PER F. SCHOLANDER
1905 - 1980
BY EDVARD A. HEMMINGSEN AND ANDREW A. BENSON

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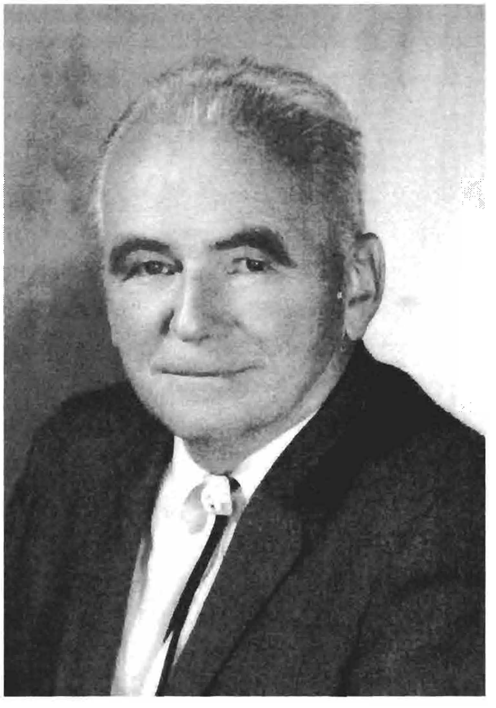


Portrait of Per F. Scholander.

Introduction

When Per Fredrik Thorkelsson Scholander, or Pete as he was known, joined the faculty at Scripps Institution of Oceanography as a physiology professor in 1958, he already had a long and distinguished scientific career. Until his arrival here, physiology and experimental biology had not been central parts of the institution's activities. That was soon to change. A new university campus was in the making, and Scholander, with his impressive academic credentials and outgoing, dynamic personality, quickly felt at home in the bustling community of scientists who were at the institution or were being recruited for the budding campus. It was a setting made for Scholander. He believed that biology at Scripps had to expand to include new areas of research directed toward more fundamental experimental approaches. Director Roger Revelle appeared to be very sympathetic to this view, while some of the more traditional Scripps biologists were less enthusiastic. But Scholander was not deterred; he frequently had gone his own way when taking on challenging tasks.

Scholander had clear visions of what he wanted to accomplish with his new opportunities. One was to establish a new research unit to conduct basic research in physiology, one slanted toward life in the sea but not limited to it. Another was to take advantage of Scripps position as an academic power operating research vessels having access to nearly all corners of the world, and with excellent scientific and political contacts in most regions of his interests. This would allow him to study unusual aspects of biology in places that otherwise would be difficult to reach. Scholander brought his visions to fruition. While he worked on the plans for a new research vessel, he established the Physiological Research Laboratory (PRL) in 1963, and served as its director until 1970. This research unit, with its own building and supporting facilities, became the center of his operations. The PRL building, finished in 1965, for a while also was a center for the Brain Research Institute, University of California, Los Angeles.

His years at Scripps were whirlwinds of activities, and numerous distinguished academic honors were bestowed upon him during this time. Among these were his election to the National Academy of Sciences (1961), the American Philosophical Society (1962), and the award of the Nansen Prize from Norway (1979). Scholander avoided placing himself in positions or circumstances that would put restrictions on the scope and breadth of his intellectual activities. Because he wanted to maximize his time for science, he avoided becoming involved with either administration or commercial ventures. Scholander continued his very productive life at Scripps and had a strong and enduring impact on the institution and many of its young scientists in physiology, biology, and other sciences. We were among these persons. One of us (EAH) was privileged to be co-author of twelve publications with him. Like so many of his colleagues, we became friends of Pete and learned to know him well as a person, and thus became quite familiar with his scientific thinking and philosophy.

Per Scholander was born on November 29, 1905, in Sweden. He grew up in Norway and studied at Oslo University. Though he earned his M.D. in 1932, he did not envision the practice of medicine as his career. Later he revealed that he chose it in order to keep from becoming a [high] school teacher. Teaching positions were among the few professions available for academic people in Norway in those times. In his teens he really wanted to become a musician, but his family discouraged this idea, probably because they recognized his other formidable talents and interests, particularly in science. While he was a medical student and was somewhat bored with those studies he became very interested in lichens and their taxonomy. He seized opportunities to visit Greenland and Svalbard to pursue his interests in lichens. These trips resulted in several publications that made him an internationally known lichenologist. He received the degree of Dr. philos. in botany in 1934, not on his specialty lichens as would be expected, but on vascular plants from Svalbard. After these adventures in medicine and botany, he obtained a research fellowship in physiology at Oslo University, where he became passionately involved with physiological studies of seals and other animals.

In 1939, Scholander applied for a Rockefeller Fellowship to continue his studies of diving animals with the distinguished physiologist Laurence Irving at Swarthmore College. But late in that year, just a few months before the Germans invaded Norway, the Rockefeller Foundation stopped granting fellowships because of the war that was developing in Europe. Scholander did not receive this message. The famous Danish physiologist August Krogh, with whom Scholander had close contact, apparently knew the Rockefeller situation and sent a note from Copenhagen to Scholander urging him to leave for the United States immediately. The following day Scholander boarded the first available ship, carrying with him only his beloved violin, a bag of personal belongings, and the precious manuscript of his diving work. Soon thereafter, he showed up at Professor Irving's laboratory, but without his fellowship. Some "strings were pulled," the fellowship came through, and a long and rewarding relationship, professionally and personally, between Scholander and Irving was established. They collaborated in numerous studies over the years. Scholander married Irving's daughter Susan in 1951. She became an invaluable and inseparable partner and wife for the rest of his life, and contributed much to his success.

After Scholander's two-year fellowship ended, he became a Research Associate at Swarthmore College for a while. But the studies there were interrupted by his wartime military service in the U.S. Air Force. After the war he returned to this college as a Research Biologist. Subsequently, he had other "soft money positions" as Research Fellow at Harvard Medical School (1949–1951) and Physiologist at Woods Hole Oceanographic Institution (1952–1955). Scholander did not consider any position offering tenure or other security until he accepted a professorship in physiology at Oslo University when he was 50 years old. Unfortunately for that university, Roger Revelle persuaded him to accept a position at Scripps just three years later. He remained at Scripps until his death on June 13, 1980.

People with outstanding minds tend to be unconventional, unusual, even colorful; Scholander was no exception. He was a complex person, not easily described with simple words. He was a rationalist and an uncompromising and dedicated scientist who sought truths and facts. For this he was forceful and tenacious, but also gentle and magnanimous. He was an artist and an aesthete; beauty he found everywhere in nature. There were a special aura and intensity about him. He stood out with his enthusiasm, constantly probing curiosity, and brilliant scientific intuition. His intuition basically was a keen eye for the mysteries of nature, combined with a sharp and penetrating logic.

Scholander was a great scientific leader who could fire up people who were associated with him, be it in the home laboratory or in the field. He could infect the people around him with curiosity and ideas more so than most other persons we have known. He would very rarely utter a harsh word to anybody or about anybody, but frequently would lavish praise and encouragement. Scholander would never use his genius to put down a person, even if the person was misguided or less than smart. But he wanted people to "use their wits," a phrase he often used to describe scientific thinking and ingenuity. An important part of Scholander's leadership qualities was his intellectual generosity, especially to students and other younger people. Another thing that stood out about him was that he always wanted to share and discuss his scientific thoughts and ideas with others. He called it "intellectual sparring." Pete consistently wondered how things work in nature, and he never hesitated to challenge existing scientific theories and dogmas when they did not make sense to him. For example, in the fifties and sixties he kept needling most geologists he met about their theories for mountain formation. He thought that their theories did not make any sense at all. And arguably they did not because at that time plate tectonics had yet to be discovered.

Scholander enjoyed giving lectures. They were always engaging and spirited, clearly separating guesses and speculations from facts; often he would dwell on fascinating problems that had not yet been resolved. However, he did not enjoy formal classroom teaching. He believed that "bringing students into a classroom and reciting textbooks to them" (as he would say) had little value; it did not encourage independent thinking. But getting the students excited in the lab by having them do experiments, or engaging them in discussions, was something else; that would make him beam! In a personal setting, he could be an excellent, indeed, mesmeric teacher to young and old alike.[1]

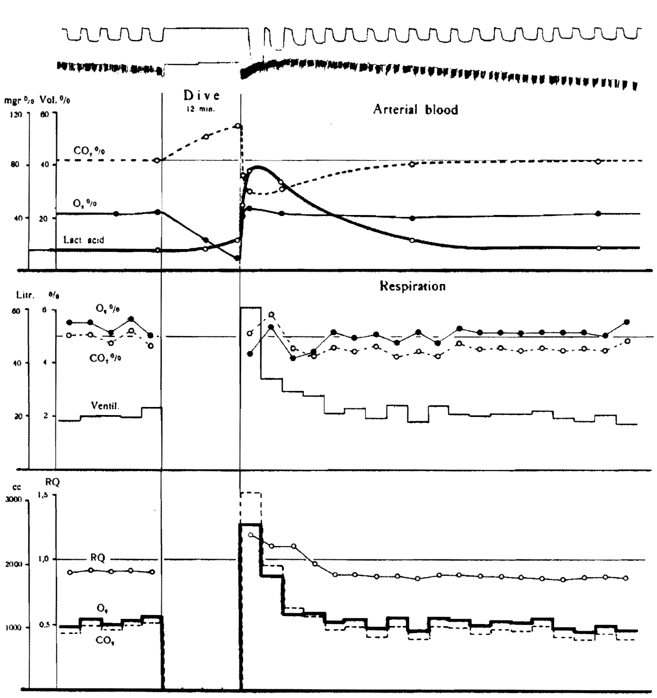
(AAB remembers: On the banks of the Colville River, Alaska, Pete and I waded through the deep lichen blanket covering the endless tundra, an entirely new environment for me. Pete, having studied lichens in Greenland and Svalbard, proceeded to educate me with the names and growth patterns of these peripolar symbiotic systems. Species we found here on the rocky ridges were the same as those in Greenland and arctic Norway. That morning, Pete taught me the Latin names of several species. Even now, forty years later, I can recall most of them. As we examined their beauty and discussed the symbiotic metabolism between their algal and fungal components, I began to feel much as a subject to a hypnotist's spell might feel—as if I were being captivated by the attractive power of a dedication to a life with the lichens. Knowing that I must escape that captivation, I struggled internally—maintaining a life-long interest in but not so far as dedicating a life to lichen science. Later on the Amazon Expedition, Pete was excited by the studies and ideas of Frits W. Went on the role of mycorrhizae in the rain forest. Even now, knowing much about arsenate metabolism in algae, I have an unending drive toward learning how fungal mycorrhizae collect arsenate in their quest for phosphate for subsequent donation to tree roots in exchange for their energy-rich sugar.)

Scholander's life was science, and science was truly fun for him. His only real diversions from science were music and being out in nature; he played his violin almost daily and was an accomplished musician. He loved chamber music and often played in quartets. He was a very charming and social person who truly enjoyed a lively party with good food and wine. The many cheerful parties that he and Susan gave in their home near Scripps will always be remembered by those who enjoyed their exuberant hospitality, bringing together students, technicians, colleagues, and Nobel prize winners, usually in settings that encouraged intermingling and conversations.

The Science

Scholander was a person with an unusual range of scientific interests, who may not have fitted well into the mold of specialization so typical for the modern day scientist. He never became consumed with a single idea or issue, except science. In a brief discourse it is difficult to touch upon more than a few of the many important contributions Scholander made. Although the few examples of his research that we cite here give justice to neither the breadth of his scientific endeavors nor their overall importance to science or even to specific areas of it, they illustrate some of his varied interests. Some of the examples are included because they specifically deal with the physiology of animals in the marine environment. Many of Scholander's studies represent collaborative efforts, which naturally often expanded Scholander's original ideas, added new ones, and enhanced the end results. Conversely, his co-authors were greatly influenced by his dynamic and stimulating personality and often became well known scientists in their own right. Scholander authored or co-authored 170 publications. He could have written many more, but he would only publish a paper when he felt he had something truly new to contribute. He loathed what he called "pot boiling," namely, publishing data that did not provide new insight into a basic problem. When he saw the results of such trivial efforts he would respond with the phrase "So, now we know that too," showing obvious indifference. Another aspect of his scientific philosophy was that the problem to be studied should be very well defined. All extraneous matters had to be peeled away from a problem so that only the clear core remained. Many younger (and older) scientists recall Scholander's reaction when they enthusiastically presented their somewhat unfocused projects or ideas to him: "What is the *problem*?"

Diving physiology. Although all his life Scholander had a deep personal interest in plant taxonomy and plant physiology, animal physiology was his primary professional interest for most of his active years. This interest appears to have been triggered or amplified during his travels to the Arctic to study lichens. He became fascinated by the diving behavior of seals and whales and wondered how they could perform their prolonged dives apparently deprived of an adequate supply of air. At that time, few facts were known about how they could manage to do their striking feats. Although some scattered physiological and behavioral observations had been made on a few diving animals, there was no understanding of what was occurring physiologically during their underwater excursions.



Physiological responses to diving in seals. The electrocardiogram tracing on top shows the changes in heart rate during an 8 minute dive. The onset of bradycardia is immediate upon submersion of the seal. The lower diagram is an example of arterial blood and respiratory data obtained in a 12 minute dive.[1]

Scholander changed that. He undertook a thorough analysis of the problem and embarked on his study. His three years of intensive and comprehensive laboratory investigations in the late thirties produced the classical work on diving mammals and birds.[1] This study was a tremendous contribution to physiology. Indeed, it is the key study that researchers in the field of diving physiology cite even today.

(AAB remembers: In the early seventies, while I was visiting the Research Institute on the shore of Lake Baikal at its entrance to the Angara River, I encountered a group of medical physiologists, from the Soviet research institute in Novosibirsk, who were studying the diving heart rates of Baikal seals in pools of pristine water. I asked what they were measuring, to which they replied "the bradycardia phenomenon discovered by Professor Scholander." Needless to say, they were impressed when I informed them that I was the present director of the Physiological Research Laboratory of Professor Scholander.)

Not only did Scholander give a clear account of the major circulatory and respiratory events that take place when an animal dives, but he also provided a new understanding of how animals, in general, respond physiologically to hypoxic stress. He showed that the animals' diving times far exceeded their capability to store enough oxygen for maintaining a normal aerobic metabolism during the dive, and more importantly, explained how they were able to do it. His innovative, in-depth experimental study on such natural diving animals as seals, porpoises, beavers, penguins, and ducks revealed that they have a finely tuned complex of physiological responses that are triggered into action even before hypoxic conditions develop. For example, immediately upon submerging a seal in water its heart rate would decrease dramatically, returning to normal soon after the animal was returned to air. This bradycardia reflex response was accompanied by a variety of other responses. Most notable, the oxygen content in the arterial blood decreased during the submersion, or dive, but far less than would be expected based on a normal rate of tissue metabolism. The lactic acid content of the blood, generated by anaerobic metabolism in the tissues, rose slightly during the dive, but rose greatly immediately upon completion of the dive. From these types of observations, Scholander concluded elegantly—among other things—that the metabolism during diving is not markedly decreased and that the limited oxygen stores in the airways and blood are conserved for the oxygen-sensitive tissues of the heart, and particularly of the central nervous system. The animals do this by constricting certain vessels, thereby almost completely shutting off the blood supply to muscles and some other tissues and forcing the tissues to use anaerobic metabolism; the resulting oxygen-debt is repaid after completion of the dive. These discoveries led to additional studies by Scholander and by others, which showed convincingly that many of the responses observed in diving animals are universal responses to hypoxia and exist in humans as well; they differ merely in degree from one case to another. Scholander viewed the bradycardia as the core reflex response, and termed it "the master switch of life" in one of his publications. In addition to their specific goals, the diving studies also offer a striking demonstration of how animals can invoke physiological defenses to extend their capabilities. The broader concepts that emerged from them have served as a foundation for many later studies at Scripps. Scholander's presence here attracted several younger investigators who wanted to pursue their interests in diving physiology and related fields. Many of these studies became highly successful and established Scripps as one of the premier sites for this field of research as well as for more general comparative physiology.

Scholander continued to work on various aspects of diving for a time after he published his initial studies in 1940, but his scientific activities soon became curtailed by the war. He enlisted in the U.S. Air Force and rose to the rank of Major while receiving commendations for heroism. These included the "Soldier's Medal for Valor" and the "Legion of Merit." In this period his research was mainly concerned with survival techniques and procedures. He did not publish any scientific papers from 1943 to 1947. The research he did in that period largely remains buried in the archives of the Air Force. After the war Scholander became more interested in areas of physiology other than diving, including some that related to the marine environment. He championed the use of comparative physiological approaches to solve many problems.

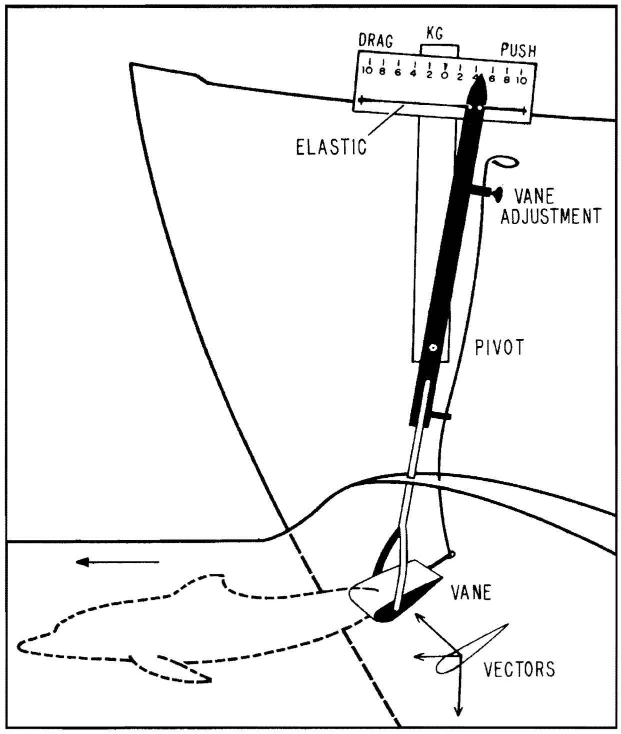
Techniques and methods. Scholander was a very clever designer of devices and instruments needed for solving research problems, and he truly enjoyed working at his laboratory bench. Throughout his working life he insisted on having a machine shop available to him and the other scientists in his laboratory; there they could do their own machine work, at any time of the day or the night. He himself would spend endless hours at the lathe, the drill press, or the milling machine, making or modifying instruments and other gadgets. Fundamentally, Scholander was an experimentalist, not a theorist or a synthesizer of information generated by others. Usually, he was quick to test his new ideas with laboratory experiments, rather than using the library to find out what the literature had to offer. When he found that methods he needed for his work were lacking or inadequate, he did not hesitate to develop new methods or improve on the old ones. His talents for developing instrumentation were evident early in his career. His methods often found widespread use beyond the specific needs for which they were developed. A respiratory apparatus developed during his diving studies and later refined by him was used as a diagnostic clinical tool for respiratory diseases for many years. Another device, ingenious in its simplicity, which he made at the end of his career has proved to be valuable in clinical research for measuring negative interstitial fluid pressures in the body.

Scholander's talents in developing new and useful tools led to many "method" papers in the forties and the fifties. The methods he developed were all used by him to solve specific physiological problems, but they also became very important as general tools in physiology and other fields until most of them gradually were replaced by electronic devices some years later. Foremost were his micro-methods for the analysis of gas contents in blood. His best known of these may be the "1/2-cc analyzer." This is an elegant and relatively simple system for accurately measuring volumetrically oxygen, nitrogen, and carbon dioxide in air and respiratory gases. The publication describing this method[2] was a Current Contents' "Citation Classic" in 1984, having been cited in over 1130 publications since 1955. But clever as Scholander was in developing instrumentation and other scientific tools, he put himself at one disadvantage: he skirted almost every problem that required the use of electronic instruments. Mentioned use of such devices for any type of laboratory measurements certainly is rare in his publications, even in his later ones when electronic devices were used in all types of research. However, he frequently admired the results obtained with such instrumentation once he was truly convinced that proper control tests and calibrations had been performed.

Swimbladder of fishes. Scholander conducted a number of studies on marine fishes, ranging from their temperature adaptations in cold and warm climates[3] to their survival when supercooled in freezing seawater.[4] His contributions in this area have been cited frequently. But the problem that may have intrigued him most about fish was how so many species are able to secrete gas into the swimbladder at great pressures. As has been long known, fishes with gas-filled swimbladders exist from shallow waters to ocean depths of several thousand meters. Because the gas pressure inside the swimbladder must equal the hydrostatic pressure to which the fish is exposed, the gas pressure can reach values of several hundred atmospheres. Yet, the blood circulating through the tissues lining the outside of the swimbladder has a gas tension similar to that of the seawater surrounding the fish, roughly one atm. At 2000 meters, the swimbladder gas would have a pressure of 200 atm, as compared with a blood gas tension of about one atm. Such a swimbladder gas pressure is higher than that of a standard laboratory gas cylinder. How can gas be deposited and maintained inside the swimbladder with such a pressure gradient? Scholander studied this gas secretion problem and wrote several papers on the subject. The research focused on the composition of the secreted gas, particularly as a function of depth, and on the structure and function of the gas-secreting gland.

In fishes living near the surface, the composition of the swimbladder gas usually is similar to that of air—about 4/5 is nitrogen and 1/5 is oxygen—with some carbon dioxide present. Scholander found that as the depth increases the oxygen content increases and becomes the main component of the swimbladder gas, to the point that it constitutes more than 90% of the total amount.[5] However, even though the relative fraction of nitrogen decreases with depth, its partial pressure increases, but less so than that of the oxygen. In most fish that live at depths the swimbladder has a special organ, a gland, from which the gas secretion presumably takes place. This gland is a magnificent structure of inflowing and outflowing blood capillaries, arranged in a countercurrent fashion for effective exchange of gas between inflowing and outflowing blood. The structure is referred to as "rete mirabile." People previously speculated that the source for the oxygen in the swimbladder was the oxygen that is bound to the blood hemoglobin, and that it was driven off the hemoglobin somehow (for example, by Bohr and/or Root effects) when the blood passed through the inside loops of the gland. The countercurrent system was mainly there to prevent the gas from escaping from the swimbladder. Scholander analyzed the physical and chemical parameters that may come into play for gas secretion to occur, and found that the limitations of the system were such that the oxygen secretion could not be accounted for by a simple release from hemoglobin, and equally or more important, it could not explain the presence of several atmospheres of nitrogen. He championed the idea that the secretion of gas resulted from a "salting-out" effect.[6] The principal concept was that when the blood passes through the rete, some solute is added to it. This in turn lowers the gas solubility by a small amount, and some gas is driven off. This effect would be multiplied by repeated passes of the blood.

In his writings and conversations, Scholander often marveled how principles known from physics and engineering were used by animals in unusual and ingenious ways. He was fascinated by the many beneficial ways the countercurrent exchange principle was used by animals to enhance their capabilities. Besides describing the use of this principle in the swimbladder gas secretion function, he published articles on other aspects of countercurrent exchange in biological systems.[6, 7] Most notably he elucidated how important such exchange is in temperature regulation, insulation, and heat conservation in many animals, in the oxygen exchange in the placenta, and in the function of the kidney. He also pointed out that countercurrent heat exchange between arterial and venous blood, particularly in extremities, made it possible for many mammals and birds to exist in cold environments. By his efforts in research and writings in this area, Scholander contributed challenging ideas that had not been expressed by others, and which have proven to be important in understanding many biological adaptations and functions.



Schematic illustration of instrument developed onboard ship to measure forward thrust in bow wave (not to scale). The stippled line shows the contour of an imaginary dolphin riding the bow wave.[10]

Ancient atmosphere. Scholander spent a large part of his life in Scandinavia and other regions where glaciers are common, and he was familiar with the fact that air became trapped in ice as bubbles. During a stay at ONR's Arctic Research Laboratory, Point Barrow, in 1947-1948, Scholander determined experimentally that air diffuses very slowly through ice. He got the idea that it may be possible to find old atmospheric air, from hundreds or thousands of years ago, buried in glacier ice. While he was professor in Oslo he developed this idea into a practical research project. The concept was this: in cold climates, snow falls and traps air in it when it settles on the ground. With continued snow fall, the snow with trapped air gradually will be compressed to ice containing cavities or bubbles filled with air. Because ice has very low gas solubility and a very low gas diffusivity, the original air trapped will remain unchanged for perhaps thousands of years, or longer. But for this to be the case, no melting must occur during the trapping and compacting process. Even in moderately cold climates in the Arctic, for example, a small surface melting in the winter by the sun would be a problem. Therefore, any hope for finding old atmosphere would be linked to glaciers in northern Greenland or central Antarctica where temperatures sufficiently cold to prevent melting exist even in the summer. After doing some preliminary work on this problem on a glacier in Norway,[8] he assembled a team of ten scientists and went to Greenland to measure the composition of the gas enclosed in glacier ice, and to carbon-date it. Ice samples were collected from icebergs spawned by a number of different glaciers on the west coast of Greenland. The bubble gas composition and pressure, the carbon date (of the enclosed carbon dioxide) and the oxygen-18 to oxygen-16 ratio of the ice water (which gives the temperature of ice formation) were determined.[9] The results obtained were inconclusive, but the basic idea of finding old atmosphere in ice certainly was not squashed. Many later studies have pursued this idea by collecting ice from the polar icecaps with coring drills. Regrettably, scientists involved in these more recent studies often do not appear to know where the idea and the earliest studies originated.

On the Greenland Expedition in particular, one of us (EAH) had his first real opportunity to observe Scholander's intensity as a scientist. His mind was always working on some problem, or a new device; no useful time was ever wasted. For example, he had an idea about how dolphins are able to ride the bow wave of a ship, with little energy expenditure. In order to obtain observations in support of his idea, he constructed a device from wooden boards, wires, and strings during transits between stations when analytical work could not be done. The project proved to be more complex for the primitive facilities and equipment than he had anticipated. Although he did not come up with a definite answer, he published a paper in *Science*[10] with the title "Wave-Riding Dolphins: How Do They Do It?" with the subtitle "At present only the dolphin knows the answer to this free-for-all in hydrodynamics." After laying out a certain scenario in the paper, he states "... as this mode of propulsion does not require that his lungs be empty, he need not take this ride in silence but may whistle to his fellow freeloaders as much as he deems fit. This, I believe, is the way dolphins ride the bow wave, and if it is not, they should try."

Facilitated diffusion of oxygen. Scholander's first study to be completed after he arrived at Scripps involved a question he had carried in the back of his mind for many years: what are the functions of myoglobin in the muscles? In diving animals, myoglobin can serve as a substantial storage reservoir for oxygen, but Scholander speculated that in addition to this function, myoglobin also may act as a transport agent for oxygen from blood capillaries to the cytochrome in muscle cells. He recognized the complexities that would be inherent in any attempt to investigate this problem with direct experiments. In true Scholander fashion, he devised a much simpler system in order to explore if such a transport effect is feasible in principle. For this he chose to work with solutions of blood hemoglobin, which also combines reversibly with oxygen in a unique way and in many other respects is similar to myoglobin. He created a thin, convection-free layer of hemoglobin solution by suspending the solution in a micropore filter separating two gas phases. He made the striking discovery that the flux of oxygen through the membrane subjected to a gradient of the gas was much higher than it was through water without hemoglobin or with the hemoglobin inactivated.[11] This was the first demonstration that the transport process termed "facilitated diffusion" or "carrier-mediated diffusion" exists and thus is a viable concept. Although Scholander did not draw any conclusions with respect to transport of oxygen by facilitated diffusion in the muscles, this question became the central theme in the numerous studies that were spawned by Scholander's basic discovery.

Water uptake and transport in plants. Two questions that Scholander often revisited were: how does sap ascend in tall trees, and how do mangroves manage to take up freshwater from seawater? Transpiration from the leaves obviously was the driving force, but the hydrostatic pressures within the plants that this process led to never had been determined. For example, in a tree that is 20 meters high, water enters the roots, moves up the tree through the xylem vessels, and evaporates from the leaves. Scholander reasoned that for this process to occur, at least in the higher part of the tree, the water must be under high tension, or "negative pressure." This presumes that water only moves passively according to gradients in biological systems, a concept almost universally accepted in the scientific community. Therefore, if the only driving force for water movement in the vessels is transpiration, it follows that the pull in the water column at 20 meters would be equal to the total weight of the water column, or 2 kg/cm^2, the equivalent of about -2 atm; even more negative if the flow resistance in the vessels is added.

Scholander measuring sap pressures in mangroves during incoming tide in a Florida mangrove swamp, 1962. Photo by E. A. Hemmingsen.

(Authors note: It is often erroneously assumed that the tensile strength of water is about 1 kg/cm^2, i.e., about one atm; that is, a water column cannot be lifted more than ten meters before it ruptures. This is not the case. In fact, water is very strong and can withstand tensile forces of hundreds of atmospheres before breaking. The theoretical basis for this is relatively easy to understand, and the empirical proofs have been provided in several cases. Based on our knowledge of intermolecular forces in water, theoretical estimates of the tensile strength have given values in excess of 1000 atm. This value has been verified by studies of water inclusions in minerals.)

The early attempts by Scholander to measure the tension in the xylem water column after he came to Scripps were unsuccessful, primarily because the water would rupture at the point where the measuring device made contact with the xylem water. Eventually, he and his co-workers succeeded in developing a method that worked.[12] It relied on a special characteristic of the xylem vessels, namely the presence of regularly spaced perforated cross-plates. These appear to be a protective mechanism, preventing air from entering the xylem vessels; the water will hang up on the nearest cross-plate when air enters. The hydrostatic pressure, negative or positive, will be maintained approximately at its normal level. Thus, when a twig is placed in a chamber with only its cut end protruding to the outside, and gas pressure is applied to the chamber, sap will appear at the cut end. At that point, the gas pressure will be equal to the negative hydrostatic pressure inside the twig. This method was used to determine the hydrostatic pressure of the xylem sap in a great variety of plants, such as tall trees, desert shrubs, and mangroves.[12] It has subsequently been applied in agriculture and forestry to obtain information about water conditions during stages of droughts.

Osmosis. The studies of the mangroves and other plants caused Scholander to examine the process of osmosis more closely, and he began to question the existing concepts of how osmosis works. He wanted to understand the mechanics of the process. The concept that the water movement was caused by differences in water concentration, or activity, was not acceptable to him; he viewed such explanations not as mechanisms, but merely as consequences of more basic phenomena. He developed a hypothesis, which essentially was as follows: when a solute is added for example to water contained in a beaker, the solute molecules will disperse because of their Brownian motion. When they reach the water surface, they will bombard it and create an expanding force, which in turn leads to a tension in the solvent (i.e., the water). If one mol. of solute is contained in one liter of solution, the solute molecules will exert a push on the surface equal to 24 atm, the equivalent to pressure that one mol. of gas will exert on the walls in a one liter container which, as we know is about 24 atm at room temperature. This expanding force on the surface of the solution will cause the solvent tension to be -24 atm. In traditional terms, the osmotic pressure potential, would be +24 atm. If a semipermeable membrane divided the beaker, and the solute was present only on one side of the membrane, then the solvent tension on this side would cause water to be taken up from the non-tension side, until the osmotic pressure on the solute side equals the solvent tension in the plain water, with opposite signs. In other words, the movement of water takes place according to *solvent pressure gradients* rather than to water concentration gradients caused by the presence of solutes. These ideas matured through interactions and collaborations with colleagues and were formulated in a series of publications. The solvent tension hypothesis, the history behind it, and its supporting evidence are discussed in some detail in the monograph on osmosis, which Scholander co-authored with his close Scripps colleague Harold T. Hammel.[13]

The solvent tensions idea did not have a major impact on the prevailing view on osmosis within the scientific community, even though Scholander communicated the idea quite vigorously in lectures and publications. He believed that the thermodynamic view of osmosis—as it generally was presented in textbooks—almost amounted to a scientific cover-up.[14] As was the case in so much of his research, Scholander did not consult the existing literature extensively before he attacked a research problem. He felt that to do so would tend to inhibit his creativity—and take some of the fun away. But he was very pleased to discover, after he had formulated his solvent tension hypothesis, that prominent physicists such as Arthur Noyes and George Hulett had proposed ideas similar to his much earlier, at the turn of the century. This hypothesis offers an illustrative mechanistical explanation of osmosis—particularly as it pertains to the movements of water in biological systems—that does not appear to violate any basic physical and thermodynamic principles. Hence, the solvent tension hypothesis may well be reconcilable with the view of osmosis derived from thermodynamic theories. The conflicts that appear to exist may reflect the different points from which the process is observed and measured more than any fundamental differences in molecular mechanisms.

R/V *Alpha Helix*

When Scholander wanted to probe a specific physiological function, he always tried to use animals in which this function had been developed most conspicuously. Thus, diving physiology was best studied in such natural divers as seals, and cold adaptations in animals exposed to low temperatures in polar regions. By knowing the features that had developed in response to extreme situations, more subtle adaptations in other animals could be detected, monitored, and better understood. This comparative approach often required both laboratory and field studies. During his numerous expeditions to polar, temperate, and tropical areas during his career, Scholander tried to integrate the two types of studies, but often this was hampered by logistical difficulties. The scientific limitations of "working out of suitcases" (as he would say) bothered him. He wanted to go into the field with technical research capabilities similar to those he had in his home laboratory, including a simple machine shop. Scripps's large fleet of research vessels was a big factor in Scholander's accepting his position, but he discovered soon after his arrival that these ships were specifically designed for oceanographic research and had very little suitable laboratory space, and no general shop facilities. This did not discourage Scholander. He found a way to rectify the situation. The vessel *Alpha Helix* was born; first as an idea, then as a project with funding from the National Science Foundation, and finally as a vessel in the shipyard of Martinac Shipbuilding Corporation, built on the engineering design of Lawrence M. Glosten and Associates.

The concept of this research vessel was unique. It was not to be used for customary oceanographic studies, or for collecting animals and other material in the open ocean. Therefore, no large winches or cranes were needed. Without such facilities, more space could be allotted for a roomy, standard type physiological laboratory, good living accommodations, and a library room for meetings and discussions. Because the vessel should be able to operate near a shore, completely self-sustained anywhere, in polar regions as well as in the tropics, heating and air conditioning were essentials. When launched in 1965, the vessel included all of these capabilities and amenities, including a minimal shop with basic machine tools.

When the plans for the vessel began to take shape in the early sixties, Scholander realized—before many of his biology colleagues—that a new kind of biology was emerging. He was familiar with the discovery of the double-helix structure of DNA by Watson and Crick, and often expressed his puzzlement about how the strands of DNA could be separated during mitosis without one strand at least spinning at very high speeds of revolution, if only for topological reasons. He also knew about the discovery by Linus Pauling of the alpha helix structure of a major protein configuration. He wanted the vessel to be named *Alpha Helix*, to signify that the structure and function of the molecules of life would become increasingly important in the study of biology.

(Authors note: Scholander wanted a symbol or expression displayed on the vessel to signify that it was directed at the quest for new knowledge. Coming from a nation with a history of seafarers and sailing ships, he decided that an artistically designed figurehead of a mermaid embracing concepts from modern science would be such a symbol. It was created based on sketches made by Scholander, donated to the vessel by him and wife Susan, and suitably placed on the bow before its maiden voyage. Beautifully cast in bronze, the sculpture depicts the figure of an ascending mermaid with her tail folded around a design of Neptune's scepter with an elegant double helix coiled around it, stylistically also projecting the magic rod of Hermes entwined by the double helix of two snakes, the traditional caduceus medical symbol. The striking sculpture was removed from *Alpha Helix* when its research program in experimental biology ended, and the ship no longer was operated by Scripps. Presumably, the sculpture will be displayed permanently at Scholander Hall in due time.)

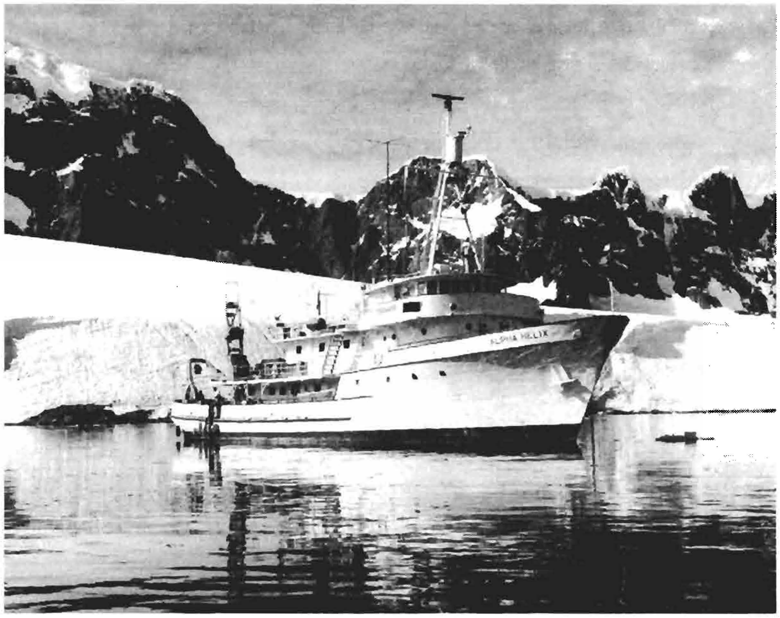
For Scholander, the purposes for obtaining this research vessel (which he insisted be a part of the home facility, the Physiological Research Laboratory) were twofold: to reach parts of the world with modern, sophisticated research capabilities he otherwise would not be able to reach, and to assemble groups of first rate scientists for such expeditionary work. He considered it important to get great minds together, undisturbed by the usual daily chores, to brainstorm and interact to solve problems. Regular group discussions and seminars while in the field were to be a valuable part of this process.

(Authors note: The plaque at the entrance to Scholander Hall contains this inscription composed by Scholander: "This building, its pools and the research vessel *Alpha Helix* were donated to Scripps Institution of Oceanography by the American people through the National Science Foundation and are dedicated to the quest for biological and medical knowledge through the study of life in the sea.")

R/V *Alpha Helix* had a large number of very successful expeditions, contributing many important scientific discoveries, which have been described in the more than 500 publications in mainstream scientific journals. This expeditionary work triggered new areas of research and inspired many of the participants to expand their scientific visions and pursue new ideas in their ongoing research in their home laboratories. This was an important aspect of the *Alpha Helix* research program, and very much in concord with what Scholander originally envisioned. Unfortunately, Scholander could take advantage of this research vessel for only a few years of his life and with less energy than he had hoped. He struggled with emphysema and other health problems associated with this disease for several years. Late in his life, the illness became a great impediment not only for the physical activities required in expeditionary work, but for creative intellectual work as well. Scholander's penetrating logic, sharp focus, and finely honed ability to convey the essence of his research, the trademarks of his writings in the earlier years, were somewhat diminished in his later years.

Concluding Remarks

Scholander's tenure at Scripps had a lasting impact on the institution. He contributed greatly to opening the door for and fostering the growth of experimental research in biology, whether this was of general fundamental nature or focused on life in the sea. In his influential position he initiated or encouraged the hiring of several outstanding faculty members and researchers to the campus. As the founder and first director of the Physiological Research Laboratory, Scholander established extensive collaborations between this unit and the campus's School of Medicine; he was influential in creating joint faculty appointments between the two units. He viewed research in animal biology and medicine as inseparable; basic research on animals had and would continue to provide crucial insight into human physiology and medicine. The term biomedicine was a natural concept for him, as was the concept that research should have no intellectual restraints. He had colleagues who supported him strongly in these views. They helped seed the growth in diversity of biological research that has taken place at the institution during the past several decades. But in other subtle ways as well, Scholander's presence at Scripps benefitted the institution. He had scientific and social contacts—and admirers—throughout the world. By his scientific stature, reputation, and activism, he helped make the institution widely known outside the narrower fields associated with the sciences of oceanography, marine biology, and the earth sciences. The Physiological Research Laboratory building deservedly was named Scholander Hall in 1989. Soon thereafter, the PRL Research Unit was merged into the Center for Marine Biotechnology and Biomedicine, with Scholander Hall becoming its primary office and laboratory facilities.



R/V *Alpha Helix* at Port Lockroy, Antarctica, 1971. Photo by E. A. Hemmingsen.

But significant as Scholander's activities were for Scripps and the campus as a whole, his impact on science in general may be more profound. His ability to peel away extraneous factors and define the fundamental core of a problem led to many important discoveries and contributions that cut across a wide spectrum of disciplines. The wealth of intellectual contributions that he left behind will affect science for generations to come. He belonged to a vanishing breed of polymaths, which soon may become an "endangered species." And those of us who knew him personally miss his genius and charm and his incredible, infectious enthusiasm for science.

We wrote this article largely using our extensive personal knowledge of Scholander and Scripps archival information, but have included facts given in his autobiography, Enjoying a Life in Science,[15] as well. This autobiography was started after the monograph on osmosis was completed, and was written mostly during the last two years of his life. It contains many facts and tidbits about Scholander's scientific work, with his complete bibliography, and many delightful stories and anecdotes from his life from childhood to late age. It illustrates so well the joy he experienced when pursuing his curiosity, ideas, science, and love of nature. However, his own assessments of the many magnificent contributions he made to science are few, and are modest and indirect when they appear. Similarly, he rarely touches upon the positive impact he had on most students and colleagues with whom he worked. We hope that this biographical sketch to some extent remedies these omissions.

(Authors note: The bibliography and a brief biography also can be found in: Schmidt-Nielsen, K. (1987). Per Fredrik Thorkelsson Scholander, 1905-1980. *Biographical Memoirs, National Academy of Sciences*, 56:387-412.)

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