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Life-time contributions of Joop Ringelberg to new approaches in aquatic ecology, father of modern aquatic ecology in the Netherlands

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Abstract

This dedication marks the retirement of Prof. Dr J. Ringelberg from the University of Amsterdam. In this article his contributions to the aquatic ecology in the Netherlands are reviewed. After his Ph.D. study on 'The positively phototactic reaction of Daphnia magna Straus, a contribution to the understanding of diurnal vertical migration' (1964), Joop Ringelberg became associate professor at the Laboratory of Animal Physiology of the University of Amsterdam. He started at the university the research group of Experimental Hydrobiology. From 1965 to the 1980s he played a very important role in the development of experimental ecology and ecosystem research in the aquatic habitats in the Netherlands. During the last ten or twelve years of his scientific career (1985- to date) Dr Ringelberg returned to his old hobby horse the 'Diel Vertical Migration (DVM)' of zooplankton, especially daphnids. Intensive field and laboratory studies during these later years, helped him and his students to get a deeper insight into DVM behaviour of the daphnids, in response to the rates of changes in light intensity in close conjunction with release of predator (fish) kairomones. In addition, Ringelberg initiated the use of micro-ecosystems and was leader of a team that has developed a flowcytometer, especially for quantitative and pigment analyses of phytoplankton. His other landmark achievements, national and international, included the chairmanship of the Dutch Hydrobiological Society and of the Aquatic Ecology division of BION (Biological Research in the Netherlands). He was a national representative of SIL (International Association of Theoretical and Applied Limnology) and during ten years a member of the Scientific Advisory Board of the Max Planck Institute for Limnology at Plön, Germany. As a guest scientist he is still continuing his scientific pursuits at the Centre of Limnology, Nieuwersluis.

Education

Joop Ringelberg was born (10 December 1931) and raised in Amsterdam. Even in the big city, his fondness for living creatures and their way of life was already distinctly manifest at an early age, as testified by his family nickname 'wormendokter' (doctor of worms). From the age of twelve, the prospective biologist joined the NJN, a legendary Dutch Youth Society for Studies of Natural History. He finished High School (HBS-B) in 1950, and joined the army as a conscript for one year before he could enter the University of Amsterdam, where he took a major in Biology. Already at that time, he showed a keen interest in life underwater. The topic he chose, after passing his first exam ('candidaats') in 1954, for his first graduation thesis under the supervision of Dr A.G. Vorstman turned out to become a life time commitment: 'The diel vertical migration in the Sloterplas'. The intriguing behaviour of waterfleas, the ascent and descent of these organisms in response to the rate of change of light intensity, has kept Joop both fascinated and preoccupied during his entire career. By a fortunate coincidence, the pike farm

NIOO contribution no. 2308.



Prof. Dr J. Ringelberg

of the Organisation for the Improvement of Inland Fisheries (OVB) in Nieuw Vennep heard about this research and saw a clear link to their own problems. The organisation was involved in a large-scale pike restocking programme, but had great difficulties collecting sufficient zooplankton in nature to feed the fry. They offered Joop a position to improve their insight into zooplankton behaviour. In consultation with Dr Vorstman, Joop's research was shifted to the Westeinderplas, another lake in the western part of the Netherlands, to study 'The vertical distribution of zooplankton'. Sampling zooplankton at different times of the day at different depths Joop clearly demonstrated that zooplankton concentrations in the surface water were considerably higher after sunset and during the night than during the day. The work provided a clear example of a 'society relevant' academic research, many years before this became *a la mode* at the university research establishments.

The OVB prolonged Joop's part-time assignment, but the distance to Amsterdam made it necessary for him to search for possibilities nearby at the University of Utrecht to complete his graduation. At that time, the Dutch Hydrobiological Society (now the Netherlands Society for Aquatic Ecology, NVAE) had just hired a few rooms in Utrecht at the Laboratory for Comparative Physiology. Prof. Dr S. Dijkgraaf was in charge of this laboratory. It was planned to found a Hydrobiological Institute, subsidised by the OVB, the Amsterdam Water Board, the Rhine Commission and the Department of Public Works (see extensive documentation in the jubilee edition of the NVAE; Zevenhuizen et al., 1996). Here, Joop made a scientific debut in doing his second graduation thesis, this time as an aquatic ecotoxicologist 'avant la lettre': 'Determining toxicity of copper and zinc for pike fry'. The project was initiated under the supervision of Prof. Dr ten Cate of the University of Amsterdam. Later, however, when Joop decided to register formally at the University of Utrecht, Prof. Dijkgraaf became his supervisor.

When the plans for setting up the Hydrobiological Institute subsided and the contract with the OVB concluded, Joop was appointed as 'candidaat assistent' with Prof. Dijkgraaf. His last, major subject was an experimental study of the mechanisms governing the vertical migration in Daphnia magna. After having obtained his M.Sc. degree in 1957, the foresight gained from this work was so promising that he continued with the same subject for his Ph.D. study. He got his Ph.D. degree in 1964 on the dissertation entitled 'The positively phototactic reaction of Daphnia magna Straus, a contribution to the understanding of diurnal vertical migration'. This study links the quantitative external light stimuli to the sensory perceptions and reactions of the animal as well as the orientation to light contrasts. It is still considered as a major contribution to our understanding of the behavioural phenomenon, that is almost universally prevalent in both freshwater and marine environments.

Animal physiology, hydrobiology, limnology and aquatic ecology

As bright and creative scientist with stimulating ideas he had no difficulties in finding an appropriate job. It is, therefore, not surprising that in 1965 Joop, at the age of 34, was appointed by the University of Amsterdam as associate professor (*lector* in Dutch) at the Laboratory of Animal Physiology under the headship of Prof. Dr A. Punt. Besides teaching animal physiology, his task was to establish a new department of Experimental Ecology. In view of his background and interests, this became in practice Experimental Hydrobiology. As his first students, the two of us (Niels Daan & Ben Flik) witnessed the 'fresh air' blowing through the old building at the Rapenburgerstraat. The experiments

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were ingeniously planned and elegantly executed, at least as long as the new technology did not fail and we did not have to spend the morning mopping up the flooded corridors. By measuring angles of orientation to light contrasts (Ringelberg et al., 1975) and sinking speeds of daphnids in response to phototactic stimuli (Daan & Ringelberg, 1969), we felt closer to what happened outside in the water column than by recording muscle contractions of frogs hung up in traditional contraptions used in animal physiology. Joop also kept a watch on what was happening in the open water. He was even once fined for using prohibited fishing gear according to the Dutch law, while fishing with a plankton net in the river Amstel on a sunday morning. However, when the corpus delicti was shown in court to the judge, charges were dropped and Joop got away with a reprimand.

In the summer of 1968, the Laboratory of Animal Physiology moved to its newly built research facility at Anna's Hoeve, where the Biological Faculty was gradually to be concentrated. Joop was in command at the fourth floor of Building II. The novel climate rooms and the spacious laboratories ameliorated research atmosphere and gave a new impulse to a great variety of modernistic experiments. Also, the strength of the research staff steadily increased. However, there remained an unrelenting conflict with the Faculty on the name of his activities. When Joop as lector became independent in 1972, he preferred Aquatic Ecology as teaching commitment, but his proposal was turned down in favour of limnology. Even after becoming professor in 1978 his teaching commitment was still limnology. Although he kept striving for a research group Aquatic Ecology, the name never got rid of the appendage 'in foundation'. In 1980 only with the arrival of the group of hydrobiologists of the Department of Zoology (Dr C. Davids, Dr P.J. Roos & Dr L. Van den Broek), his section could be formally called Department of Aquatic Ecology. Later, his department was affilliated to the group of applied entomologists of Prof. Dr M.W. Sabelis and the research group 'Fundamental and Applied Ecology' was established. This group comprised three sections: Aquatic Ecology, Aquatic Ecotoxicology and Population Biology.

Irrespective of the name, Joop's department had at least become more independent from animal physiology, which enabled him to steer the research programme to a new direction. His prime interests had gradually shifted from the organisms to the ecosystem level. The experimental work evolved in the 1970s toward energy flow through Daphnia magna populations (Kersting, 1973). Besides, Joop was convinced that experimental studies should be firmly entrenched in fieldwork, to both develop appropriate hypotheses and to verify the experimental results. The primary production measurements in an incubator (de Roos & Flik, 1985; Flik & Keyser, 1981; Flik, 1985; Meulemans, 1989; Vermij et al., 1985) clearly reflected the direct links that were maintained between field and laboratory. An excursion with his students in 1970 to Besse-en-Chandesse to investigate the crater lakes in Auvergne, France (Flik et al., 1973; Hallegraeff et al., 1976) marked the start of a comprehensive study of the pelagic fresh water ecosystem. However, finding a suitable research object in the Netherlands was not as easy as in Besse. It was only after preliminary experiments in the Barlosche Kolk (Wijhe) and the Gat van Ham (Nijkerkerveen) that the group finally chose the Maarsseveense Plas as a study object. This newly dug out mesotrophic lake was not too far from the Westeinderplas where he had set up his research on vertical migration.

Joop made a great effort, together with the Limnological Institute (now the Centre of Limnology) at Nieuwersluis, to procure a programme subsidy from the Foundation for Fundamental Scientific Research (ZWO) in order to carry out a large scale, multidisciplinary ecosystem study. To this end, he wrote down his ideas in a so-called 'Red Booklet': 'The ecology of a stratified lake, a multiform approach of an ecosystem'. It personified an ambitious blue-print of plans that involved work at three levels: fully controlled microecosystems in the laboratory, open outdoor mesocosms and the Grote Maarsseveense Plas serving as reference. Regretfully for Joop and his group, the grant was awarded to a terrestrial group.

Nevertheless, the group did as much as possible with the limited manpower and resources at its disposal. Kersting (1975) developed a first prototype of a small, closed micro-ecosystem with three compartments, one each for phytoplankton, zooplankton and decomposers. The system has since then operated, virtually uninterrupted for twenty years. Meanwhile, Joop, together with D. de Zwart and C. Bruning, worked on the development of somewhat larger systems (Ringelberg, 1976, 1977; Bruning et al., 1978; Ringelberg & Kersting, 1978). The mesocosms did not yield the expected results. Although they were developed for back-up studies of phenomena observed in the pelagic phase of the open lake, the oxygen regime turned out to be completely determined by



Joop on a sampling spree (pelagic ecosystem of Barlosche Kolk, Wijhe 1972).

periphytic wall growth (Lingeman, 1980). The field programme included monthly sampling of phytoplankton, zooplankton and abiotic factors from a raft in the Maarsseveense Plas by an enthusiastic group of students. However, the ambitious programme was gradually stripped down, probably also under influence of the outcome of the International Ecology Congress (INTECOL) in The Hague in 1975. The international thrust for this type of research appeared to be dwindling, partly because the analytical problems appeared to be prohibitive. Thus, the emphasis shifted to population development and seasonal succession of the dominant phyto- and zooplankton species in the Grote Maarsseveense Plas in order to describe the phenomena and to explore the underlying mechanisms in experimental studies. After Hallegraeff (1976) finished his doctorate thesis on phytoplankton species diversity and phytoplankton pigments, a large number of individual grants were actually obtained during later years for individual components of the proposed programme. This resulted in several Ph.D. theses (Hulsmann, 1983; Van Donk, 1983; Vermij, 1987; Bruning, 1991; Veen, 1991). However, the surplus value expected from a

simultaneous, integrated approach has not been realised.

The group paid attention not only to the open water of the lake, but also to the demersal and littoral systems. Members of the staff concentrated on the epiphyton of reed (Dr P.J. Roos), dynamics of chironomids (Ten Winkel, 1987) and mites (Dr C. Davids), snails (Dr J. Dorgelo), and desmids (Dr P. Coesel). The binding force between all these studies was the Maarsseveense Plas, where a simple field laboratory facilitated round the clock studies.

An important new development was that as the society relevant studies became current in university research departments, it became increasingly difficult to defend and carry out fundamental research in a relatively deep and unpolluted water body. This because most of Dutch surface waters are shallow and threatened by pollution. This clash of choice for research objects and priorities marked the weakening of coherence and integration of the group, and the group was subsequently split in two sub-groups, Aquatic Ecology and Aquatic Ecotoxicology. The section of Aquatic Ecology under Joop had dwindled

markedly in size so that the idea of community ecology had to be abandoned. Instead, the new research approach became more restricted and focussed on problem oriented studies. As far as Joop is concerned there was one blessing in disguise - the old hobby horse of Joop, the vertical migration, was rejuvenated, but clearly with a greater emphasis now on balance between field observations and laboratory experiments. An intensive sampling programme of the hybrid Daphnia galeata \times hyalina (from 1989–1993), to study the relationship between vertical distribution and light stimuli, revealed that the migration behaviour of daphnids was limited in time to approximately six weeks during June and July. Before and after this period no significant changes in the vertical distribution of the animals were observed. Moreover, the onset of the vertical migration behaviour coincided with the time that large numbers of juvenile (post-metamorphosis) perch (Perca fluviatilis) appeared in the surface waters (Ringelberg et al., 1991a, b). This suggested the possibility that fish exudates (kairomones) might trigger the migration behaviour, in addition to the food conditions and stratification. In 1989, Joop found convincing evidence that a fish exudate enhanced the phototactic reaction to relative changes in light intensity (Ringelberg, 1991). His results were received with considerable scepticism at the Congress of the Societas Internationalis Limnologiae (SIL) in Munich 1989, but since then the role of fish kairomone has been firmly established. New experiments were initiated to reveal how adaptive goals of diel vertical migration are realised by the behavioural mechanisms. Therefore, the effect of different concentrations of kairomones as well as food concentrations on phototactic behaviour of Daphnia hybrids was tested (van Gool & Ringelberg, 1995), leading to the quantification of a 'Decision Making Mechanism' (van Gool & Ringelberg, in prep.).

In 1985 an entirely new issue was addressed, when Joop became head of the Optical Plankton Analyser (OPA) project subsidised by the Foundation for Applied Sciences (STW). In the 1980s, the idea had been launched by the Department of Public Works (RWS) and Applied Physical Research (TNO) to apply flowcytometric techniques for routine counting of phytoplankton. Joop's interests clearly stemmed from the many laborious counts made under his supervision in relation to the community research programme. In close co-operation with other partners, a project was formulated for the development of a flowcytometer that was specifically tailor-made for phytoplankton quantitative analysis. TNO was responsible for the technical development, but the biological interpretation linked to the measurements were investigated by the group in Amsterdam (Balfoort et al., 1991, 1992). Thanks to a financial injection by the European Union, the flowcytometer has now evolved to an operational model, called EUROPA.

Other commitments

Joop was heavily involved in the management of the university, probably the least satisfying side of his career, and in the national and international coordination of hydrobiology, limnology and aquatic ecology. He was secretary of the Dutch Hydrobiological Society from 1959-1962 and chairman from 1971-1977, which engaged him deeply in the promotion of aquatic sciences among Dutch professionals and amateurs. In 1996 Joop became honorary member of the Netherlands Society for Aquatic Ecology. Together with, among others, Prof. Dr L.R. Mur, he played a crucial role during these years to found the BION (Biological Research in the Netherlands) sub-division Aquatic Ecology (BION was an organisation responsible for prioritising academic studies to be financed by the ZWO, then the Foundation for Fundamental Scientific Research). Also, he was for many years the national representative of SIL (International Association of Theoretical and Applied Limnology). From 1984 onwards, he served for ten years on the scientific advisory board of the Max-Planck-Institut für Limnologie in Plön, Germany.

Joop also provided a key contribution to the establishment of the research and advice bureau AquaSense, which was set up ten years ago by two of his former Ph.D. students, Dr E.H. Ten Winkel and Dr J.T. Meulemans. In his role as adviser of this consultancy, he still serves as a highly appreciative 'sound-board' in scientific matters.

Retirement

After a thirty year contract with the University of Amsterdam, Joop retired and was accorded the emeritus status in 1996. He was strange with university management and all the controversies that went with it, but not with his pet animals, the daphnids, and with his scientific ambitions. He took his experimental toolbox and his last graduate student Erik van Gool with him to the Centre of Limnology in Nieuwersluis to continue to work on an integrated behavioural model to explain vertical migration in *Daphnia galeata* \times *hyalina*. The void left by his departure from Amsterdam will perhaps never be filled. But we do not only look back upon the many stimulating years with a great scientific leader, an original thinker, a careful experimenter, and a very good friend, but we also look forward to new opportunities to work together again. We wish Joop a very good health and success in his scientific pursuits.

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