Diving Adaptations of the Weddell Seal

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Collapsible lungs and a spleen that functions as a scuba tank are apparently among the features that enable the seal to swim deeper, and to hold its breath longer, than most other mammals

by Warren M. Zapol

A person who can swim unaided to a depth of 20 meters and stay submerged for three minutes is considered an expert diver. Yet such an accomplishment pales when compared with that of another mammal, one able to plunge more than 500 meters and remain underwater for more than 70 minutes. This diving virtuoso is the Weddell seal (*Leptonychotes weddelli*), a member of the Phocidae family of true, or earless, seals.

The animal, which flourishes on the shores and coastal ice of Antarctica, plows deep into the cold sea not to set endurance records but in search of food. A quarter of a mile from land, within 50 feet of the 250- to 600-meter-deep sea floor, lives its staple diet: the large Antarctic cod *Dissostichus mawsoni*.

Weddell seals readily withstand water temperatures that fall to −1.9 degrees Celsius by virtue of their large size (adults weigh from 350 to 450 kilograms) and a thick layer of insulating blubber. Diving, which forces the animals to cope with a lack of air and with intense undersea pressure, constitutes a more complex challenge. Indeed, unraveling the adaptations to this challenge has required decades of laboratory research by many investigators and, more recently, a spate of field studies. The field studies suggest that certain long-held beliefs based on laboratory studies may need to be modified. Forcing a seal confined in a laboratory to put its face underwater does not necessarily evoke the same response as a dive undertaken freely in the sea.

The specific problems posed by diving are considerable. Above all, the seal must provide its tissues with oxygen. At the same time it must limit the buildup in the blood of carbon dioxide, a by-product of the oxidation of glucose for energy. This gas is generated by the tissues and then carried in the blood to the lungs for removal. When an animal is submerged, the gas can accumulate in the blood, upsetting the fluid's delicate *p*H balance.

The animal also has to avoid the many ills that extreme pressure can cause. For every 10 meters of depth, an animal or a person is subject to an additional "atmosphere" of external pressure—that is, to the push exerted at sea level by a 14.7-pound force on one square inch of area, or the pressure exerted by a 760-millimeter column of mercury. One potential effect of underwater pressure is an increase in the excitability of nerve cells, which can result in convulsions. Pressure also squeezes air pockets, such as the air sinuses in the human head. The squeezing can cause pain, and if the body cannot deliver enough air to the pockets to equalize the external pressure, blood vessels may expand into the air spaces and burst.

Pressure also compresses gases, posing a danger when it affects the nitrogen in the alveoli, the tiny gas sacs in the lungs. (Body fluids and fluid-filled organs are compressed only minimally underwater.) Nitrogen gas constitutes some 78 percent of the air. Normally it passes harmlessly into the circulation, but when the air in the lungs is put under great pressure, as it is during descent, excess nitrogen dissolves in the blood and tissues; it may then lead to narcosis, a disorder that divers call rapture of the deep. Narcosis is identified by such symptoms as intoxication, loss of coordination and vision, drowsiness and unconsciousness. During ascent, a too rapid trip to the surface can cause the nitrogen tension in the blood and tissues to be greater than the external pressure on the body. Then dissolved nitrogen may come out of solution and bubble ("the bends"). In addition to producing pain in the joints and elsewhere, the bubbles may block vessels in the brain and spinal cord, leading to paralysis and even death. ouch

Laboratory studies, in spite of their limitations, have revealed many of the strategies by which the diving seal appears to ensure an adequate supply of oxygen and avoid the disorders described above. I shall therefore review those strategies and then indicate instances in which field studies contradict or clarify earlier results.

One major and still undisputed laboratory finding is that the seal stores an abundance of oxygen—almost twice as much per kilogram of body weight as a human being does. It also concentrates the oxygen where it is most needed during a dive: in the blood and, to a lesser extent, in the muscles. People are particularly dependent on the lungs for oxygen, keeping 36 percent of their total supply in the lungs and 51 percent in the blood, but the seal stows only 5 percent in the lungs and a full 70 percent in the blood. Similarly, a person stores just 13 percent of its oxygen in the muscles, but the Weddell seal keeps about 25 percent there, bound to the oxygen-carrying pigment myoglobin.

Vast amounts of oxygen can be maintained in the seal's blood in part because the volume is enormous. In 1969 Claude J. M. Lenfant, then at the University of Washington, discovered that in contrast to the blood of human beings, which typically accounts for 7 percent of the body weight, the blood of the Weddell seal accounts for 14 percent of the animal's weight. (This comparison actually underestimates the amount of blood that is available to working tissues, because blubber, which constitutes about a third of the r2 animal's mass, receives little blood.) Moreover, the seal's blood has great Hb quantities of hemoglobin, the oxygen-carrying pigment of red blood cells. When my group at the Massachusetts General Hospital drew blood from seals in the laboratory, we found that red cells accounted for some 60 percent Hct of the volume of each drop; in human beings these cells occupy only from 35 to 45 percent of the volume.

Although the Weddell seal's oxygen supply is impressive, it is not infinite. Like other diving animals, the seal has therefore devised ways to conserve its fuel. When any mammal puts its face in the water, neural impulses trigger the brain to induce the so-called diving reflex: as the animal stops breathing, 1 bradycardia (a slowing of the heart rate) ensues and certain arteries be2come constricted, limiting the blood that flows to the organs they feed.

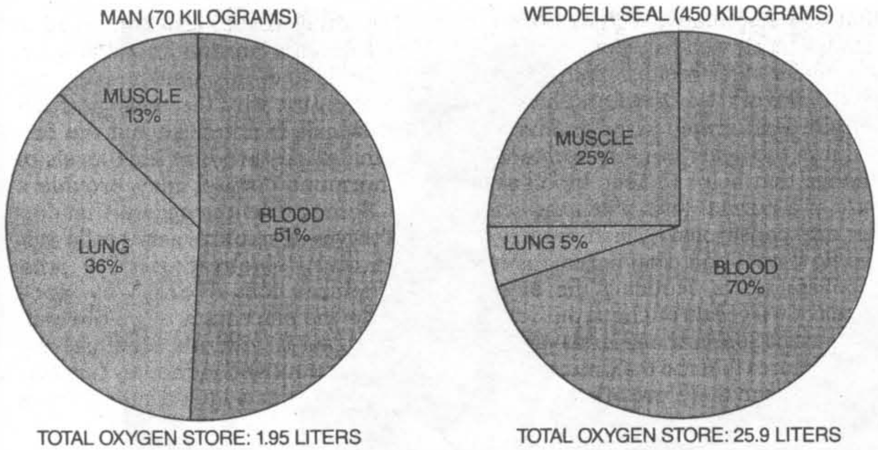
The rapid onset of bradycardia at the start of a dive has been recognized in animals for more than 100 years. It happens in human beings but appears to be most profound in species that dive habitually, such as seals and whales. A slowed heart rate is beneficial underwater because it enables the heart to work less hard and hence to require less oxygen. Bradycardia also reduces the heart's output of blood, a change that helps to keep blood pressure at a normal level when the arteries are constricted. Furthermore, as the flow of blood diminishes, the metabolism slows, reducing the oxygen needs of tissues throughout the body.

Constriction of the arteries presumably ensures that the maximum supply of blood, and therefore of oxygen, will be available to the tissues that are most crucial to survival. My colleagues and I recently measured blood flow to various tissues in the seal during a laboratory dive. Consistent with earlier findings, we found that the seal continued to supply blood at a normal rate to the retina, brain and spinal cord, all of which are vital to navigation and motor control. (As would be expected, the heart received blood but the amount was reduced to match the organ's reduced workload.)

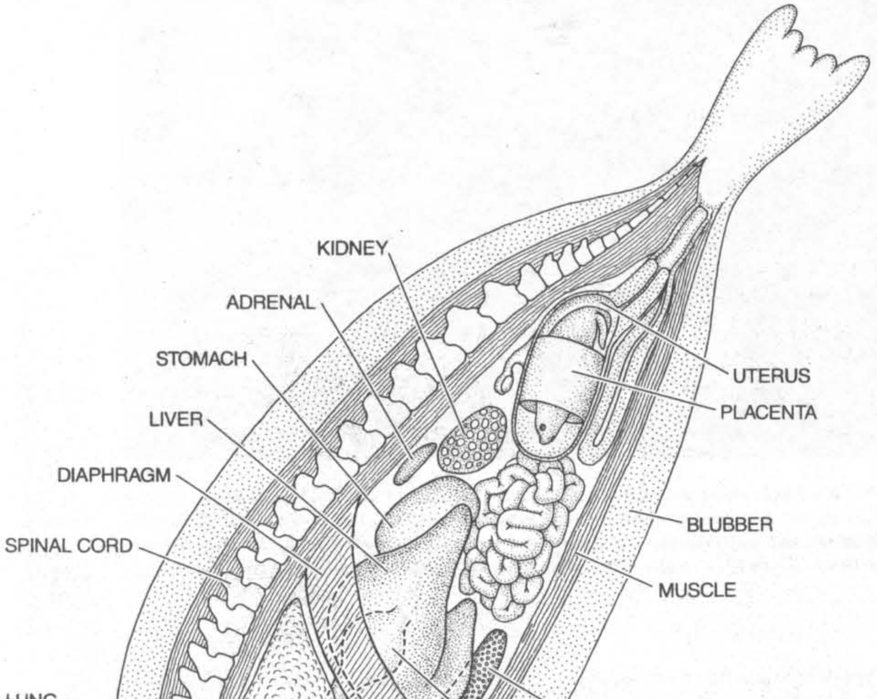
Two other tissues also continued to benefit from a normal flow: the adrenal glands and, in pregnant seals, the placenta. Just why the body perfuses the adrenals is not clear, but the fact that the glands produce high levels of the hormone cortisol may provide a clue. Some evidence suggests that cortisol serves to stabilize nerve cells during a dive, thereby preventing pressure-induced convulsions. Why blood flows to the placenta is more obvious. This organ is vital to fetal gas exchange and must continue to function if the submarine within a submarine is to survive.

Our studies of oxygen distribution also confirmed that the seal essentially shuts off the flow of blood to most other organ systems and tissues during laboratory dives. When this flow ceases, many of the affected tissues A (such as the kidneys) stop functioning until the animal comes up for air. Certain other tissues apparently switch to anaerobic, or oxygen-independent, B metabolism if they have cru-

WEDDELL SEAL returns to a manmade ice hole for air after a dive in the Antarctic Ocean. Most dives are fishing trips that last for about 17 minutes and take the animals as deep as 500 meters or more. Other dives may last for more than an hour. To survive even short forays the animal must supply oxygen to its tissues and avoid such pressure-associated ills as nitrogen narcosis and decompression sickness ("the bends"). Randall W. Davis of the Sea World Research Institute in San Diego made the photograph.



DISTRIBUTION of oxygen differs markedly in a man and a Weddell seal. The seal stores about twice as much oxygen per kilogram of body weight as the person. The animal is also less reliant on its lungs, keeping more of its oxygen store in its blood and muscles.



cortisol

TISSUES that continue to receive normal amounts of oxygen-laden blood (*colored labels*) during laboratory dives include the retina of the eye, the brain and the spinal cord, all of which are crucial to navigation or motor control. The adrenal glands, which produce a hormone that may protect the brain from pressure, also receive a normal flow, as does the placenta in pregnant seals. Not knowing how long they will be underwater, the seals apparently prepare for the worst by dramatically reducing blood flow to many other tissues, including their extensive muscular system. When oxygen stores have been depleted, the muscles obtain energy by initiating anaerobic, or oxygen-independent, metabolism.

cial tasks to perform. The telling by-product of anaerobic metabolism is lactic acid; when seals surface after forced dives, the levels of lactic acid in the blood soar above the resting state.

Although initiating anaerobic metabolism can be important when oxygen is lacking, it can also be extremely dangerous. High levels of lactic acid lower the *p*H of the blood and can lead to acidosis, which may cause cramping, a weakening of the heart's ability to contract and even death. Laboratory studies by P. F. Scholander of the Scripps Institution of Oceanography, who studied the diving reflex in the 1930's, suggested that the seal avoids acidosis by confining anaerobic metabolism to the skeletal muscles and other tissues that are isolated from the blood supply during laboratory dives. With the blood flow shut off, these tissues cannot release lactic acid into the blood until the animal surfaces. At that time the liver, lungs and other organs can clear out the by-product.

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Laboratory work has also attempted to explain how the Weddell seal handles external pressure. In addition to raising the possibility that elevated cortisol levels may prevent convulsions, the studies have shown that the seal lacks the potentially troublesome air sinuses of other mammals. The seal likewise has ways of avoiding nitrogen narcosis and the bends. Its lungs are small for its weight, and so they have a reduced capacity for storing nitrogen that might diffuse into the blood in the course of a dive. Moreover, the animal exhales before submerging. The obvious effect is to reduce the buoyancy that impedes descent, but exhalation has the added benefit of reducing gas volume in the lungs still further.

exhales

During a dive, seawater pressure on the animal's collapsible rib cage undoubtedly squeezes most of the remaining nitrogen out of the alveoli and into the bronchial air-duct system. According to anatomical studies done by Gerald L. Kooyman and his co-workers at the Scripps Institution, the seal's bronchi and bronchioles are supported by rings of cartilage that enable the airways to serve as an armored gas-storage reservoir. Because these passages, unlike the alveoli, have no direct contact with the blood, they do not introduce nitrogen into the circulation. (Some oxygen is certainly sequestered in the seal's airways as well, but not much; only 21 percent of inhaled air is oxygen.) In contrast, the bronchi and bronchioles of human beings would close down under intense pressure and so could not store excess nitrogen.

Several years ago Kooyman also determined, on the basis of forced dives in a compression chamber, that the

ATTACHING a combination computer and blood sampler to the back of a seal enabled Roger D. Hill of the Massachusetts General Hospital (*right*), the author and their colleagues to measure the physiological responses of seals throughout free dives at sea. Journeys shorter than 17 minutes evoke a less dramatic response than dives in the laboratory.

influenced behavior?

seal's lungs collapse when the animal reaches a depth ranging between 50 and 70 meters. Collapsed lungs would halt the flow of nitrogen into the blood and hence limit the total amount of nitrogen that accumulates there.

More recently Kooyman and his coworkers have carried out some field studies that have caused many of us to wonder whether the seal in the ocean responds to a dive the way it does in the laboratory. When Kooyman's group attempted to study seals engaged in voluntary dives in the ocean, their data suggested that the animals may not always exhibit a pure diving reflex. Those early studies were not definitive, however, because the available equipment could not monitor complete dives.

After Roger D. Hill of Massachusetts General developed software and constructed a battery-operated, eight-bit computer that would make it possible to evaluate the seal's physiological and metabolic responses throughout free dives at sea, a group of us from laboratories around the world converged on the National Science Foundation's research station on the shore of McMurdo Sound in Antarctica. With any luck, the portable computer, which weighed less than four pounds and had 64 kilobytes of random-access memory, would enable us to clarify the extent to which the Weddell seal exhibits the diving reflex in its natural habitat. It would also add insight into how the seal deals with pressure.

Hill's diving computer, which was encapsulated to withstand 500-meter depths, did everything but steer. It recorded heart rate and depth at predetermined intervals for several days. It also controlled an electric pump that took up to seven arterial-blood samples at specified times (such as 10 minutes into the dive) and depths. After collecting the samples the computer pumped the blood into a bag or syringes tethered to a six-foot fiber-optic line, which itself had additional functions when the seal surfaced.

We gathered seals from nearby colonies and sledged them to the study site, a hole three feet in diameter drilled through ice six feet thick. There we anesthetized a subject with harmless techniques devised by Robert C. Schneider of Massachusetts General, inserted the necessary catheters and attached the computer, which was fastened to a rubber sheet glued to the seal's dorsal fur. (When the animals molted later in the summer, they readily shed the rubber appendage.)

Once rigged with our computer and recovered from general anesthesia, the seal was free to enter the hole and swim off. We were confident it would return with blood samples and data because we adopted a rather reliable tactic devised by Kooyman. Knowing that Weddell seals can swim only a few kilometers underwater, he studied the animals at isolated holes drilled in broad ice sheets; the seals had to return to the site of origin in order to breathe.

After a subject went on its way, we placed a fishing hut (with a large circle cut out of the floor) over the hole, providing shelter both for us and for a computer that would later retrieve data from the diving computer. When the seal returned, we quickly connected its fiber-optic line to the stationary computer. Within 10 seconds the larger machine collected data stored in the diving computer and, when appropriate, gave it new instructions.

We found, as Kooyman had earlier, that some 95 percent of the seal's voluntary dives last for less than 20 minutes. These tend to be feeding dives in which the animals head directly for their prey and then return. The seals embark on the 5 percent of dives that last longer than 20 or 30 minutes when they explore distant routes or must escape from predators.

Studying the all-important distribution of oxygen to tissues, Peter W. Hochachka of the University of British Columbia showed that the seals do not release lactic acid into the circulation during or after sea journeys that last for up to 20 minutes. This indicated that during short natural dives—that is, the majority of the seals' journeys—the muscles do not resort to the anaerobic metabolism observed in laboratory dives and must receive some blood. (The muscles would probably account for most of the lactic acid in the blood because they are abundant and also do work when the animal dives.) With little or no lactic acid to break down after a dive, the seal often resumes fishing within minutes after taking a few breaths at the surface.

We wondered how Weddell seals supply oxygen to the muscles without depriving the brain and other vital tissues of their rightful supply. No one yet knows the answer, but Hill did find a hint. He noted that the heart rate slows at the start of every dive but does not remain at a constant level throughout the shorter excursions; instead it quickens and slows in accordance with the seal's swimming speed, never outpacing the resting rate. When the heartbeat quickens, cardiac output must also increase. The extra blood has to go somewhere, and it may well be channeled to the skeletal muscle. If this is the case, it implies that the total constriction of blood flow to muscles, assumed for so long to characterize every dive, does not in fact take place in the course of most natural dives.

In contrast to the feeding dives, the seal's occasional long excursions do evoke the classic diving response seen in the laboratory. The long forays are characterized by profound bradycardia with little variability of heart rate. After (but not during) such dives the Weddell seal releases lactic acid into its blood, indicating that the animal shuts off the blood flow to its muscles and meticulously conserves oxygen while diving. Having switched to anaerobic metabolism in the muscles, the seal can stay underwater for an hour or more. It pays a price, though: when it finally surfaces, it does not dive again until it has cleared away the lactic acid released by the muscles, a process that can take up to an hour. Why do even short laboratory dives elicit a response characteristic of long field dives? In the laboratory the seal does not know how long it will be submerged and so prepares for the worst.

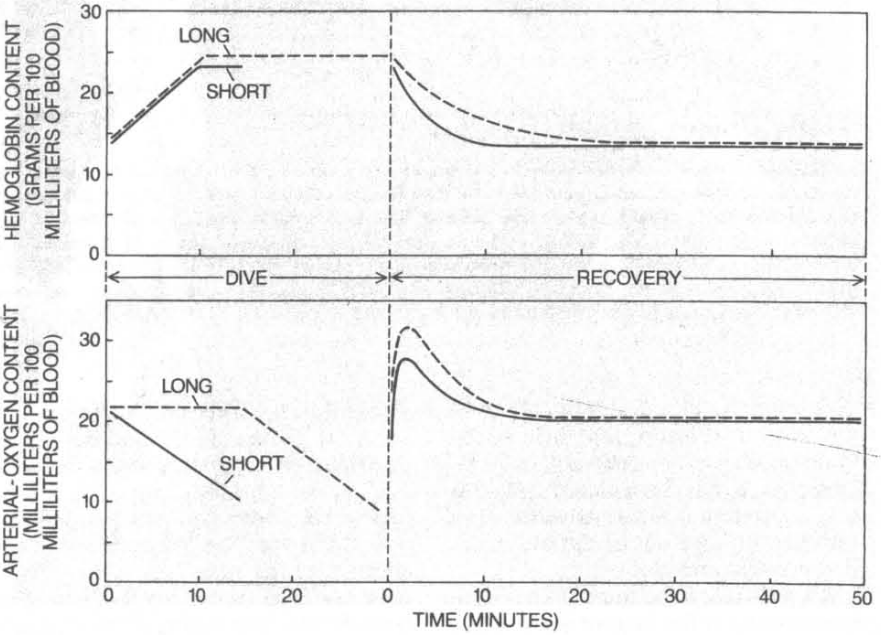
also not swimming

Other studies of oxygen delivery indicate that early in both feeding and exploratory dives at sea the seal actually increases the concentration of red blood cells in the circulation, thereby maximizing the hemoglobin level in the blood and thus the amount of oxygen available to the tissues. In a remarkable discovery Jesper Qvist of Herlev Hospital in Copenhagen, who was a part of our Antarctic team, found that the red-cell concentration in the arteries increases by 50 percent in the first 10 to 15 minutes of a dive. In contrast to my group's laboratory findings, which suggested that the levels are always high, Qvist showed that the cells initially account for only 35 or 40 percent of the circulating blood volume and then rise to 60 percent during a dive. (The levels return to normal within 10 minutes after the animal surfaces.)

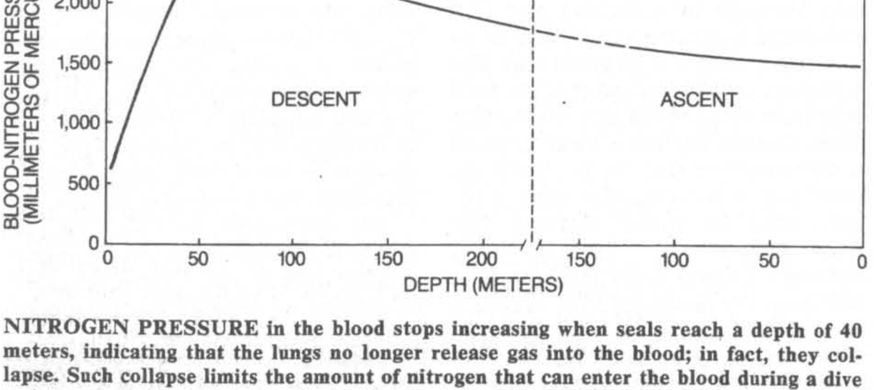
RBCs

Where might the bounty of new cells come from? The spleen is a reasonable guess. This poorly understood organ is known to contract when the sympathetic nervous system is activated, as it *
is when a mammal dives or is frightened. (Indeed, fear may explain why some seals have elevated red-cell levels when they are confined in a laboratory.) Contraction of the spleen could well inject stored oxygen-rich red cells into the seal's highly expandable venous system; the heart could then deliver them to the arterial circulation as needed. After the seal returned to the surface for air, the circulating red cells would be readily reloaded with oxygen and stored again.

An oxygen-supplying role for the spleen is not unprecedented; the organ is known to infuse red blood cells into the circulation within minutes after a racehorse begins intensive exercise. More direct evidence of the spleen's importance to the seal comes from an-

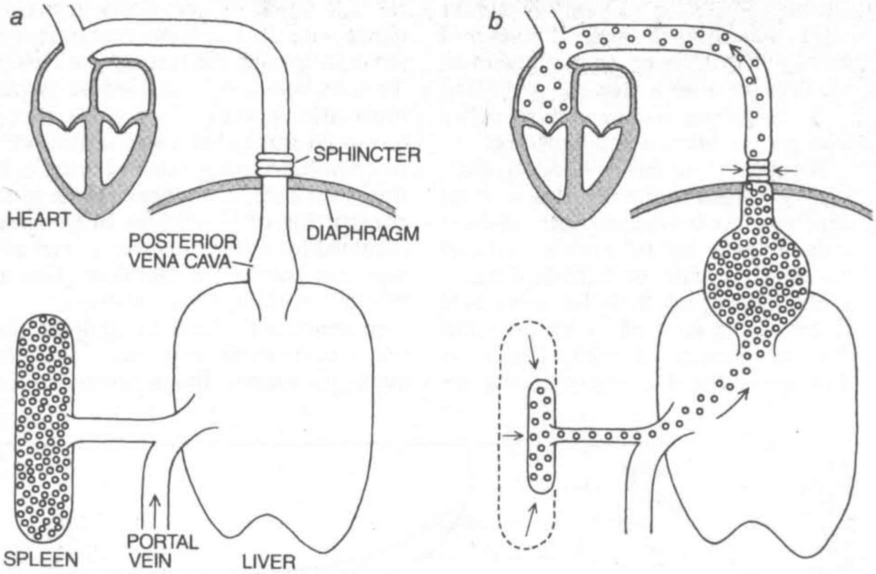


CONCENTRATION OF HEMOGLOBIN (*a*), the oxygen-carrying pigment of red blood cells, rises in the blood during the first 10 to 12 minutes of voluntary ocean dives, preventing the oxygen levels in the seal's blood (*b*) from falling precipitously. In excursions that last for more than 17 minutes (*broken line*), when the muscles switch to anaerobic metabolism, the influx of hemoglobin into the blood actually balances oxygen consumption for about 15 minutes. In trips of less than 17 minutes (*solid line*), when the muscles apparently burn oxygen, the added hemoglobin cannot fully counteract oxygen consumption by tissues; hence the level of oxygen in the blood declines gradually from the start.



NITROGEN PRESSURE in the blood stops increasing when seals reach a depth of 40 meters, indicating that the lungs no longer release gas into the blood; in fact, they collapse. Such collapse limits the amount of nitrogen that can enter the blood during a dive and thereby helps to protect the seal from nitrogen narcosis and the bends. As the dive progresses, uptake of nitrogen by the muscles and the blubber further reduces the risks.

atomical studies of several mammals. On comparing organ weight with body weight I found that the size of the Weddell seal's spleen is particularly large, matched only by that of the southern elephant seal, another long-diving species. In human beings, dogs and even baleen whales the organ is considerably smaller for the animal's bulk. On the basis of organ size and the degree to which hemoglobin levels rise during a dive, my colleagues and I estimate that the Weddell seal warehouses approximately 60 percent of its total red-cell supply in the spleen, whereas a human maintains less than 10 percent there. Indeed, the seal's spleen appears to be something of a contractile scuba tank in its ability to store and release oxygen needed for a dive.



LARGE SPLEEN probably collects oxygen-rich red blood cells when the seal breathes air at the surface (*a*) and injects the cells into the circulation when the animal submerges (*b*). Such activity would explain the finding that hemoglobin levels are elevated at the start of ocean dives. The author suggests that the spleen stores about 24 liters of red blood cells. It contracts when the dive begins, squeezing much of its contents into the portal vein, through the liver and into the expandable posterior vena cava. A sphincter allows the reservoir to release cells to the heart and to the arterial circulation as needed.

The effects of an oxygenated red-cell infusion become particularly apparent in long dives. In the period when the red-cell concentration is rising, the blood's oxygen content remains constant, indicating that the amount consumed by the brain, heart and other crucial tissues is somehow being replaced. The same plateau is not seen in feeding dives, where the muscles consume oxygen; then oxygen levels fall steadily. In this instance the oxygen burned by the seal's muscles probably outstrips the ability of the splenic blood-storage system to inject red cells into the circulation.

In addition to providing oxygen during a dive, the inflow of fresh red blood cells into the circulation probably serves another important purpose: the dilution of gases dissolved in the blood. Such an effect would explain why the carbon dioxide concentration rises surprisingly little in the course of field diving. Dilution would also help to explain why nitrogen does not cause narcosis or the bends in the seal. The field studies suggest other explanations as well. For instance, our international group has found, as others had suggested, that the lung collapses. It does so at about the 40-meter mark, somewhat earlier than predicted.

We determined the point of collapse on the basis of work by Konrad J. Falke of the University of Düsseldorf, who painstakingly measured nitrogen pressures in blood specimens drawn from the arteries of free-diving seals. (Pressure is a good indicator of nitrogen concentration because the tension in the blood rises and falls with the concentration.) Falke found that the blood-nitrogen pressure, which measures 550 millimeters of mercury when the animal breathes at the surface, increases as the seal descends, peaking at from 2,000 to 2,400 millimeters when the animal reaches 40 meters. Beyond 40 meters the pressure falls. We think the drop in pressure that follows the lungs' collapse happens not only because the spleen infuses red cells into the circulation but also because some nitrogen diffuses out of the blood and into muscles and blubber.

As we studied the many remarkable adaptations of the mature seals in McMurdo Sound we became increasingly curious about the responses of the seal fetus. Does it exhibit a diving reflex when the mother descends at sea? Work by Robert Elsner of the University of Alaska at Fairbanks had suggested that it might. He found that the fetal heart rate, like the mother's, slows during laboratory dives.

We do not yet have a complete answer to our question, but we were able to collect some field data when Graham C. Liggins of the National Women's Hospital in Auckland and Hill succeeded in placing a heart-rate monitor on the back of a pregnant seal. The computer record showed that the fetal heart rate does indeed slow during free dives, but the decline is more gradual and less marked than the mother's; the heart rate also accelerates more gradually after the mother surfaces. The fetus "knows" when its parent dives, although exactly what informs it is not clear. We must complete additional studies to determine whether alterations in the fetal heart rate are accompanied by changes in cardiac output and in the distribution of blood flow. If they are, the finding would indicate that the fetus conserves oxygen for vital tissues as the mother dives and replenishes its store at the surface.

As a whole our field studies demonstrate that the Weddell seal's responses to its occasional long dives look much as laboratory dives predict they should. The diving reflex is in full force: the heart rate slows and remains low throughout the dive, and the muscles switch from aerobic to anaerobic metabolism, indicating that their supply of blood is shut off, probably because their arteries are constricted.

In the majority of dives, in contrast, the profile is rather different. When the seal embarks on a feeding excursion, the diving response is modified. The heart rate slows but is more variable, speeding up as the seal swims faster. Moreover, the muscles continue to rely on aerobic metabolism; apparently they continue to receive some blood, indicating that vascular constriction is modulated. Early in its dive the seal apparently "decides" whether its foray will be long or short and whether or not it must resort to draconian measures to conserve oxygen.

The mechanism by which the seal makes the decision is one of many puzzles left to be solved. Given the rapidly advancing technology now available, it may not be long before the question is answered and added insights are gained into the complex adaptations of the Weddell seal, one of the world's most impressive diving machines.