Resolution of Respect

W. Thomas Edmondson, Limnoecologist:

1916–2000

W. Thomas Edmondson, an international leader in the study of lakes, the causes and effects of eutrophication, the processes controlling plankton population growth rates, and the biology of rotifers, died on 10 January 2000 in Seattle, Washington. His approach to ecological research was unconstrained by prevailing fashion or dogma: he was a rule-breaker without being a rebel. He asked the questions that he thought were the most interesting to answer, and obtained his answers by the means he found most appropriate. In the late 1950s, he began an investigation of Lake Washington that became a model of long-term ecological research well before the value of developing such study systems became widely recognized. During the 1960s and 1970s, when population and community ecology were drifting apart from ecosystem science, he studied lakes as if no such distinction existed. Through this research, and in his development of an elegant method for determining vital rates in natural populations, Edmondson showed by example how the study of natural ecosystems could provide new and correct insights into ecological processes, despite the absence of possibilities for replication and control. Edmondson understood that all approaches have advantages and limitations, and so simply ignored one-approach-fits-all depictions of how ecology should be carried out.

Tommy, as he was known to his friends, developed his interest in fresh waters within a decade of his birth in Milwaukee, Wisconsin on 24 April 1916. By the time he was a pre-teen, he had his own microscope for looking at the contents of local pools and lakes, and his own copy of Ward and Whipple's *Freshwater Ecology* to aid him in identifications. After his move to New Haven, Connecticut as a teenager, his high school teacher, Ms. Ruth Ross (for whom he later named the rotifer *Trichocerca rossae*) recognized his talents and found a way for Tommy to attend a course in invertebrate zoology taught at Yale University by G. E. Hutchinson. This highly fortuitous connection resulted in Tommy having his own corner in Hutchinson's laboratory. There he had access to plankton samples from all over the world with which he could pursue his passion for rotifers. More importantly, he gained an extraordinary mentor. By the time he had obtained his Bachelor of Science degree from Yale in 1938, he had published eight papers, primarily on the diversity of rotifers collected from Hispaniola and the Himalayas as well as sites across the United States.

As a graduate student continuing his education with Hutchinson at Yale University, Edmondson studied the population ecology of sessile rotifers. He demonstrated, among other observations, that there was a substantial gain in survival experienced by animals living in colonies compared with those living as solitary individuals (Edmondson 1944). It is a result that presaged, by several decades, investigations of similar questions for marine invertebrates. Before Tommy completed his Ph.D. in 1942, Hutchinson arranged for him to spend a year at the University of Wisconsin, where Chancey Juday provided him with an assistantship to work at the Trout Lake laboratory with the agreeable assignment of studying sessile rotifers. While in Wisconsin, Tommy took Juday's course in limnology and there encountered a scientific perspective, grounded in induction, that was famously distinct from that of Hutchinson and his students (e.g., Cook 1977). Beckel (1987:25), in her history of the Center for Limnology at the University of Wisconsin, quotes Tommy as reporting that:

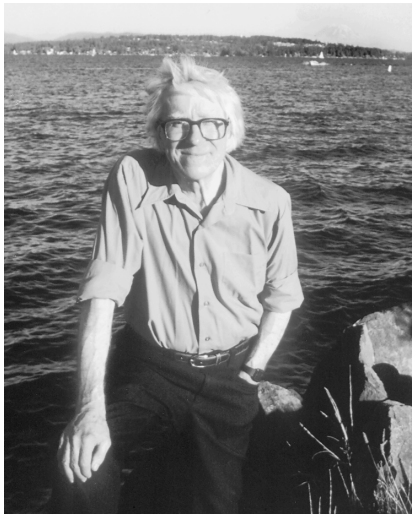

Photo by Benjamin Benschneider of the *Seattle Times*. August 4, 1985.

> *Yale and Wisconsin were vastly different. The Wisconsin emphasis seemed to be to assemble measurements of some property from a large number of lakes, finding ranges and means ... There was a little but not much attempt to notice relations between variables, and minimal attention to the limnological processes that would connect them together ... In New Haven, there was plenty of data gathering, but it was directed at something other than just statistical description of a population of lakes ... some ideas had been thought out ahead of time and the particular samples were collected for a purpose beyond just finding out what was there.*

A fellow student in Juday's course was Yvette Hardman, who was completing her own Ph.D. at Wisconsin on microbial ecology. They helped each other with field work, discovered interests in common (Edmondson 1989), and were married in 1941.

The Second World War broke out during the period when Edmondson was completing his Ph.D., and begin-

ning in 1942 he worked as a civilian for the U.S. Navy. Having passed a college course in advanced differential equations, he was given a Research Associate position as physical oceanographer working on predicting wave heights for aid in amphibious assaults and mine-laying in enemy harbors. His participation in these studies began at the American Museum of Natural History, but after a year, Tommy moved to Woods Hole Oceanographic Institution, where he worked with Walter Munk, Henry Strommel, and George Clarke. A later project at WHOI, under Maurice Ewing's direction, involved attempts to use sound refraction in the ocean to locate downed aircraft. While Tommy was at the New England coast — on board ship measuring wave heights under the most extreme conditions, or dropping depth charges into the water by hand to measure sound transmission—Yvette was teaching at her alma mater, Bennington College in Vermont. After the war ended, Tommy initially stayed at WHOI and then moved to Harvard in 1946 to become a lecturer in a general education course. During this period, he began research with Yvette on the effects of nutrient enrichment on primary production, a topic that a decade later became a major theme in his scientific career.

In 1949, the Edmondsons traveled to Seattle, where he had accepted a faculty position in the Department of Zoology at the University of Washington. It was there that he spent the remaining half-century of his career, and it was not long before he began the studies for which he became so well known. In 1955, one of his students brought back a water sample from Lake Washington that showed telltale signs of eutrophication. In the years and decades to follow, Edmondson used this environmental problem arising from a growing human population as a whole-lake experiment, valuable for understanding the mechanisms underlying the ecological effects of nutrient enrichment. He was among the first to show clearly that phosphorus was the key component in municipal wastewater causing noxious algal blooms, and predicted early on that sewage diversion would quickly reverse the effects in Lake Washington. His publications and testimony were used locally, nationally, and internationally to push legislation regulating phosphorus inputs to freshwaters. His observations were used in the Seattle area to effect the significant political changes needed to tie together sewage treatment facilities from different communities around the lake into a single common system to eliminate inputs. The rapid favorable response of the lake served at the time as an important test of proposed ecological mechanisms, and serves today as a clear demonstration of how scientific understanding can be put to use for the public good (Edmondson 1991).

Data collection from Lake Washington by Edmondson and members of his laboratory continued essentially uninterrupted for four decades, beginning first with the understanding of the causes and consequences of eutrophication. Later, they began documenting the role of a major consumer (*Daphnia*) in determining algal abundance and water clarity, the impact of construction in the watershed on lake alkalinity, and most recently, the effect of fisheries manipulations on zooplankton community structure. Each piece of research depended on the base of long-term data that he had accumulated over time, and each demonstrates the value of continuing data collection in a single system. This is an approach that he took with purpose, and that he advocated frequently (e.g., Edmondson 1991).

In addition to his seminal long-term studies, Edmondson was well known for devising one of the most valuable tools available for determining the ecological factors underlying increases and declines in plankton population numbers. The "Edmondson egg ratio method," and its various modifications, takes advantage of the fact that many of these organisms either carry their eggs or divide conspicuously, allowing a direct estimation of instantaneous birth rates. When combined with estimates of realized population growth rates, this makes possible an estimation of death rates (Edmondson 1960, 1968). As vital rates change over time, the causes of population fluctuations become much clearer. What makes the technique so valuable is that it can be applied to natural populations under unmanipulated conditions. As with his use of long-term ecological research, the method demonstrates how much can be learned about a wild population without a requisite of experimental manipulation. The egg ratio method has become an essential tool worldwide for investigating plankton dynamics (Lampert and Sommer 1997).

Edmondson developed his egg ratio method while on sabbatical leave with Yvette at the Istituto Italiano di Idrobiologia in Pallanza, and it was on that trip to Europe that the two of them amplified the network of international friends and colleagues that became a hallmark of many of their day-to-day interactions. Shortly after returning to Seattle, Yvette herself became an international figure in aquatic sciences when she took over editorship of *Limnology and Oceanography*. During the 19 years of her tenure, she was instrumental in helping to establish it as the premier journal in the field. Both of them retired in 1986, but remained extremely active. Tommy continued to maintain his research program on Lake Washington, to attend scientific conferences, and to produce insightful publications.

Edmondson's uniquely valuable contributions to our science were formally recognized by his election to the National Academy of Sciences in 1973. In that same year, the NAS presented him with the Cottrell Award for Environmental Quality. A decade later, the Ecological Society of America presented him with our Eminent Ecologist award. Edmondson was also the recipient of the American Society of Limnology and Oceanography's Hutchinson Medal and the August Thienemann–Einar Naumann Medal of the Societas Internationalis Limnologiae. These and other awards were presented to him in recognition of his scientific contributions. On the occasion of his retire-

ment, the legislature of Washington State passed a special resolution recognizing his contributions to the public welfare. Not adequately covered by these accolades is the depth of the friendships that Tommy built with his colleagues and students. His enthusiasm for the sciences of ecology and limnology was genuinely unbounded, as was his delight in new ideas, revealing data, and the interesting people who generate them.

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A complete list of W. T. Edmondson's publications through 1988 is given by Lehman 1988. More recent works can be found by searching standard website databases.

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