

Temporal dynamics of lipids in the zooplankton of two tropical reservoirs of different trophic status

Ricardo M. Pinto-Coelho, M. K. Amorim and A. R. da Costa

Introduction

Lipids make up the most important energy reserves of zooplankton (GOULDEN & HENRY 1988). In freshwater ecosystems, copepods, cladocerans and rotifers are the dominant groups and all are known to accumulate lipid as energy reserves (VIJVERBERG & FRANK 1976, KOKOVA et al. 1982). Lipids in zooplankton occur mostly as triacylglycerides, phospholipids, acetone mobile polar lipids, free fatty acids and sterols (VANDERPLOEG et al. 1992).

A vast literature exists on lipids from marine zooplankton (e.g. RAYMONT et al. 1971). More recently, some information on lipid dynamics of freshwater zooplankton from temperate regions has been published. These works are basically limited to a few studies on seasonal patterns (e.g. SIEFKEN & ARMITAGE 1968, HILL et al. 1992, WAINMAN & LEAN 1990, WAINMAN et al. 1993, VANDERPLOEG et al. 1992).

There is a great lack of information about the biochemical composition of zooplankton from tropical regions. Are the data on lipid content comparable to the existing data from higher latitudes? Can we isolate temporal patterns of energy storage in tropical zooplankton?

This study aimed to investigate the temporal dynamics of lipids of zooplankton in two reservoirs: a) the turbid and hypereutrophic Pampulha Reservoir ($A = 2.4 \text{ km}^2$, $\text{vol} = 14 \times 10^6 \text{ m}^3$, $Z_{\text{max}} = 16 \text{ m}$, $\text{loc.} = 19^\circ 55' \text{ S}$, $43^\circ 56' \text{ W}$), situated in the city of Belo Horizonte; and b) the oligo-mesotrophic Furnas Reservoir ($A = 1459 \text{ km}^2$, $\text{vol} = 21.0 \times 10^9 \text{ m}^3$, $Z_{\text{max}} = 88.5 \text{ m}$, $\text{loc.} = 20^\circ 40' \text{ S}$, $46^\circ 19' \text{ W}$). This reservoir is situated in south-eastern Minas Gerais State. The temporal dynamics of lipids was investigated at two different time scales: annual and diurnal cycles.

Methods

Zooplankton was collected monthly from February 1993 to December 1994 by means of vertical net tows using a 22 cm diameter net with $90 \mu\text{m}$ mesh size at a central sampling point in Pampulha Reservoir ($Z = 10 \text{ m}$). Two diel cycles were investigated in Pampulha Reservoir: in April and August 1994, respectively. In Furnas Reservoir, two diel cycles were investigated: in July 1994 and in February 1995.

Zooplankton samples for counting were also taken. Organisms were immediately fixed using formalin (4% of final concentration) buffered to pH 7. Counting was done using a stereo-microscope Zeiss microscope. Every specimen was measured and allometric equations were used for estimation of dry weights (PINTO-COELHO 1991b).

Contents of net tows for biochemical analyses were placed in an insulated 5 L container filled with lake water from the epilimnion, and transported to the laboratory within 20 minutes. At the laboratory, organisms were filtered on an inox gauze with $160 \mu\text{m}$ mesh size. These filters were placed on 10 cm diameter Petri dishes and immediately stored in a freezer (-25°C).

Zooplankton organisms were then freeze-dried according to the technique proposed by BERBEROVIC & PINTO-COELHO (1989). Dried organisms were transferred to small pre-weighed aluminium 'boats' and dry weight was determined using a Mettler high precision balance (0.000001 g). Weighed zooplankton was homogenized with 1.0 ml of distilled water using an electrical micro-homogenizer ELGIN.

Chemical digestion, as proposed by MEYER & WALTHER (1988), was applied to the homogenized material. Total lipids were determined spectrophotometrically ($h = 546 \text{ nm}$) using the sulpho-phosphovanillin reaction (ZÖLLNER & KIRSCH 1962).

Results and discussion

The biomass of total zooplankton of Pampulha Reservoir fluctuated between 1.0 and $4.0 \text{ mg DW} \cdot \text{m}^{-2}$ in 1994 (Fig. 1, top). This community was dominated by large cladocerans *Daphnia gessneri*, *D. laevis*, *Diaphanosoma* spp. were the most important organisms. Small cladocerans, such as *Bosmina* spp. and *Ceriodaphnia cornuta*, were occasionally abundant but their contributions to total biomass can be neglected. Copepods were dominated by *Thermocyclops decipiens*. Other cyclopoids, such as *Mesocyclops* spp., *Metacyclops* sp. and *Scolodiatomus corderoi* were also occasionally present. Total zooplankton biomass peaked in June–July,

DeBusk (1991) observed that microbial retention of phosphorus from macrophytes caused an acute reduction of C:P ratios of detrital biomass attached to the root zone of *E. crassipes* in the first 40 days of observations. Nevertheless, these microbial community attached to the root zone of *E. crassipes* is a key factor for the decomposition of these macrophytes, since decomposition rates are faster in the root zone of hyacinth mats than at the sediment water interface (Reddy & DeBusk, 1991). As an example, the microbial flora and fauna attached to young *E. crassipes* plants required only 26 days to recycle its biomass completely in other lakes (Singhol et al., 1993). The decomposition rate will depend strongly on the prevailing metabolism of the attached microbes: aerobic respiration, facultative anaerobic respiration and anaerobic respiration. The aerobic respiration, however, may be the major metabolic pathway of biomass decomposition of dead macrophyte tissue in the root zone (Reddy & DeBusk, 1991).

Conclusions

The higher excretion rates of zooplankton and biomass turnover rates of macrophytes found in this study indicate that the zooplankton community and the macrophyte *E. crassipes* may be the keystone organisms in the internal cycling of phosphorus in Pampulha reservoir. On some occasions, like at the end of the rainy season, both communities were able to recycle as much as 43% d⁻¹ of the available phosphorus in lake water. Furthermore, it was also clear that there was a time lag between the maximum of return rates of phosphorus due to these communities. Zooplankton released more phosphorus during the dry season when its biomass was high, whereas the water hyacinths released more phosphorus at the end of their growing season when biomass turnover peaked. This period coincided with the end of the rainy season and a low zooplankton biomass.

The temporal differences in maximum P-release due to zooplankton and macrophytes possibly have important consequences. The regular monitoring program over several years has shown that the phosphorus concentrations in the water usually reach a minimum at the end of the rainy season (Pinto-Coelho, 1998). At this time, the water hyacinth population is recycling more phosphorus. Therefore, the decomposition of macrophyte biomass is not only a major source of phosphorus for the existing biota in the reservoir, but

is possibly the most important source of regenerated phosphorus during some periods of the year.

Acknowledgements

This study was supported by the Fundação Nacional do Meio Ambiente – FNMA, convênio FUNDEP 2279, Coordenação de Aperfeiçoamento de Pessoal Docente do Ministério da Educação e Cultura do Brasil – CAPES, and by Fundação de Amparo à Pesquisa do Estado de Minas Gerais – FAPEMIG (CBS 152/92). We also thank the biologists Raquel Teixeira de Moura and Carla Fernandes Macedo for support in the experiments of zooplankton excretion.

References

- Alcaraz, M., E. Saiz & M. Estrada, 1994. Excretion of ammonia by zooplankton and its potential contribution to nitrogen requirements for primary production in the Catalan Sea (NW Mediterranean). *Mar. Biol.* 119: 69–76.
- Bartell, S. M., 1981. Potential impact of size selective planktivory on phosphorus release by zooplankton. *Hydrobiologia* 80: 139–145.
- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig & I. Hillbricht-Ilkows, 1976. A review of some problems in zooplankton production studies. *Norw. J. Zool.* 24: 419–456.
- Brönmark, C., 1989. Interactions between epiphytes, macrophytes and freshwater snails. *J. redl. Stred.* 55: 299–311.
- Carpenter, S. R., K. L. Cottingham & D. E. Schindler, 1992. Biotic feedbacks in lake phosphorus cycles. *Trends Ecol. Evol.* 7: 332–336.
- Center, T. D. & N. R. Spencer, 1981. The phenology and growth of water hyacinth (*Eichhornia crassipes* (Mart.) Solms.) in a eutrophic North-Central Florida lake. *Aquat. Bot.* 10: 1–32.
- Center, T. D. & T. K. Van, 1989. Alteration of water hyacinth (*Eichhornia crassipes* (Mart.) Solms.) leaf dynamics and phytochemistry by insects damage and plant density. *Aquat. Bot.* 35: 181–195.
- Conner, J. B. & R. G. Wetzel, 1992. Uptake of dissolved inorganic phosphorus compounds by phytoplankton and bacterioplankton. *Limnol. Oceanogr.* 37: 23–243.
- Christoffersen, K., B. Riemann, A. Klysner & M. Sondergaard, 1993. Potential role of fish predation and natural populations of zooplankton in structuring a plankton community in eutrophic lake water. *Limnol. Oceanogr.* 38: 561–573.
- Debusk, T. A., J. H. Ryther, M. D. Hanisak & L. D. Williams, 1981. Effects of seasonality and plant density on the productivity of some freshwater macrophytes. *Aquat. Bot.* 10: 133–142.
- Ejsmont-Karabin, J. & I. Spondniewska, 1990. Influence on phytoplankton biomass in lakes of different trophic by phosphorus by phosphorus in lake water and its regeneration by zooplankton. *Hydrobiologia* 191: 123–128.
- Ejsmont-Karabin, J., 1984. Phosphorus and nitrogen excretion by lake zooplankton (rotifers and crustaceans) in relationship to individual body weights of the animals, ambient temperature and presence or absence of food. *Ekol. Pol.* 32: 3–42.

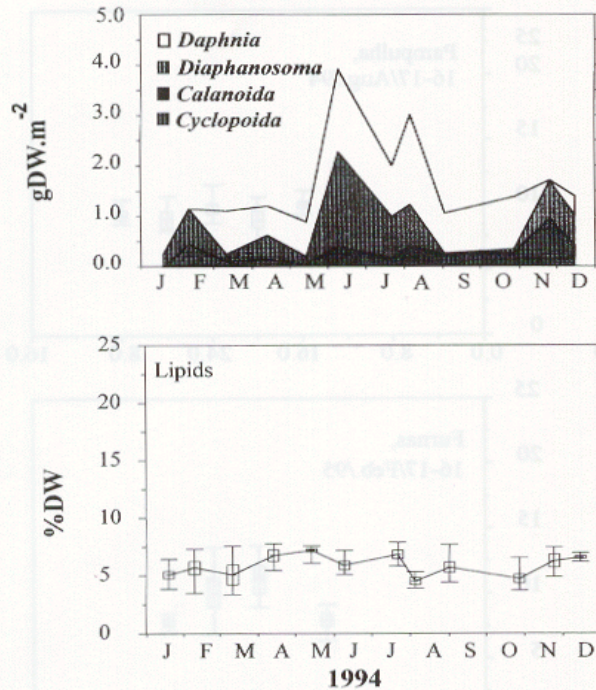


Fig. 1. Annual course of biomass and lipid content of zooplankton from Pampulha Reservoir, Brazil in 1994. Ranges, standard errors and mean values are indicated.

mostly due to an increase of cladoceran populations. Copepods were more abundant in the rainy season (November–March).

The lipid content of total zooplankton in 1994 remained always below 10% of total biomass (Fig. 1, bottom). In spite of the seasonality observed in the biomass of cladocerans and copepods, seasonal fluctuations in the lipid content were minimal. The mean annual value for total lipids was 5.8 ± 0.8 % DW. Zooplankton of Furnas Reservoir also exhibited low values of lipid in its biomass. The overall mean values for the two diurnal cycles undertaken in 1994 were 8.4 and 9.2 % DW, respectively.

Freshwater zooplankton of higher latitudes has generally higher lipid values (HILL et al. 1992, VANDERPLOEG et al. 1992). The lipid contents of zooplankton also increases with depth in the oceans (CHILDRESS & NYGAARD 1974). In both cases, it seems that zooplankton stores higher amounts of lipids in colder waters. Tropical zooplankton possibly has a higher energetic demand since they are living permanently in warmer waters ($>18^\circ\text{C}$). The oxygen

consumed is positively affected by temperature increases (TOTH & DRITS 1991) and, therefore, tropical zooplankton would have to allocate more energy to basal metabolism and this should cause lower lipid storage patterns.

Poor food quality can also induce lower levels of lipid content (LA ROW et al. 1975). Phytoplankton in Pampulha Reservoir is dominated by Cyanobacteria (*Microcystis* spp.). Recent investigations have demonstrated that zooplankton in this lake mostly consumes detritus and small heterotrophs (ARAÚJO 1995). It is well known that assimilation efficiency is very low in any detrital food chain (MARGALEF 1977).

The daily cycles of lipid content of zooplankton showed different results in each of the reservoirs studied. In Pampulha Reservoir, the two diel cycles showed different trends (Fig. 2, top). In the diel cycle of April/94, the coefficient of variation, c.v., was 15.5%, higher than the c.v. obtained for the whole year of 1994 (c.v. = 14.4%). Nevertheless, the same mean value of lipids (8.2%) was observed in three different times of the cycle: at 20:00 hs, 24:00 hs and 08:00 hs, respectively. The maximum value (10.2%) was measured at 20:00 hs.

In the diel cycle from August of 1994, lipid values remained quite comparable (c.v. = 5.6%). The ANOVA confirmed the absence of a diel pattern (F-Ratio = 1.907, $P < 0.122$, $N = 37$). The mean values varied within a narrow range: 8.8–10.1% for all times (Fig. 2, top). The highest values of the diel cycle were 11.6% and 11.5%, observed at noon and midnight, respectively.

In Furnas Reservoir, there was a clear trend for higher lipid values at night in both dates (Fig. 2, bottom). In July 1994, the highest values (both mean and maximum values) occurred at 04:00 am. The mean value at 04:00 hs. am was 10.8% clearly much higher than all mean values observed during the day (6.7–8.7%). The c.v. of 17.8% also indicates the existence of a marked diel fluctuation in the lipid content of zooplankton (F-Ratio = 4.232, $P < 0.021$, $N = 18$).

Higher lipid values at night were again observed in February 1995. Night values of lipids were 11.1% and 10.1%, observed at 20:00 hs. and 24:00 hs., respectively. These values were clearly more elevated than the mean daily values (7.7–7.9%). The c.v. calculated for the whole cycle was 15.5% (F-Ratio 4.119, $P < 0.026$, $N = 19$).

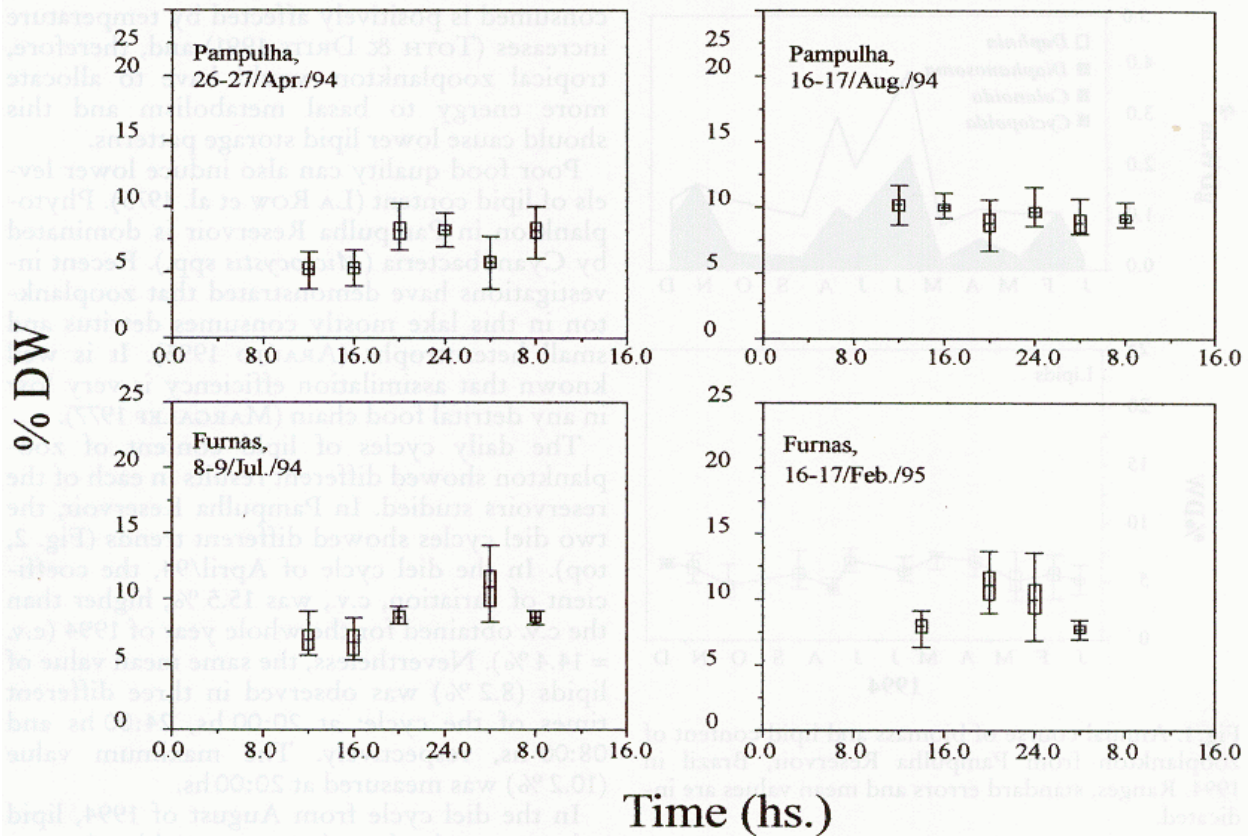


Fig. 2. Diurnal course of lipid values in zooplankton (% DW) in two reservoirs of Minas Gerais, Brazil. Ranges, standard errors are indicated.

Why has zooplankton in Furnas Reservoir higher lipid values at night, whereas this trend could not be observed in Pampulha Reservoir? This survey was undertaken in an oligotrophic part of Furnas Reservoir, near the Turvo River Bridge. Herbivore zooplankton in this part of Furnas is largely dominated by the calanoids *Argyrodiaptomus furcatus*, *Notodiptomus iheringi*, *Scolodiptomus corderoi* and large cladocerans such as *Daphnia* and *Diaphanosoma* (REID & PINTO-COELHO 1994). At least *S. corderoi* is known to be an efficient algal filter-feeder (PINTO-COELHO et al. 1988). Transparency of the water column at this point in Furnas is high (Secchi disk > 4.0 m).

The higher lipid values of zooplankton at night suggest that the classic food chain (phytoplankton-zooplankton) plays a major role in this environment. Large herbivores are known to have higher filtering rates at night (PINTO-COELHO 1991 a). Consequently, they

would stock lipids at night. On the other hand, Pampulha Lake is a very turbid reservoir (Secchi disk < 1.5 m) and zooplankton nutrition is mostly based on heterotrophic organic carbon (ARAÚJO 1995). The lack of a pattern in the diurnal rhythms of lipid dynamics would be expected in a detrital/heterotrophic food chain in a turbid reservoir since there would be no selective advantage for zooplankton to wait until dark to enhance filtering rates.

Conclusions

The lower lipid values of zooplankton found in different tropical ecosystems seem to confirm the latitudinal trends observed in the lipid content of zooplankton. Furthermore, the differences found in the diurnal cycles between Pampulha and Furnas reservoirs indicate that food quality possibly plays a major role in the dynamics of lipids in zooplankton. The comparison between diel and seasonal cycles of lipid contents of zooplankton seems to confirm the

idea that short temporal variations are more important in most ecological processes occurring in the water column of tropical waters.

Acknowledgements

This study was supported by Brazilian National Research Council (CNPq, Procs: 521513/93-6 and 400630/92-3) and by the Federal University of Minas Gerais, PRPq/UFMG (Proc N. 23072.050293/94-17).

References

- ARAÚJO, M. A. R., 1995: *Produção e Consumo de carbono na comunidade planctônica do Reservatório da Pampulha*. – MSc. Thesis.
- BERBEREOVIC, R. & PINTO-COELHO, R. M., 1989: Dry first, measure later: a new procedure to preserve and measure zooplankton for ecophysiological studies. – *J. Plankton Res.* 11(5): 1109–1116.
- CHILDRESS, J. J. & NYGAARD, M., 1974: Chemical composition and buoyancy of midwater crustaceans as function of depth of occurrence off Southern California. – *Marine Biology* 27: 225–238.
- GOULDEN, C. E. & HENRY, L. L., 1988: Lipid energy reserves and their role in cladocera. – In: MEYERS, D. G. & STRICKLER, J. R. (eds.): *Trophic interactions within aquatic ecosystems*: 167–185. Selected Symposium AAAS, Washington, DC.
- HILL, C., QUIGLEY, M. A., CAVALETTO, J. F. & GORDON, W., 1992: Seasonal changes in lipid content and composition in three benthic amphipods *Monoporeia affinis* and *Pontoreia femorata*. – *Limnology & Oceanography* 37(6): 1280–1289.
- KOKOVA, V. V., TRUBACHEV, I. N. & BARASHKOV, V. A., 1982: Biochemical composition of certain aquatic invertebrates. – *Gidrobiologicheskij Zhurnal* 18: 86–94.
- LA ROW, E. J., WILKINSON, J. W. & KUMAR, K. D., 1975: The effect of food concentration and temperature on respiration and excretion in herbivorous zooplankton. – *Verh. Internat. Verein. Limnol.* 19: 966–973.
- MARGALEF, R., 1977: *Ecología*. 2 Ed. – Ediciones Omega, S.A., Barcelona, 951 pp.
- MEYER, E. & WALTHER, A., 1988: Methods for the estimation of protein, lipid, carbohydrate and chitin in fresh water invertebrates. – *Arch. Hydrobiol.* 113(2): 161–177.
- PINTO-COELHO, R. M., 1991a: Zooplankton grazing in Lake Constance: seasonal and day-night “in situ” measurements. – *Verh. Internat. Verein. Limnol.* 24: 842–845.
- 1991b: *Zooplankton grazing in Lake Constance: In situ measurements of temporal variations, relative contributions of size fractions and major herbivores, regulatory factors of specific filtering rates and potential impact as loss factor for phytoplankton*. – PhD Thesis, Universität Konstanz.
- PINTO-COELHO, R. M., LIMA, S. S. & PELLI, A., 1988: Estudos experimentais sobre a alimentação em fêmeas adultas de *Diatomus* (s.l.) *corderoi* (WRIGHT 1936) copepoda calanoida do reservatório da Pampulha, Belo Horizonte, MG. – *Acta Limnologica Brasiliensia* 11: 605–620.
- RAYMONT, J. E. G., SRINIVASAGAM, R. T. & RAYMONT, J. K. B., 1971: Biochemical studies on marine zooplankton. IX. The biochemical composition of *Euphausia superba*. – *J. Marine Biol. Assoc. United Kingdom* 51: 581–588.
- REID, J. W. & PINTO-COELHO, R. M., 1994: Planktonic copepoda of Furnas Reservoir: Initial survey of species (1993) and review of literature. – In: PINTO-COELHO, R. M., GIANI, A. & VON SPERLING, E. (eds.): *Ecology and Human Impact on Lakes and Reservoirs in Minas Gerais*: 93–114. SEGRAC, Belo Horizonte.
- SIEFKEN, M. & ARMITAGE, K. B., 1968: Seasonal variation in metabolism and organic nutrients in three *Diatomus* (Crustacea: Copepoda). – *Comparative Biochemistry Physiology* 24: 591–609.
- TÓTH, L. G. & DRITS, A. V., 1991: Respiratory energy loss of zooplankton in Lake Balaton (Hungary) estimated by ETS-activity measurements. – *Verh. Internat. Verein. Limnol.* 24: 993–996.
- VANDERPLOEG, H. A., GARDNER, W. A., PARRISH, C. C., LIEBIG, J. R. & CAVALETTO, J. F., 1992: Lipids and life cycle of a hypolimnetic copepod in Lake Michigan. – *Limnology and Oceanography* 37(2): 413–424.
- VIJVERBERG, J. & FRANK, T. H., 1976: The chemical composition and energy contents of copepods and cladocerans in relation to their size. – *Freshwater Biology* 6: 333–345.
- WAINMAN, B. C. & LEAN, D. R. S., 1990: Seasonal trends in planktonic lipid content and lipid class. – *Verh. Internat. Verein. Limnol.* 24: 416–419.
- WAINMAN, B. C., MCQUEEN, D. J. & LEAN, D. R. S., 1993: Seasonal trends in zooplankton lipid concentration and class in freshwater lakes. – *J. Plankton Res.* 15: 1319–1332.
- ZÖLLNER, N. & KIRSCH, K., 1962: Über die quantitative Bestimmung von Lipoiden (Mikromethode) mittels der vielen natürlichen Lipoiden (allen bekannten plasmalipoiden) gemeinsamen sulfophosphornilen Reaktion. – *Z. f. die Ges. Experim. Med.* 135: 545–561.

Authors' address:

R. M. PINTO-COELHO, M. K. AMORIM, A. R. DE COSTA, Depto. Biologia Geral ICB UFMG, P.O. Box 2486, 31270 010 Belo Horizonte (MG), Brazil.

- Ferreira, W. P., 1992. Atlas Nacional do Brasil. Instituto Brasileiro de Geografia e Estatística – IBGE. Rio de Janeiro: 42 pp.
- Giani, A., R. M. Pinto-Coelho, S. M. Oliveira & A. Pelli, 1988. Ciclo sazonal de parâmetros físico-químicos da gua e distribuição horizontal de nitrogênio e fósforo no reservatório da Pampulha (Belo Horizonte, MG, Brasil). *Ciência e Cultura* 40: 69–77.
- Greco, M. K. B., 1996. Determinação da Produção de *Eichhornia crassipes* (Mart.) Solms. na Represa da Pampulha, BH/MG, Através dos Métodos Tradicional e Demográfico. Programa de Ecologia Conservação e Manejo da Vida Silvestre, Universidade Federal de Minas Gerais, 71 pp.
- Gerber, M. A., M. A. Watson & R. Furnish, 1992. Genetic differences in clonal demography in *Eichhornia crassipes*. *J. Ecol.* 80: 329–341.
- Gophen, M., 1976. Temperature dependence of food intake, ammonia excretion and respiration in *Ceriodaphnia reticulata* (Jurine) (Lake Kinneret, Israel). *Freshwat. Biol.* 6: 451–455.
- Gopal, B., 1987. *Water hyacinth*. Elsevier. Amsterdam. The Netherlands.
- Gopal, B., 1994. The role of ecotones (transition zones) in conservation and management of tropical inland water. *Mitt. int. Ver. Limnol.* 24: 17–25.
- Gutelmakher, B. L. & E. S. Makartseva, 1990. The significance of zooplankton in the cycling of phosphorus in lakes of different trophic categories. *Int. Rev. ges. Hydrobiol.* 75: 143–151.
- Henrickson, L., H. G. Nyman, H. G. Oscarson & J. A. E. Stenson, 1980. Trophic changes without changes in nutrient loading. *Hydrobiologia* 68: 257–263.
- Henry, R. & J. G. Tundisi, 1983. Responses of the phytoplankton community of a tropical reservoir (Sao Paulo, Brazil) to the enrichment with nitrate, phosphate and EDTA. *Int. Rev. ges. Hydrobiol.* 68: 853–862.
- Hutchinson, G. E., 1973. Eutrophication: the scientific background for a contemporary practical problem. *Am. Sci.* 61: 269–279.
- Jacobsen, T. R. & G. W. Comita, 1976. Ammonia nitrogen excretion in 'Daphnia pulex' *Hydrobiologia* 51: 195–200.
- Jeppsen, E., P. Kristensen, J. P. Jensen, M. Sondergaard, E. Moresen & T. Lauridsen, 1991. Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. *Mem. Ist. ital. Idrobiol.* 48: 127–148.
- Kleeberg, A. & H.-P. Kozerski, 1997. Phosphorus release in Lake Grosser Müggelsee and its implications for lake restoration. *Hydrobiologia* 342/343: 9–26.
- Larcher, W., 1980. *Physiological Plant Ecology*. 2nd edn. Springer-Verlag, Berlin.
- La Row, E. J., J. W. Wilkinson & K. D. Kumar, 1975. The effect of food concentration and temperature on respiration and excretion in herbivorous zooplankton *Verh. int. Ver. Limnol.* 19: 966–973.
- Lehman, J. T., 1980a. Nutrient recycling as an interface between algae and grazers in freshwater communities. In Kerfoot, W. C. (ed.), *Evolution and Ecology of Zooplankton Communities*. The Univ. Press of New England: 251–263.
- Lehman, J. T., 1980b. Release and cycling of nutrients between planktonic algae and herbivores *Limnol. Oceanogr.* 25: 620–632.
- Likens, G. E., 1972. Eutrophication and aquatic ecosystems. *Proceedings of the Symposium on Nutrients and Eutrophication: The limiting-nutrient controversy*. ASLO: 3–13.
- Masundire, H. M., 1994. Mean individual dry weight and length weight regressions of some zooplankton of lake Kariba *Hydrobiologia* 272: 231–238.
- Mayzaud, P., 1976. Respiration and nitrogen excretion of zooplankton and the influence of starvation on the metabolism and the biochemical composition of some species. *Mar. Biol.* 37: 47–58.
- McCauley, E., 1984. The estimation of the abundance and biomass of zooplankton in samples. In Downing, J. A. & F. H. Rigler (eds), *A Manual on Methods for the Assessment of Secondary Production in Freshwaters*. IBP Handbook no. 17, Blackwell, Oxford, U.K: 228–265.
- Methy, M. & J. Roy, 1993. Morphogenetic changes induced by a low red far radiation and their growth consequences in water hyacinth (*Eichhornia crassipes*). *J. exp. Bot.* 44: 1275–1280.
- Murphy, J. & J. P. Riley, 1962. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta* 27: 31–36.
- Peters, R. & D. Lean, 1973. The characterization of soluble phosphorus released by limnetic zooplankton. *Limnol. Oceanogr.* 18: 270–279.
- Pieczynska, E., 1990. Lentic aquatic-terrestrial ecotones: their structure, functions, and importance. In Naiman & H. Déchamps (eds), *The Ecology and Management of Aquatic-Terrestrial Ecotones*. Unesco & Phaternon Publishing Group, Paris: 103–140.
- Pinto-Coelho, R. M., 1994. Limnological perspectives for the control of eutrophication in large tropical reservoirs. In Pinto-Coelho, R. M., A. Giani & E. vom Sperling (eds), *Ecology and Human Impact on Lakes and Reservoirs in Minas Gerais*. SEGRAC. Belo Horizonte: 11–26.
- Pinto-Coelho, R. M., R. T. Moura & A. Moreira, 1997. Zooplankton and bacteria contribution to phosphorus and nitrogen internal cycling in a tropical and eutrophic lake: Pampulha Lake, Brazil. *Int. Revue. ges. Hydrobiol.* 82: 185–200.
- Pinto-Coelho, R. M., 1998. Effects of eutrophication on seasonal patterns of mesozooplankton in a tropical reservoir: a 4-year study in Pampulha Lake, Brazil. *Freshwat. Biol.* 40: 159–173.
- Reddy, K. R. & W. F. DeBusk, 1991. Decomposition of water hyacinth in eutrophic lake water. *Hydrobiologia* 211: 101–109.
- Schindler, D. W., 1977. Evolution of phosphorus limitation in lakes. *Science* 195: 260–262.
- Singhol, P. K., L. Varghese & L. Talegaonkar, 1993. Abiotic and microbial decomposition of pre and post-bloom leaves of water hyacinth (*Eichhornia crassipes* (Mart.) Solms). *Hydrobiologia* 259: 115–119.
- Stephen, D., B. Moss & G. Phillips, 1997. Do rooted macrophytes increase sediment phosphorus release? *Hydrobiologia* 342/343: 27–34.
- Sucharit, S., C. Harinasuta, T. Deesin & S. Vutikes, 1981. Studies of aquatic plants and grasses as breeding hosts for mosquitoes. *J. Trop. Med. Publ. Health* 12: 462–463.
- Thomas, F. I. & A. J. Atkinson, 1997. Ammonium uptake by coral reefs: effects of water velocity and surface roughness on mass transfer. *Limnol. Oceanogr.* 42: 81–88.
- Urabe, J., M. Nakanishi & K. Kawabata, 1995. Contribution of metazoan plankton to the cycling of nitrogen and phosphorus in Lake Biwa. *Limnol. Oceanogr.* 40: 232–241.
- Westlake, D. L., 1965. Some basic data for investi A.J. gations of productivity of aquatic macrophytes. *Mem. Ist. ital. Idrobiol.* 18: 229–248.
- White, J., 1979. The plant as a metapopulation. *Ann. Rev. Ecol. Syst.* 10: 109–145.
- Zauke, G. P., R. G. Niemeyer & K. P. Gilles, 1992. *Limnologie der Tropen und Subtropen*. Ecomed. Bonn. 171 pp.

