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What is a fish? The life and legend of David L.G. Noakes

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Abstract David Lloyd George Noakes (1942–2020) is best known for his insatiable curiosity, his quick wit and dry sense of humor, his scientific contributions to the field of animal behaviour, and his ability to form and maintain long-lasting connections. His research interests were vast but remained grounded in early life history, behaviour, social behaviour, the evolution of behaviour, behavioural genetics, and evolutionary ecology. David had a remarkable ability to establish and maintain strong connections within the international academic community. David was also internationally recognized for his numerous contributions as a scientific editor, promoting accessibility to the international community that he served. We memorialize David's legacy in this tribute article, ensuring that his accomplishments and the momentous impact he had on the scientific community are not soon forgotten.

Keywords David Lloyd George Noakes · Memorial · Tribute · Scientific contributions · Lifetime achievements

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The early years

David Lloyd George Noakes, named for his three uncles David, Lloyd, and George, serving overseas in the Canadian military, was born on 3 August 1942, in Hensall, Ontario, Canada. He was the second oldest in a family of eight children. He grew up playing baseball, road hockey, fishing, and taking guitar lessons. He helped his father Leonard and brother Bill maintain a very large vegetable garden. As it was an equal-opportunity household, David did not escape household chores. As a reward for cleaning their rooms and closets on Saturday morning, they were allowed to bake in the afternoon.

From an early age, David was a keen reader (Fig. 1). His sister Jean introduced him to the town library when he was five. He challenged himself to read all the non-fiction books, including government publications, at the Hensall public library, a task he completed before starting high school. He attended Hensall Public School where he excelled at his studies. His love for books was surely linked to his unquenchable thirst for knowledge and continued into his high-school years.

Even from a young age, David was drawn to books about history and science, two passions that remained with him throughout his life. His insatiable curiosity and encyclopedic mind were reflected in David's broad interests and knowledge of just about everything — sports, military history, airplanes, Samurai movies, and so much more. There appeared to be no trivia that David did not know, from lyrics and composers of bluegrass music to stats of baseball players and everything in between. Most of all, from an early age, David was interested in finding answers to various questions, and that interest led him to science.

The remarkable career

After high school, David headed to the University of Western Ontario (now Western University), in London, Canada, where he was enrolled in the honours physics and chemistry program, making him the first in his family to go to university. David was required to take two additional courses to round out his first year and opted for a botany and a zoology course. He was told that this would position him well to become a high school science teacher. Today we are thankful that David found the chemistry and physics courses "boring" and "tedious" (David's words!) and switched into the biology option after his first year. He completed his B.Sc. Honours in Biology in 1965 and continued to complete a M.Sc. in Zoology in 1966, where his interest in animal behaviour continued to grow, focusing his graduate work on fish behaviour and specifically on northern longear sunfish *Lepomis megalotis* behaviour.

David met Patricia Huntley at Western, and they married in September 1966, the day before they took the train to the University of California Berkeley where David would begin his Ph.D. studies. Pat was David's closest friend and companion (Fig. 2). Her long career teaching elementary students in Guelph and the surrounding area included many years working with children who had special needs. She was an enthusiastic supporter of his work, frequently hosting their wide circle of friends and colleagues from around the world. She went with him to a great number of scientific meetings and on many sabbaticals, participating in various science-related recreational activities, of which David was so fond. David and Pat have one son, Jeffrey Noakes, who holds a Ph.D. in military history and is a historian at the Canadian War Museum, and one grandson, William.

In the 1960s, University of California Berkeley was one of the very few places in North America where you could study Ethology, the European approach to the study of animal behaviour. The ethological approach was started by Karl von Frisch, Konrad Lorenz, and Niko Tinbergen and emphasized studying animal behaviour for its own sake, in its natural context. It was thought to be useful to distinguish species, in the same way that physiology and morphology were explored and applied at the time. It focused on the adaptive aspects of behaviour and is strongly based in evolutionary theory. Everywhere else in North America, animal behaviour was taught as a branch of Psychology, from a human perspective. At the time, most universities did not offer courses in animal behaviour.

The year David started his Ph.D., 1966, was a pivotal year at Berkeley. George Barlow had just arrived, after leaving the faculty at the University of Illinois (Fig. 3). Although he was hired as an Ichthyologist, George was also a "card carrying" ethologist, having spent a 2-year postdoctoral fellowship in the laboratory of Konrad Lorenz at

Fig. 1 David as a young boy and an avid reader (photo courtesy of Pat Noakes)

the Max Planck Institute in Seewiesen, Bavaria. There, George worked with cichlid fishes, which would become the focus of his career. Lorenz's 1966 book "On Aggression" had just been published in an English translation. It became a best-seller and popularized the Ethological approach to behavioural studies.

In 1967, David became a student in George's first Ichthyology class at Berkeley, which Gene Helfman, a fellow member of the lab (Fig. 4), described as "legendary". All four undergraduate students, David, and the teaching assistant went on to become tenured faculty in biology, most in Ichthyology. David maintained life-long contact with them and they were

Fig. 2 Pat and David during a visit to Lofoten, Norway, in 2015 following the Charr Symposium in Tromsö (photo courtesy of Skúli Skúlason)

Fig. 3 David, George Barlow, and Gene Helfman during a field trip to a whaling station in Richmond, CA, in 1967 (photo credit: Howard Schein)

important to his network. As George's first student at Berkeley, David helped develop and set up George's fish laboratory.

When Jeff Baylis arrived in Berkeley to join George's lab in 1968, David was the first person he met. If George was not present, David was in charge of the lab, which had become a major cichlid breeding enterprise requiring close attention. Additionally, a new ethologist, Richard Dawkins (Fig. 5), a new hire from Oxford University, taught his first animal behaviour course at Berkeley in 1968. David was Richard's first teaching assistant and Richard would serve on David's Ph.D. committee. Again, a life-long contact. Besides his skill in the laboratory, David was also a dedicated field biologist (Fig. 6). On one dangerous trip, he and Jerry Meral drove from Berkeley to Nicaragua in 1969 to work on cichlids, narrowly escaping harm as they made their way through the "Soccer War" in Honduras during their passage home. The Nicaraguan fish studies contributed to his dissertation on the ontogeny of behaviour in red devil cichlids *Amphilophus labiatus*.

David finished his Ph.D. in 1970 (Fig. 7) and left Berkeley for the University of Edinburgh, Scotland, to do a postdoctoral fellowship in the laboratory of Aubrey Manning (Fig. 8), working on behavioural genetics. There, he met another life-long contact, John Endler. David's work focused on animal behaviour, which fit well with the Manning lab; however, he was the first lab member to conduct research on fish.

University of Guelph

After completing his postdoctoral studies, David returned to Canada in 1972 to join the College of Biological Science in the Department of Zoology at the University of Guelph focusing on animal behaviour (Fig. 9). David's skill set complemented the well-established faculty at the

Fig. 4 Howard Shein, David, and Gene Helfman posing in a museum cabinet outside of George Barlow's office at the University of California Berkeley in 1967 (photo courtesy of Pat Noakes)

Fig. 5 Ron Brooks, David, and Richard Dawkins pictured conducting field work at Sasajewun Dam at the Algonquin Wildlife Research Station in 1982 (photo credit: Ron Brooks)

Fig. 6 David as a teaching assistant sampling stream-side with students during a field course near the University of California Berkeley campus (photo courtesy of Pat Noakes)

Fig. 7 David (right) and Alan Bond at a reception after David's Ph.D. exit seminar at the University of California Berkeley (photo credit: Jeff Baylis)

Fig. 8 David (right) relaxing with Aubrey Manning, and Margaret Bastock at their home outside of Edinburgh, on the outskirts of Ormiston (photo courtesy of Pat Noakes)

Fig. 9 David during his early years at the University of Guelph (photo credit: College of Biological Science, Zoology Department)

University of Guelph that emphasized research on fish biology. For example, William Beamish was already on the faculty, with an established research program in fish physiology. David's background in fish behaviour and early ontogeny added breadth to the program.

When David came to the University of Guelph, he drew on his background in animal ecology and ethology but this time applied it to coldwater fishes such as salmonids (i.e. charrs) and sturgeons. His interest remained grounded in early life history, behaviour, social behaviour, the evolution of behaviour, behavioural genetics, and evolutionary ecology for the length of his illustrious career at Guelph. David's teaching activities included courses, field courses, undergraduate projects, advising graduate and postdoctoral students, and sitting on graduate student committees. At Guelph, he worked closely with Mrs. marie Thérèse Rush-Smyth where they developed innovative and engaging curricula (Fig. 10). David taught undergraduate and postgraduate courses in animal behaviour, aquaculture, experimental ethology, ichthyology, and fish biology and ecology, among others. It is not uncommon to hear fisheries professionals state that the pivot point in their career — the moment they knew they were choosing the right path — occurred while taking David's 3rd year Ichthyology course, or his 4th year Environmental Biology of Fishes course. He initiated an interdisciplinary course called "Darwin in London", focusing on biology, history, and philosophy that was offered at the University of Guelph London House for several years.

In 1980, David went to Oxford University, where he spent the first of many sabbaticals and research-focused international trips, including to Japan; California, USA; Iceland; Germany; Zanzibar; China; and Thailand. David chose Oxford University for his first sabbatical as he knew that it was one of the premiere universities to study behaviour and to explore the theory of animal behaviour. David returned to Guelph where, as he had always done, he shared the knowledge he had gained with those who surrounded him.

In 1989, a key event occurred at Guelph when Herbert R. Axelrod donated a $20 million collection of Cretaceous fish fossils from the Santana Formation of northeastern Brazil to the university. The result of that gift was the founding of the Axelrod Institute of Ichthyology in 1990, with David as the founding Director. He served as Director of the institute off and on until 2002. The Axelrod fossil collections were incorporated into David's ichthyology labs on structural diversity of fishes and techniques in the study of fish taxonomy. David appreciated the significance of the collection of fossils and gave many opportunities for colleagues and students to explore this collection (Fig. 11). He also brought the collection to children from kindergarten to high school and presented an engaging "fish and fossil" presentation followed by a "hands-on" experience to observe the features present

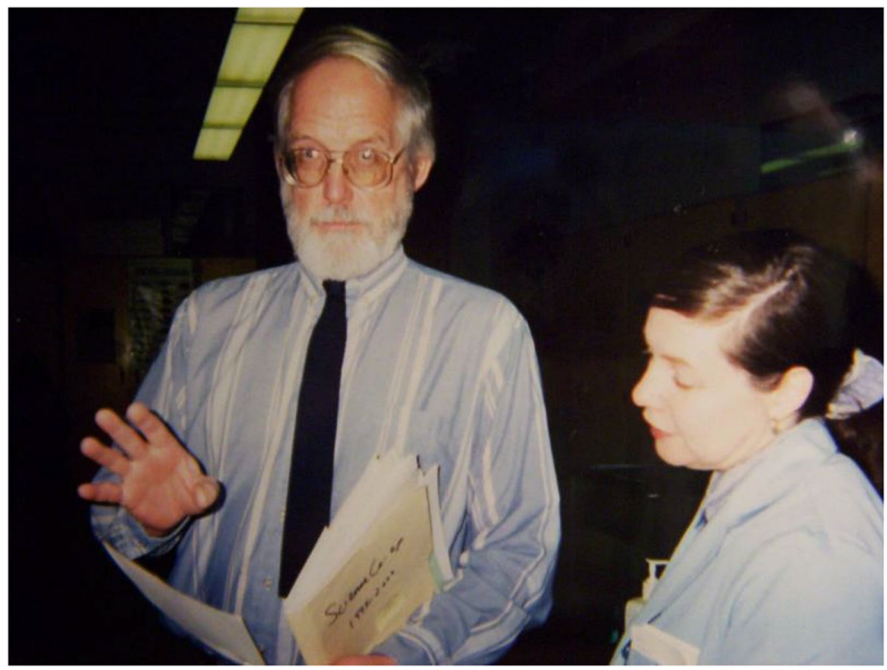

Fig. 10 David and marie Thérèse Rush-Smyth at the University of Guelph in 2004 (photo credit: candid photo from summer co-op student)

Fig. 11 David explaining the significance of the Axelrod fish fossils to a group of undergraduate students at the University of Guelph (photo credit: D.L.G. Noakes and m.T. Rush. 2004. Principles of Ichthyology course manual)

on these exceptional specimens. The collections continue to be an invaluable teaching resource.

During David's time at the University of Guelph, he oversaw the construction of a new campus building to house the Axelrod Institute of Ichthyology. In the initial years, the institute resided in an old house across the street from the Zoology Building. In 1996, it was moved to its newly constructed home, which included office space for the administrative staff of Environmental Biology of Fishes, for graduate students, postdoctoral researchers, visiting scientists, and later, two research labs equipped for fish age estimation and energetics studies. Throughout this time, David also worked tirelessly to cultivate the institute as a meeting place for anyone interested in fishes. David also created opportunities for social interactions at the institute by initiating Friday morning coffee breaks where he and others would supply homemade baked goods. David would actively round up anyone in the vicinity of the institute to participate. The institute was an intellectually rich and exciting research base for graduate students, postdoctoral fellows, and research associates from Austria, Brazil, Canada, Iceland, Japan, and the UK. It was also a highly regarded place to visit for scientists and historians from neighbouring universities and from universities farther away, including Cambodia, Iceland, Japan, the UK, and the USA. Scientists and fishery managers from government agencies in Canada and the USA, industry leaders in the aquarium and pet trade, and representatives from Indigenous groups regularly visited the institute. Many of these people made extended visits for sabbaticals or recurring visits.

David was foremost an ethologist. Throughout his career at Guelph much of his research can be encapsulated as focusing on two themes. One involved investigations applying Tinbergen's four fundamental questions about the biological basis of behaviour (causation, development, adaptive value, and evolution). The investigations focused on early life history to reveal the mechanisms behind the creation of ecological diversity within and among populations, within species of management or conservation interest, particularly salmonids. These studies have contributed to our understanding of the processes involved in creating new biodiversity in fishes. The second theme comprised the application of behavioural principles to applied studies of fishes aimed at enriching our understanding of the processes behind losses in the biodiversity of fishes in response to anthropogenic change.

The first theme was explored via two concurrent and complementary series of investigations of charrs. One series began with investigations of heritability and behavioural flexibility in aggression and water column use of brook charr *Salvelinus fontinalis* and lake charr *S. namaycush* (Ferguson and Noakes 1982,

1983a, b, c). Those investigations were followed by field studies applying optimality principles to assess the adaptive value of foraging, aggressive, territorial, and escape behaviour in the field (Grant and Noakes 1986, 1988; Grant and Noakes 1987a, b, c; Grant et al. 1989); studies identifying alternative foraging tactics related to water column use and diet (Biro et al. 1997; Grant and Noakes 1987b; McLaughlin et al. 1999, 2000); potential mechanisms explaining the tactics and quantifying the consequences for short-term growth rate, an index of Darwinian fitness in juvenile fishes (McLaughlin et al. 1999; de Kerckhove et al. 2006); and behavioural and environmental influences on the development of alternative morphotypes (Imre et al. 2002). These studies laid the foundation for more recent investigations of the molecular and neuroendocrine basis for individual differences in charr behaviour (Wilson and McLaughlin 2010; Farwell et al. 2014; Hale et al 2021). A second series of investigations focused on the diversification of polymorphic Arctic charr *S. alpinus* in Iceland. Here, David had a hand in studies assessing how the interactions between genetic differences, the timing and location of spawning behaviour, and environmental rearing conditions shape the development of alternative phenotypes and lifestyles in sympatric morphs of Arctic charr (Skúlason et al. 1989a, b; Skúlason et al. 1996; Kristjánsson et al. 2018). David was also involved in initial assessments of the evolutionary relationships among the morphs (Danzmann et al. 1991) and detailed examinations of the ecology of specific morphs (Skúlason et al. 1993; Kristjánsson et al. 2012). These studies motivated deeper exploration of ecology, evolution, and developmental biology perspectives on the origins of resource polymorphisms (Skúlason et al. 2019). David extended his interests in this theme to complementary studies of polymorphic threespine stickleback *Gasterosteus aculeatus* in Iceland (Kristjánsson et al. 2002a, b) and polymorphic lake charr in Great Bear Lake in Canada (Blackie et al. 2003; Noakes 2008a).

The second theme consisted of an ensemble of diverse studies conducted over David's career at Guelph. Members of his lab used behavioural studies of juvenile brook and lake charr to assess the sublethal and lethal effects of acid rain and contaminants in northern Ontario Canada (Gunn and Noakes 1986; Gunn et al. 1987), field studies to evaluate the relationship between groundwater inflow and selection of spawning sites by brook charr, and the implications of this relationship for managing water flow and adjacent land use (Curry et al. 1994, 1995; Curry and Noakes 1995). Additional studies involved field experiments to reveal the ways interactions with exotic Pacific salmon could be limiting efforts to re-introduce Atlantic salmon *Salmo salar* to Lake Ontario (Scott et al. 2003; Scott et al. 2005a, b). David also took a major leadership role in the multi-university Biological Impacts of Low-Head Barriers project that showed how small, in-stream barriers across the Great Lakes basin contributed to local losses of fish species (Dodd et al. 2003) by restricting upstream movements (Porto et al. 1999) among species that were impacted most by the presence of barriers (McLaughlin et al. 2006).

Given his curiosity, it is no surprise that David's contributions were not limited to just these themes. David had a long interest in the reproductive development of clonal mangrove killifish *Kryptolebias marmoratus* (Cole and Noakes 1997; Minamimoto et al. 2003; Sakakura and Noakes 2000; Sakakura et al. 2006). He also oversaw research contributions to a major project developing an individual-based model of population dynamics for smallmouth bass *Micropterus dolomieu* (Scott et al. 1997; Friesen 1998; Mackereth et al. 1999), co-advised research improving our understanding of several fishes of conservation concern, including Atlantic salmon, lake sturgeon *Acipenser fulvescens* (Noakes et al. 1999), native lampreys (Neave et al. 2006, 2007), and redhorse suckers (Clarke 2004). Through his participation in the University of Guelph's M.Sc. Aquaculture program, David helped make fundamental contributions to the use of clove oil as an anaesthetic for research on fishes (Keene et al. 1998; Grush et al. 2004; Holloway et al. 2004). Finally, David actively facilitated research on the genetics, ageing, and ecology of lake whitefish *Coregonus clupeaformis* to support the management of commercial and traditional Indigenous fisheries (Muir 2004; Bernard et al. 2009; Macpherson et al. 2010).

David spent 33 years, or some may say an entire career, before leaving for Oregon State University to expand his study of fishes and share that passion with new colleagues and students in the Pacific Northwest.

Oregon State University

In 2005, David joined the faculty of Oregon State University (OSU), as the first Director of the Oregon

Hatchery Research Center (OHRC), a joint venture between Oregon State University and Oregon Department of Fish and Wildlife (ODFW). The OHRC was designed to invite world class scientists to bring the best science to bear on the question of how to manage and minimize the impacts of hatchery fish on wild fish. David was proud of the unique resources that OHRC offered: four outdoor artificial stream channels that simulated actual stream conditions, four concrete raceways, a tank farm comprising 44 fibreglass tanks, an analytical lab, and a complete wet lab with heated, chilled, filtered, and UV-treated water. His role as director was multi-faceted, a position for which he was ideally suited and that allowed him to work full time with his beloved salmonids.

He enthusiastically brought researchers who came from local, national, and international programs studying freshwater and marine systems, with diverse interests spanning genetics, physiology, ecology, and behaviour, especially fish movement, to this extraordinary venue. David worked hard to connect hatchery staff, agency scientists, managers, and leadership to ensure that OHRC was focused on the issues most relevant to ODFW. Teams including his students, post-doctoral fellows, and OSU colleagues studied the effects of developmental physiology on migration (Self et al. 2018a, b; Billman et al. 2014; Thompson et al. 2016) and examined the details of in-river movements (Pollock et al. 2020; Whitmore et al. 2021). Replicate outdoor streams facilitated innovative studies such as one examining the effects of riparian shade on bird predation on coastal cutthroat trout *Oncorhynchus clarkii* (Penaluna et al. 2016). Laboratory experiments explored diverse effects of temperature including those on fish behaviour and development (Miura et al. 2013; Munakata et al. 2017), and insect emergence (Li et al. 2011).

Seminal work on magnetic orientation included significant contributions not only to our scientific understanding of fish movement but also to salmonid conservation and management (Putman et al. 2013, 2014a, b; Scanlan et al. 2018; Naisbett-Jones et al. 2020). David's work painted a complete picture of magnetic navigation in salmon, effectively setting the benchmark for researchers of other taxa to follow. He led the studies demonstrating that salmon use magnetic cues throughout their life cycle, as they move out of their gravel nests at swim-up, as juveniles to locate oceanic foraging grounds, and as adults to navigate back to their natal river (Putman et al. 2018). In Putman's (2022) introduction to a special issue on magnetosensation, which was dedicated to David, recalled that David "would often paraphrase U.S. President John Kennedy's 1962 speech setting the goal for humans to explore the Moon, saying that we choose to study questions on magnetic orientation "…not because they are easy, but because they are hard, because that goal will serve to organize and measure the best of our energies and skills, because that challenge is one that we are willing to accept, one we are unwilling to postpone, and one which we intend to win…".

In his role as OHRC director, David was an effective communicator to audiences beyond academe. He presented important, complex issues in ways easily understood by the Oregon legislature and the highly political OHRC Board. His ODFW colleague, Bruce McIntosh, declared "When David spoke, he commanded the room in his understated and charming way, a way that engendered trust and confidence in the OHRC and the man in charge", On the OSU campus, he was a wise mentor to faculty and grad students, long-serving member of the university animal care and use committee, enthusiastic teacher, and all-around driving force who made the department a happy place.

David brought his energy and passion for teaching not only undergrad and graduate university students, but also while collaborating with ODFW staff. He regularly taught a graduate course in fish ecology that began as a "living laboratory" at OHRC during Spring Break followed by innovative lectures and activities. To introduce them to the wonders of international collaboration, David arranged remote sessions for students to learn from others half-a-world apart (e.g. Iceland and Japan). With his students and postdoctoral fellows, he organized a range of workshops for agency and tribal personnel. David whole-heartedly embraced the Center's mission of outreach to the community, actively engaging school kids, their teachers, and the general public to explore the OHRC and its surrounding environment (Fig. 12). With OHRC staff, he established the wildly popular Fall Festival that was timed to coincide with Chinook salmon spawning at Fall Creek, and featured diverse educational activities and served free salmon meals to the public. Early in his tenure at

the Center, he co-wrote a National Science Foundation Grant that brought kindergarten through grade 12 teachers from coastal schools to OHRC for annual workshops. These teachers subsequently visited the Center with classrooms of children. David, with a twinkle in his eye, and aided by his

Fig. 12 David streamside at Oregon Hatchery Research Center at Oregon State University (photo credit: Oregon Hatchery Research Center Archives)

staff, delighted the kids as they learned about the conservation of salmon and stream habitats.

The dedicated scientist

David was the kind of scientist who was open to the wonders of nature, with deep curiosity for understanding the diverse patterns we see in life on Earth, and a quest for understanding the processes that lie behind these patterns. The vast diversity of fishes allowed for numerous avenues of exploration and David took full advantage, publishing scientific papers on a total of 38 species in 16 families (Cooke et al. 2022; Muir 2022). David's focus was broad and connected many important aspects, but he particularly combined studies of individual early embryonic and juvenile development with questions on the ecology and evolution of diversity within and among populations and species. This focus extended to his more recent work at OSU where he led research describing the factors limiting wildness of hatchery reared salmonids (Cogliati et al. 2022). Behaviour was often the key phenotypic attribute he would consider. He was fortunate with his university training and the mentors he interacted with, as described earlier, which naturally contributed greatly to the development of his research focus and helped him to become the critical and creative thinker that he was. David's combination of ecology, evolution, and development in his research philosophy was not only original, but directly and indirectly a part of a movement within the broader field of evolutionary ecology that focused on rapid evolution of diversity and adaptive divergence, a discipline that is now cutting edge. Incredible, recent intraspecific diversification among a number of fish species lend itself to this kind of research. David's special attention to cichlids, salmonids, eels, and sticklebacks is therefore not surprising; they all represent examples of rapid diversification and show how behaviour plays an important role in such evolutionary processes. Furthermore, his research emphasis included the significance and application of ecology, evolution, and development to management and conservation strategies. These also underscored his strong commitment to contribute to society and to the welfare of ecosystems — including humans.

David was highly productive, with more than 200 papers in peer-reviewed journals (see Muir 2022). He also authored book chapters and edited books. In addition, he served as an editor and organizer of numerous scientific meetings. While clearly illustrating his primary research themes and diverse projects within these, his publications also demonstrate his vast network of coworkers and institutions all over the world (Muir 2022). Indeed, his respect for students and coworkers was unlimited. For example, his mentorship of students targeted their own interests, understanding, and abilities in a fundamental way — their development and wellbeing came first. He listened carefully and then advised. Unselfishness and generosity were the hallmarks of David's method of scientific training and research collaboration. As a result, the future careers of his graduate students and postdocs, their happiness and success — both in basic academia and in applied science — have been greatly elevated. Many good examples exist of how ideas and guidance provided by David shaped subsequent research and teaching of the students with whom he worked, in some cases having noticeable academic and societal impacts. And the same applies to his research partners and collaborators. Overall, these personal qualities were fundamental to his success and achievements in science. He was a dynamic member of the ethos that should characterize all universities and research institutions, where academic freedom and responsibility, critical thinking, and respect for the opinions of peers are emphasized.

The exceptional personality

Everyone who knew David agreed that he was "charr"ismatic, warm and friendly, and sometimes a bit quirky. Without a doubt, David's most well-known personality traits were his wit and dry sense of humour (Fig. 13). For those who did not know David well, these personality traits may have been surprising or off-putting, and it did take a while to get accustomed to them. However, for his close family, friends, and colleagues these traits were incredibly endearing and are fondly remembered and missed. In front of an audience, or when chatting one-on-one, he could first look stern, speaking in a deep, serious voice, but characteristically injected his deadpan, often subtle, humour and in an instant would make a connection. He often used his humour to make an important point or to capture people's attention. Great examples were David's famous exam questions "What is a fish?" and

Fig. 13 Candid photo of David (photo courtesy of Pat Noakes)

"What do fish want?". David's memorable signature "Charrs, David" captured his personality perfectly, demonstrating both his serious and playful sides.

David was a considerate and generous person who cared deeply and equally for his students, department staff, and colleagues; he showed incredible compassion for people in general. His door was always open to anyone seeking his advice and knowledge and he showed a genuine interest in each person he met. Countless examples of his kind and thoughtful gestures evidence his caring personality. One of the most well-known gestures was the effort he and Pat put into sending personalised and individually-signed holiday greeting cards to their very large network (Fig. 14). In his memorial, a friend left the following note for Pat: "Looks like they had many, many fishy friends all over the world. Pat—what was your annual postage bill for Christmas cards? You must have sent out hundreds every year!".

Another one of David's prominent personality attributes was his ability to connect people and build networks. He was a leader in developing successful meetings, especially the Ecology and Evolutionary Ethology of Fishes (EEEF) conference and the International Charr Symposium, where he played pivotal roles in their success. In these meetings, he talked broadly to participants and was eager to introduce students, postdocs, and those beginning their career to leading scientists in the field. It was not uncommon to hear David say "Do you know < insert name > ? They are an expert in < insert field or discipline > . The two of you have a lot to talk about.", and of course, he would add an interesting story about them as well.

David was also keen to create a spirit of belonging in his department. He was well known for sharing his homemade baked goods (including his famous strawberry shortcake and apple crisp) after the "Loaves & Fishes Seminar" at the University of Guelph and at the "Friday morning coffee sessions" at both University of Guelph and Oregon State University (Fig. 15). It was not uncommon to walk by a room filled to the brim with students, colleagues and visiting fellows all enjoying one of David's treats. He was also famous for his legendary celebrations to commemorate Darwin's birthday, which was yet another occasion to bring people together.

David's interests ranged from the trivial to the non-trivial and he had an uncanny ability to purposefully blur those lines. For instance, he used the history of the automobile or golf clubs and balls in his lectures to teach about evolutionary processes. His general knowledge spanned automobiles, typewriters (Fig. 16), birds, airplanes, military history, sports, music (Fig. 17), and baked goods, and the origin of exotic ingredients for such goods, among many others. He had a large and eclectic collection of trivia books and was known for opportunistically posing trivia questions whether related to ongoing

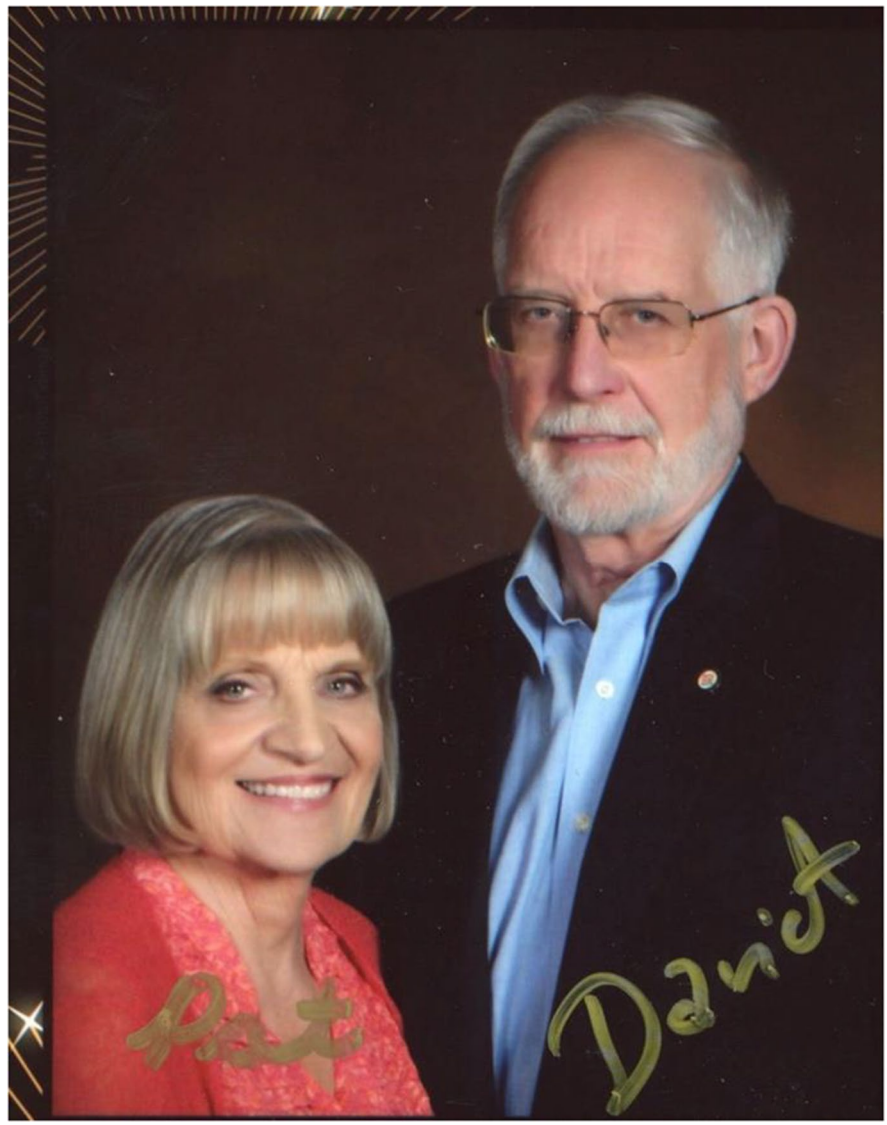

Fig. 14 An example of one of David and Pat's well-known personalised and individually signed holiday greeting cards that was sent to their very large network of friends and colleagues (photo courtesy of Pat Noakes)

conversation or as conversation starters. David had a strong "artistic component" and recognized the overlap between science and art. Photography and video were tools employed in his lab to document and study fish behaviour (e.g. McNicol and Noakes 1981; McLaughlin and Noakes 1998) and ecological diversity. He taught scientific fish illustration as part of his ichthyology labs and celebrated the works of J.L.B. Smith with illustrations by his wife Margaret M. Smith, Joseph Tomelleri, and others. In the late 1990s, David was introduced to Paul Vecsei, a physical geography student at Concordia University, Montreal, and brought him to Guelph to do an M.Sc. in his Ghoti lab. Paul had an encyclopedic knowledge of fishes, military tanks, and camouflage patterns, but most importantly, he was one of the most promising young fish illustrators in North America who flourished under David's supervision and became one of the most accomplished fish illustrators globally.

Throughout his career, David was an active mentor and supervisor of students at all levels, from high school students to post-doctoral fellows (Table 1). He had an uncanny ability to sense a person's need and would take on the role that would serve the greatest good, whether it be a fellow researcher, agency

Fig. 15 David provided homemade baked goods, of which he was famous for, at the Friday morning Coffee Sessions at both the University of Guelph and Oregon State University (photo courtesy of Pat Noakes)

Fig. 16 A few typewriters from David's personal collection. David was well known to gift typewriters to the children of friends and colleagues so they could gain an appreciation for the lost art of typing (photo credit: Amanda Pollock)

professional, departmental staff, parent, or student. He was a good listener and master of empathy.

David's supervision did not end at his office door, or at graduation for that matter, as he took a genuine interest in his students' and their family's wellbeing. David treated everyone he met as an equal and students were no exception. Students naturally reciprocated the respect they were shown and it formed the basis of many long-lasting relationships. David put his students first, and it was not uncommon for a student to receive a fully marked up version of their thesis one day after handing it in.

Fig. 17 David and Hiram Li sharing their love for country music (photo courtesy of Pat Noakes)

David's mentorship style was one of groundskeeping (sensu Montgomery 2020). He recognized the roles of exams, grades, and defences — the gatekeeping of academia — but devoted his energy and effort into creating a learning methodology supporting networking, collaboration, and success. The groundskeeping began with his liberal selection of mentees which, over his career, included many women, early researchers from foreign countries, and mentees that were not necessarily stellar academically, but had exceptional passion for, interest in, or experience with fish biology, behaviour, and conservation outside of university classes. Almost all of David's mentees have gone on to successful careers in research- or management-related professions. David's groundskeeping continued through the myriad of venues he created for mentees to connect with peers and senior colleagues. One such example was the weekly Loaves and Fishes seminar series that David organized religiously every semester at the University of Guelph. He created a venue where senior undergraduates and graduate students could interact with faculty, as well as develop their presentation chops in a collegial atmosphere. David insisted the seminar series not lapse when he was away on research leave. Of course, David urged mentees to attend national and international conferences but he was particularly creative and adept at creating opportunities where mentees could take lead roles in the organization of conferences and symposia, as well as at creating unique venues for mentees to connect with senior people in the field. These were often tributes, such as special conference sessions, book signings, and invitations that brought well known scientists to the Institute of Ichthyology for extended visits.

Along with the support for networking and collaboration came David's patience and loyalty. David understood that the path to becoming an excellent researcher can be indirect, long, and challenging. He did not belabour instances when a mentee did not perform at their best, when progress was slow because an experiment was not working, or if equipment was lost. He appreciated the value of making mistakes and recognized that a career was determined by years of incremental successes and not a handful of bad days. In a similar way, David was not a hard critic, although he had a critical mind. Based on his actions, David appreciated that students were encountering challenges and criticism on a regular basis and did not need more from him. If you were stuck with an experiment or had an idea that required forging into a new discipline, David was laser focused on connecting you with people who could help you overcome any hurdles in your path. Finally, David's gatekeeping was done with incessance. Once you were rooted in his circle of influence the groundskeeping did not lapse. He perpetually fostered personal connections and learning. It might be when you approached him for insight on a topic, or him directing

Table 1 Compilation of all graduate students (Master of Science (MSc), Doctor of Philosophy (PhD)) and postdoctoral research fellows (PDF) under David's mentorship over the course of his career

Last name	First name	MSc	PhD	PDF	Year	Thesis title
University of Edinburgh, Scotland						
Thomas	Dorothy	X				
University of Guelph, Canada						
Armstrong	Edward (Ted)	X			1977	Reproductive biology and ecology of the mourning dove in southern Ontario
Bernard	Andrea	X			2006	Cryptic structure and diversity of lake whitefish (*Coregonus clupeaformis*) in Ontario waters
Biro	Peter	X			1996	Space-use by juvenile brook charr (*Salvelinus fontinalis*) in lakes: the central-place territorial model does not apply
Carey	Wayne	X			1981	Comparative ontogeny of photobehavioural responses of the Salmonidae
Clark	Josh	X			2004	Redhorse suckers (*Moxostoma*) in the Grand River, Ontario: how do six ecologically similar species coexist?
Clément	Marie		X		2003	The feasibility of the restoration of Atlantic salmon (*Salmo salar*) into the Lake Ontario basin
Cole	Kathleen	X			1976	Social behaviour and social organization of young rainbow trout, *Salmo gairdneri* of hatchery origin
Crabbe	Sarah	X			2000	Use of small streams by juvenile Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, in the Ponoi River, Russia
Curry	Allen		X		1994	Hydrogeology of brook charr (*Salvelinus fontinalis*) spawning and incubation habitats: linking aquatic and terrestrial ecosystems
DePasquale	Deborah	X			2006	Predicting the sensitivity of non-target fishes to low-head stream barriers
Ferguson	Moira	X			1982	Behaviour-genetics of lake charr (*Salvelinus namaycush*) and brook charr (*S. fontinalis*)
Friesen	Trevor		X		1998	Effects of food abundance and temperature on growth, survival, development and abundance of larval and juvenile smallmouth bass
Grant	James W.A. (Jim)		X		1987	Foraging tactics and social behaviour of young-of-the-year brook charr, *Salvelinus fontinalis*
Grush	Julian	X			2000	The efficacy of clove oil as anaesthetic for the zebrafish, *Danio rerio* (Hamilton)
Gunn	John		X		1987	The role of episodic acidification in the extinction of lake charr (*Salvelinus namaycush*) populations
Imre	Istvan	X			1999	Developmental response of young-of-the-year brook charr (*Salvelinus fontinalis*) to water velocity
Keene	Joel	X			1995	The efficacy of clove oil as an anaesthetic for rainbow trout, *Oncorhynchus mykiss* (Walbaum)
Kristjansson	Bjarni	X			2001	Divergence of Icelandic threespine stickleback, *Gasterosteus aculeatus*, to two substrate types in lakes and recently formed lagoon
Kristjansson	Bjarni		X		2008	Fine scale phenotypic diversity of Arctic charr in relation to ecological characters (2008)
Lau	Michael	X			2003	The efficacy of argon gas as a pre-slaughter sedative for farmed rainbow trout, *Oncorhynchus mykiss* (Walbaum, 1792)

Table 1 (continued)

Last name	First name	MSc	PhD	PDF	Year	Thesis title
Locke	Brian	X			1995	An investigation of relationships between otolith age and growth and foraging behaviour in recently emerged brook charr *Salvelinus fontinalis*
Mackereth	Rob		X		1995	Size-based variation in the allocation of energy to parental care by male smallmouth bass, *Micropterus dolomieu*
Manzanilla	Silvia	X			1988	El Niño southern oscillation as a natural marker in the teeth of dusky dolphins, *Lagenorhynchus obscurus*, from Peruvian waters
McLaughlin	Rob			X	1992	
McNichol	Richard	X			1979	Territory defense among juvenile brook charr, *Salvelinus fontinalis*, in an artificial stream channel
Meisenheimer	Peter	X			1990	Condition, thyroid hormones, and emergence behaviour of brook (*Salvelinus fontinalis*) and lake (*S. namaycush*) charr
Ming	Frederick W	X			1978	Spawning site selection and competition in male fathead *Pimephales promelas* and bluntnose *P. notatus* minnows (Pisces: Cyprinidae)
Muir	Andrew	X			2004	Age estimation of lake whitefish (*Coregonus clupeaformis*) in Lake Huron: Reducing the uncertainty
Neave	Fraser B	X			2005	The utility of meristic, morphometric, pigmentation and gonad analysis in the identification of *Ichthyomyzon* lamprey larvae
Newlands	Josh	X			1995	The effect of feeding on aggressive behaviour and growth in juvenile rainbow trout
Noltie	Douglas			X	Late 1980s	
Nunan	Christopher P		X		1987	Environmental influences on movements of salmonid embryos within artificial redds
Porto	Louise	X			1997	The effects of low-head barrier dams on fish movement
Pot	Willem		X		1986	Competition for nests, paternal care, and female choice in the bluntnose minnow, *Pimephales notatus*
Ross	Marlene D	X			2002	Effects of low-head barriers on species richness in streams within the Laurentian Great Lakes basin
Rossiter	Andrew			X	Early 1990s	
Sakakura	Yoshitaka			X	1999	
Scott	Bob	X			1993	The influence of parental care behaviour on space use by adult male smallmouth bass, *Micropterus dolomieu*
Scott	Bob			X	2001	
Skulason	Skuli	X			1986	Embryo size and early head shape in four sympatric morphs of Arctic charr (*Salvelinus alpinus*) in Thingvallavatn, Iceland
Skulason	Skuli		X		1990	Variation in morphology, life history and behaviour among sympatric morphs of Arctic charr: an experimental approach
Soto	Cristina	X			1988	Relationship of coloration to gonadal status in the self-fertilizing fish *Rivulus ocellatus*
Valiant	Emma	X			2000	The evaluation of carbon dioxide and argon gas as humane euthanizing agents for fish
Vecsei	Paul	X			2000	Sexual dimorphism of North American sturgeons, Acipenser species
Veenstra	Ronald	X			1987	Ecomorphological comparisons of early development in an altricial (*Lucania parvaan*) in a precocial (*Lucania goodei*) cyprinodont
Wanzenbock	Josef			X	1992	
Walton	Clement	X			1979	Growth of alewives, *Alsoa pseudoharengus* from two marine watersheds
Ward	Colette	X			2008	Long-term correlates of lake whitefish recruitment in eastern Lake Ontario spanning an ecosystem regime shift
Oregon State University, USA						

Table 1 (continued)

Last name	First name	MSc	PhD	PDF	Year	Thesis title
Cogliati	Karen			X	2019	
Kamran	Maryam			X	2020	
Leblanc	Camille		X		2011	The importance of egg size for the diversity of salmonids
Lemanski	Joseph	X			2015	Effects of current hatchery practices on salmon odor recognition and responses
Lewis	Sierra	X			2013	Reconnecting aquatic habitats: Validating historical habitat use by anadromous fishes using telemetry and stable isotope analysis above barriers
Pollock	Amanda	X			2019	Comparing migratory patterns and survival between wild and wild fish surrogate juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*)
Putman	Nathan			X	2014	
Quelch	Glenn	X			2015	
Romer	Jeremy	X			2010	Survival and behavior of juvenile steelhead trout (*Oncorhynchus mykiss*) in two small estuaries in Oregon
Scanlan	Michelle	X			2015	An evaluation of the effects of hatchery and management practices on geomagnetic orientation behavior in juvenile Pacific steelhead trout (*Oncorhynchus mykiss*)
Schlemmel	Eva	X			2009	Managing adult hatchery summer steelhead for a recreational fishery with reduced hatchery and wild interactions
Self	Katherine (Kate)	X			2017	The effects of tank structure and egg size on the production of wild steelhead (*Oncorhynchus mykiss*) surrogate fish

others to you for assistance. And David would subtly, yet firmly involve you in initiatives he felt would benefit you and others. Like an experienced groundskeeper, David knew where and when his care would be beneficial, often before you did, and placed you in opportunities where you would continue to grow and thrive.

The career as an editor

In 1975, a new international fish journal, Environmental Biology of Fishes (EBF), was launched. Environmental Biology of Fishes was based out of the University of Guelph, which was now something of a powerhouse in ichthyology, and especially in physiology, ontogeny, ecology, and behaviour, with David being a key player. Environmental Biology of Fishes would provide a publication outlet not readily available elsewhere for researchers to publish on these topics. David became an "in house" co-editor for the journal and set about using his contacts for soliciting papers that would provide content for the fledgling enterprise.

In 2001, David became the editor-in-chief of Environmental Biology of Fishes and also editor of Springer's Fish & Fisheries Monographs, positions that he maintained until his passing in December 2020. Environmental Biology of Fishes underwent an incredible evolution and transformation during David's tenure as editor-in-chief. This transformation not only reflected new technologies and services coming online for scientific journals, shifting from mailing out manuscript review packages and hand-written postcard reminders of upcoming review deadlines, but more importantly also reflected a transformation in terms of inclusivity and accessibility.

David was ahead of the times in terms of understanding societal issues, such as gender and racial inequality. David not only understood these issues but also brought them to the forefront and actively sought ways to improve them. He deliberately and strategically sought diverse representation on the Environmental Biology of Fishes advisory editorial board. He worked hard to build gender equality within the board and also ensured that the board mirrored the international community that it served.

David always advocated that Environmental Biology of Fishes was a platform that was open to the international community of researchers to publish their work. He strongly supported authors from developing countries and non-native English-speaking authors. He saw value in providing these authors a platform to publish their research and often offered free English editorial services to ensure that language was not a barrier to publication of their important research.

The Icelandic connection

David was deeply connected with Iceland, a relationship that began at the University of Guelph and extended during his time at Oregon State University. This relationship began in 1984, when he accepted to supervise a graduate student from Iceland, Skúli Skúlason, who focused his research on the evolution and development of four different morphs of Arctic charr in the lake Þingvallavatn, work that was also closely linked with Sigurður S. Snorrason at the University of Iceland. The association with Iceland grew rapidly reflecting David's exceptional skills, interest, and respect for diverse cultures and communities. On the research side, David continued to be involved in projects on Icelandic Arctic charr for over three decades and was also a promoter of research on threespine stickleback and European eel *Anguilla anguilla* in Iceland.

Over the years, David's research efforts seeded several other long-term research collaborations between Iceland and the University of Guelph. He not only supervised many graduate students who focused their research in Iceland (Fig. 18), but his incredible ability to network introduced other researchers to this dynamic area who subsequently built strong connections through their own research programs. Most notably, one of David's first graduate students was Moira Ferguson. Moira's research program had a strong connection to Arctic charr in Iceland and has subsequently supervised more than six graduate students on the topic. Beren Robinson also developed an important research program focused on Icelandic stickleback, spending two sabbaticals in Iceland. Furthermore, several of David's students who have become professors themselves at various academic institutions have also supported Icelandic graduate studies. For example, Stefán Óli Steingrímsson completed his graduate studies with Jim Grant (PhD. 1987 with David) at Concordia University studying juvenile behaviour of Atlantic salmon. David's connections to Iceland were driving factors in bringing the Ecological and Evolutionary Ethology of Fishes (EEEF) meeting to Iceland in 2004, which was the first time it was held outside of North America, as well as bringing the Charr Symposium to Iceland in 2006.

David's relationship with Iceland involved much more than collaborative studies of fishes. David was instrumental in creating an agreement, first signed in 1995, that outlined a broad collaboration between the University of Guelph and four Icelandic institutions: the University of Iceland, University of Akureyri, and the Agriculture Colleges at Hvanneyri and Hólar. The latter two are now accredited universities, the Icelandic Agricultural University and University of Hólar. In this effort, David joined forces with another life-long friend of Iceland, Steven Cronshaw, at that time a professor of psychology at the University of Guelph and who had Canadian-Icelandic heritage. The agreement included diverse academic disciplines across multiple departments and faculties of the institutions involved, setting the stage for the Iceland-Guelph Institute at the University of Guelph. For example, there has been active collaboration in the areas of rural studies as well as hospitality and tourism. Numerous people from both countries have, in one way or another, participated in the Guelph-Iceland relationship, and it has remained active to this day. It has facilitated numerous projects, including exchange of students, faculty, and people. One of the drivers of the relationship was a bi-annual credited multidisciplinary field course in Iceland for Guelph students running from 1996 to 2006.

David was also one of the organizers of a Guelph-Iceland friendship conference, held in 1998 at Guelph. The highlight of this event was when the former president of Iceland, Vigdís Finnbogadóttir, was given a Doctor of Law (LL.D) honorary degree from the University of Guelph. During his time at Guelph, David was active in bestowing such an honour on a number of people. As a result, the University of Guelph established a fund in Finnbogadóttir's name that has supported a number of Icelandic students to do graduate work at Guelph. This was the beginning of a lifelong friendship between David, Pat, and Vigdís (Fig. 19). Over the years, David and Pat became integrated with the Icelandic community as they were deeply interested in the history and culture

Fig. 18 Bjarni Kristjánsson, David, Camille Leblanc, and Skúli Skúlason during one of David's visits to Hólar University in August 2017. Bjarni, Camille, and Skúli completed their Ph.D. degrees under David's supervision; Bjarni and Skúli completed their M.Sc. degrees with David as well (photo credit: Sólrún Harðardóttir)

of the country. Not surprisingly, they formed friendships with a number of Icelandic people within and outside academia.

Hólar Agricultural College became an accredited university over the period of 2000–2008. David played an instrumental role in this accreditation that involved direct and active academic support from the University of Guelph, including two visits to Iceland in 2004 and 2006 by the current president of the University of Guelph, Alastair Summerlee. David, along with Steven Cronshaw, was the driver behind this process, and it would not have happened without his initiative and respect for Iceland. Similar to the relationship David fostered between the University of Guelph and Iceland, David continued to grow his connection to Iceland after moving to Oregon State University. In 2006, David was instrumental in negotiating Memoranda of Agreement between Oregon State University and Hólar University, the University of Akureyri, and the University of Iceland.

David and Pat last visited Iceland in 2017, and among other things, they went to Þingvallavatn, the place which first connected David to Iceland. One of major inlet ground water faults to the lake is named Davíðsgjá, or David's Canyon, which is of course very appropriate (Fig. 20).

The Japanese connection

David was well known as a friend of Japan and his passing has caused many Japanese scientists to grieve deeply (Maekawa and Munakata 2021). David first

Fig. 19 David, Pat, Sólrún Harðardóttir, and Vigdis Finnbogadóttir, former president of Iceland at her home in August 2017 (photo credit: Skúli Skúlason)

Fig. 20 Skúli Skúlason and David at Davíðsgjá, one of the major inlet groundwater faults to Þingvallavatn during David's last visit to Iceland in August 2017 (photo credit: Sólrún Harðardóttir)

met Japanese fish ecologists at the First International Charr Symposium held in Winnipeg, Canada, in 1981 and visited Japan for the first time in 1988 to attend the Second International Charr Symposium held in Sapporo (Maekawa et al. 2021). Since then, David strengthened academic and cultural exchanges between Japanese and North American scientists and students.

David collaborated with Hiroya Kawanabe, a well-known Japanese ecologist. In 1995, Kawanabe received a Doctor of Science honorary degree from the University of Guelph, nominated by David. David facilitated academic exchanges between many Japanese scientists and researchers at the University of Guelph (i.e. Mikio Azuma, Koji Maekawa, Akira Goto, Seiji Kondo, Izumi Nakamura, Yoshitaka Sakakura, etc.). When David moved to Oregon State University his research focus changed somewhat from behaviour and evolution of freshwater fishes to fish migration (e.g. salmonid and eel migration). During this transition, David continued his work with Japanese scientists and took the opportunity to extend his network of Japanese researchers and their students. Some of these achievements were edited as a 1998 special issue of Environmental Biology of Fishes (EBFI volume 52, issues 7–8).

David visited and stayed in Japan for conferences and two of his sabbaticals. In 1994, he stayed at National Research Institute of Fisheries Science, collaborating on studies of the ecology of salmonids with Koji Maekawa, Osamu Katano, and Kei'ichiro Iguchi who converted David's name to Japanese kanji (Chinese characters) "出人能玖珠", which were made memorialized on David's business card. David had a keen interest in research on eel migration, which further connected him to Japanese scientists. He became close companions with Katsumi Tsukamoto, University of Tokyo, who discovered the spawning ground of the Japanese eel *Anguilla japonica*. David and Katsumi's laboratory collaborated on the migration of eels worldwide. David joined a 2000 research cruise for Japanese eel *Anguilla japonica* with Katsiumi Tsukamoto, Jun Aoyama, Michael Miller, Mari Kuroki, and many of their students. He was invited to a 2001 international symposium "Advances in Eel Biology" that was a satellite symposium of the 70th Anniversary of the Japanese Society of International Science. David and Pat spent time in Japan during his sabbatical in 2003 (Figs. 21 and 22), and during this time, David helped establish the Academic Exchange Agreement between the University of Guelph and Nagasaki University, Japan. Every time David visited Japan, he gave excellent lectures as well as provided mentorship to the young Japanese students, which motivated them to pursue scientific studies. His impact on young Japanese students was perhaps one of David's greatest contributions.

The first nation and tribal connection

David recognized early in his career the importance of giving First Nation and Tribal communities a voice. He recognized that he had a role to play in

Fig. 21 Welcome party for David and Pat at a sushi restaurant in Tokyo, Japan, in 2003 (photo credit: Jun Aoyama)

removing barriers that had been historically placed on these communities and advocated to provide Indigenous communities with an opportunity to voice their perspectives and concerns and share their fishery priorities.

David was instrumental in establishing a faculty position at the University of Guelph, jointly funded by the Chippewas of Nawash Unceded First Nation and the university. Stephen Crawford was hired as Management Biologist for the Chippewas of Nawash

Fig. 22 Group photo of David and Pat Noakes in Tokyo Japan in 2003 with the eel group from Ocean Research Institute, University of Tokyo (photo credit: Michael Miller)

and tasked with bridging traditional and non-Indigenous knowledge systems to advance science and management decision making around important fisheries, particularly lake whitefish in southern Georgian Bay, Lake Huron. This study helped lay the groundwork for the signing of a 2000 Fishing Agreement between the Province of Ontario and the Saugeen Ojibway Nations.

When David moved to Oregon he continued his support of Native Americans, seeking opportunities to work with tribes of the Pacific Northwest. Gabe Sheoships, member of the Confederated Tribes of the Umatilla, praised David's sincere interest and very open approach in working particularly with Native American students enrolled at OSU. His support of their interests in Pacific lamprey *Entosphenus tridentatus* contributed to research collaborations with coastal and inland tribes. David fostered research on coho salmon *Oncorhynchus kisutch* and Pacific lamprey with the Confederated Tribe of the Siletz, whose native lands include the Alsea River where OHRC is located. The Center held summer camps focused on natural resource education for Siletz Tribal members and students. In southern coastal Oregon, OHRC collaborated with the Cow Creek Tribe studying anadromous rainbow trout *Oncorhynchus mykiss* and lamprey and sponsored an acclimatization workshop that drew agency and tribal participants. In 2019, he and post-doc Maryam Kamran travelled inland to participate in a workshop examining recovery of wild Warm Springs River Chinook salmon *O. tshawytscha*, cooperating with Warm Spring Tribal and Columbia River Intertribal Fish Commission staff to outplant hatchery-reared Spring Chinook, and re-introduce sockeye salmon *O. nerka* in the Columbia River.

The Ecological and Evolutionary Ethology of Fishes Conference

In 1976, David, Jeff Baylis, and Jack Ward went to a regional meeting of the Animal Behavior Society that they described as very disappointing. Their fish talks were put into inappropriate sessions, the conference's emphasis being on mammals and birds. The threesome decided it would be best to hold their own regional meeting, and Jack, the most senior among the three, volunteered to host one at Illinois State University-Normal.

The first meeting was held in 1977 as the Ethology and Behavioral Ecology of Fishes (EBEF) Conference, and it was decided that the meeting was to be held on a biennial basis. The first meeting was quite small, but it grew quickly over the years becoming large and lively. Normal was a great location for the meeting, as it was within a day's drive from Ontario, Michigan, Wisconsin, and many universities and colleges throughout the mid-west and southern USA. The founders all envisioned the meeting as a place where students could attend, learn, meet, and give presentations about their research. Every year David, Jeff, and Jack would bring all of their students who were working on fishes to EBEF.

Jack Ward still held the position of lead organizer in 1981; however, he was joined by 15 other faculty from throughout North America, including David, Jeff, and Gene Helfman. Gene organized a symposium on *Behavioral Tactics of Predators and Prey*, and Mary Henry organized a symposium on *Applied Aspects of Fish Behavior*. These symposia formed the core of a special issue of Environmental Biology of Fishes in 1983 (EBFI volume 8, issues 3–4). The 1983 meeting was to be the last time it was held at Illinois State University-Normal, as Jack Ward unexpectedly passed away in December 1982. After Jack's passing, it was a given that David would now take the position of lead organizer, as he was the main driving force behind the EBEB by that time.

David hosted the next meeting at Guelph in 1985, and it has continued to occur every two years ever since as Ecological and Evolutionary Ethology of Fishes (EEEF), moving to a new location each time (Fig. 23). Fittingly, in 2021, University of California Berkeley, David's alma matar, was the host campus, but for a virtual meeting. David had hoped this would provide the opportunity for a lab reunion but unfortunately it was not meant to be; however, a special session was dedicated to David's legacy.

The International Charr Symposium

The International Charr Symposium began in Winnipeg, Canada, in 1981, and to date has included a series of nine international symposia dedicated to charrs, the salmonid genus *Salvelinus*. The symposium has been held in various locations across the globe where charrs live, with the most recent

Fig. 23 Group photo from 2018 EEEF meeting at Concordia University in Montréal, Canada. David can be seen in the back row at the far right (photo courtesy of Pat Noakes)

occurring in Duluth, MN, USA in 2018 (Fig. 24). David provided important contributions to many of the meetings by promoting the symposium, supporting its organization by participating in steering committees, and sharing research through keynote talks and contributed papers. He also facilitated the publication of conference proceedings focused on the symposium, for which he edited contributed papers.

David became involved in the second symposium in Sapporo, Japan, in 1988 by editing the proceedings together with the convenor of the symposium, Hiroya Kawanabe, and Fumio Yamazaki. This was a major task as 85 contributed papers were submitted, more than double of any of the other proceedings. The papers appeared as a special volume of Physiology and Ecology Japan (Kawanabe et al. 1989). David also contributed a paper to this special issue in which he presented research on juveniles of the two most common Canadian charrs, brook charr and lake charr, and demonstrated genetically determined differences in behaviour between them (Noakes 1989). Brook charr have an aggressive and territorial but also plastic behaviour whereas lake charr are non-aggressive, non-territorial, and less plastic. David related these differences to their habitats, i.e. the predictable, unidirectional water movement in streams and the unpredictable and shifting movements of water in lakes. This was an early study indicating the importance of behaviour in charr evolution. From this point, the Charr Symposium continued to be published as a special issue and David, as an experienced editor, played a critical role in this evolution.

In 2000, the Charr Symposium was held for the second time in Canada, in Trois Rivières, Québec (Fig. 25). A total of 123 presentations (72 talks and 51 posters) were given at the symposium, which attracted more than 160 scientists from 12 countries. David again played an essential role as he co-edited the proceedings that resulted from the meeting, with 32 papers published as a special issue of Environmental Biology of Fishes (EBFI volume 64, issues 1–3) titled "Ecology, behaviour and conservation of the charrs, genus *Salvelinus*" (Magnan et al. 2002).

A second Charr Symposium special issue was published in Environmental Biology of Fishes (EBFI volume 83, issue 1) in 2006 after the symposium was held in Reykjavik, Iceland (Fig. 26). David took part in the planning of the symposium as a member of the Scientific Committee. In the introductory paper to the proceedings (Noakes 2008b), he first pointed out the tribute that Gyselman (2008) gave to Lionel Johnson, the foremost Canadian charr researcher and the convener of the first charr symposium. David also delivered the keynote presentation titled "Charr Truth:

Fig. 24 International charr symposia has been held nine times, from Winnipeg, Canada, in 1981 (upper left) to Duluth, USA, in 2018 (lower right). Proceedings from all except the first were published as separate issues in different journals. David contributed importantly to many of them: in the planning committees and as keynote speaker, author, and editor (photo credit: Øyvind Grønvik)

sympatric differentiation in *Salvelinus* species", published as Noakes (2008a). After a brief account on how sympatric speciation had come back to evolutionary theory after a long period of being dismissed (strongly influenced by the forceful rejection by Mayr (1963)), he again pointed to the importance of process in the evolution of charr species. He also continued the focus from the Sapporo meeting on foraging and social behaviour in juvenile charr. David's keen sense of humour and gift for introducing complex themes with few words can be seen in the title of his keynote presentation. Another example is the first sentence of the paragraph that discusses charr evolution. It reads "Charrs are enigmatic fishes". Here, he discussed sympatric trophic polymorphism, with ample reference to the research effort on Arctic charr in Þingvallavatn, with many influential papers, not the least Skúlason and Smith (1995) that made the front page of a Trends in Ecology & Evolution issue. He was important in the Þingvallavatn research, via his involvement in several papers and through colleagues, some of whom were his former students from Guelph.

At the Reykjavik meeting, David also continued the focus from the Sapporo meeting on foraging and social behaviour in juvenile charr. Charr behave in two alternative ways, as "movers" or "stayers". Movers move, have low levels of antagonistic behaviour, and feed mostly on prey at the stream surface or the substrate. Stayers, in contrast, are aggressive, move little, and feed on invertebrate drift. Both tactics give

Fig. 25 Participants of the Fourth International Charr Symposium in Trois-Rivières, Québec, Canada, before the opening banquet during a six-hour cruise on the St. Lawrence River. David is center left in the front row (photo credit: Satoshi Kitano)

high fitness as measured by growth rates, whereas fish that combine tactics have lower fitness. There are more stayers in swift streams and more movers in slow streams. The mover tactic is dominant in lakes, both in brook charr and lake charr. These studies led to the proposal of a model for sympatric differentiation based on initial behavioural differences where fitness is a critical feature.

The 150th anniversary of Darwin's "Origin of Species" was celebrated all over the world in 2009. As far as we know, Darwin did not know charrs but the symposium in Stirling, Scotland, in 2009 marked the anniversary by presenting and discussing research on charrs that exemplify the variation in form, function, and ecology in a way that would undoubtedly have fascinated Darwin (Adams et al. 2010). David was invited to provide a keynote talk. He engaged the audience with his typical wit with a lecture titled "Charles and Charr: 200 years on". His talk was considered to be a great success and inspired the design of the official T-shirt of the symposium, which portrayed Darwin, charrs from different areas of the world, and the words "Charles and Charr". The Scottish Cabinet Secretary of the Environment, Roseanna Cunningham, who had opened the symposium, and had heard the keynote talk, remarked that it was very entertaining (C. Adams, pers. comm.).

Fig. 26 Group photo of delegates to the 2006 International Charr Symposium during the excursion to Þingvallavatn. David can be seen in the second row near the middle (photo courtesy of Bjarni Kristjánsson)

David also came to the Charr Symposium in Tromsø, Norway in 2015, this time without giving presentations or having any official commitments. But as usual, he enjoyed himself very much, met friends and colleagues, and took part in the meeting and the excursions to north Norwegian charr lakes. David remained a member of the organizing committee for the next meeting, which was held in Duluth, USA, in 2018. However, the meeting in Tromsø was the last meeting he attended in person after having had a significant influence on the symposia, and on research on his favourite fishes, the charrs.

Preserving the legacy

There is an incredible importance in preserving the legacy of a scientist, whether that be through written memorials or a published synopsis of research. Such efforts can provide the opportunity for not only the reader, but also the author, to tap into the power of reminiscence and can help one through the grieving process. Memorials can shed light on an individual's lifetime accomplishments, assuring that the impact these accomplishments had on others and on their field of research does not fade with passing years and generations. David must have known the cathartic nature of this process as he took it upon himself to ensure that the legacy of so many of his peers was properly captured. He memorialized such greats as Ethelwyn Trewavas (Noakes 1993, 1994a, b, c), Bill Ricker (Noakes 2006), and Eugenie Clark (Noakes 2015) and also encouraged others to do the same for Rosemary Lowe-McConnell (Bruton 1994), Hans Peters (Fishelson 1997), R. Jan F. Smith (Chivers et al. 1999), Shigeru Nakano (Fausch 2000), and Lionel Johnson (Gyselman 2008). It does feel as though we have now come full circle, taking this opportunity to do the same for David's legacy, ensuring that his accomplishments and the momentous impacts he had on so many are not forgotten. Without a doubt, David made the most of the opportunities that were presented to him and enabled such opportunities for so many others. He led a full and happy life for himself and all those who were fortunate enough to cross his path and left the world much improved for having been here.

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