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The Physiological Ecology of Whales and Porpoises

Like other mammals, these marine species have a high-energy way of life. In pursuing it they evolved particular adaptations of their own, notably the ability to dive deep for long periods

by John W. Kanwisher and Sam H. Ridgway

It is not generally realized that 70 species of entirely marine mammals—the whales and porpoises—play as crucial a role in oceanic ecosystems as the terrestrial mammals do on land. The broad success of the land mammals at the end of the Mesozoic era (some 65 million years ago) was due in large part to their high-energy way of life, including such features as warm-bloodedness and an expanded central nervous system. When some of these terrestrial mammals later filled a marine ecological niche, they evolved further adaptations of the same high-energy type.

How have the whales and porpoises—the Order Cetacea—overcome the many physiological obstacles presented by living in the ocean? Consider, for one thing, their severely stressed life cycle. Initially expelled from a submerged birth canal into water that can be close to the freezing point, the newborn calf must struggle to the surface unaided before it can even take its first vital breath of air. To be suckled by its mother the calf must hold its breath and return underwater. When eventually it can feed itself, it may have to develop an entirely new behavioral repertory: diving in order to find its prey. Finally, once the cetacean is an adult, it must master a further repertory of complex gymnastics before it can reproduce and thereby give rise to the offspring that initiate the next life cycle.

Consider also the surprising diversity of the cetaceans, both in geographic distribution and in size. Whales and porpoises are plentiful in all the oceans, from the Tropics to the edge of the polar ice, both north and south. Many species even migrate seasonally from cold seas to warm ones and back again. The largest adult blue whale is some 20,000 times heavier than the smallest newborn porpoise, yet both large and small species are found in tropical and polar seas. The toothed whales—the odontocetes—include small porpoises such as the har-

bor porpoise at one end of their size range and the great sperm whale at the other. How is it that the sperm whale is the cetacean that dives the deepest and stays submerged the longest? How does it avoid the "bends" and other physiological problems human beings encounter when they dive to much shallower depths? The porpoises, being smaller than the smallest of their larger toothed-whale cousins, have a much higher surface-to-volume ratio. How do they manage to stay warm in cold waters? Questions of this kind led us to the first of several investigations: the thermal physiology of porpoises.

Our observations of captive porpoises at Marineland in Florida showed us that the animals were able to maintain a stable internal temperature close to the human one and similarly well regulated. Since water removes heat from an object much faster than air does, we found this observation intriguing. We had thought these thermally stressed mammals might exhibit the more variable body temperatures typical of terrestrial hibernators. This not being the case, we were led to calculate the stringency of the thermal problem faced by a small porpoise living in the cold waters of high latitudes.

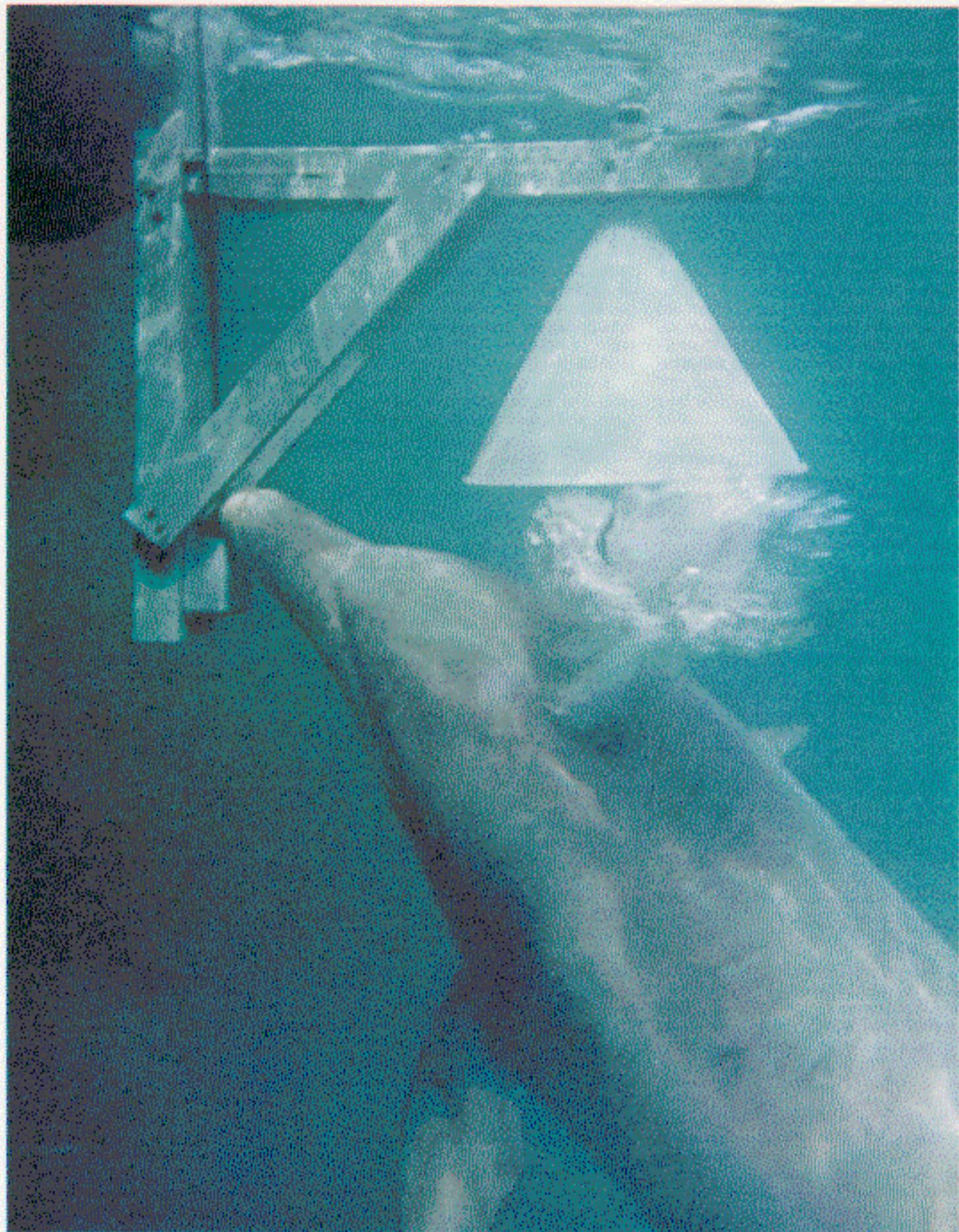
For the purpose of heat-flow calculations a cetacean may be regarded as a uniformly warm fleshy core surrounded by a surface layer of insulating blubber. The outward flow of heat from the core, encountering the thermal resistance of the blubber layer, must be great enough to maintain the temperature difference between the surrounding water and the warm inner core. It is known that this difference is equal to the product of the thermal resistance of the blubber times the outward flow of metabolic heat generated in the core. When the insulation is insufficient, more body heat must be generated if the animal is to maintain a constant core temperature. For exam-

ple, if the core temperature of a terrestrial mammal falls by as little as .5 degree Celsius, the mammal will begin to shiver in order to increase its metabolism. Over longer periods any such imbalance can be corrected by increasing the amount of insulation. The land mammal grows a winter coat and the whale in polar waters develops a thicker layer of blubber.

When the animal is active, such an increased thermal barrier may actually be too much of a good thing. For example, when a whale swims fast, the increase in its metabolic activity will cause its core to overheat. The whale then has recourse to a circulatory stratagem. An increase in blood flow near the body surface, particularly through the flippers and flukes, thermally bypasses the insulating blubber and returns the core temperature to normal. In cetaceans generally a steady body temperature is mainly achieved by such changes in blood flow. The same is true of human beings: when they are too warm, more blood is shunted to the surface of the body, producing the flushed appearance that is the opposite of being "blue from the cold."

There are fundamental differences, however, between the physiology of human beings and the physiology of whales. For example, cetaceans have no sweat glands; evaporative cooling in an aquatic environment is impossible. By the same token, for their surface insulation human beings have only a very poor equivalent of blubber. Human divers have now learned to imitate whales by wearing insulation in the form of foam-rubber suits. Ashore human beings overcome the handicap of their essentially tropical origins by covering themselves with, among other things, winter insulation grown by other terrestrial mammals.

Even before we began our investigations we were well aware that the smallest cetaceans would be the ones that



BOTTLENOSE DOLPHIN, one of the small whales trained by the U.S. Navy for underwater tasks, worked for the authors in experiments on the physiology of breath-holding. This dolphin, known to

his trainers as Tuffy, submerged on signal and after various intervals responded to a second signal by nudging a buzzer and exhaling into a funnel, so that his remaining oxygen supply could be measured.

faceted the greatest problem in maintaining a normal mammalian temperature. Considering the total surface area that is constantly losing heat to the surrounding water, the smaller the animal, the smaller the core volume that generates the metabolic heat required to maintain the necessary temperature differential across the blubber. In addition to the disadvantageous geometry of surface-to-volume ratios, considerations of linear scaling also work against any small porpoise trying to stay warm in cold water. Because of their smaller dimensions, the smaller animals will tend to have a thinner layer of blubber.

Regardless of their size, cetaceans maintain a normal mammalian internal temperature of about 37 degrees C. In the Arctic, where the water tempera-

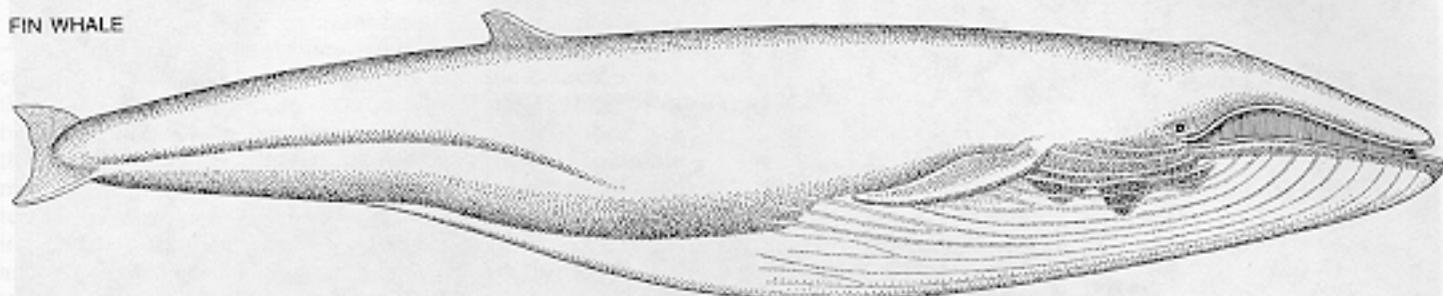
ture may be -2 degrees C., the temperature difference across the blubber barrier is nearly 40 degrees. In the Tropics, where the water temperature may be 30 degrees C., the temperature gradient across the barrier would be only a fifth of that in Arctic waters. Thus a porpoise adapted to warm water would seem to be headed for serious thermal trouble on entering polar seas. Yet one of the smallest cetaceans, the harbor porpoise (*Phocaena phocaena*), is found mostly in cold northern waters.

To determine the dimensions of the problem faced by harbor porpoises in cold water we calculated how much metabolic heat they would have to generate in order to keep warm. To determine the total surface area and the

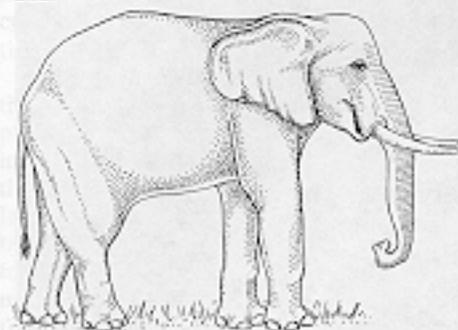
thickness of the porpoise's insulating blubber we made direct measurements on a dead harbor porpoise that had washed ashore. When our figures were entered in the formula for heat loss, the only conclusion to be drawn was that with only a normal mammalian metabolic heat supply a porpoise that small could not keep warm in northern waters. Yet there the harbor porpoises were, sporting in the same chill seas that should have killed them.

Such a paradox is upsetting to biologists who have come to expect orderliness when they examine any parameter common to different animal groups. The amount of metabolic heat production in animals of different sizes is one such comparison that seemed well enough understood. For example, the

FIN WHALE



ELEPHANT



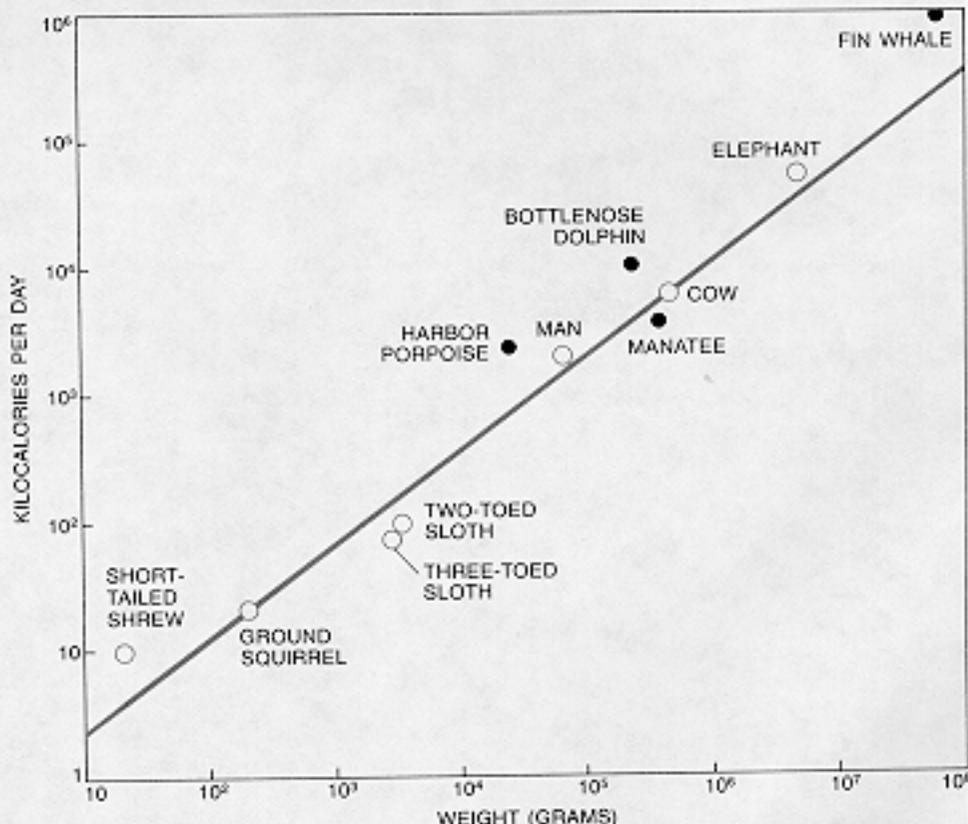
BOTTLENOSE DOLPHIN



HARBOR PORPOISE



GROUND SQUIRREL



"MOUSE TO ELEPHANT" CURVE, shown as a solid line (color) in the graph at the right, was devised in the 1930's by Francis G. Benedict of the Carnegie Institution of Washington as a rough means of estimating the basal metabolism of various mammals, expressed in kilocalories per day, on the basis of 75 percent of their weight. Large colored circles show how selected terrestrial mammals closely fit the curve, which is constructed on a logarithmic ordinate and ab-

scissa. (The ordinate has a top value of one million kilocalories and the abscissa extends to 100 million grams.) Direct measurement of the metabolism of harbor porpoises (*Phocaena*) and bottlenose dolphins (*Tursiops*) and an estimate for fin whales (*Balaenoptera*) based on lung volume (black dots) all lie well above the terrestrial-mammal curve. Weight for weight, however, the metabolism of fin whales is lower than that of such sluggish terrestrial mammals as sloths.

metabolic rates of numerous terrestrial mammals have long been arrayed in what is called the "mouse to elephant" curve. It was believed that given the animal's body weight one could closely estimate from this curve the metabolic heat production of any mammal. Our estimate of the metabolic rate needed to keep the porpoise warm in cold water, however, was so high that it was in clear disagreement with the data from terrestrial mammals.

There were two possible ways to explain the paradox. The first was, quite simply, that the metabolism of the cetaceans does not conform to the terrestrial mammals' mouse-to-elephant curve. This is to say the cetaceans may have an intrinsically higher rate of basal metabolism that allows even a small cetacean to survive in cold water. The second possibility is that cetaceans have a "normal" (which is to say a terrestrial) basal rate of heat production but that by exercising all the time when they are in cold water they can generate enough extra heat to keep themselves from getting too cold. To us the only way to choose between these two explanations was to present the question to the porpoises. Which of these thermal strategies had evolution chosen for them?

With the skilled help of Gunnar Sundnes, a physiologist at the Havforskningssinstitutt in Bergen, we set up a heat-loss experiment. First we learned how to keep young harbor porpoises more or less contented in captivity in a large tank. We then transferred them for testing to a smaller box, filled with seawater, that served as a whole-body calorimeter. The young of the species weigh as little as 15 kilograms. Although they are born with blubber that is only one centimeter thick, the difference between their normal body temperature and the temperature of the surrounding seawater can be as much as 25 degrees C.

The porpoise being tested would lie quietly in its box as the metabolic heat it was generating passed through its insulating layer of blubber and warmed the surrounding water. We found we could put a thermistor in the box and with a little amplification produce a curve plotting temperature against time on a chart recorder that was sensitive to within .001 degree C. Taking into account the volume of water in the box, the slope of the temperature curve provided a running record of how much metabolic heat the porpoise was losing at any moment.

Our results proved to be quite clearly in favor of the first of our two possible explanations: these small porpoises had a metabolic rate two to three times higher than the rate of terrestrial mammals of the same weight. This increased heat production is not achieved without cost: the small porpoises must obtain three

times as much food as a terrestrial mammal of the same weight and must rise to the surface and breathe three times more often than they would if their metabolic rate were terrestrial.

On the basis of the porpoise data we went on to make similar thermal calculations for larger cetaceans to see how much more easily a large mammal, with its more favorable geometry, could keep warm in cold water. We first considered a theoretical whale weighing 1,000 times more than a harbor porpoise; since the two sea mammals are similar in shape, the whale's linear dimensions must increase about tenfold. The theoretical whale therefore has 1,000 times more tissue to generate metabolic heat but the heat passes out to the surrounding water through a surface area only 100 times larger than the porpoise's.

Consider this diminished heat loss in terms of blubber insulation only. Whereas the small porpoise could balance its heat loss with the aid of a blubber layer two centimeters thick, the 1,000-times-heavier whale, given the same metabolic rate as the porpoise, could make do with a blubber layer no more than two millimeters thick. Actually, however, such a whale would have a blubber layer some 20 centimeters thick and even in polar seas would face a cooling problem. Such a large cetacean appears to be 100 times overinsulated.

If the large cetacean's blubber layer is far thicker than considerations of insulation require, what other functions does it serve? First, the fatty tissue, which is low in specific gravity, provides enough buoyancy to offset the negative buoyancy of the whale's muscle and skeleton. Second, the blubber constitutes a food store large enough to take care of the whale's metabolic needs on the animal's seasonal migrations, often across thousands of miles of food-poor waters.

Because of the general rule that relates the metabolic rate of mammals to their size, we would expect a whale to have a rate of heat production per kilogram of tissue considerably lower than the rate we had established experimentally with harbor porpoises. We could see no way to check this expectation by direct measurement of the metabolic rate of a 40-ton animal, and so we were left with estimating the whale's heat production on the basis of anatomical considerations only.

At Steinshamn, a Norwegian coastal whaling station, we dissected out the lungs of a 48-foot fin whale (*Balaenoptera physalus*). We determined the whale's lung volume by first inflating the organs with compressed air and then emptying them through a gas meter. We assumed that the volume of expelled air was equal to the volume of air the whale inhaled with each breath. From observations at sea we were able to determine

how often a fin whale breathes. The normal diving pattern for the species is to surface for five quick breaths and then to stay underwater for five minutes; thus in effect a mature fin whale breathes on the average about once a minute.

From the combination of lung volume and breathing rate we could estimate the amount of air a fin whale breathes: 2,000 liters per minute. Now, mammals in general utilize about 6 percent of the oxygen in the air they breathe (21 percent of the total atmospheric mixture of nitrogen, oxygen and other gases). Because each cubic centimeter of oxygen the animal consumes will generate five calories of heat, we were able to estimate, albeit crudely, the fin whale's rate of metabolism. The figure we got was, like that for the harbor porpoise, significantly above the curve for terrestrial mammals. On a weight-for-weight basis, however, the fin whale's metabolic rate is even lower than that of sloths, which have a rate reflecting their lethargic movements.

When one takes into consideration both the large whales' lower absolute metabolic rate and their ability to accumulate a food reserve in the form of blubber, it becomes evident that all large whales are relatively independent of local food supplies. They can satisfy their energy needs for three to six months simply by living off half of their supply of blubber. This leaves them free to feed in the rich polar seas and to give birth to their young thousands of miles away in warm tropical waters.

In comparison the small harbor porpoise leads a much more restricted life. Its higher metabolic rate makes its need for food much more pressing and limits the time available for migration. Moreover, its higher rate makes it more difficult for it to hold its breath: when the porpoise dives to search for food, it must depend on such oxygen as it can take along. Just how the porpoise makes do with what oxygen it has become the focus of our next investigations.

We already knew that the mammals' high-energy way of life had been made possible by a correspondingly larger consumption of oxygen; this in turn depended on a parallel evolutionary development of respiratory and cardiovascular systems that were more competent than those of amphibians and reptiles. When the terrestrial mammals that were ancestral to the cetaceans abandoned the land (with its unlimited access to oxygen) in favor of an aquatic life, a still further evolutionary development favoring greater oxygen storage and transport was called for. How had this been accomplished?

Consider the sperm whale, the cetacean with one of the most impressive of all underwater capabilities. Whereas the porpoise can stay submerged for only a

few minutes, sperm-whale dives can last for as long as an hour. Yet even the porpoises' briefer underwater performance puts an unassisted human diver to shame. The answer, for large and small cetaceans alike, is that they can take more oxygen down with them than a human diver can.

One factor in this performance is the cetaceans' considerably greater volume of blood: up to two or three times more blood per unit of body weight than is the case in human beings. The cetaceans' blood also has a somewhat greater oxygen-carrying capacity than human blood. In addition the whale carries a further store of oxygen in combination with myoglobin in its muscles. The myoglobin (a protein that is actually a subunit of the oxygen-carrying

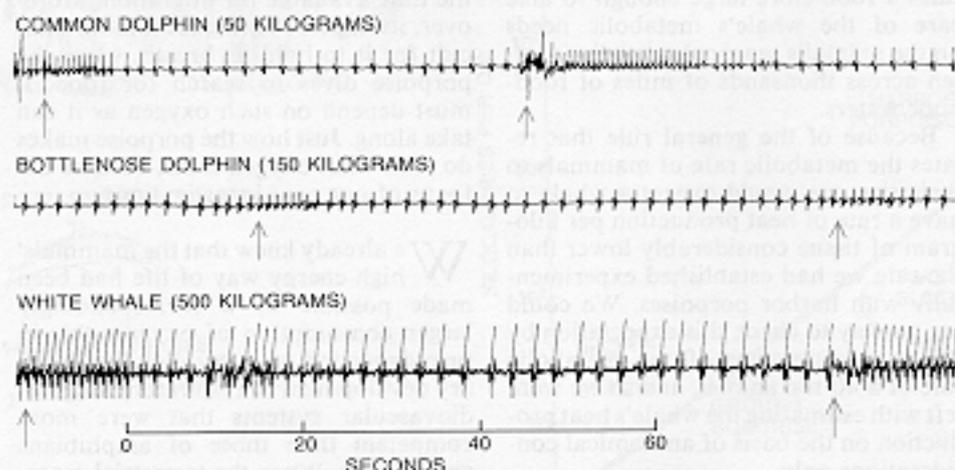
hemoglobin of the red blood cells) is responsible for the muscles' characteristic dark red color. Indeed, in some cetacean species there is enough myoglobin in the muscles to carry more than half again as much oxygen as the animal's red blood cells do.

When a whale comes to the surface after an extended dive has depleted both these oxygen stores, its highly efficient vascular system rapidly passes the blood through the lungs for oxygen replenishment with the aid of a particularly powerful heart and a circulatory system that features large networks of capillaries (*retia mirabilia*, or "wonderful nets") and large sinuses in the venous system. Although the exact function of these unusual structures can only be guessed at, it seems likely that they facilitate the

rapid reloading of the red blood cells with oxygen. The fast circulation of the blood is reflected in the fact that while the animal is breathing at the surface it has a higher heart rate. This constitutes a fundamental respiratory difference between cetaceans and terrestrial mammals, whose breathing is usually regular and whose blood flow is relatively smooth.

Meanwhile the recharged red blood cells convey part of their oxygen load to any oxygen-depleted myoglobin in the animal's muscle cells. The transfer is easy because myoglobin has a much lower oxygen-loading tension than hemoglobin. Myoglobin thus binds oxygen more tightly than hemoglobin does, inhibiting it from reentering the circulatory system. It is best to think of the myoglobin-bound oxygen as a purely local oxygen resource, available to the surrounding muscle in the course of a dive. Most of it lies within easy diffusing distance of the muscle cells' mitochondria: the intracellular particles where respiration occurs.

Myoglobin is present in the muscles of terrestrial mammals too, but in much smaller amounts. One of its functions in terrestrial mammals is to serve as a local oxygen source for muscle during contraction, when intramuscular pressure tends to throttle capillary blood flow, cutting off the normal supply of oxygen carried by red blood cells. It is evident that the much more abundant supply of oxygen carried by cetacean myoglobin is another example of a diving adaptation that has arisen through the enhancement of a preexisting mammalian capability.



TOOTHED WHALES' HEARTBEATS WERE RECORDED, by telemetry for bottlenose dolphins such as the one carrying an ultrasonic transmitter in the photograph at the top and directly in the case of the remaining electrocardiograms. These show the heartbeat of a 50-kilogram common dolphin (*Delphinus delphis*) and that of a 500-kilogram white whale (*Delphinapterus leucas*). Arrows in color indicate the start of inhalation in each instance. The heartbeat of all three animals accelerated as they inhaled, an action that would have accelerated oxygen uptake. Thereafter, whether the animals were diving, were resting on the surface or were out of the water altogether, their heartbeat decelerated until a basal rate was reached. Earlier experiments (conducted by the physiologist P. F. Scholander with seals and ducks under restraint) had shown a radical decrease in heart rate following involuntary submergence, but the three cetaceans did not show such a decrease. The authors' findings suggest that the reaction of animals under restraint was one of alarm as they were involuntarily submerged.

When we began our study of cetacean diving capabilities, a widely accepted explanation of the long dive times characteristic of aquatic animals already existed. It derived from experiments done by P. F. Scholander of the Scripps Institution of Oceanography demonstrating that when a restrained animal (a duck or a seal) was forcibly submerged, its heart rate decreased abruptly and the reduced blood flow was shunted in such a way as to largely shut off the circulation of blood to the animal's muscles and viscera. The reduced cardiac output went almost entirely to the brain and the heart, organs that were considered to have a need for a continuous supply of oxygen. (For example, a few seconds' interruption in the flow of blood to the human brain causes unconsciousness.) All that was available to the oxygen-deprived muscles of Scholander's subjects was an anaerobic energy pathway that resulted in an accumulation of lactic acid as a metabolic by-product.

This logical sequence of events has become the standard textbook explanation of the extended diving capacity not

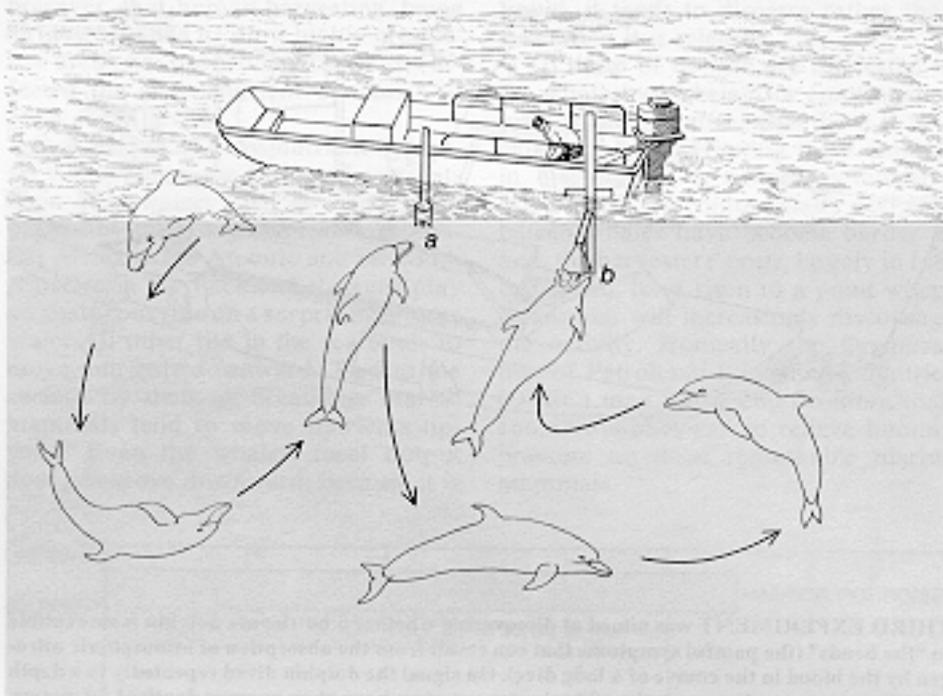
only of ducks and seals but also of other waterfowl and of marine mammals in general. There were, however, virtually no physiological data for cetaceans. Indeed, the one time a restrained porpoise was experimentally deprived of air in this way it went into shock and died. We undertook to collect evidence on this hypothetical diving reflex from free-swimming cetaceans.

As a first step we fitted porpoises with ultrasonic transmitters so that we could monitor the animals' heartbeat as they swam. We were surprised, first of all, to find no evidence of the abruptly diminished heartbeat on diving that was characteristic of forcibly submerged ducks and seals. The porpoises seemed to maintain a relatively high level of general circulation throughout their dive. We therefore set out to find a more direct measure of how quickly the porpoises depleted their store of oxygen while they were submerged.

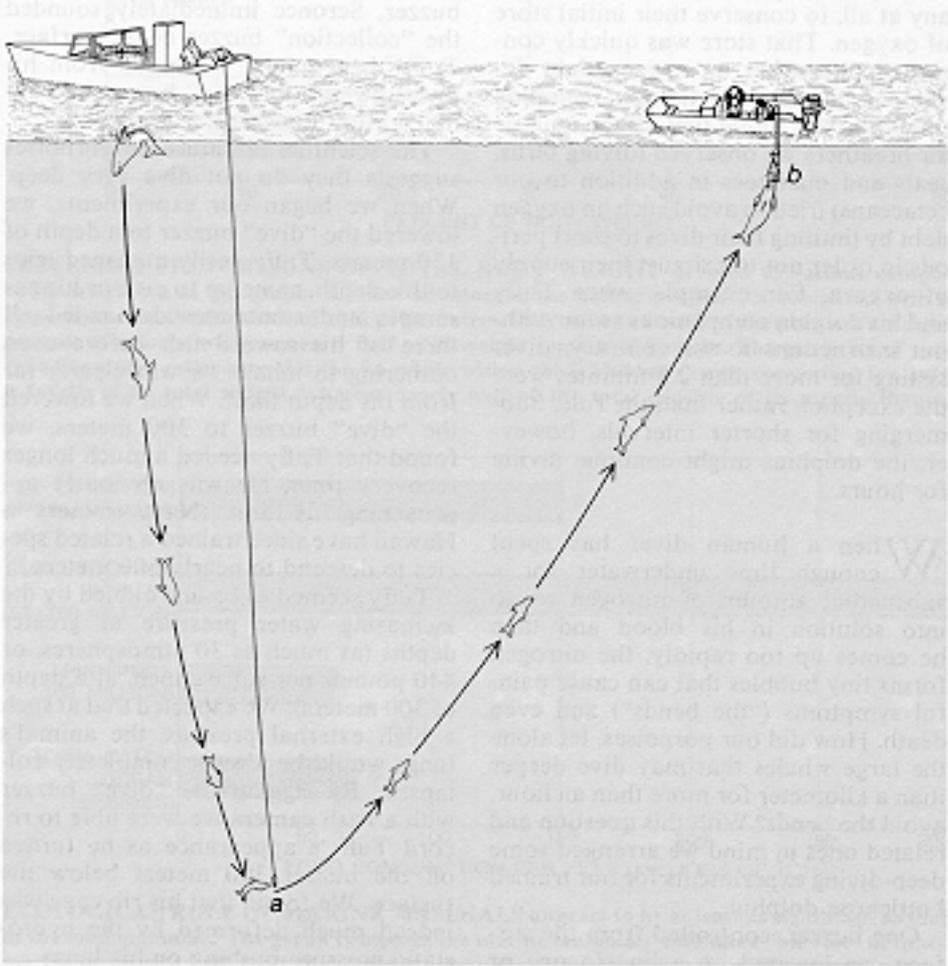
Fortunately for us the U.S. Navy at that time was training bottlenose dolphins (*Tursiops truncatus*) to act as messengers for deep-sea divers. One Navy trainer, William Scrone, undertook to train one of the dolphins, named Tuffy, to exhale on command into an underwater funnel so that we could collect the expired breath for analysis. An underwater buzzer was Tuffy's signal to perform. If he pushed his snout against the buzzer and exhaled into the funnel, he received three fish as a reward. Another buzzer served as a signal for Tuffy to begin his dive. By varying the interval between the sounding of the "dive" buzzer and the "collection" buzzer we could obtain air samples over an entire range of breath-holding times. Tuffy could easily hold his breath for as long as six minutes, but after a much shorter time he grew increasingly impatient as he waited for the "collection" buzzer to sound; looking up through the water at us, he would even gnash his teeth.

Studying the data Tuffy provided us, we were surprised to see how quickly the oxygen concentration in the porpoise's lungs dropped off. For example, after only three minutes the gas in Tuffy's lungs had fallen from its normal atmospheric level of 21 percent oxygen to less than 2 percent. For the remaining three minutes of these "easy" dives, therefore, he was virtually anaerobic. After such a breath-hold he would not perform again until he had spent four or five minutes breathing rapidly on the surface, obviously repaying the oxygen debt he had just incurred. After dives of two minutes or less, however, he would readily dive again following only a brief breathing interval at the surface.

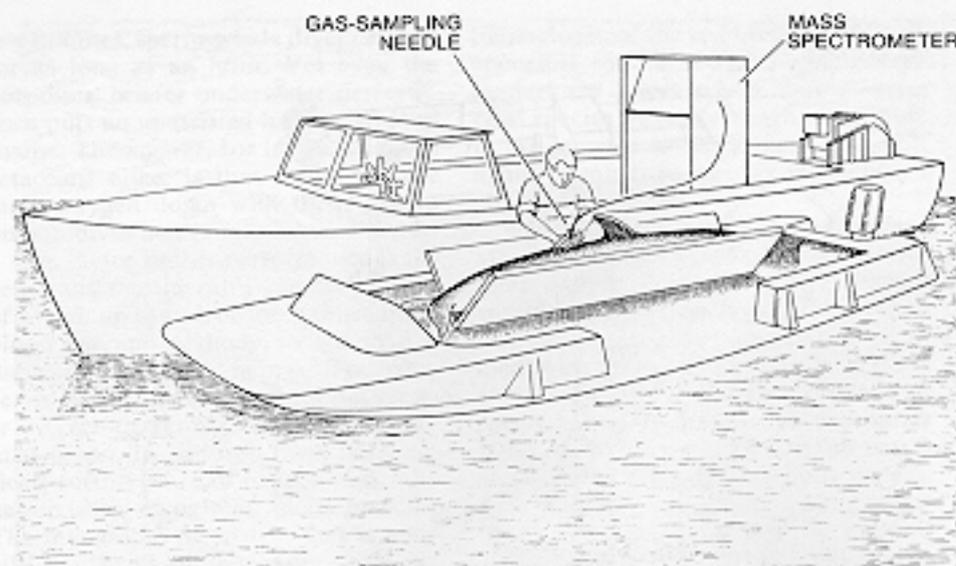
We could now understand why we had failed to observe an abruptly diminished heart rate when our ultrasonically equipped porpoises dived. Like Tuffy, they had made only a partial effort, if



NAVY-TRAINED DOLPHIN TUFFY was taught as is shown here to submerge when one buzzer (a) sounded and to stay underwater until a second buzzer (b) sounded. Tuffy then swam to the second buzzer, touched it with his snout and exhaled into a funnel. After he exhaled he received a reward of three fish. The study showed that Tuffy could remain underwater comfortably for six minutes but had exhausted almost all his oxygen supply within three minutes.



DEEP-DIVING ABILITY OF THE DOLPHIN was tested in a second experiment. First a buzzer and a switch (a) were lowered to a depth of 150 meters. Turning the buzzer on was Tuffy's signal to dive and switch it off. The dolphin then returned to the dinghy, to touch a second buzzer (b) and claim his reward. Tuffy had no difficulty with 150-meter dives but needed time at the surface to recover after turning off the "dive" buzzer at a depth of 300 meters.



THIRD EXPERIMENT was aimed at discovering whether a bottlenose dolphin is susceptible to "the bends" (the painful symptoms that can result from the absorption of atmospheric nitrogen by the blood in the course of a long dive). On signal the dolphin dived repeatedly to a depth of 100 meters, spending more than 20 minutes out of an hour at an average depth of 50 meters. The animal then swam onto a floating couch next to a boat containing a mass spectrometer; the experimenters pushed a gas-sampling needle through its blubber layer and into its muscle. The dolphin's muscle proved to be saturated with nitrogen to an extent dangerous to a human diver. The authors attribute the dolphin's freedom from the bends to a diving adaptation.

any at all, to conserve their initial store of oxygen. That store was quickly consumed; thereafter an oxygen debt developed in all their tissues, including the brain. We found that all the aquatic air breathers we observed (diving birds, seals and manatees in addition to our cetaceans) tried to avoid such an oxygen debt by limiting their dives to short periods in order not to exhaust their supply of oxygen. For example, when Tuffy and his dolphin companions swam without instructions to the contrary, dives lasting for more than 2.5 minutes were the exception rather than the rule. Submerging for shorter intervals, however, the dolphins might continue diving for hours.

When a human diver has spent enough time underwater for a substantial amount of nitrogen to go into solution in his blood and then he comes up too rapidly, the nitrogen forms tiny bubbles that can cause painful symptoms ("the bends") and even death. How did our porpoises, let alone the large whales that may dive deeper than a kilometer for more than an hour, avoid the bends? With this question and related ones in mind we arranged some deep-diving experiments for our trained bottlenose dolphin.

One buzzer, controlled from the surface, we lowered on a line to one or another of a variety of chosen depths. Tuffy was trained to swim down to the buzzer when we sounded it and turn it off by pushing a switch with his snout. When the animal turned off this "dive"

buzzer, Scronce immediately sounded the "collection" buzzer at the surface. Tuffy then quickly swam up from his dive to the "collection" buzzer and exhaled into the collection funnel.

The scientific literature on porpoises suggests they do not dive very deep. When we began our experiments, we lowered the "dive" buzzer to a depth of 150 meters. Tuffy easily managed trips to this depth, came up to give us his gas sample and sometimes demanded all three of his reward fish before even bothering to inhale; he was clearly far from his depth limit. When we lowered the "dive" buzzer to 300 meters, we found that Tuffy needed a much longer recovery time. He was obviously approaching his limit. (Navy trainers in Hawaii have since trained a related species to descend to nearly 600 meters.)

Tuffy seemed to be untroubled by the increasing water pressure at greater depths (as much as 30 atmospheres, or 440 pounds per square inch, at a depth of 300 meters). We expected that at such a high external pressure the animal's lungs would be almost completely collapsed. By rigging the "dive" buzzer with a flash camera we were able to record Tuffy's appearance as he turned off the buzzer 300 meters below the surface. We found that his rib cage was indeed much deformed by the hydrostatic pressure pushing on his lungs.

We next tried to give another trained dolphin the bends by directing it to dive repeatedly. As soon as its surface breathing indicated its recovery from the previous dive we would send it down

again, until in the course of an hour it had remained below 50 meters for more than 20 minutes. The dolphin still showed no apparent sign of distress. Then, with the help of Robert S. ("Red") Howard of the Scripps Institution, we measured the actual amount of nitrogen accumulated in the animal's muscles as the result of these many consecutive submergences. It was no easy task. First the dolphin was trained after such a sequence of dives to swim onto a floating couch alongside our boat. That enabled us to insert a small gas-sampling needle through its blubber layer into the underlying muscle. A tube led from the needle to a mass spectrometer (aboard a second boat) that could directly measure the concentration of nitrogen dissolved in the muscle. Doing all this while at sea in small boats makes a substantial demand on the experimenter's patience.

Again we got a surprise. The concentration of dissolved nitrogen in the dolphin's muscle tissue was indicative of a degree of supersaturation that in a human diver would have been dangerous. We could only conclude cetaceans can tolerate nitrogen concentrations that would give a human diver the bends. How they do so we cannot yet say, but the capability is, of course, what one should probably expect of a well-adapted order of deep-diving mammals.

What has the evolution of this superior diving capacity meant to the ecology of the world's oceans? Some aquatic mammals, for example the sea otter and the manatee, have evolved to more or less nibble at the edges of the oceanic food chain. Others, such as the carnivorous suborder of pinnipeds (seals, sea lions and walrus), are more at home in the open ocean but still need to go ashore for mating and reproduction. Only cetaceans have evolved to deal with a fully oceanic way of life. What they gained thereby is a vast food supply in the form of other marine animal life. The whales and porpoises have established themselves as harvesters at the very top of the marine food chain.

The success of these physiologically adept marine predators may be judged by their numbers. Many species of cetaceans are commonly thought to be in imminent danger of extinction; this conclusion is based largely on a misperception of their current population levels. For example, the total number of blue whales is greater by at least one order of magnitude than the total number of such endangered terrestrial species as the orangutan or the giant panda. In fact, most cetacean species exist in substantial numbers, and some populations are even reaching the level where they serve as entertainment. Whale watching is a growing winter sport on the California coast, and in the Atlantic excursion boats putting out from the Boston area

assure tourists of frequent whale sightings after a trip of only an hour or two.

Sperm whales were probably twice as numerous in the generations before modern whaling began than they are today, but even so their modern number is far from low. The British cetologist Malcolm R. Clarke reckons the present population of sperm whales at about a million (others say 1.5 million) and estimates that they annually consume some 100 million tons of deep-sea squid, an oceanic resource that is otherwise scarcely touched. It is instructive to compare the predation of this single cetacean species with the total of the world's annual fishery yields: 60 to 70 million tons.

An annual-consumption estimate for the next-ranking aquatic mammals, the pinnipeds, has been made by Michael E. Q. Pilson of the University of Rhode Island. Pilson's estimate has the advantage of better-known population numbers, since pinnipeds must come ashore for breeding and can be more accurately counted than the 70 cetacean species. Censuses have been taken at most pinniped breeding areas, and their annual food needs are known from the feeding of captive species. Pilson estimates that the seals, sea lions and walrus consume 60 million tons of fish per year, or approximately the amount harvested by man. Extrapolating from the number of porpoises killed annually by the operations of the tuna fishery in the eastern Pacific, the worldwide stock of porpoises and dolphins may approach 100 million. Even if the population is only half this size, its annual food consumption must total some 150 million tons.

Such large numbers may come as a surprise, and we hasten to add that they must be considered tentative. Indeed, unless oceanic animals are harvested by man either accidentally or deliberately, the size of their populations is not likely to be well known. Two examples will suffice. Until recently Fraser's dolphin was known only from a single skeleton collected in 1954. Now that people are aware of the species, Fraser's dolphins have been sighted in schools numbering in the hundreds in Philippine waters, and the animals appear to be widely distributed in the tropical zones of the Pacific and Indian oceans. The North Pacific population of Dall's porpoise was estimated at only a few tens of thousands. Since it became known that Japanese fishermen kill as many as 10,000 Dall's porpoises every year, new surveys have raised the population estimate to a million or more.

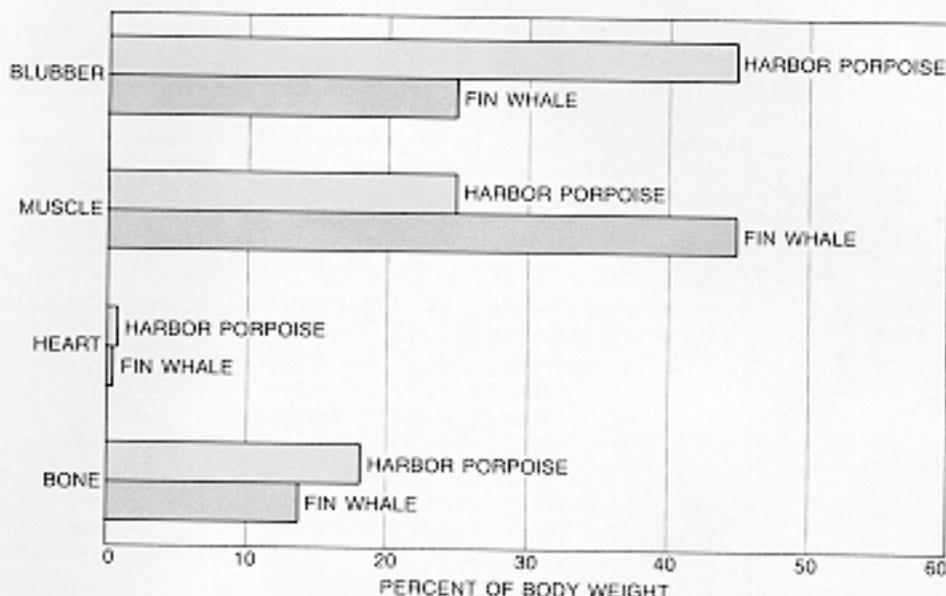
Thus it is evident that the cetaceans' role in marine food chains is far greater than man's. This does not mean that man's overfishing has not heavily depleted local fish stocks, as it has the stocks of some whale species, particularly in the Antarctic. It does indicate,

however, that human harvesting, being largely confined to a few highly productive areas, has probably not seriously affected the gross nutrient dynamics of most ocean areas.

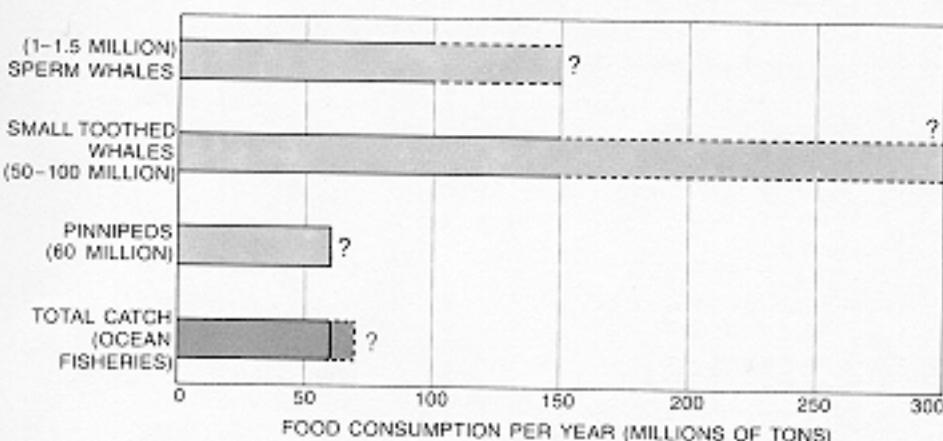
One feature of gross nutrient dynamics is upwelling: the lifting of nutrients from deep waters such as that accomplished by the rising currents off southern Africa in the Atlantic and off South America in the Pacific. Cetaceans play an analogous role on a surprisingly large scale. All other life in the sea tends to move nutrients downward. Tied to the surface by their air-breathing, marine mammals tend to move nutrients upward. Even the whales' fecal output does not move downward: because it is

liquid, it tends to disperse rather than sink when it is released.

To those of us who are interested in the whales' well-being for emotional as well as biological reasons there is new cause for hope. Hunting these animals in distant seas is an energy-intensive activity. As the commercially desirable baleen whales have become harder to find, the harvesters' costs, largely in fuel consumed, have risen to a point where economics will increasingly discourage the activity. Ironically the Organization of Petroleum Exporting Countries (OPEC) may in the end do more than conservationists can to relieve hunting pressure on these remarkable marine mammals.



DIFFERING PROPORTIONS OF TOTAL BODY WEIGHT devoted to various components are shown in this graph. A small odontocete, the harbor porpoise, is compared with a large mysticete, the fin whale of cold polar waters. Only about a fourth of the porpoise's weight consists of muscle, whereas nearly half of its weight consists of blubber. The geometry of surface-to-volume ratios provides the fin whale with a thick blubber sheath accounting for only a fourth of its total weight, whereas nearly half of the total consists of its muscle tissues.



ECOLOGICAL ROLE OF MARINE MAMMALS appears to be at least as significant as that of the land mammals. The graph compares the marine mammals' estimated "harvest" of other marine organisms with the total recorded international catch of fish. A million sperm whales consume some 100 million tons of squid each year (more if sperm whales are actually more numerous). The 50 to 100 million porpoises and other small odontocetes consume between 100 and 300 million tons of fish. Estimates of consumption by whales other than the sperm are less reliable, but seals, sea lions and walrus consume 60 million tons of fish annually. The total catch by marine fishermen worldwide is somewhere between 60 and 70 million tons (color).