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OBITUARY

Fifty years of research on plankton ecology, biomanipulation and restoration of shallow lakes in the Netherlands: a tribute to Dr. Ramesh Datt Gulati (1935–2019)

Brij Gopal · S. S. S. Sarma · S. Nandini

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Late Dr Ramesh D. Gulati (28 Sept 1935–23 Dec 2019). (Photo by S. Nandini during the 14th International Rotifer conference in České Budějovice, Czech Republic. 30 Aug–4 Sept 2015)

Background of Dr. R. D. Gulati

Born on the 28th of September 1935, in Piplan (in erstwhile Panjab, now in Pakistan), young Gulati lost his parents during the 1947 war following the partition between India and Pakistan. He arrived as a refugee with his brothers and sisters in New Delhi where he had his school and university education (see also Parma, 2003). He obtained his B.Sc. honours in Zoology (1956), and M.Sc. in Fish and Fishery Biology (1958) from the Department of Zoology, University of Delhi. For his PhD degree (1964, University of Delhi), he had investigated several shallow and deep lakes including Lake Nainital and Lake Bhimtal in the Kumaon Himalaya. He had studied thermal stratification, plankton ecology, algal blooms and lake eutrophication. These studies, however, remain unpublished. He taught zoology to graduate students from 1959 to 1968 at Delhi University, before moving to the Netherlands.

Career in the Netherlands

The waterscape of the Netherlands is dominated by a large number of freshwater lakes, besides the rivers

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B. Gopal (✉)
Centre for Inland Waters in South Asia, 41B Shiv Shakti Nagar, Jaipur, Rajasthan 302017, India
e-mail: brij.ciwsa@gmail.com

S. S. S. Sarma · S. Nandini
Laboratory of Aquatic Zoology, Division of Research and Postgraduate Studies, Universidad Nacional Autónoma de México, Campus Iztacala, Av. de los Barrios #1, Los Reyes, Iztacala, 54090 Tlalnepantla, Mexico, Mexico

and canals. These lakes, created since the early 17th century by dredging out peat, have undergone eutrophication since early 1950s due to growing input of nutrients from agriculture and polluted waters from the rivers and canals (Gulati & van Donk, 2002). As elsewhere in Europe and North America, the problem of eutrophication of lakes attracted much attention in the Netherlands as well, leading to the establishment of the Hydrobiological Institute in 1957. After the sudden untimely demise of its first director, Dr. E. Nicolai, Dr. H.L. Golterman, the only other scientist in the Institute at that time, became its Director. Dr. Golterman laid the foundations of research in physical–chemical limnology, focusing especially on the phosphorus dynamics, both in the water column and in the mud-water interphase. Recognizing the need to investigate the role of biological components of lake ecosystems, Dr. Golterman inducted several scientists and got the Institute renamed as Limnological Institute in 1968.

In May 1968, Dr. Golterman invited the young Indian aquatic biologist, Dr. Ramesh Datt Gulati, as a Post-Doctoral Fellow (with Dutch Ministry of Foreign Affairs fellowship) and in December 1970, gave him a permanent position in the Institute (see also Parma, 2003). Dr. Gulati continued to serve this Institute (later becoming a part of the NIOO-KNAW) until his formal retirement in 2000 and remained associated as emeritus scientist until his death on 23 December 2019. Dr. Gulati contributed immensely and significantly to the development of our understanding of lake ecosystems, especially the shallow lakes in the Netherlands, over five decades of dedication to the Institute and the science of limnology. He leaves behind a legacy of limnological research, his beloved wife, Toshi, and a son and a daughter.

In this article, we who have had the privilege of decades-long association and interaction with Dr. Gulati present a summary of his major contributions related to the ecology of phyto- and zooplankton interactions and the impacts of whole-lake biomanipulation for the restoration of lakes in the Netherlands. In addition, because Dr. Gulati was a far-sighted biologist and a pioneer in many fields of aquatic research, he also studied temperature effects, food quality and fatty acid studies, riverine zooplankton, egg ratio studies and analysis of cost of reproduction, to name a few. Some of his important contributions in these areas are also touched upon in this overview.

Research in the Netherlands

Well equipped with the knowledge of phyto- and zooplankton and fish, limnology of deep and shallow subtropical lakes and the issues concerning eutrophication, Dr. Gulati, soon after arrival in Nieuwersluis, The Netherlands (1968), started with the study of primary production by phytoplankton using the radioisotopic technique, in Lake Tjeukemeer. Shortly thereafter, he moved to a comprehensive limnological survey of a large and 31 m deep (mean depth 11.4 m) lake Wijde Blik. His publications on its physical–chemical conditions, plankton and primary production (Gulati, 1972a, b) were the first on this lake.

Zooplankton–phytoplankton interactions

These studies revealed the dominance of *Microcystis* during July to September period of 1968 in Wijde Blik whereas the zooplankton comprised of several copepod species including *Acanthocyclops robustus, Cyclops strenuus, Diacyclops bicuspidatus* besides the cladocerans (mainly composed of *Bosmina longirostris*) and the rotifer genera such as were *Brachionus, Synchaeta, Polyarthra, Hexarthra* and *Trichocerca*.

Dr. Gulati was fascinated by the intra-plankton interactions and their feeding relationships. For the next few years (1972-1978), Dr. Gulati concentrated his studies more on the herbivory (also referred to as grazing) by zooplankton on phytoplankton based on both field and laboratory investigation. He became the senior scientist at the then Limnological Institute in 1974, headed the working group “Primary and Secondary Production”, one of the three working groups at Nieuwersluis and remained in this position until 1987. During this period, on the one hand, Dr. Gulati presented valuable quantitative data on the crustacean and rotifer species feeding on algae, and on the other, contributed to the development of the methodology for estimation of secondary production by zooplankton communities (Gulati, 1974, 1975.

Dr. Gulati’s other studies centered on grazing, assimilation and excretion rates of zooplankton communities in Lake Vechten (Gulati, 1976) and later on the role of zooplankton in eutrophication and the restoration of lakes of Loosdrecht area (Gulati, 1978; Bakker et al., 1985; Gulati et al., 1982, 1985; Gulati, 1985; Davidowicz et al., 1988). His studies also involved stoichiometric changes in seston and zooplankton in response to eutrophication control measures. For example, feeding studies on *Euchlanis dilatata* during the late 1980s showed that a feeding time of 15 min. was adequate for gut filling (Gulati et al., 1987). This work also provided the basis of food selectivity in *Euchlanis* (Ejsmont-Karabin et al., 1993, Gulati et al., 1993). Grazing studies were expanded by the use of radioactive tracers (Gulati, 1985) and led to research in yet another important area of limnology: control of toxic cyanobacteria. Series of experiments conducted by him yielded valuable information on how to control toxic cyanobacteria. Interestingly, Gulati et al. (2001) found that the detritus derived from filamentous cyanobacteria can still be used for feeding daphniids. This study reported that when both the living and detrital filaments of *Oscillatoria* were fed, the latter were ingested more efficiently.

The role of zooplankton in nutrient dynamics and the stoichiometry

It is well known that cyanobacteria lack adequate nutritional quality to support the survival and reproduction of zooplankton. Therefore, when the cyanobacteria are supplemented with edible diet such as green algae, several species of zooplankton grow under culture conditions. Feeding and assimilation efficiencies of the zooplankton species depend strongly on the diet quality (Gulati et al., 1985). While it is also well known that the toxic cyanobacteria reduce the feeding rates of zooplankton, studies on the nutritional quality of algae in influencing the growth and reproduction of cladocerans have received much less attention. For example, Pérez-Martínez and Gulati (1999) showed the differences in the P and N excretion rates of daphniids fed normal, phosphorous-limited and nitrogen-limited algae. Further studies on the P-deficient studies have received considerable high recognition (DeMott et al., 1998; DeMott and Gulati 1999) indicating the importance of such studies in understanding the complex interactions between nutrients and plankton.

The role of food quality in zooplankton was elegantly reviewed by Gualti and DeMott (1997). This is the most cited work of Dr. Gulati according to Web of Science 2020. This paper is a review summarizing the presentations of the first international workshop of the Plankton Ecology Group on the theme of food quality for zooplankton held during 17–21 March 1996, at the Centre of Limnology in Nieuwersluis. In their review, Gulati and DeMott (1997) pointed out four mechanisms in which food affects consumers: (i) size and shape of the food particles, food selectivity, feeding inhibition and ingestion rates; (ii) morphological defences against digestion; and (iii) nutritional inadequacy (P, N and fatty acids); and (iv) presence of toxins. Since their review, several workers have followed these research lines in food quality studies. Amongst the most common types of field-based studies are those on changes in the elemental composition of both phyto- and zooplankton. Because of their complex role in the biology of plankton, several studies on the role of temperature on the life history and fatty acid composition of zooplankton are noteworthy (Gama-Flores et al., 2015). In the conclusion of their volume on the State of the Art in zooplankton feeding studies, Gulati and DeMott (1997) stated that the experiments conducted on single species of zooplankton need to be extended to field conditions. This aspect is yet to be realized in different regions, especially tropical countries.

For about a decade Dr. Gulati collaborated also with Chinese scientists on several aspects of lake management and zooplankton–cyanobacteria interactions. This collaborative research resulted in several articles of scientific interest and of applied value. Zhang et al. (2017) clearly show that Tilapia, an invasive species in many regions of the world, has an adverse effect on shallow lake ecosystems by increasing nutrients, especially phosphorus and turbidity in the water column. They also suggest the eradication of this species, whenever possible, to improve water quality. Many studies also focused on the effect of cyanobacteria, especially *Microcystis*, on cladocerans. While the literature emphasizes the adverse impact of cyanobacteria and cyanotoxins on cladocerans, Chen et al. (2013) showed that lysed microcystins are not always toxic. These findings have been corroborated by research elsewhere: e.g. Zamora Barrios et al. (2017) show that cyanotoxins from blooms in different sections of Lake Texcoco in Mexico are not toxic, sometimes even at high concentrations. With Luo et al. (2015), Dr. Gulati worked on the utility of cyanobacteria and showed that during the decay of blooms, the fatty acid content increases and improves the nutritional quality of decomposing cyanobacteria to cladocerans.

Top-down approach in biomanipulation and lake restoration

Already in the 1970s, the need was felt for an ecosystem approach to control eutrophication (Patten, 1973). The role of biomanipulation in regulating the growth of algal blooms by means other than zooplankton (Shapiro et al., 1975) had been highlighted. During the 1980s, the concept of biomanipulation had gained ground. In the Netherlands, the first biomanipulation experiments were conducted in 1986 in small drainable ponds of 0.1 ha, where the impact of 0 + fish on zooplankton was investigated (Meijer et al., 1990a). Later, Lake Zwemlust (area 1.5 ha, mean depth 1.5 m) was selected for long-term studies. The first ever whole-lake study on biomanipulation involved the removal of planktivorous fish (bream) in March 1987 after emptying the lake. This resulted in increased transparency (2.5 m) during the summer of 1987 and rapid colonization by submerged macrophytes. Subsequently, in 1988 and 1989 macrophytes multiplied and colonized more area and the clear water phase persisted. It was observed that macrophyte abundance contributed to transient N-limitation of phytoplankton (Ozimek et al., 1990). In 1987 experiments were started also in other natural lakes and ponds (Van Donk et al., 1990a; Van der Vlugt et al., 1992; Driessen et al., 1993; Meijer et al., 1990b, 1994). This led to the organization of the first Conference on Biomanipulation in 1989 (see Hydrobiological Bulletin 23(1), 1–4, 1989).

Encouraged by the successful restoration results, a whole-lake food-web manipulation was attempted on a large scale at around the same time (Van Donk et al., 1990a, b). A large shallow lake, Breukeleveen (area 180 ha, mean depth 1.45 m) was selected for biomanipulation. In spring 1989, most of the planktivorous and benthivorous fish (bream, *Abramis brama*) populations were removed, and migration from other lakes was prevented. Large-sized daphnids and pike (*Esox lucius*) were introduced. Two macrophyte species, *Chara globularis* and *Nuphar tutea*, were also introduced. However, water transparency did not increase during summer and autumn owing to (1) rapid increase of the biomass of planktivorous fish who fed on zooplankton community, (2) suppression of the large daphnids by the filamentous cyanobacteria and (3) high turbidity from the sediment resuspension.

The working group of Dr. Gulati also investigated the role of macrofauna associated with macrophytes (periphytic organisms and benthic fauna) (Kornijow et al., 1990; Kornijow & Gulati, 1992). Vascular plants became food for zoobenthos and phytal-fauna, once they were decomposed. Invertebrates also stored significantly large amount of nutrients in their biomass. The success and failures of lake restoration by biomanipulation measures were summarized with due explanations in a review paper by Gulati and Van Donk (2002) and Gulati et al. (2008). They highlighted the roles of accumulated phosphorus in sediments, ability of cyanobacteria to withstand large variation in their P content, water level fluctuations, wind- and fish-induced resuspension of sediments, piscivore fish populations and the shoreline macrophytes in the outcomes of restoration interventions. A later review on restoration of lakes (Gulati et al., 2006) further elaborated on the subject.

Other contributions to limnology

Even after his retirement, as an emeritus scientist at the NIOO-KNAW, Dr. Gulati remained highly active with research, and equally, if not more, productive with his publications in his chosen fields of plankton ecology, biomanipulation and lake restoration (e.g. Gulati & van Donk, 2005; Hessen et al., 2005, Hosper et al., 2005; Bakker et al., 2013; Leoni et al., 2014; Gama-Flores et al., 2015). Dr. Gulati's limnological research extended to a wide geographical extent outside Europe and to different climatic regions. He revived his early interest in the tropics when he worked on the zooplankton and their feeding ecology in Parakrama Samudra in Sri Lanka (Duncan & Gulati, 1981, 1983a, b), by joining the studies in subtropical China (Chen et al., 2011, 2014; De Kluijver et al., 2015) and Mexico (Sarma et al., 2005; Nandini et al., 2017). For several years, Dr. Gulati was actively involved in the studies of meromictic lakes in Siberian Russia (Degermendzhy & Gulati, 2002, Degermendzhy et al., 2002, Rogozin et al., 2009; Tolomeev et al., 2010; Zadereev et al., 2017). In recognition of his contributions to Russian limnology, as an honorary senior scientist of the Russian Hydrobiological Society, Dr. Gulati was awarded in 2014, by the Siberian

Academy of Sciences, with an honorary PhD and professorship in limnology. A complete list of his publications is provided as an electronic supplement (online resource 1).

Dr. Gulati's services to scientific journals and organizations are also exemplary. He served as Editor in Chief for Aquatic Ecology (1996–2015), Editor of SIL News (2006–2019) and figured on the editorial boards of several prestigious journals including Hydrobiologia of which he edited more than 12 special volumes.

Dr. Gulati was very generous with his advice and help to the limnological community throughout the world. He had a particularly soft corner for young scientists. Despite his age, he was willing to travel long distances to impart courses. He visited Mexico four times and gave courses on limnology, lake management, scientific writing and plenaries during two international conferences. He also went on field trips and during one such trip to the River Antigua in Veracruz (Mexico) he wistfully remembered his days as a PhD student in Delhi, collecting samples on the River Yamuna. This trip led to a project and then a paper, one of the first long-term studies on a river in Mexico (Nandini et al., 2017). He also gave courses on scientific writing in Indian universities. Many students were beneficiaries, in terms of international awards, of his positive evaluation of their enthusiasm and research potential.

The legacy of Dr. Gulati's pioneering research in the areas of trophic interactions among plankton and the biomanipulation at whole-lake level for restoration will continue to guide and inspire aquatic ecologists who strive to understand the complexities of the Earth's inland water ecosystems and restore them from the increasing anthropogenic stresses. Aquatic biologists, especially those who were fortunate to have known and learnt from him personally, will miss him badly. Our continuing efforts to reverse the deterioration of our lakes and reservoirs will be a fitting tribute to late Dr. Gulati.

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