The Journal of Experimental Biology 214, 2453-2454 © 2011. Published by The Company of Biologists Ltd doi:10.1242/ieb.060970

OBITUARY

Bruce D. Sidell

20 March 1948 - 8 February 2011

The discipline of comparative and evolutionary physiology suffered the loss of one of its most creative scholars earlier this year, with the all-too-young passing of Bruce Sidell. As all who knew Bruce - either personally or from reading his many excellent publications - realize, his science exemplified the 'curiositydriven' approach to investigation that commonly leads to the most novel and fascinating of discoveries. Bruce marched to the beat of his own drum, and the pathway he followed throughout his career was intellectually, technically and geographically wide-ranging and adventurous. He spotted questions that others in his field had missed and taught us many lessons about 'how animals work' that we otherwise might not have learned. Bruce's approach to science also taught us much about the importance of collegiality, candor and collaboration in advancing the scientific enterprise. Bruce's personal model not only helped to shape the career approaches of his many graduate students but also served as an exemplar to his peers and colleagues of how best to pursue a life in science. In preparing this tribute, we were again reminded of all that Bruce meant to us as a friend, collaborator and intellectual catalyst of his field. We hope that our words serve as a clear reminder not only of what Bruce discovered but also of what he taught us about the most effective - and enjoyable - modes of fostering discovery.

Throughout his scientific career, Bruce manifested a remarkable talent for formulating novel and important questions and then choosing the right organisms and methodologies to get the answers. The science from his laboratory was always well crafted in design, executed with precision, and interpreted with the right balance of conservatism and speculation. His success is reflected in a career of uninterrupted funding from the National Science Foundation (USA). The output from his laboratory at the University of Maine was impressive in quantity and quality and continues to serve as an intellectual springboard for studies on a wide spectrum of questions in thermal biology.

Bruce's decision to pursue a career in biology can probably be traced to his introduction to research at his undergraduate alma mater, Boston University, in the laboratory of Frank Belamarich, whom he admired greatly. From there, Bruce moved to the laboratory of C. Ladd Prosser at the University of Illinois, which at the time was a leading center for study of the thermal biology of animals. Bruce's primary interest quickly became the impact of low temperature on the biochemistry of fish. Whereas he cut his intellectual teeth in work with temperate eurythermal species, most of the latter half of his career was spent investigating Antarctic fish that live close to the freezing point of seawater and die at temperatures only a few degrees above zero. Bruce's curiosity led him to investigate a great many facets of the thermal biology of these and other species of fish. Indeed, much of Bruce's success may be attributed to his ability to appreciate the full jigsaw puzzle of thermal biology, from biochemical and molecular mechanisms to physiological ecology and evolutionary biology. He was able to work on sections of the puzzle throughout his career, often at the



Bruce Sidell on Cormorant island, Antarctic Peninsula, with Mt William in the background, in 2009. Photo courtesy of Dr Jody Beers.

same time, but most important of all, he saw how the pieces fit together with an intellectual skill that elevated him above his peers. The combination of exquisite experimental detail and over-arching intellectual synthesis that one finds in Bruce's publications is remarkable and truly the hallmark of his contributions to our field.

Bruce's first interest, and one that continued throughout his life, was energy metabolism. Work in this area included his contributions to metabolic fuel preference at low temperature, the role of fatty acid binding proteins, and the control of lipid degradation at the hormonal and enzyme levels. Just as examples, his laboratory was the first to compare metabolic enzyme capacities in laboratory-acclimated fish with those in field-captured fish, and the first to show the metabolic preference for unsaturated fatty acids in Antarctic fish. Recognition that ATP supply was only one component of the metabolic story set the stage for experiments related to energy demand in red and white muscle. His integrative studies on striped bass, which covered isolated contractile proteins, biophysics of contractile fibers, fiber recruitment at the wholeanimal level, and calcium management provided the first comprehensive picture of the impact of temperature on swimming performance. A third broad area that captured Bruce's interest, one in which he again filled in key pieces of the puzzle about mechanisms of adaptation to low temperature, was how oxygen moves from the sarcolemma to mitochondria. Conceptual advancements on this front included ultrastructural modifications at the mitochondrial level to reduce diffusion distances and the exciting and novel idea that lipid pools may serve as a conduit for oxygen movement. He demonstrated lipid-mediated oxygen transport in an elegant series of experiments, using a device he designed and fabricated himself.

Deeper understanding of oxygen delivery was enhanced with a series of papers on myoglobin function that elegantly exploited the

2454 Obituary

large variability of this protein among species. Bruce focused strongly on the hearts of Antarctic icefish, some of which lack myoglobin entirely. He elucidated the different mechanisms underlying the loss of this putative 'essential' component of the oxygen transport system, showing that different molecular lesions were found in different lineages. Using a combination of physiological approaches, he showed that loss of cardiac myoglobin reduced cardiac aerobic capacity. He also studied the function of myoglobins in these highly cold-adapted fish, demonstrating that these proteins had an unprecedented ability to unload oxygen rapidly at extremely low temperatures.

Bruce's final line of investigation perhaps most clearly illustrated his ability to 'connect the pieces of the puzzle' in an insightful and synthetic fashion. These efforts were directed to building an integrated perspective that comprises the roles of heme-containing proteins (hemoglobin and myoglobin), the production of nitric oxide, and angiogenesis. He built a strong case that the lack of heme-containing proteins in icefish resulted in decreased conversion of nitric oxide (NO) to nitrate, leading to higher steadystate levels of NO that subsequently triggered both mitochondrial proliferation and angiogenesis. In this way, he showed the evolutionarily downstream consequences of the loss of hemoglobin and myoglobin in this lineage of Antarctic fish. His later studies also revealed the importance of oxygen-carrying pigments in setting the upper thermal tolerance limits of Antarctic fish. He showed that the hemoglobin-less icefish are much less tolerant of elevated temperatures than their red-blooded relatives. Consequently, icefish may be especially susceptible to the effects of climate change.

It was this type of multi-level, highly integrative thinking that put Bruce a step ahead of his peers. Although Bruce's experiments were often specifically focused on questions in the context of cold thermal biology, the conceptual impact was far reaching in yielding insights into fundamental principles, especially as related to mechanisms of metabolic control, muscle performance, and oxygen delivery. His contributions thus taught us a great many new things about nature and, equally importantly, illustrated the types of approaches to research that are most fruitful and fun. We also note that he was as comfortable on a freezing deck trawling for specimens off the Antarctic Peninsula or the South Shetland Islands as he was conducting experiments in his laboratory in Maine or at the U.S. Antarctic base at Palmer Station.

It would be unfair, and certainly incomplete, to restrict our comments to the strictly scientific side of Bruce's contributions. He was an academic man in full, a strong contributor to the teaching and administrative activities of his university and an important participant in the Antarctic scientific community, including his long service to the Palmer Area Users Committee and the Antarctic Research Vessel Oversight Committee. In the latter role, as the sole scientific advisor on a \$100 million future facilities contract, he had to maintain his characteristically balanced and objective approach in the face of political pressures from industry and legislative constituencies. In recognition of his long career of research and service to the Antarctic scientific community, in 2010 the Sidell Spur on Brabant Island in the Palmer Archipelago, overlooking an

area where he often fished for specimens, was named for him by the National Science Foundation and the United States Geological Survey.

Bruce's entire career as a professor was spent at the University of Maine. There, he taught a series of highly acclaimed undergraduate (Cell Biology; Vertebrate Biology; Biology of Fishes; Integrative Marine Science) and graduate (Physiology of Fishes; Biochemical Adaptation) courses and mentored generations of graduate students, who are now successful in their own rights. He did yeoman service as the founding Director of the School of Marine Sciences, where he brought together a diversity of marine biologists, oceanographers and aquaculturists, as well as economists and policy and management specialists, to form an academic department that is consistently at or near the top in research funding and productivity at his university. Bruce's success in administrative tasks was based on the same personal characteristics that helped account for his success as a scientist: high intelligence, extraordinary attention to detail, an ability to inspire loyalty and a high level of effort in the colleagues and collaborators he chose to work with, and a unique sense of humor that helped him bear the diverse burdens associated with academia. In recognition of the esteem in which he was held, his friends, colleagues, and former students established the Bruce D. Sidell Scholarship for deserving students in the School of Marine Sciences.

Bruce's success as an academic was paired with a rich and supportive family life. He enjoyed the companionship of a wonderful wife, Mary, their three daughters, Amy, Jessica and Amanda, and their husbands, and, later, six grandchildren. Bruce would also want us to recognize his canine companions who, along with his family, carried him through the challenges of his professional life.

Bruce Sidell manifested the mixture of deep curiosity about nature, creativity in experimentation, cooperativeness in working with colleagues, caring and fairness in mentoring students, and commitment to the diverse expectations of academic life that underlies a most successful career. Proud of his liberal education, Bruce was mindful of his broader audience and the role of science in society, and had underlined these words in his copy of William Zinsser's book 'On Writing Well': '...they all come across first as people: men and women finding a common thread of humanity between themselves and their specialty and their readers. You can achieve the same rapport, whatever your subject.' His passing will be deeply felt by all in our field, but his rich legacy will continue to shape our thinking about our science and inspire us to carry out our activities in research and education in the creative and thoughtful way that Bruce exemplified.

William Driedzic Ocean Sciences Centre, Memorial University of Newfoundland

J. Malcolm Shick School of Marine Sciences, University of Maine

George N. Somero* Hopkins Marine Station, Stanford University *Author for correspondence (somero@stanford.edu)