where the diversity of the prey species is widest. Especially after migrating to pelagic waters, *L. miodon* uses besides zooplankton also shrimps and larvae of *S. tanganicae* as food (Ndugumbi *et al*. 1976, after Mannini *et al.* 1996) .

Lates stappersii has a similar life history with *S. tanganicae* and they are thought to share same niche; both live their life in the pelagics and therefore the larvae of *S. tanganicae* are exposed to predation by *L. stappersii. L. miodon* avoids predation caused by *L. stappersii* by spending its larval stage in littoral. When migrating to the pelagics, *L. miodon* is big enough to avoid predation. Another possible reason for *L. miodon's* littoral stage is the smaller food items needed at the larval stage (Blaxter 1969, Kamler 1992); littoral zone contains small sized rotifers, while simplified pelagic fauna is poorer by its

diversity, forming mainly of copepod -crustaceans. In this study, interspecific competition between *Stolothrissa tanganicae* and *Limnothrissa miodon* in terms of habitat overlapping was investigated for the first time at the species' larval stage. The size distribution of young fish of lake Tanganyika is poorly known and therefore the density analyses of the newly recruited individuals are important in understanding the stock size fluctuations. (May 1974, Ponton *et al.* 1988, Helminen 1994).

2. STUDY AREA

Lake Tanganyika is an ancient, tectonic and meromictic lake situated at East African Rift valley system (3°20'-8°48' S, 29°03'-31°12' E). It is 673 km long, 48 km wide and has a surface area of 32 900 km^2. The maximum depth is 1470 m and the mean depth is 700 m. The volume is 18 880 km^3, it contains one fifth of all the free freshwater in the world (Coulter 1991).

This study focused on three pelagic areas of Lake Tanganyika: (1) Kigoma sub-basin, (2) delta of river Malagarasi and (3) Moba sub-basin (Appendix 1). The sub-basin of Kigoma is deep (mean depth of sampling points 962 m) situated in the central part of lake. The sub-basin of Moba is shallower (mean depth of sampling points 270 m) situated in the southern part of Lake Tanganyika. The delta of Malagarasi differs from the other two areas being shallow (mean depth of sampling points 154 m) and heavily loaded by organic input of Malagarasi River (Coulter 1991).

3. MATERIAL AND METHODS

3.1 Sampling of larval clupeids

Fish larvae were sampled with the GULF-V sampler (pulling speed 3 - 4 knots) (Snyder 1983). Samples were collected around midday, dusk, midnight and dawn during March 11 – 31, 1998. One GULF-V sampling haul took 25 minutes. Sampling depths were adjusted by the wire length and verified by Koden Color Sonar ESR 150 (Fig. 1). The larvae caught were immediately preserved in 5 % formaldehyde solution.

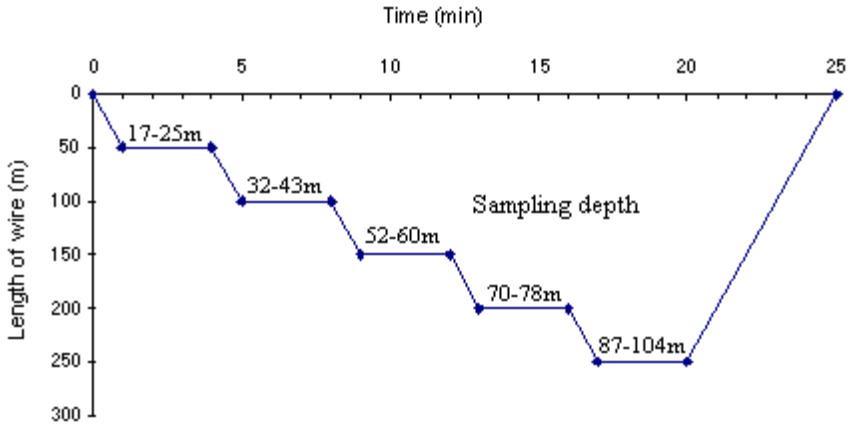

Figure 1. GULF-V sampling procedure; sampling time and relation of given wire to sampling depth.

Quantification of the larval density was based on the volume sampled. The volume of a sample was calculated according to formula (1):

(1) $Q = a * l$

where Q is the volume filtered by the sampler (m^3), a is the area of the sampler's mouth opening (m^2) and l is distance that the sampler has moved (m). Before density analysis samples were subsampled (to 1/3 or 1/4) using the HMLB method (Alden *et al*. 1982).

3.2 Sample treatment

The fish densities were calculated as individuals per cubic meter (ind./m^3). From each sample 10-30 larvae were measured and grouped into 1 mm length classes. Habitat overlap (α) was calculated according to the percentage similarity index (Renkonen 1938; Schoener 1968).
Analysis of variance and Sheffe's pairwise comparison was used to compare preferences between three pelagic areas, and differences in length distribution.

4 . RESULTS

4.1 Distribution of clupeid larvae

There was no significant differences in abundance of larvae *Stolothrissa tanganicae* between studied areas (p = 0.2, n = 28, ANOVA). The highest density was found in Kigoma sub-basin (12.2 ind./m^3), and lowest in delta of Malagarasi (8.8 ind./m^3). Malagarasi differed from other areas being the only location where the eggs of clupeids were found at one sampling point (abundance: 15.7 eggs/m^3, depth: 142 m, date: 31 March).

The abundances of *L. miodon* were significantly lower than *S. tanganicae* in every sampling areas ($p < 0.001$, n = 28, ANOVA) and the abundances differed also between studied areas ($p < 0.001$, n = 28, ANOVA). The highest densities were found in sub-basin of Moba (4.0 ind./m^3), where the main spawning areas are located (Coulter 1991). The density was lowest in sub-basin of Kigoma and delta of Malagarasi (density < 0.5 ind./m^3).

4.2 Length distribution

There were significant areal differences in the length distribution of the *Stolothrissa tanganicae* larvae: Kigoma sub-basin: mean length = 5.8 mm (SD = 1.5); Moba sub-basin: mean length = 6.8 mm (SD = 2.2); Delta of Malagarasi: mean length = 4.7 mm (SD = 1.7) ($p < 0.01$, n = 441, ANOVA).

The length distribution of *Limnothrissa miodon* larvae caught in Moba sub-basin differ significantly ($p < 0.05$, n = 144, Sheffe's test). Larvae were longer with the mean length of 8,1 mm (SD = 2.5) whereas in Kigoma sub-basin the mean length was 6,3 mm (SD = 2.2) and in Delta of Malagarasi 7.0 mm (SD = 2.5).

4.3 Habitat overlap

A significant habitat overlap between *Stolothrissa tanganicae* and *Limnothrissa miodon* was detected only in Moba sub-basin, where Shoener's index showed both habitat overlap ($\alpha_h = 0.75$). On the contrast, there were no significant niche overlap neither in Kigoma sub-basin ($\alpha_h = 0.54$) or delta of Malagarasi ($\alpha_h = 0.54$).

5. DISCUSSION

5.1 Abundance and length distribution of *S. tanganicae* and *L. miodon* larvae in studied areas

The study concentrated on pelagic zone of Lake Tanganyika. In respect of abundances of larvae, our results support the previous studies. The larvae of *S. tanganicae* were abundant in all studied areas, whereas the absence of *L. miodon* fits the assumption that it spends its larval stage in littoral zone. On the other hand, Stolothrissa is known to be in all life stages more narrowly specialized for pelagic life. (Coulter 1991, Mannini *et al*. 1996).

The larvae of *S. tanganicae* were unevenly distributed in all studied areas. The existence of *S. tanganicae* also in Malagarasi delta leads to conclusion that, *S. tanganicae* prefers shallow waters with reduced transparency, as a spawning site. The larvae caught from the delta of Malagarasi were also significantly shorter than in other areas being probably newly hatched. The finding is also supported by the fact, that the delta of Malagarasi was the only area where the eggs of clupeids were found. Because the

larvae of *L. miodon* were very infrequent in delta area, the eggs found were most likely *S. tanganicae*.

The result, that larvae of *S. tanganicae* were abundant also in deeper areas (Kigoma sub-basin) could be due to two reasons: first, newly hatched planktonic larvae can drift along the currents coming from Malagarasi river or second, *S. tanganicae* could have a pelagic spawning form (Matthes 1967). The highest mean length of larval *S. tanganicae* in Moba sub-basin may indicate an earlier spawning peak. The major annual spawning in southern parts of Lake Tanganyika (Zambia) is in August-December, when in Tanzania (Kigoma) there appears to be a later spawning peak (Coulter 1991), while Moba is located in between. Another explanation may be the better feeding efficiency and therefore faster growth, when compared with Malagarasi where the low visibility may reduce prey-predator encounter rate.

L. miodon was more present in southern part of lake. The sub-basin of Moba can be shallow enough as spawning area of *L. miodon* (Coulter 1991, Mannini *et al.* 1996), when the other studied clearwater area, the sub-basin of Kigoma, was evidently too deep. Absence of *L. miodon* in the shallowest area, the delta of Malagarasi, indicates that *L. miodon* avoids dark, turbid water, or at least does not spawn there.

Schooling behaviour, which is typical to *S. tanganicae* (Coulter 1991), can cause variation in density estimations. If the larvae school stays between the sampling depths (Fig. 1), the abundance of larvae will be underestimated. In this respect, the best sampling time could be the dusk, when the schools are known to be more disperse (Coulter 1991). However, estimates of abundance in this study were higher than obtained in previous studies. According to Coulter (1991), the abundance of fish larvae in Lake Tanganyika is < 1 to 10 m^{-3}.

5.2 Habitat overlap between *Stolothrissa tanganicae* and *Limnothrissa miodon* larvae

The habitat overlap occurs when two or more species share the same habitat. According to our results *S. tanganicae* and *L. miodon* are only partly competitors at the larval stage in the pelagial, since no significant numbers of *L. miodon* were found in this zone. There was evidence of habitat overlap only in the sub-basin of Moba, where the Shoener's index showed habitat overlap between larval *Stolothrissa tanganicae* and *Limnothrissa miodon*. This does not however mean that these species compete all the time, but during certain size classes only. More detailed studies are needed for evaluation of smaller scale partitioning of food and habitat resources, before making final conclusions on possible niche competition between *S. tanganicae* and *L. miodon* Besides habitat and food selection also the behavioural strategies involving optimal feeding and avoidance of predation should be involved in future studies.

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NUTRITIONAL VALUE OF SEVEN FOOD FISH SPECIES IN LAKE TANGANYIKA - HOW SUITABLE PEROXIDE AND FREE FATTY ACID VALUES ARE IN FISH LIPID QUALITY ANALYSES

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1. INTRODUCTION

Fisheries of Lake Tanganyika has great importance to regional protein consumption and employment involving about 40 000 full time and twice as many part time fishermen. Multiple number of people are engaged in primary and secondary sectors of fishing infrastructure (Leendertse et.al, 1991). Protein malnutrition is still the major nutritional problem in the third word. On a global basis, fish represent about 14% of animal protein and about 5% of total protein eaten and fish protein is an excellent source of animal protein (Mayre, 1962). It is estimated that 60% of people in developing countries obtain 40 - 100 % of the animal protein in their diets from fish. (NRI, 1996). It is also estimated that 25 - 30 % of total catch are lost because of post harvest fish losses (Ward et al., 1997). The losses due to spoilage and insect infestation occur mainly in traditional/artisanal and small-scale fisheries operations, in remote rural areas without any infrastructural facilities and supplies necessary for the proper handling, processing, storage (lack of cold chain) and marketing of catch. The spoiling of fish is mainly micro biological and it starts immediately after catching. The chemical spoiling starts usually with changes of lipid fatty acids and protein. The main reasons for spoilage of fatty acids are hydrolysing and auto-oxidation caused by sun and oxygen. The highly unsaturated lipids of fish are readily susceptible to attack by molecular oxygen. In this study the spoilage process of fats was assessed with peroxide value and free fatty acid value which are adequate for analysing fat quality in food. The spoiling reaction of fats proceeds by a free radical mechanism, and it is therefore characterised by an induction period followed by an accelerating rate of oxygen absorption with concurred developments of peroxides, rancid odours, and polymerised products. The rate of initiation of free radical chain is increased by light, heat, irradiation and heavy metals. Nutritional damages from the ingestion of oxidised fish lipids is caused by the toxicity of the peroxides (Olcott, 1962).

This study was made in Kigoma and it aimed at finding out if peroxide value and free fatty acid value are adequate for analysing fat condition in fish. The second goal aimed at assessing nutritional value of local fish species (*Lates stappersii,, Lates mariae, Lates angustifrons, Lates microlepis, Stolothrissa tanganicae, Limnothrissa miodon*, *Bathybates graueri*).

MATERIALS AND METHODS

Samples

Fish was caught by mid water trawling in front of Kigoma or bought on fish market in Kigoma during March and April 1998. Nutritional analyses were made in clupeids as whole fish and in others only in muscle taken from middle and back site of the fish (dried in oven ~12 h, ~60 ºC). *Stolothrissa* divided in tree size groups were analysed for the energy content. Sun dried clupeid from fish market in Kigoma were analysed for ash content. Fatty acid analyses were made in *L. miodon* (size 7-8 cm and 10.5-11.5 cm) and in *S. tanganicae* (size 7-9 cm) muscle with skin, *L. stappersii* (size 28-30 cm) and *L. mariae* were analysed in muscle (size 50-70 cm). Self caught clupeids *L. miodon* and *S. tanganicae* were immediately frozen, and kept under sun on ship deck for 1 h and frozen thereafter, or dried in oven (~12 h, ~60 ºC) for quality analyses. *L. stappersii* were bought from fish market (air temperature 26,5ºC) about 4-9h after catching. Fish were taken to controlled temperature (26.2℃-29.6℃ in the shade) and samples were analysed immediately, after 4h and 8h.

Nutritional analyses

To assess water content a representative sample was weighed accurately, dried in oven (about 12 h, 60℃) and re-weighed according to Connell (1995). The mineral content was determined by burning off at a high temperature (600 C, 4 h) the organic part of a known quantity of the product and weighing the residue of ash (Connell, 1995).

Total protein content was assessed by determining the nitrogen content of the sample and multiplying it by a factor 6,00 (Hendrik, 1974) representing the inverse of the known nitrogen content of the protein. Nitrogen content were determined by using the Kjeldahl method, recommended by the Association of Official Analytical Chemists. Total lipids were determined by using extraction method of Frings & Dunn (Dunn *et al*, 1969). Fatty acid fractions were extracted according to Folch *et al*. (1957), separated using a slightly modified method of Ågren *et al*. (1992) and Zhu *et al*. (1995) and methylated in methanol. The fatty acid methyl esters were analysed with gas chromatography (HP 5890 Series II, Hewlett-packard Company, Waldbronn, Germany) fitted with FID and equipped with HP-FFAP capillary column. Total energy content were determinated by using autobomb (Gallenkamp Autobomb, GWB) and calculated with following energy rations: 23.8 kj/g protein, 39.7 kj/g fat.

Methods for fat quality analyses

Peroxide value and assessment of free fatty acids are used to analyse fat quality in food. Peroxide value means the number of peroxides (milliekvivalents) in 1 kg fat. Peroxides are oxidised products of lipids that are created during the early state of oxidation. Degree of fats spoilage

can be estimated via the peroxide value during the early state of oxidation. Peroxide value of fresh fats should be < 10 mekv/kg and the values exceeding > 10 indicate the oxidation of fats. Free fatty acid value means the amount of fatty acids which are released from glyseride because of lipolytical enzymes, water and temperature. The value > 1 indicates that hydrolytic spoilage of sample is in progress. Fish fats were extracted and analysed according to Food chemistry laboratory practicals, University of Helsinki, 1992.

RESULTS AND DISCUSSION

Nutritional components

Pelagial species *L. miodon, S. tanganicae* and *L. stappersii* included less protein than *L. mariae, L. angustifrons* and *L. microlepis* which are more benthic in their ecology. Littoral dwelling *B. graueri* also contained slightly more protein than pelagial species (table 1). Hendrik et al. (1974) reported a little lower protein content for *S. tanganicae* 69.7 % , *L. miodon* 63.3 % and *L. stappersii* 77.0 %. Usually differences in protein content are small between fish species (Kukucz, 1962) and this was also true in studied species.

S. tanganicae and *L. miodon* had the same fat composition when analysed as whole fish. The fat content in *B. graueri* was higher in muscle than in whole clupeids. *L. stappersii* had greatest fat- % in muscle of these species. Fat content in other Lates were on other hand very low; *L. mariae* 3.2 %, *L. angustifrons* and *L. microlepis* 1 - 1.2 %. But this may also be because muscle samples were taken from dorsal part of fish and fat content also depend on the tissue studied. The accumulation of fat is considerably greater in the ventral than in the dorsal part of the body (Kukucz, 1962). In some Finnish fish species fat content of muscle has been low, in pike 0,7 % and perch 1,3 % (Nutritional components of food, 1993).

The water content is in inverse proportion to the amount of fat and energy content (Kukucz, 1962) which was clearly seen in this study. *L. stappersii* had highest fat and lowest water content (74.1 %) and *L. angustifrons* had lowest fat and highest water content (80.0 %).

Clupeids had higher ash (mineral) content than others but this was because they were analysed as whole fish including the bones and others only for muscle. *L. stappersii* had on the other hand also quite high ash content in muscle (almost as high as clupeids). Sun dried clupeids from fish market had greater ash content than in oven dried clupeids, which was probably because of sand contamination.

Table 1. Average composition (Mean ± SD) of different species, DM = dry matter, SD = standard division

Species	N=3	Protein % (DM) N% x factor	Fat % (DM)	Water %	Ash % (DM)
L. miodon (Adult)	3	12.5 x 6 = 74.8±1.77	5.2±0.67	79.2±0.29	12.5±1.41
S. tanganicae (Adult)	3	12.7 x 6 = 76.0±0.58	5.4±0.65	76.5±1.41	10.9±1.27
L. stappersii	3	12.4 x 6 = 74.5±0.30	7.1±0.38	74.1±1.45	10.4±0.58
L. mariae	3	13.7 x 6 = 82.3±1.96	3.2±0.43	80.7±4.56	5.2±0.07
L. microlepis	3	13.2 x 6 = 79.4±0.55	1.2±0.08	79.0±1.80	5.6±0.41
L. angustifrons	3	18.9 x 6 = 83.2±0.76	1.0±0.07	80.0±0.39	5.8±0.25
B. graueri	3	12.9 x 6 = 77.8±0.92	6.0±0.14	75.4±0.30	6.7±0.67
Dry Clupeid (market)		-	-	-	13.4±1.46

The energy content goes side by side with fat and protein content. Clupeids had lowest fat and protein content and also lowest energy content. *L. stappersii, L. angustifrons* and *L. microlepis* had almost similar energy content. *L. mariae and B. graueri* had highest energy content (*L. mariae* had high protein content and *B. graueri* had high fat and protein content). The energy content did not differ between different sizes of *S. tanganicae* but adult *L. stappersii* had higher energy content than fish of 8- 10 cm. Calculated energy contents were lower than the determinated and the differences between species also became smaller. The calculated energy content is less accurate because energy standards used for protein and fat are not species specific (Hendrik *et al.*, 1974)

Table 2. Energy value (Mean ± SD) of different fish species

Species	n	Energy (kj/g) Determinated (autobomb)	Energy (kj/g) Calculated (via protein and fat)
L. miodon			
(adult)	3	21.3 ± 0.26	19.9
S. tanganicae	3		20.2
4 - 5 cm *	2	21.9 ± 0.14	---
6 - 8 cm	3	21.0 ± 0.64	---
8 - 10 cm			
(adult)	3	21.3 ± 0.35	---
L. stappersii			
(adult)	3	24.3 ± 1.17	20.5
8 - 10 cm	3	21.2 ± 0.21	---.
L. mariae	3	24.0 ± 1.59	20.9
L. angustifrons	3	22.5 ± 0.36	20.2
L. microlepis	3	22.5 ± 0.00	19.4
B. graueri	3	23.7 ± 0.17	20.9

Fatty acids

The proportion of unsaturated (mono/poly) fatty acid is higher than the proportion of saturated fatty acid in all species. On the other hand *L. stappersii* and *L. mariae* contain less polyunsaturated than saturated fatty acids and the proportion of monoenes is higher than that of clupeids. All these species contain more ω - 3 fatty acids than ω - 6 fatty acids. Many Finnish fish species like pike (*Esox lucius*) (18.6 %), whitefish (*Coregonus lavaretus*) (17,0 %), perch (*Perca fluviatilis*) (21.9 %), vendace (*Coregonus albula*) (25.2 %) and rainbow trout (*Oncorhynchus mykiss*) (22.3 %) have much lower proportion of saturated fatty acids than studied species and they also contain more ω - 3 fatty acids than ω - 6 fatty acids (Ågren *et al.*, 1987; Anonym, 1993). Australian freshwater fish callop (*Macquaria ambigua*) have also lower proportion of saturated fatty acid (30,6 %) than Lake Tanganyika species but higher than Finnish species (Gibson, 1983). High amount of unsaturated fatty acids may thus show adaptation of temperate species to fluctuations of temperature.

The proportion of saturated (16:0) palmitic acid was highest in all species studied. All species contain also quite much monoen (18:1 ω -9) oleic acid and polyunsaturated (22:6 ω -3) docosahexaenoid acids (PHA). The proportion of (18:3 ω -3) linolenic acid is quite same in all species as well as the proportion of (20:4 ω -6) arachidonic acid and (20:5 ω -3) eicosapentaenoic acid. Polyunsaturated fatty acids like EPA and DHA reduce the amount of triglycerides in serum by diminishing the formation of VLDL and promote it's catabolic reactions. The amount of important linolenic acids (2.4 % - 3.3 %) didn't vary between species. It can be said that all studied species have similar fatty acid profile as Australian callop and are for the consumers a quite good source of fatty acids with positive health implications. For example, Japanese and Eskimos consume large quantities of fish and show a low incidence of coronary heart disease (Bang *et al.*, 1972 and Kagawa *et all.*, 1982).

Table 3. The relative proportions (mol %) of the main fatty acid classes in muscle of *L. miodon*, *S. tanganicae*, *L. stappersii*, and *L. mariae*.

	L. miodon	*S. tanganicae*	*L. stappersii*	*L. mariae*
Total lipids (% in DM)	5.2*	5.4*	7.1	3.2
Saturated	40.2	39.8	45.8	44.2
Monoenes	10.4	11.3	26.8	36.2
Polyunsaturated	49.4	48.9	27.4	19.6
ω - 3	35.5	34.6	18.2	10.6
ω - 6	13.9	14.3	9.2	9.0

* total lipids in whole fish

Table 4. The relative proportions of main fatty acids of muscle in *L. miodon, S. tanganicae, L. stappersii and L. mariae.* Values are means ± SD

Fatty acid (mol%)	*L. miodon*	*S. tanganicae*	*L. stappersii*	*L. mariae*
Total lipids (% in DM)	5.2*	5.4*	7.1	3.2
16:0	30.95±0.8	28.35±3.7	31.57±1.3	29.37±2.2
18:1 ω -9	6.60±0.4	7.30±2.7	18.77±2.0	25.77±4.3
18:3 ω -3	2.40±0.6	3.30±1.0	3.03±1.1	3.03±0.9
20:4 ω -6	7.45±1.2	6.65±0.2	3.55±0.3	3.67±3.0
20:5 ω -3	4.80±0.7	3.95±0.4	1.43±0.3	1.13±0.2
22:6 ω -3	27.05±1.3	25.85±3.7	12.20±2.0	5.10±3.9

* total lipids in whole fish

Fat quality analyses

Values of peroxide and free fatty acids can be compared with these of fresh fats that is < 10 mekv / kg for peroxide value and < 1 for free fatty acids (table 5).

Table 5. Value of peroxide and free fatty acids

Sample	n	Mean ± SD Peroxide value (mekv/kg fish fat)	Value off free fatty acids
Clupeid fresh	3	1.3±0.25	0.4 ± 0.35
Clupeid 1h sun + oxygen	3	2.3±0.23	3.8 ± 0.31
Lates 4-9 h after caught	3	7.2±1.41	1.2 ± 0.51
Lates 4h sun exposure	3	13.0 ± 0.80	2.9 ± 0.15
Lates 8h sun exposure	3	11.9 ± 0.66	2.9 ± 0.56
Fresh fish		< 10 mekv / kg	< 1

Peroxide value of fresh clupeid was very good in fish, indicating a low oxidation ration. Free fatty acid value was close to 0.5. After 1 hour peroxide value had not risen radically but free fatty acid value was clearly increased tenfold. This indicated high hydrolysing ration of fat in fish. It seems like drying decreases the oxidation of fat but not hydrolysing of fats and in this case drying may help maintaining a good quality of fats. This means drying so drying of clupeids seems to be an effective way to store fish. On the other hand, it is known that quality of fat decreases also in dried fish. Peroxide value of recently caught *L. stappersii* was below 10 mekv/kg but much higher than the value of self caught clupeid. Free fatty acid value of fresh *L. stappersii* was far above 1, so it was likely that fats were getting spoiled before the fish reached the consumer. After 4 hours, peroxide value was getting even higher exceeding 10 mekv/kg and free fatty acid value was also rising. After 8 hour peroxide value decreased a little which is likely because peroxide value tells the early state of oxidation and peroxides disappear from fish. Free fatty acid value remained on same level. Laitinen's (1999) sensory

analyses and K-value results of the same fish showed similar trends as my own results even thought they don't measure the same thing and peroxide value does not always correlate well under all circumstances with sensory impressions of rancidity (Torry research, 1989).

CONCLUSIONS

In conclusion, all species studied are a good source of protein and fatty acids foe human consumption. The analyses were successful despite the problems in the field and laboratory (irregular supply of electricity, poor equipment etc.). The two chemical fat quality analyses demand a lot of chemicals witch makes them less appropriate for field conditions than the sensory methods and K-value as tested by Laitinen (1999). Although a great deal of research has been done to find chemical or biochemical methods to measure deterioration in fish, it seems unlikely that in the near future these methods will replace sensory methods from their dominant position in the fish industries (Connell, 1995). One new tool for quality analyses is an electronic nose lately tested on the field, but there are still a long way to go into accurate, reliable and fast methods particularly suitable for conditions in developing countries.

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MEASURING OF FISH FRESHNESS IN THE FIELD

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1 INTRODUCTION

In Africa, 45-85% of animal protein in human consumption comes through fish, making fish in many countries the most important source of animal protein. (Clucas et al., 1996). In Kigoma area, where the present study was conducted fish provides 37,6% of animal protein (Gréboval et al., 1994). About 30% of fish are eaten fresh and the rest mostly dried. The average fish and seafood consumption in Africa is about 6,8 kilos/person/year, which is less than the worldwide average 14,3 kilos/person/year, but in Tanzania the average consumption is 11,1 kilos/person/year (FAO statistics 1996: http://www.fao.org)

On Lake Tanganyika about 45,000 full time fishermen are employed in fishery or fish for subsistence. Up to one million persons are assumed to work in secondary employment; processing, marketing, boat building, services etc. (Coenen 1995). Fisheries are an important source of employment and provide food for about 10 million people at Lake Tanganyika. The yearly catch of the whole lake is about 150 000 tons which mainly consist of the clupeids (*Limnothrissa miodon, Stolothrissa tanganicae*), and a predatory (*Lates stappersiii*). 95% of the fishermen are artisanal or traditional fishermen. There are 45 artisanal and 55 traditional units, and only four purse seiner units in the region of Kigoma. (Bosma et al., 1997).

In Tanzania a major interview was made among fishermen by Bosma et al. (1997). In the region of Kigoma fishermen were worried about sales problems, high transportation costs or otherwise poor transport. Weak points were also pitiful stores and stallfacilities and consumers being undemanded of the fish quality. Fisherwomen thought that the main problems are decreased catches, high prices of fish and low income. (Bosma et al., 1997).

It has been estimated that physical, economic and nutritional losses due to 25% of produced dried fish provide nothing for a consumer or a producer. Worldwide the post-harvest losses of traditionally produced fish are about 5 million tons/year in less developed countries (wet and cured fish) (Clucas et al., 1996). Fresh fish is more valuable than the dried one, and therefore it is crucial also on Lake Tanganyika to utilise the whole catch and avoid the unnecessary losses. (Bosma et al., 1997).

The purpose of my research was to measure fish freshness by chemical, physical and organoleptic methods, and by these methods to assess the time of fish becoming spoiled in the conditions of Kigoma. Also I evaluated the usefulness of those methods to measure fish freshness in tropical circumstances.

2. MATERIAL AND METHODS

2.1 Sampling procedure

Fresh fish to test and calibrate the methods were caught with trawl on the LTR Project R/V Tanganyika Explorer. Fish samples were collected at Kigoma market and Kibirizi village, a few kilometres north from Kigoma. The third place was Mwanga market, one kilometre south from Kigoma. Mr. E. Mondoga from Fisheries Department assisted in interviews and communication with fishermen and salers. Once the permission was obtained, the Torrymeter readings were recorded (individually or as the average of sixteen). Gills were smelled, eyes were checked and surface was touched to get a general view of the fish. The temperature of salesplace was measured and also temperature and pH of the fish were measured if possible. I used nonparametric tests by SPSS (Kruskal- Wallis and Mann-Whitley U Wilcox + Bonferon`s multiplier) because my results were not normally devided.

2.2 The K- value

The Fresh Tester is a colorimetric, highly reliable method to determine freshness of fish. After death follow rigor mortis, autolysis and putrefaction. K- value enables to see the process of autolysis before the early putrefaction. The Fresh Tester shows degradation of ATP (adenosinetriphosfase) to ADP (adenosinediphosfase), then ADP degradiates to AMP (adenosinemonophosfase) and AMP to IMP (inosinemonophosfase), and results in the formation and accumulation of HxR (inosine) and Hx (hypoxanthine). K-value represents the percentage of HxR and Hx in total amount of ATP degradation products:

$$K\ (\%) = \frac{(HxR + Hx)}{(ATP + ADP + AMP + IMP + HxR + Hx)} \times 100$$

Low percentages appear in fresh fish and ATP has not degradationed.

All stages were carried out following the manual (Transia Fresh Tester FTP II; Ref: FT 302). I used Minigrip plasticbags (0,2 l) and fingers for homogenise fishflesh with Buffer II.

2.3 Torrymeter

Torrymeter is an electrically operated (chargeable), quick and portable device to assess the fish freshness. Testing does not damage or mark the sample at all. It can be used the climate range of -25 C - + 45 ^{o}C and fish being 0 C - +20 ^{o}C of temperature. Certain dielectric properties of fish skin and muscle alter in a systematic way during spoilage when a tissue component degrades. These alterations

occurring at the microscopic level, are strongly associated with the gross changes in appearance, odour, texture and flavour which take place during spoilage and which are normally used by consumer for judging freshness. Torrymeter has two pairs of concentrically arranged electrodes. An alternating current is passed through the fish between the other parts of electrodes and the resulting voltage sensed by the inner pair. The phase angle between the current and voltage is measured and converted electronically for digital display on a convenient scale in the range 0 to 16. Zero value means definitely spoiled and sixteen is a very fresh fish. The phase angle and the reading of the meter decrease on spoilage. Between the measuring electrodes there are two auxiling electrodes one of, which contains a thermistor measuring the fish temperature and automatically correcting the reading. (Torry Research Station, 1989).

2.4 pH and temperature

I used Knick Portamess 752 calimatic and Metrohm <<L>> combined pH glass electrode 6.0236.100 for measuring pH in the fish muscle below the dorsal fin. Temperature was measured simultaneously with pH, keeping both electrodes in the same hole of the fish muscle.

2.5 Sensory testing

In the organoleptical evaluation the European Union Council's evaluation scales of freshness was followed. (EU Council's statute No: 2406/96). Secondary, the Finnish Veterinary and Food Technology Department's (EELA) standards for organoleptical evaluations of fishes were used. Evaluation scales were 5 (fresh), 4 (good condition), 3 (satisfied condition), 2 (poor condition), 1 (very poor condition), 0 (not for any consumption).

3. RESULTS

3.1 Effects of time for *Lates stappersii*

Because there were no control for fresh *Lates stappersii*, values for fresh *L. stappersii* had to estimate (fresh fish got f.ex. organoleptical values 5). Between estimated control and samples (n= 10) there were no scientific differences (p> 0,48). However fishes became spoiled by the end of day. At 10am ATP of the *L. stappersii* was degraded by 8,3%. Already at noon ATP was degraded by 17,5% and when the fishes were definitely spoiled the percentage was as high as 21,7%.

3.2 Effects of place on fish freshness

The organoleptic values odour (p= 0.000, n= 61) and outlook (p= 0.002, n= 60), and Torrymeter readings (p= 0.001, n= 64) for market fish (all measured species) differed significantly from these of fresh fish (n= 39-40). The physical texture had weakened less dramatically.

3.3 pH and temperature

The pH of fresh fishes (mean 6,1) did not change during the day. The temperatures of the fishes were very close to the air temperatures. The bigger fish (*Lates sp.*) were cooler than the smaller ones.

3.4 Spoilage by species at market places

There were no particular differences in fish appearance freshness between the species (Figures 1 and 2), although fishermen handle bigger and valuable fishes (Lates sp.) more carefully than clupeids. Fishes that were less than one kilo in weight usually were sold in piles. Bigger fishes were cut into pieces, but only if a customer was sure to buy.

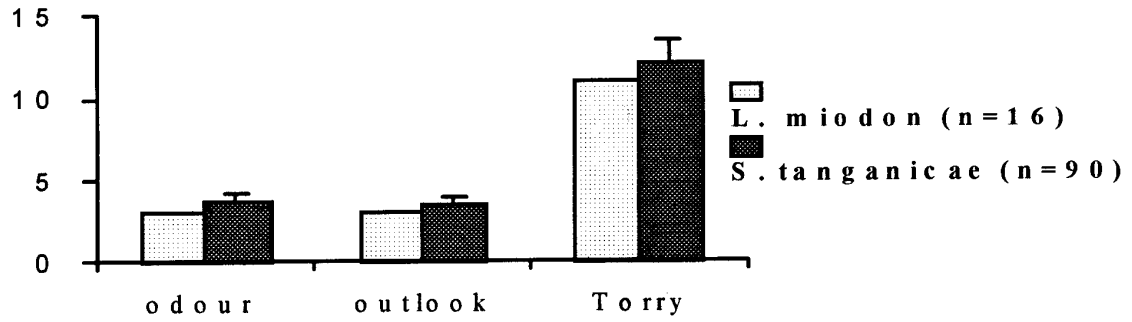

Figure 1. Quality values and ± SD of clupeids at various market places in Kigoma.

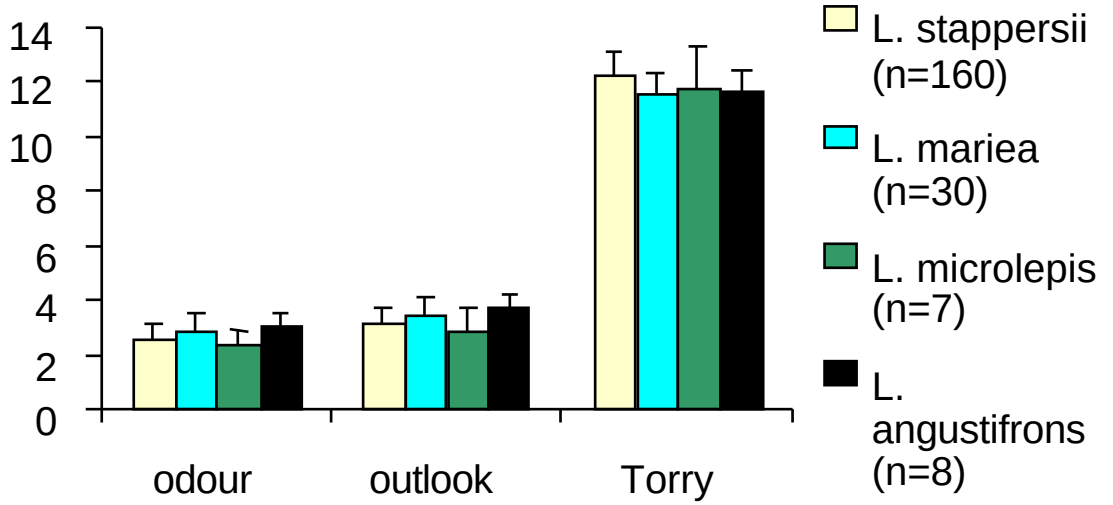

Figure 2. Quality values and ± SD of *Lates sp.* at various market places in Kigoma.

4. DISCUSSION

4.1 Evaluation of methods

The K-value is a quick method giving results within 20 minutes, but as a disadvantage for the test one must cut a piece from a dorsal muscle which harms the fish. The K-values from the fresh fishes were promising (5-15%), but the values of the fishes definitely spoiled were only slightly higher (15-25%). The method showed only the increasing trend, but quantitatively not so pronounced results possibly due to the storage temperature of the test stripes. After arrived in Kuopio, the kit was put into the freezer. According to the instructions the stripes must be kept below 0 ^{o}C but the storage temperature of the FTP II buffer have to be + 18-30 ^{o}C. The buffer was completely frozen when I opened the box. Our trip to Kigoma took nearly 60 hours and the stripes were without proper freezing for such a long period. There were styrox-flakes and long lasting ice pack in the cartoon box. The guide promised that the stripes could be stored for 3-4 days at the room temperature (+ 20-25 ^{o}C). But the temperature was higher than + 20-25 ^{o}C and in Kigoma the electricity was constantly off (mainly every afternoon). The freezer was also off, but it never melted completely down and the lacks of the electricity took not longer than a few hours. So storing temperatures of the stripes went up and down all the time (nearly four weeks).e trend of the result was correct but the sun might have been a problem. Using Torrymeter was quite acceptable amongst the people in Kigoma. The local people paid a lot of attention and interest on my work and therefore I could do my measurements quite easily (except in Kibirizi). According to Torry guide, readings should not be taken on fish left under direct sunlight, especially in hot countries. In this experiment, most of the fishes were definitely at some stage of transportation or selling exposed to the sunlight. The fishes were carried in different kind of baskets or bags. The salesmen washed and put them in shadow. Small clupeids were carried in plastic bags or –buckets and put just on a table or sand. Most of the fishes were sold before noon, as were measurements also made. Torrymeter does not directly measure the freshness as defined in sensory terms, but the readings are strongly associated with it. In some measurement a bit odd results were got when compared with other methods (especially the sensory

The variations of pH values were non-significant. It was quite difficult for do pH measurements from muscle, because this had to be done when the salers cut bigger *Lates sp.* to pieces. With clupeids I had no chance to do measurements without buying those fishes.

To success in sensory method needs some experience, which I hardly had. I represented more like a consumer who makes decisions to buy. The sensory method is subjective especially when you are working alone. In most cases I did my estimations at market places, where light, odours,

temperature, wind, humidity etc. was not stable, but however, typical conditions of the fish markets.

4.2 Fish freshness

The decreasing freshness of fish during the hours before noon on the markets was recorded chemically (K-value), physically (Torrymeter) and by organoleptic measurements of odour and outlook. Only the latter three measurements gave statistically significant results. The pH values did not change largely. The organoleptic classification that is subject to the investigator's personal view, gave the most clear results of quality changes which reflects also the consumer's preferences and means of freshness assessment.

The time dependence of the freshness was followed in *L. stappersii* only, because other *Lates* species were so big and expensive (about a 300g piece, costed 1500 Tsh ~ 15 Fmk). *L. stappersii* was cheaper (five specimens *L. stappersii* cost 1000- 1500 Tsh ~ 10-15 Fmk) and easy to get and handle. Smaller species *S. tanganicae* and *L. miodon* dried so quickly and were therefore inappropriate for testing the spoilage process.

The fish on market is no longer fresh when it arrives to the market place even nine hours after the fishermen lift their first catch in lift net. First catch is caught around midnight. The lift net fishermen can get two to six lifts in the night, depending on the size of the net (the bigger net – the fewer lifts), the target species (for *Lates stappersii* more frequently) and the weather conditions (in bad conditions the net works like an anchor). So some kind of spoilage process has already started when the fishes are sold on the shore. (Chitambebwa, 1998 pers. comm.).

The fish spoils very easily in tropical environment. High temperatures and sunlight allows rapid putrefaction and spoilage begins at very early stages. For example fishes surfaces dry quickly which was seen in fish outlook, smell and texture.

When the fish get killed the microorganisms and enzymes are free to invade or diffuse into flesh. The microbial enzymatic action causes changes in odour and flavour compounds. Such as reducement of the odourless compound TMAO (trimethylamine oxide) to TMA (trimethylamine), which causes ammoniac smell. TMAO has been found also in Nile perch. At later stages also proteolytic enzymes soften the flesh of the fish. These actions affect the appearance and physical properties of several components of the body. The slime becomes discoloured, the skin gets rough to touch, and the peritoneum can be easily detached from the internal body wall. On death the large number of different enzymes become involved in predominantly degradative reactions. The glycogen of muscles becomes lactic acid by gradual hydrolysis and that causes rigor mortis. Lactic acid

decreases pH and prevents the microbiological spoilage. When rigor mortis has stopped lactic acid concentration decreases and pH rises again. Microbiological action provides basic nitrogenous compounds such as TMA and ammonia that raises the pH. In this field study these changes in pH were not differed significally. Autolysis and microbiological has been started and the fish is no longer valid for consumption. (Connell, 1995).

4.3 Test assessment

To conclude the suitability of the studied methods basic requirements are that the test must be quick and cheap and it must not damage the fish. The results should be comparable regardless of circumstances and person. The test must be objective, reliable and easy to use, and the results must be self explanatory to the consumers and authorities. The most non-sensory methods like Torrymeter have those advantages. The sensory method, respectively, predicts better the consumers' reactions because it is based on the same criteria that the ordinary buyer uses when making the decisions to buy or not to buy a fish. (Torry research station, 1989).

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SOCIO- ECONOMIC STUDY AT LAKE TANGANYIKA IN KIGOMA REGION IN TANZANIA: INTERESTS, ATTITUDES AND EARNINGS OF FISHERMEN

Janne Hänninen

1. INTRODUCTION

In Lake Tanganyika there are estimated 10 - 12 000 fishing units. In average 3- 4 fishermen are working in one unit: in primary employment of fisheries a total of ~ 45 000 fishermen. Up to one million persons are assumed to work in secondary employment; processing, marketing, boat building, services etc. (Coenen, 1995). Fish provides 37,6% of animal supply in the area (Gréboval et al., 1994). Fisheries is an important source of employment and food for about 10 million people at the Lake Tanganyika. As one respondent explained: " Fishing is crucial for Kigoma, without it there would be no nutrition, no employment – nothing." During past decades total catch has increased from only 16 200 tons in 1964 to 80 525 tons in 1992 from Tanzanian part of Lake Tanganyika. Since that the total catch has decreased (Table 1.) One reason to this trend is obviously decreased catchable stocks and apparent overfishing, as clearly seen from CPUE of all fishing types in Table 2 . For fishermen this has meant decreased income and uncertanities about future. This study aims at explaining the current socio-economic situation of fishermen in Kigoma region.

Table 1. Fish catch in tons of all sectors in Tanzanian part of Lake Tanganyika

YEAR	CLUP	LST	LSSP	TILAPIA	OTH	TOTAL
1991	36 518	11 958	2 463	-	-	63 503
1992	54 021	14 170	5 038	-	-	80 525
1993	39 963	30 962	643	415	2 747	71 130
1994	29 242	23 932	282	13	774	54 125
1995	40 764	11 546	435	203	1 704	54 652

CLUP=clupeids; LST= *Lates stappersii*; LSSP= *Lates spp.*; TILAPIA= *Tilapia spp.*; OTH= other catch

1.1. Structure of fisheries

Artisanal fishery is the most common fishing type (60% of fishermen) in the Kigoma region (Reynolds, 1997). The artisanal fishery accounts for more than 99% of the total catch in the region (Coenen, 1994). It is carried generally from catamarans using standard lift net, other common artisanal gear is day and night beach seine.Lift net unit "kipi" operates during nights, except fullmoon period, thus during ~22 days in a month. The crew (3-4 persons) harvest with 4-8 lights as attraction. Catch remains to net when lift net is weighed. The net is hauled 1- 3 times per night; x= 1,7 hauls/ night and average catch is 50,2 kg per night in 1995, as seen in Table 2. (Coenen et al., 1998).

In night beach seine unit "kokoro" there is a special attraction unit of some boats with 2 to 3 lamps in each boat. Boats are paddled so that fish is able to follow the

light. When close enough to the shore, the beach seine is taken around by another light boat. The net is pulled by 6 to 15 men. Day beach seine is operated similarly but without attraction boats. The average catch of beach seine unit was according to Tanzanian statistics 47,9 kg per day (Coenen et al., 1998).The three main target species of the pelagic artisanal fishery are two clupeids (on average 63% of catch*); Stolothrissa tanganicae, Limnothrissa miodon* and the predatory (36%) *Lates stappersii.*

Traditional fishery is carried out on single non- motorized dugout canoes or planked canoes, using gillnets, traps, hooks and lines. Normally one or two persons harvest with one or several gears for his family during day time. In traditional fishing more coastal fish communities (cichlids, lungfishes, catfishes etc.) are targets of harvesting attempts.

Table 2. Catch Per Unit Effort CPUE for some gears in Tanzanian territorial waters of Lake Tanganyika, source Tanzania`s fisheries statistical system (Coenen , 1998).

YEAR	LIFT NET unit	BEACH SEINE unit	GILL NETS unit
1993	104,0	50,4	35,0
1994	110,8	51,4	21,9
1995	50,2	47,9	17,8

1.2. Aims of the study

”The economy of affection" theory by Hyden (1983) has affected the formulation of this study. The main idea of this theory is that economical behaviour is based on affection. In a society (often in developing countries) where the economy of affection dominates, the primary objective is not the realization of surplus and its reinvestement into new productive activities as in modern capitalistic economy (cited in Jul- Larsen 1992). In 1997 a lakewide socio- economic survey was conducted at the LTR project to collect data on local fishermen of whom a great deal fish for subsistence and processors. This new information gave an idea to investigate more deeply some matters, which have not been addressed in former survey.

Primarily, the aim of the study was to clarify the reasons that influence the decisions to choose between fishing and other work: good catches, income, lack of fertile land or way of living. What is the importance of parttime occupations? Is the timing of various activities related to the annual cycle e.g. duration of dry and rainy seasons? How important fishing is for fishermen`s families as source of food and income? Further is there difference between attitudes of traditional and artisanal fishermen towards fishing and earning? All these questions were clarified during the participatory interview, which was made as a one- time survey.

2. MATERIAL & METHODS

Seventy fishermen were interviewed during 12.3.-4.4.1998 in Kigoma in northern Tanzania. Questionnaires made in English were translated and presented in Kiswahili to the interviewee by a local guide. Forty- two (42) artisanal fishermen, who work with/ in a crew on catamaran – lift net or beach seine fishing and twenty- eighth (28) traditional fishermen, who harvest mostly alone or pairwise were met. Interviewees were found with the help of Tanzanian Fisheries Research Institute (TAFIRI) Kigoma staff. Interviews were made in the villages nearby Kigoma. The interviews were told that the study is a part of FAO`s project with the aim of clarifying fishermen` s socio- economy incomes, family, education and other occupations. Samples were taken randomly on the beach upon the fishermen arrival or while they were overhauling equipment. One interview took approximately 30 min. The last interviewees were selected by their fishery type (artisanal- traditional) to reach intended proportion.

Answers were recorded by author of this study. Truthfulness was intended to be achieved with simple questions and appropriate sample size. Collected data was saved with MS Excel and processed with SPSS. Special theme discussions were held with persons with professional experience. The other translator was an employee in Fisheries Department and he had good knowledge in fisheries. These discussions gave an useful scope to evaluate critically the former interviews. Also I had possibility to join lift net and hand line units on their fishing trip. This experience gave a realistic view to fishermen’s work and practices in fishing. Discussions with fishermen and their family as well as with other local people gave a wider look to fishermen` s socio- economy.

3. RESULTS

Table 3. Sufficiency of incomes during bad seasons by fishery type

	Fishery Type	
Sufficiency	Artisanal	Traditional
Bad	42,9 %	14,8 %
Sufficient	57,1 %	**85,2 %**
Total	100,0 % (n= 42)	100,0 % (n= 27)

Pearson`s chi- square p-value= 0,015

There is statistically remarkable difference in felt incomes sufficiency between the artisanal and traditional fishermen. Traditional fishermen find (85,2%) that income is sufficient also in bad seasons (usually end of dry season; November). Plenty of artisanal fishermen find that the sufficiency of incomes is poor during bad seasons.

Table 4. Land owning by fishery type

	Fishery type	
Owned land	Artisanal	Traditional
0 acre	35,7 %	37,0 %
1-2 acres	38,1 %	40,7 %
3-6 acres	26,2 %	24,6 %
Total	100,0 % (n= 42)	100,0 % (n= 27)

p= 0,931

Worth noticing is that there is no statistically remarkable difference in land owning between interviewed fishermen groups. Approximately 1/3 of fishermen have no land for farming, 2/5 of fishermen have 1-2 acres and 1/4 have 3-6 acres. Hypothesis was that traditional fishermen (especially with gillnet) have more cultivation activities and land, because spent time in fishing is only 1-3 hours per day. But results do not show any evidence to former proposition.

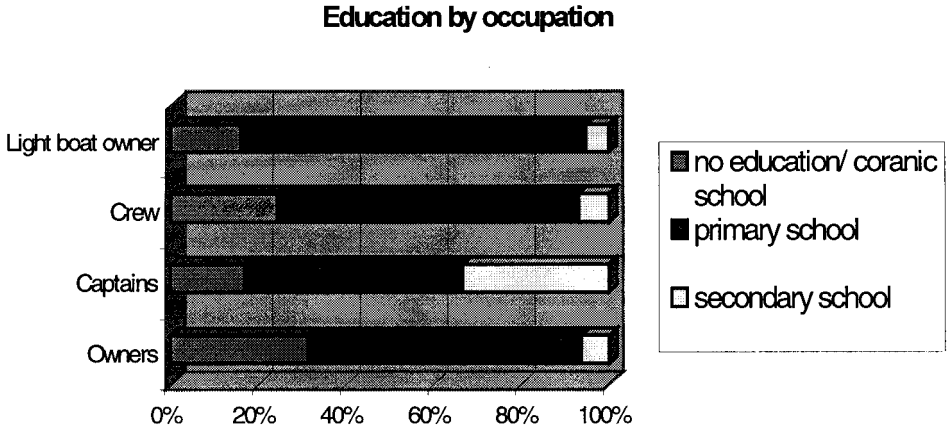

Figure 1. Level of education in main occupation groups

Data shows there is no difference between other occupation groups and level of education. Secondary education seems not to be more probable among owners and captains than among crew and light boat owners. Fishermen with no education means generally, people who had learned to read Coran but never went to real school.

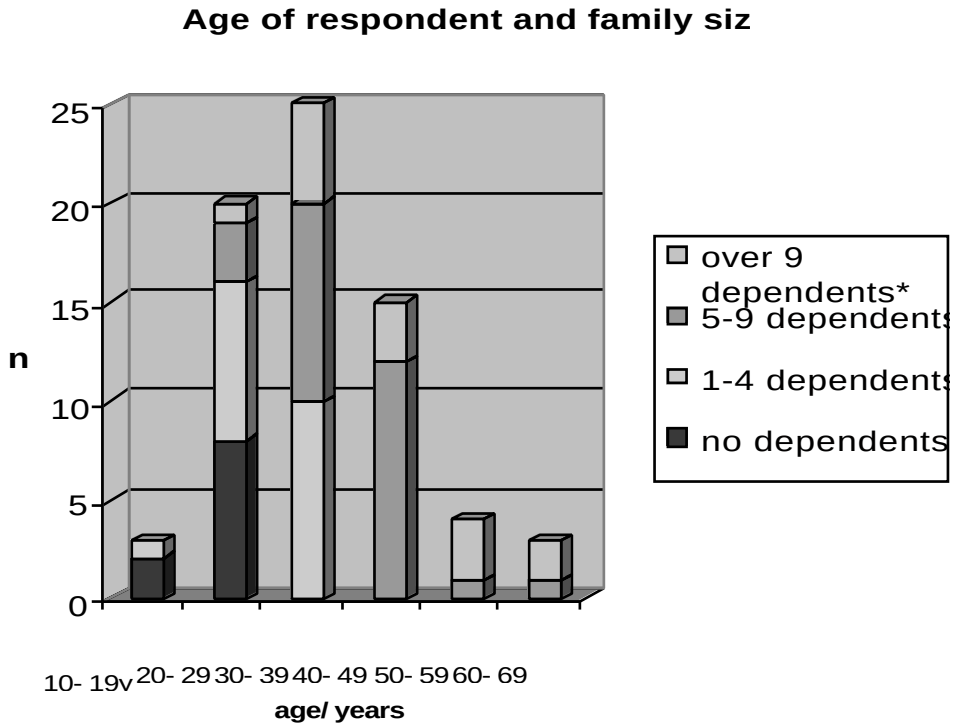

Figure 2. Age of respondent and family size

There are many families with over 9 dependants. Unmarried fishermen could be found only in the age of less than 30 years. The youngest interviewee was 17 years old. An average fisherman is 35 years old and has five to six dependants. Some quite old fishermen, over 60 years, had fishing still as occupation. They work during daytime with their hand line. Elder fishermen have more children naturally. There is no significant difference in the family size between artisanal and traditional fishermen. Artisanal fishermen get slightly more probable bigger family: 20,9% of artisanal and 11,1% of traditional fishermen has more than six dependants.

Table 5. Satisfaction to life in age classes

	Satisfaction to life as fisherman		
Age	Yes %	No	Total
17- 29 years	25,0	**50,0**	32,9
30- 39	33,3	**40,9**	35,7
40- 49	29,2	4,5	21,4
50- 70	12,5	4,5	10,0
Total	100,0	100,0	100, 0

There are satisfied fishermen in all age classes. Respondents of 17- 29 years are the most unsatisfied. Elder fishermen in general are more satisfied to life.

4. DISCUSSION

4.1. Sufficiency of incomes

Generally fishermen find that their incomes are sufficient even during bad seasons (Table 3). Slightly bigger part (57,1 %) of artisanal respondents think that their income is sufficient. These respondents were owner of units and someone had even another occupation. Clearly bigger amount (85,2%) of traditional fishermen find that their family income is sufficient also during bad season. The sufficiency of incomes was regarded bad among 42,9% of artisanal fishermen in this study. The difference is statistically remarkable and it is one of the most important new findings. The reason, why there is still “old fashioned” traditional fishermen, is, that their income is more stabile than artisanal fishermen, who are not able to fish in fullmoon and often in dry seasons when pelagic fish shoals may disperse. Majority of fishermen (97,1%) informed to fish both in dry and rainy seasons. A fairly reasonable income level amongst the artisanal fishermen in Kigoma region was also found by Reynolds (1997), who reposted the unit owners to earn some USD 640 per year that is twice as much as estimated for an average worker`s income. In Southern part of Lake Tanganyika, Skjonsberg (1982) also noted the beach seine unit members to earn considerably higher incomes than the ordinary farmers.

4.2. Land owning and parttime occupations

Up to 81,5% of traditional interviewés and 50,0% artisanal interviewés regarded themselves part time. It was expected, that traditional fishermen would cultivate more because they have more time outside fishing activities but this was not seen in sizes of owned land that are similar in both groups. Natural reason for small cultivated land size are steep slopes surrounding the Lake. Agriculture is the most common (60%) part- time occupation, paid job (9%) and fish trade (3%) give also extra income to fishermen. In 68% of cultivators cultivated products are consumed only in family and the rest is sold outside. One third of fishermen`s family process caught fish themselves. As a general rule when fisherman has an own family, he concentrates in fishing and probably helps in fullmoon and rainy season in farming but otherwise wife and children take care of cultivation and fish processing. For 88% of artisanal and for 70% of traditional fishermen fishing is the most important source of annual income showing the great importance of fish in income generation. The difference is not statistically significant ($p= 0,12$)

4.3. Education

The principle of better education leading into better vacations was not evidenced in this study. One reason might be that educated persons have got better occupations for example in administration. Secondary school fees are expensive for normal fisherman`s family, 30 000 Tsh (50 USD)

a year and few family can afford that for more than one child. The finished secondary school was not a reason to enter fishery by owners and captains but this was mostly due to heritage (45.7%). In the rural area there is not too many source for employment and nutrition. Learning and access to occupation goes naturally from father to son.

4.4 Age, family size and satisfaction

Older men have naturally more children. Another reason for growing number of children during lifespan is that in Islamic culture the number of wife is a mark of welfare (Figure 2.). The very interesting phenomen is that there seems to be a correlation between family size and satisfaction to life as fisherman (Table 5.). Young fishermen are unsatisfied and many of them are single. Elder fishermen have one, usually two to three wives and many children. Older fishermen seems to be also more satisfied to life.
Young people may still think leaving Kigoma but elder people have settled down; they have decided to be satisfied. Among young people there are relatively more crew members whose salary is small (commonly 1/3 of unit`s catch given to crew). It is one reason for unsatisfaction.

4.5 Socio-economic problems

1. In macro scale ignorancy, poverty, diseases and poor infrastructure are socio- economical problems, which make e.g. modern fish processing and transportation impossible (Marwa, pers. comm.).
2. Poor hygiene is mentioned as a big problem (Petit, 1997).
3. Lack of local and institutional support, lack of land and lack of wood are seen as socio- economic matters in the region (Petit, 1997). Many fishermen say, that modern fishing materials and methods is needed. Reynolds (1997) states that for most serious problem fishermen (57%) found lack of inadequate gears. Artisanal fishermen found for the most serious occupational problem lack of security (61%) and traditional ones lack of inadequate gears (50%) (Bosma, 1997). Negative influence of modern gears to fish stocks in southern Lake Tanganyika is apparently one important factor (Coenen, 1998).
4. Many fishermen in the villages north from Kigoma; Mwangongo, Mtanga and Gombe, where beach seining has been important source of employment, have criticised strongly banning. Beach seining has been banned since 1998, after researchers` findings of destructive influences to fish stocks and biotope (Petit, 1997).
5. The unstable political situation in neighbour countries (Burundi, Congo) have had lot of influence during past years into fisheries in the region. E.g. in Mtanga fishing village 63% of 465 fishermen are aliens. Great increase in fishing has caused decrease of fish price even 80% (Petit, 1997). Since today invasion has not caused great violences. But the refugees` camps have caused rise in prices (high demand), which reduces the inhabitants purchasing power.

6.Independent initiative is needed for better future. People have used to foreigners and their introduced new gears and grants.

4.6 Happiness

The economy of affection (see 1.2.) was easy to notice, the prevailence of African attitude was seen e.g. in boats, engines and nets. Anyway fishermen generally seemed and said to be at least as happy as Scandinavian city dwellers. The importance of family is great, when no kind of social security from the state can be expected. The study showed too that family has a mentally important role, young men without family are more unsatisfied. To summarise, the role of women is weak and their hard working attitude and positive concern towards the family welbeing should be better utilized. This requires, however, changes in the schooling system and mentality in the whole society dominated by the men.

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