

## OBITUARY

# David (Dave) John Randall (1938–2024), Fellow of the Royal Society of Canada, Fellow of the Brazilian Academy of Science

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Legendary comparative physiologist, Dave Randall, passed away peacefully and unexpectedly at home on 4 April 2024. He will be missed deeply by his family and by his many friends and colleagues.

After growing up in East London, Dave attended the University of Southampton, UK, where in 1960 he obtained a BSc in classical Zoology with a parallel course in comparative animal physiology, taught partly by Dr Gerald Kerkut, founder of the journal *Comparative Biochemistry and Physiology*. He shared undergraduate courses with Ted Taylor, a lifetime friend. Dave went on to be the first postgraduate student of Professor Graham Shelton and obtained a PhD in 1963, entitled ‘The regulation of breathing and heart rate in teleost fish’. Shortly after graduation, Dave received competing offers to either manage a banana plantation on a small island in the Caribbean or accept an Assistant Professor position in the Department of Zoology at the University of British Columbia (UBC), Canada.

Fortunately, for science, he accepted the latter. Dave remained at UBC until his retirement, after which he was named Professor Emeritus in Zoology. During his 40 years at UBC, Dave was a highly inspirational faculty member and a key member of a dynamic group within that faculty that helped establish the field of comparative animal physiology. He also served as Associate Dean, Graduate Studies and as an elected member of the University Senate. Dave served two terms as Chair and Professor in Biology and Chemistry at the City University in Hong Kong (2000–2005, 2009–2012) and was an Honorary Professor in the Department of Anatomy, Chinese University of Hong Kong (2005–2008). While in Hong Kong, he served as a Trustee of the World Wildlife Fund.

Dave was an elected fellow of both the Royal Society of Canada (1981) and the Brazilian Academy of Sciences (2013). He received the Fry Medal, the highest honour bestowed by the Canadian Society of Zoology (CSZ; 1993), an Award of Excellence from the American Fisheries Society (1994), and delivered the Bidder lecture for the Society of Experimental Biology (2000). He was a Guggenheim Fellow (1968–1969), a Killam Fellow (1981–1982) and NATO Scholar (1991), and received the Murray Newman Award from the Vancouver Aquarium (2008). Dave was President of the CSZ (1984–1985) and of the Western Canadian Universities Marine Biological Society (1998–2000). He held visiting professorships at several Universities and served on numerous editorial boards, including *Journal of Experimental Biology* (JEB)



between 1981 and 1984 and to which he contributed more than once a year on average (51 research articles, 4 reviews and 1 JEB Classics article between 1967 and 2014).

## Shaping science

Great people make the world a better place and Dave Randall did just that. He did much to shape and promote the field of fish physiology. His interests were broad and his knowledge was huge.

Dave travelled widely; he loved meeting new scientists, especially those with different backgrounds and cultures; he had a knack for bringing researchers together and organizing ambitious programmes.

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For many years, he ran an exchange programme in environmental toxicology with Russia and other countries in association with the US Environmental Protection Agency (US EPA). Dave was a Sinophile. He taught and mentored research at several universities in China, and was passionate about bringing Chinese science to the West, and Western science to China. Dave was among the first to host Chinese scientists after the Cultural Revolution had ended.

### Mentoring

Dave's legacy will endure through those he mentored, and many have benefited greatly from being on the shoulders of a giant.

His legacy of graduate and post-doctoral training is truly remarkable, having trained 22 MSc students, 30 PhD students and 14 post-doctoral fellows. Of these, 32 secured faculty positions at universities and research institutions around the world. Today, his lineage can be traced through his own trainees to a third generation of family that populates the global academic community. Yet, his mentoring extended well beyond formal supervision of undergraduates, graduates and post-doctorates. It could be informal with someone he happened to meet during a conference and would ask about their research.

### Books

Dave's influential books represent another legacy. With Dr Roger Eckert and later with Drs Warren Burggren and Kathleen French, Dave co-authored the premier undergraduate textbook in animal physiology: *Animal Physiology* (W. H. Freeman). This textbook, which extended to six editions, was widely adopted in universities throughout the world and was translated from English into five other languages.

Dave conceived and began co-editing the *Fish Physiology* series (Academic Press and later Elsevier) in the late 1960s, with Dr Bill Hoar, his life-long colleague at UBC. This monograph series was hugely successful, and its influence greatly contributed to establishing fish physiology as a mainstream field of research and still does so today, with a recent celebration of its 50th anniversary. Volume 40A is now on bookshelves, making it the longest ongoing reference book series in zoology. With a total of 48 books (several volumes have two books) containing almost 500 chapters, the content of the *Fish Physiology* volumes has evolved. The initial volumes focused on the basic mechanisms and principles of fish physiology and their application to natural environmental conditions. More recent volumes have incorporated evolutionary principles while relating fish physiology to the challenges of a changing world and thereby informing on conservation, sustainability and management. Dave had signed off on the contents of Volume 40A shortly before he passed away.

### Scientific expeditions

Dave participated in many research expeditions, investigating a wide range of animals. These included: R/V *Alpha Helix* to Palau to study land crabs; more on land crabs in Moorea; spawning salmon in Bella Coola, Canada; blood flow regulation in skates in Port Aransas, TX, USA; mudskippers and weather loaches in Singapore; baby wallabies in Australia; sturgeon in Italy. This list could go on. However, two initiatives stand out because they helped to entrench comparative physiology research in two countries, Kenya and Brazil, with programmes that continue to this day.

In 1976, he and the late Peter Hochachka organized the now legendary expedition to the Amazon aboard the R/V *Alpha Helix* – a research vessel associated with the Scripps Institution of Oceanography and funded by the National Science Foundation.

The expedition ran for 2 months, from September to October 1976, and included 33 international researchers and graduate students who lived and worked aboard the vessel moored near Lake Janauaca, located 1200 km up the Amazon River, southwest from Manaus. An entire volume of the *Canadian Journal of Zoology* (1978, volume 56) was devoted to the research findings from this trip, resulting in a stunning 43 peer-reviewed articles! Also, a synthetic monograph, *The Evolution of Air-breathing in Fishes* (Randall et al., 1981), which he co-authored with a post-doctorate fellow and two PhD students in his laboratory at that time, integrated these discoveries more broadly.

In 1987, Dave led an expedition to Lake Magadi, Kenya, to study the unique physiology of a fish that thrives at pH 10. This resulted not only in an article in *Nature* (Randall et al., 1989) documenting the only 100% ureotelic teleost fish, but to many further collaborations of North American and African scientists.

### An incredible ideas man

Dave used to say 'we should spend more time thinking, less time doing experiments' and 'ideas are easy, good ideas are harder, and doing good experiments to test them is really hard'. We all share memories of arriving at his office with an inexplicable dataset only to leave an hour later with a cogent and often creative explanation of what it likely meant, and ideas for experiments to test the interpretation. At this point, he would usually say 'Now, just get on with it'.

Dave was not protective of his ideas, and he shared them with anyone who cared to listen. He advised his students to do the same. Dave thought that ideas got better through the sounding board of others. Indeed, a number of the ideas that he pioneered and published were eventually proven wrong, some by his own subsequent research (!), but those ideas were critical in moving the field forward.

### Chronic cannulation techniques

In the early 1960s, techniques for the placement of chronic indwelling catheters in blood vessels and the buccal and opercular cavities of fish were developed. Dave quickly realized their potential for understanding what was actually happening inside the fish in real time. Working with his early graduate students Don Stevens and George Holeyton, he measured blood gases, heart rate and blood pressure during exercise and hypoxia for the first time in fish. This work resulted in a series of five papers published together in a single issue of JEB (Holeyton and Randall, 1967a,b; Stevens and Randall, 1967a,b; Randall et al., 1967). These papers revolutionized fish cardiovascular and respiratory physiology, having been cited hundreds of times and forming the cornerstones of our present understanding in these areas. This suite of papers was deemed so important that it was featured in the JEB Classics series (Stevens, 2008), 'designed to revisit JEB articles that created paradigm shifts in understanding or established new fields' (Knight, 2013). Dave's firm belief in the power of new technologies was passed on to his mentees, who then pioneered numerous new techniques that have been accepted and applied worldwide.

### Carbon dioxide

In the 1960s, few had considered the problem of carbon dioxide (CO<sub>2</sub>) excretion in water-breathing animals such as fishes. Carbon dioxide is very soluble in water, and it was thought that if conditions were sufficient for oxygen uptake, they would be more than sufficient for CO<sub>2</sub> excretion. Dave was the first to appreciate the integrated function of three proteins – carbonic anhydrase, haemoglobin and Band 3 – in the red blood cell, which was

critical to both CO<sub>2</sub> excretion and blood pH regulation in fish (Haswell and Randall, 1978). This sub-field, which started with a theory-based chapter on CO<sub>2</sub> in *Fish Physiology* (Randall, 1970), has since flourished.

### Ammonia

Dave was the first to appreciate that in fishes, ammonia, produced by metabolism at a rate of about 10% of CO<sub>2</sub> excretion, behaves as a respiratory gas. Like CO<sub>2</sub>, ammonia exists both as a dissolved gas that moves along partial pressure gradients and as an ion that moves through transporter and channel proteins. He posited that blood pH was cleverly situated midway between the functional p*K* of the ammonia and CO<sub>2</sub> systems, allowing integrated control of the flux of the ionic and gaseous forms. This work demonstrated that conditions in the boundary layer water next to the gills could be very different from those in the bulk water, and this allowed the fish to maintain ammonia and CO<sub>2</sub> homeostasis in the face of fluctuating water pH (Wright et al., 1989). This theoretical understanding allowed him to develop ammonia water quality guidelines for the US EPA, guidelines that are widely used today.

### Osmorespiratory compromise

While working one summer at the Max Planck Institute in Göttingen, Germany, Dave conducted a series of experiments with radioactive <sup>22</sup>Na in quiescent and exercised trout in freshwater. The results (Randall et al., 1972) led to the novel idea that the design of fish gills reflects a trade-off between the needs for high permeability for respiratory gas exchange and low permeability for ion conservation. Although Dave did not use this term, we now know this concept as the ‘osmorespiratory compromise’, which remains a very active research area today.

### Environmental toxicology and regulations

Dave moved easily between physiology and toxicology, driven by his belief that ideas were paramount and could help him cross disciplinary boundaries. For example, his idea that ammonia was a respiratory gas (Randall and Ip, 2006) helped him to understand ammonia toxicity (Hillaby and Randall, 1979; Randall and Tsui, 2002) and develop environmental water quality criteria for ammonia (Wicks et al., 2002). The influence of water pH on ammonia toxicity further fuelled his experiments on how ammonia is distributed across cell membranes in fish tissues (Randall and Wright, 1987). His understanding of the osmorespiratory compromise enabled him to develop models predicting the uptake of organic pollutants across the gills as a function of O<sub>2</sub> uptake rate in fish. This also led to his highly cited paper in *Chemosphere* (Randall et al., 1998), showing the bioaccumulation of lipophilic chemicals in fish occurs via the gills rather than via the diet.

### Society

Dave Randall was a socialist and activist, and he campaigned for parties that supported socialist ideals. He was very concerned about childhood education and served on the school board in his own community. Whenever he got involved in something, he invariably ended up leading it, whether it was the tenant’s association of his apartment block, the Emeritus Faculty Association at UBC, the Governing Council of Bamfield Marine Sciences Centre, or the Canadian Society of Zoologists, to name but a few.

### The unforgettable character and the sportsman

To many Dave was an unforgettable character – excellent company with his acerbic wit and insightful opinions about the human

condition. He loved sports, especially football (soccer) and closely followed Manchester United. He was naturally competitive and a good athlete himself. He enjoyed playing football, squash, tennis and, in his later days, badminton and table tennis. He loved card games, especially bridge, which he sometimes played for hours with graduate students or a group of elderly ladies in Hong Kong. His free spirit led him to bet on anything, from horse racing to equity stock price forecasts. In one instance, while in Palau, he laid a friendly wager on which insect on a wall would next be eaten by a gecko.

A message we received from Dr Larry Fiddler beautifully summarizes Dave:

“David Randall was one of those rare human beings who enriched, and often changed, the lives of those he came into contact with. I am indebted to him for the sharing of his enormous knowledge, understanding, patience and friendship – all delivered with a generous portion of humor, humility and, at times, mischief. Truly, for those of us who had the good fortune of his friendship, David was and will always remain an unforgettable character. I often find myself remembering the good times I had at UBC – all due to David Randall.”

Tony Farrell (Canada)  
Colin Brauner (Canada)  
David McKenzie (France)  
Steve Perry (Canada)  
Jodie Rummer (Australia)  
Ted Taylor (England)  
Chris Wood (Canada)

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