



ADVANCES IN THE ECOLOGY OF LAKE KARIBA

Edited by Jacques MOREAU



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ISBN 0-908307-54-3

First published in 1997 by
University of Zimbabwe Publications
P. O. Box MP 203
Mount Pleasant
Harare
Zimbabwe

Cover and inside photographs supplied by Nils Kautsky and Gertrud Cronberg

Cover Top: Typical ringnets as utilized in Kapenta fisheries on Lake Kariba

Bottom: Lake Kariba: The littoral area and draw-down zone

Back cover: Lake Kariba: The ecology of the littoral area is strongly influenced by wildlife.

Printed by Print Holdings

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ACKNOWLEDGEMENTS

The present investigations were sponsored for many years by the University of Zimbabwe Research Board and by the Swedish Agency for Research Cooperation with Developing Countries (SAREC).

The Zimbabwean Department of National Parks and Wildlife Management gave permission to undertake research and assisted one of us (K. Hustler) by shooting Reed Cormorants and collecting chicks for experimental purposes from the Kariba Recreational Park.

The contributors are particularly grateful for all the assistance and encouragement given by the staff at the Department of Biological Sciences at the University of Zimbabwe.

They also wish to thank the Directors of the University Lake Kariba Research Station (ULKRS): Dr Lars Ramberg (1982–85) and Professor Chris Magadza (from 1986) for their generosity in providing the facilities, including boats and logistic support, and thus making the investigations reported here possible. Many thanks are due as well to all the staff of ULKRS for help in the laboratory and for the assistance during long fieldworks on Lake Kariba. In addition, the staff of the ULKRS contributed with knowledge on past and present conditions in the lake area.

G. Cronberg would like to thank Mrs Karin Ryde for correcting the English language of her contribution.

C. Skarpe wishes to thank all participants in the project for cooperation, and particularly Mats Eriksson for help with the tedious measurements of *P. repens* shoots. Ingvar Backéus constructively commented on her manuscript. Krister Surell kindly agreed to the inclusion of his data and vegetation maps.

Ian Games is indebted to his supervisor, Professor John Loveridge for help throughout the project.

The study by Kit Hustler was supervised by Brian Marshall and Mats Eriksson whilst Peter Mundy and Peter and Sue Frost provided valuable assistance and encouragement. Joel Chisaka fed the captive birds during the absence of K. Hustler from Kariba.

The assistance of the following colleagues in editing some of the contributions presented here has to be gratefully acknowledged: M. Ericksson, B. Marshall, H. Dumont, L. Kautsky, J. Talling.

J. Moreau is extremely grateful to U.Z. and SAREC for appointing him as chief editor and allowing him to share Lake Kariba knowledge with all the participants.

In Toulouse, Delphine Lambert has drawn all the figures and Annick Corrège prepared the camera ready copies for submission to the publisher.

Finally, thanks are due to the University of Zimbabwe Publications for a quick publication of the book.

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CONTRIBUTION OF NITROGEN FIXATION TO THE NITROGEN BUDGET OF LAKE KARIBA

Stanley M. Moyo

INTRODUCTION

Dinitrogen (N_2) constitutes about 80% of the atmosphere and is important for primary production in aquatic and terrestrial systems (Postgate 1978). A wide variety of organisms are able to fix elemental atmospheric nitrogen either in the free-living state or in symbiotic relationships. The reduction of N_2 to ammonia is referred to as biological nitrogen fixation (BNF) and is an energetically expensive reaction catalysed by nitrogenase or dinitrogenase (Postgate 1978, Carr and Whitton 1982). However, nitrogen fixation may provide significant inputs to a large variety of ecosystems (Postgate 1978). BNF is carried out by a wide range of autotrophic and heterotrophic bacteria. Most nitrogen is fixed in aquatic ecosystems where cyanobacteria are the dominant plankton (Howarth *et al.*, 1988). This is so particularly if the cyanobacteria can form heterocysts (Postgate 1978, Stewart *et al.* 1967). The phytoplankton of Lake Kariba is known to be dominated by heterocystous cyanobacteria in the hot season (Ramberg 1984, Cronberg this vol.) There was sufficient reasons to expect that BNF might be an important process in the lake.

There is very little information about nitrogen fixation in tropical lakes in general and even less in tropical man-made lakes (Thornton 1986, Wetzel 1983). The literature reveals that apart from the processes of nitrification and denitrification there is a dearth of information on nitrogen cycling in African aquatic ecosystems (Thornton 1986). There is no information on the relative contribution of cyanobacterial N_2 fixation to the nitrogen budget of Lake Kariba. Such information can be of vital importance as this input of nitrogen might be one important source of nitrogen. This is particularly important for Lake Kariba as it is located in a basin which is not only highly leached but has inflows that are low in nutrients (Begg 1970, Coche 1974).

The main objectives of the current study were therefore to determine (1) the rates of BNF in the lake (2) the spatial and temporal variations and (3) the importance of BNF to the nitrogen economy of Lake Kariba.

MATERIAL AND METHODS

The study site

The study site was Lake Kariba (Zimbabwe/Zambia) whose characteristics have been thoroughly discussed elsewhere (Coche 1974, introduction in this volume). The stations that were sampled during the study period (1986–1988) are depicted

in Figure 2.1. They have been used for other sampling procedures (see, for instance, Machena this volume, Kautsky this volume).

Methods of evaluation of BNF

Rates of BNF were measured by the simple and sensitive acetylene reduction assay that was developed during the 1960s (Stewart *et al.* 1967; Hardy *et al.* 1968). Five millilitres of lake water were pipetted into 15 ml Hungate tubes that were then sealed with butyl-rubber septa and screw caps and kept in dark prior to incubation. To initiate the assay, 2 ml of acetylene, which had been scrubbed through concentrated sulphuric acid and water, were injected into each of the tubes. The incubations were carried out in triplicate with two blank tubes; one without acetylene and the other containing 0.15 ml of Lugol's iodine to kill and preserve the phytoplankton. Incubations were either conducted on-board, in deck incubators (in 1986 and 1987) or under *in situ* conditions (during 1988). Incubations lasted two hours, after which time acetylene reduction was terminated by injecting 0.15 ml of Lugol's iodine. The tubes were then stored upside-down (to minimize ethylene loss) in darkness prior to ethylene analysis. Correction for possible loss of ethylene during storage was operated according to Leonardson (1984). Prior to analysis for ethylene, samples were first equilibrated to room temperature and then shaken for 30–60 seconds. One millilitre of the gas phase was then withdrawn for ethylene measurement using flame ionisation gas chromatography on a Shimadzu 4-CM (PF) gas chromatograph fitted with a stainless-steel column (4 m long by 1/8 inch internal diameter). The column was packed with Porapak T (mesh 80–100 and obtained from Waters Assoc., Inc. Framingham, Mass., USA) and operated at 110°C. The carrier gas used was N₂ at a flow rate of about 60 ml min⁻¹. Chemically pure ethylene standards (Alfax Ab. Malmo, Sweden) at a concentration of 2.1 and 4.2 × 10⁻¹⁰ mol ml⁻¹ were used for calibration. The conversion rate from ethylene reduced to N₂ reduced was the theoretical ones of 3:1 (Peterson and Burris 1976, Stewart *et al.* 1967) since the acetylene reduction assay was not calibrated with the N15 isotopic measurements in this study.

Other parameters recorded

Simultaneously, additional parameters were monitored: carbon dioxide fixation (CDF) (phytoplankton primary production), light penetration (LP), turbidity (TU), alkalinity (ALK), conductivity (CON), concentrations in phosphates (PO₄), ammonia (NH₄), nitrate-nitrite (NO₃N), chlorophyll *a* (CHLA) and phaeopigments. The methods used in order to measure these parameters are given in Moyo (1991).

Data analysis

The whole data set was initially split into littoral and pelagic data on the basis of expected differences in the productivity of these two zones and then analysed using multi-variate methods, the rationale of which was to summarize the data set and to determine the relationships between the variables measured. Multi-variate techniques used were principal component, factor analysis and multiple regression analysis (see Moyo 1991 for details). The whole set of data is available on request to the author.

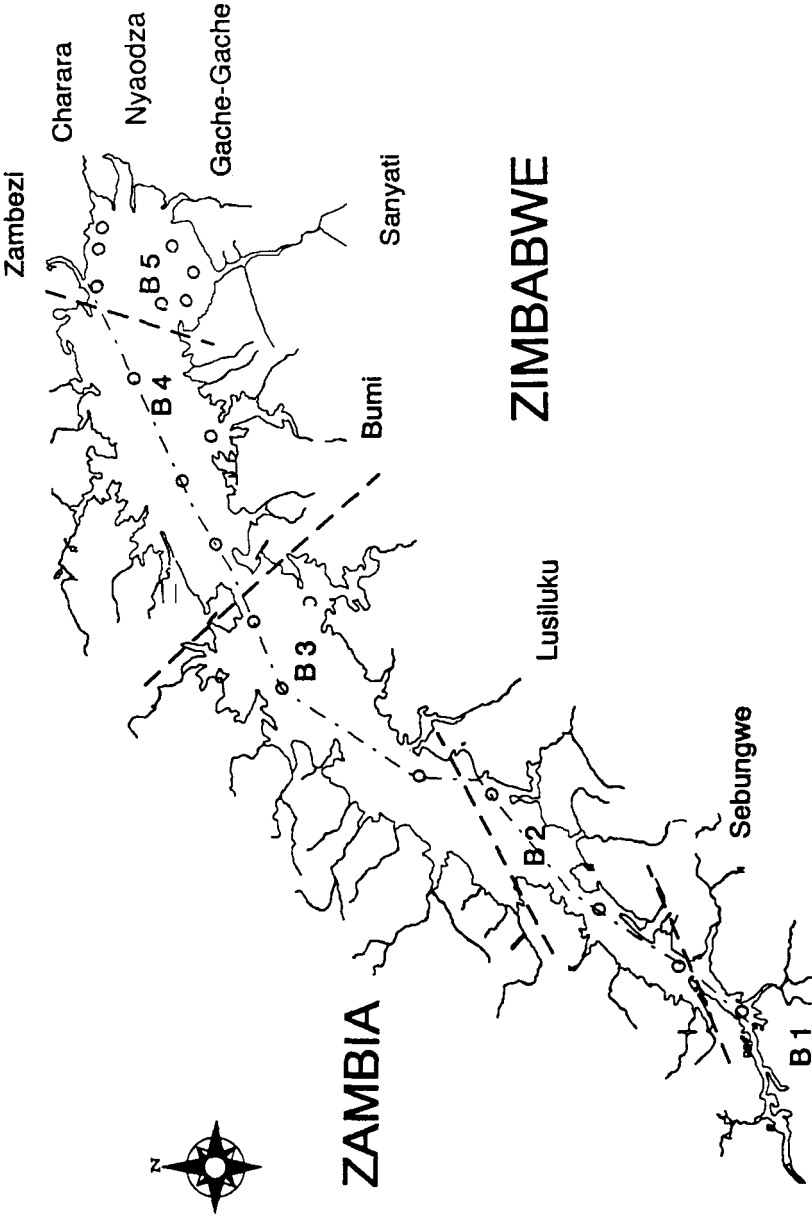


Figure 2.1 Map of Lake Kariba showing sampling locations

RESULTS

Volume based rates of BNF ranged from 0 to 5 $\mu\text{g N l}^{-1} \text{h}^{-1}$ (Figure 2.2). After integration on a surface area basis, rates of BNF ranged between 0.040 and 0.202 $\text{g N m}^{-2} \text{yr}^{-1}$ with an average of 0.121 $\text{g N m}^{-2} \text{yr}^{-1}$.

Values of BNF varied with time (Figure 2.2). BNF was usually highest in the hot season (October–February), although peaks occurred much earlier than this in the more lacustrine basins of the lake. Variations of BNF on the longitudinal axis were noted with rates being higher in the lacustrine basins (Basins 3, 4 and 5) compared with in the riverine basins (Basins 1 and 2).

The values of BNF measured here were used in the construction of a nitrogen budget for Lake Kariba (Table 2.1).

Table 2.1 Nitrogen budget for Lake Kariba (tonnes yr^{-1})

Inputs		Outputs	
Source	Amounts	Source	Amounts
Surface inflow		Outflow	
Zambezi	1199 ^a	Zambezi	793.1 ^e
Other rivers	147 ^b		
BNF	630 ^c	Fish harvesting	830.1 ^f
Rainfall	100 ^d		
Total	2,026	Total	1,623.2

Notes:

(a) Value calculated on the assumption that the concentration of the Zambezi River is 40.54 $\mu\text{g l}^{-1}$ and the flow is 29.58 $\text{km}^3 \text{yr}^{-1}$ (Coche 1974)

(b) Value calculated on the basis of the value of Nitrogen concentration of 50 $\mu\text{g l}^{-1}$ for secondary rivers in the Zambezi basin (Davies 1986). The inflow of these river (2.925 $\text{km}^3 \text{yr}^{-1}$) was computed from data provided by the Zambezi River Authority and by the Meteorological Office of Zimbabwe.

(c) Value based on results of current study (0.121 $\text{g m}^{-2} \text{yr}^{-1}$) for the whole surface of the lake during the study: 5 000 km^2

(d) Value calculated on basis of rainfall measurements at Kariba and Binga (Meteorological Office, Harare) with a content of 17.4 $\mu\text{g N l}^{-1}$ (Caulton unpublished)

(e) Data from Magadza *et al.* (1986) where nitrogen in the outflow is given as 26.8 $\mu\text{g l}^{-1}$ and the flow is 29.58 $\text{km}^3 \text{yr}^{-1}$

(f) Calculated from assumption that

(i) Kapenta catches are 29615 t (Lupikisha, 1992) and inshore catches are 3590 t for the whole lake (Sanyanga *et al.* 1990, Scholtz and Mweetwa 1990)

(ii) 2.5% of the wet weight of kapenta is nitrogen (Chemistry and Soil Research Institute Laboratory Report No 1489/GF, June 1980). This value has been used for every fish species.

From this budget, it appears that BNF contributed about 32% of the total annual nitrogen inputs into Lake Kariba during the study period.

Factor analysis of biological nitrogen fixation and other limnological parameters measured produced the factor diagram shown on Figure 2.3.

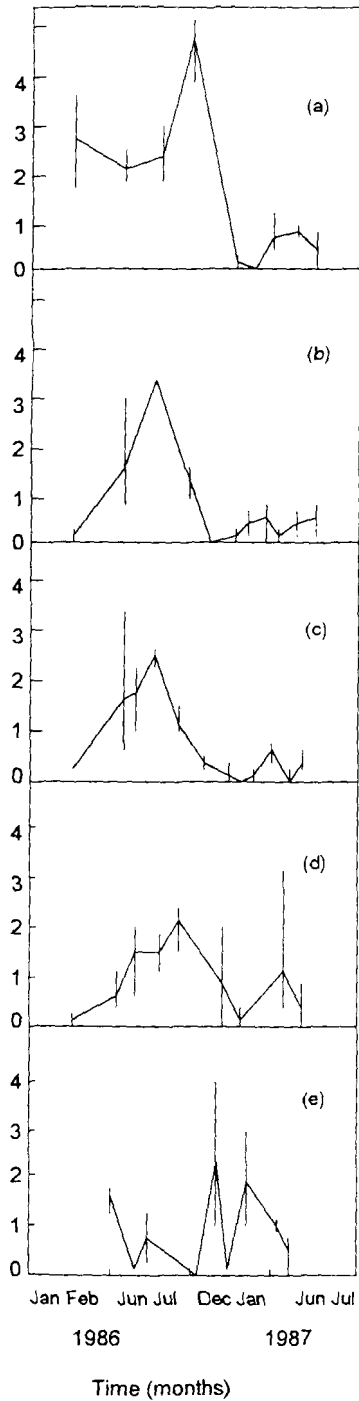


Figure 2.2 Variation of BNF (ordinate: unit $\mu\text{g l}^{-1} \text{h}^{-1}$) with time in each basin

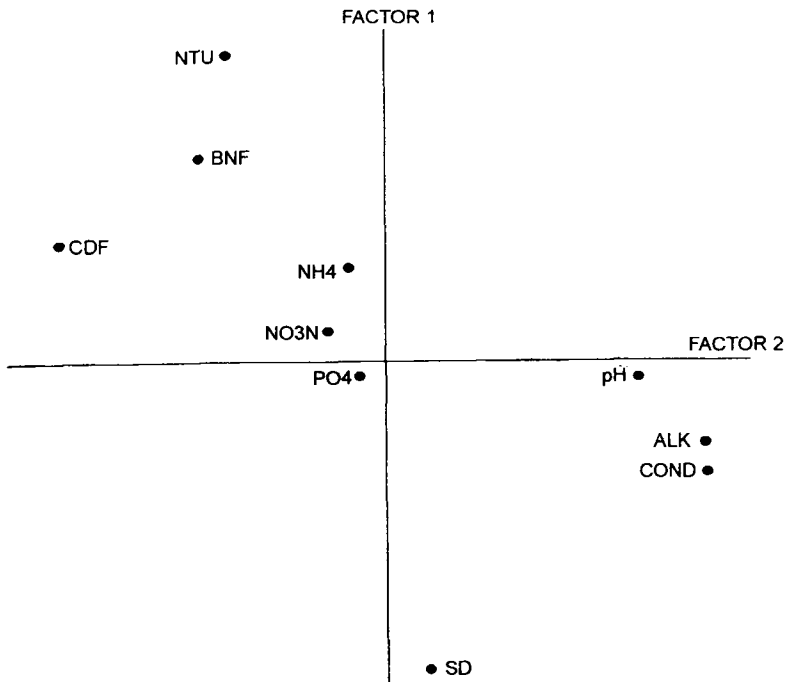


Figure 2.3 Results of factor analysis of cyanobacterial N_2 fixation and other limnological parameters

Three clearly distinct clusters of variables are evident when the first two components were plotted. The analysis showed that the group comprising pH, alkalinity and conductivity was inversely related to that of BNF, phytoplankton primary production and turbidity.

The equations obtained when the data set was subjected to multiple regression analysis are given below. They show the relationships between BNF and various limnological parameters:

$$\text{BNF} = 12.79 - 0.51 \text{ LP} + 0.002 \text{ PO}_4 - 0.97 \text{ pH} - 0.02 \text{ NH}_4 + 0.020 \text{ CON} - 0.01 \text{ TU} - 4.61 \text{ ALK} \quad (R^2 = 0.371)$$

$$\text{Log BNF} = 13.79 - 0.47 \text{ Log TU} + 0.32 \text{ Log pH} - 0.11 \text{ Log CHLA} - 5.90 \text{ Log ALK} - 0.073 \text{ Log PO}_4 - 0.33 \text{ Log NH}_4 - 0.34 \text{ Log LP} - 1.49 \text{ Log CON} \quad (R^2 = 0.88)$$

$$\text{Log BNF} = 11.84 - 4.13 \text{ Log ALK} - 1.97 \text{ Log CON} \quad (R^2 = 0.79)$$

It should be noticed that there was no inverse correlation between BNF and ammonia N or nitrate-nitrite N. However, alkalinity, conductivity, light penetration and pH are potentially the most useful predictors of the BNF in Lake Kariba.

The temporal variation noted for BNF correlates well with the abundance of *Cylindrospermopsis raciborski*, a heterocystous cyanobacterium, as quoted by

Ramberg (1984 and 1987). The latter noted an increased cyanobacterial biomass in the hot dry and hot wet season (between October and April) whereas the lake experiences high temperatures, stratification and nutrient inflow. These parameters are possibly the major determinants of cyanobacterial biomass increase.

The basin-related spatial variations observed in BNF levels may be a result of the differential riverine influence on the sampling stations. Stations in riverine basins 1 and 2 are markedly affected by the Zambezi River which, although low in nutrients, exerts itself lumetrically. The lacustrine basins 3 and 4 have no major riverine unputs, whereas lacustrine basin 5 (Sanyati basin) is under the influence of the nutrient rich Sanyati River which drains agricultural lands.

DISCUSSION

The rates of BNF found in Lake Kariba ($0-5 \mu\text{g N l}^{-1} \text{h}^{-1}$) are comparable to those from other lakes and the oceans (Goering, Dugdale and Menzel 1966, Horne and Goldman 1972). Aerial cyanobacterial nitrogen fixation rates in Lake Kariba ranged from 0.04 to $0.202 \text{ g N m}^{-2} \text{ yr}^{-1}$, values which lie at the lower end of the range ($0.92 \text{ g N m}^{-2} \text{ yr}^{-1}$) given by Howarth *et al.* (1988).

The contribution of BNF to the total annual nitrogen inputs in Lake Kariba is higher than those given for a few aquatic ecosystems (e.g. Carr and Whitton 1982, Horne and Fogg 1970, Horne and Viner 1971, Leonardson 1984, Toetz 1983). The contribution of BNF by cyanobacteria to the nitrogen budget in Lake Hefner was 1.5% (McFarland and Toetz 1988). In the Western Sargasso, *Oscillatoria (Trichodesmium) thiebauti*, a non-heterocystous cyanobacteria made an insignificant input of nitrogen (Carpenter and McCarthy 1975).

On the opposite, BNF has been shown to be a quantitatively important source of nitrogen for the nitrogen budgets of a number of lakes. This process contributed up to 80% of the annual nitrogen supply to Lake Erken, Sweden (Granhall and Lundgren 1971), and 43% in Clear Lake, California (Horne and Goldman 1972). In eutrophic Rietvlei dam, South Africa, the process contributed between 1.4 and 46.5% of the total nitrogen (Ashton 1981). In oligotrophic Skaha Lake, Canada, a cyanophyte bloom contributed up to 60% of the annual nitrogen income into the lake (Findley *et al.* 1973). In Pyramid lake, nitrogen fixed by a short-lived bloom of *Nodularia* sp. constituted 99.5% of the alga's needs and 81% of the nitrogen input (Horne and Galat 1985). The value reported for Lake Kariba is as high as the 33% attributed to this process in Lake George, Uganda (Horne and Viner 1971). Possible reasons for the similarity of the two figures could be investigated: Cyanobacteria are abundant in the two lakes which are both mesotrophic or even eutrophic.

Factors influencing BNF were investigated for instance by Horne and Fogg (1970) who concluded that although nitrogen fixation was confined to periods of low nitrate N, there was no significant negative correlation noted. Horne and Goldman (1972), in their multiple regression equation, found that fluctuations in NBF were best explained by variations in heterocysts, cyanobacterial biomass, orthophosphates levels, nitrate levels and temperature. In Lake Kariba, a model incorporating alkalinity and conductivity may be of significant predictive value for BNF.

BNF showed spatial variation along the longitudinal axis of Lake Kariba. This observation is similar to that made for BNF and heterocyst frequency in Lake Valencia (Levine and Lewis 1985). Spatial variations of several other variables have been reported in Lake Kariba. For example, Coche (1974), Moyo (1991) and Lindmark (this volume) noted variations of several physico-chemical variables along the longitudinal axis of the lake. Magadza (1980) also found that riverine influences affected the distribution of plankton in the Sanyati basin.

CONCLUSION

The present study aimed at quantifying the level of BNF in Lake Kariba and finding out how this process was related to biological physical and chemical parameters in the lake. Such knowledge can be of useful modelling and predictive value, particularly when attempting to approach the transfers of nutrients and biomass inside the whole ecosystem.

SUMMARY

There is no information on the relative contribution of cyanobacterial N_2 fixation to the nitrogen budget of Lake Kariba. The main objectives of the current study were therefore to determine (1) the rates of BNF in the lake (2) the spatial and temporal variations and (3) the importance of BNF to the nitrogen economy of Lake Kariba.

Volume-based rates of BNF ranged from 0 to 5 mg $N\ l^{-1}\ h^{-1}$. After integration on a surface area basis, rates of BNF ranged between 0.040 and 0.202 g $N\ m^{-2}\ yr^{-1}$ with an average of 0.121 g $N\ m^{-2}\ yr^{-1}$.

Values of BNF varied with time. BNF was usually highest in the hot season (October–February), although peaks occurred much earlier than this in the more lacustrine basins of the lake. Variations of BNF on the longitudinal axis were noted with rates being higher in the lacustrine basins (Basins 3, 4 and 5) compared with in the riverine basins (Basins 1 and 2).

The values of BNF measured here were used in the construction of a nitrogen budget for Lake Kariba which shows that BNF contributed about 32% of the total annual nitrogen inputs into Lake Kariba during the study period. A factor analysis was also performed which helped to establish that alkalinity, conductivity, light penetration and pH are potentially the most useful predictors of the BNF. Lake Kariba is compared with other water bodies for BNF contribution to the nitrogen budget of the lake.



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