

## **Joel E. Keizer, 1942 – 1999**

### **Nonequilibrium Statistical Thermodynamics**

Joel Keizer wasn't quite 57 years old when he succumbed to lung cancer after a battle of 6 months. He was at the peak of his scientific abilities when this occurred and many friends and collaborators mourned his premature death. A special symposium was held in his honor at the University of California at Davis in September of 1999. As you will glean from the excerpt of an obituary written at the time <http://universityofcalifornia.edu/senate/inmemoriam/joelekeizer.html> , Joel had two scientific careers, a first one as a nonequilibrium statistical thermodynamicist and a second one as a computational cell biologist.

“[As a graduate student], Joel started to work with Sidney Bernhard and published two papers in experimental biochemistry, but then, enamored by the power of theory, switched to theoretical chemistry. He received his Ph.D. degree in chemical physics in 1969 under the supervision of Terrell Hill, one of the founding fathers of modern theoretical biophysics, who pioneered studies on statistical thermodynamics, muscle contraction and polymer dynamics. Joel's thesis work was highly mathematical and appeared as papers in the *Journal of Statistical Physics* in 1970. The interplay between experiment and theory would characterize his work throughout his career. As a postdoctoral fellow at the Battelle Memorial Institute in Columbus, Ohio, from 1969 to 1971, Joel developed his theoretical skills and started to publish prolifically. He began his long association with UC Davis in 1971 in the chemistry department and rapidly rose in rank to full professor in 1978.

Throughout the 1970s, Joel's research interests focused on non-equilibrium thermodynamics. In more than 60 journal publications, he pioneered a quantitative description of non-equilibrium steady states and collaborated with experimentalists to test his theories. This stage of his scientific career culminated in a very successful monograph "Statistical Thermodynamics of Nonequilibrium Processes." In the following years, Joel's powerful intellect turned to mathematical modeling of cell biological phenomena (from 1993, he held an appointment as professor of biology). In the 1980s and 1990s, he developed novel mathematical models of insulin secretion, pancreatic beta-cell oscillations and intracellular calcium dynamics. His research resulted in a burst of papers published in prestigious journals such as the *Proceedings of the National Academy of Sciences (PNAS)*, *Biophysical Journal* and *American Journal of Physiology*. Joel's best known work, a model for insulin secretion published in *PNAS* in 1992, has been cited about 100 times and had a major impact on our understanding of this fundamental biomedical phenomenon. By the end of his life, Joel published more than 120 journal articles and book chapters.

Highly unusual for a theoretical biologist at the time, this modeling work was much appreciated and heavily cited by biologists, with whom Joel often collaborated producing joint experimental/theoretical papers that were at the onset of the modern quantitative revolution in biology. Respect and admiration for Joel's radically innovative modeling work and his insightful collaborations with experimental biologists translated into NSF and NIH grants for his research. His last NIH grant was for theoretical research on calcium waves in frog eggs, which was highly unusual at the time, and started a trend that continues to today."

At the symposium I was the only collaborator of Joel's who had participated intimately in his first career. The article that follows was written to expand on the talk I gave. All the other talks appeared in the *Journal of Theoretical Biology* (Volume **210**, Issue 2, pp. 133-263 (21 May 2001)). It was thought that my paper wasn't really appropriate for *JTB* and I thought about where else it might appear, and eventually forgot about it altogether. Recently (Sept., 2012) the manuscript was unearthed and I decided that at the very least it should appear on my web site [www.fefox.com](http://www.fefox.com). Since my lost/found manuscript was not digital I had to scan it and convert it to a pdf file in order to obtain good resolution. The scanned file is [Nonequilibrium Statistical Thermodynamics](#).