

3. Diving dolphins

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DIVING DOLPHINS

The range of cetacean body size is immense. The smallest dolphin neonate may weigh as little as 3 kg while the largest blue whale (Bryden 1972; Lockyer 1976) may weigh almost 200 000 kg – over 60 000 times as large. These air-breathing mammals are present in all the oceans of the world, and four of the smaller species live only in freshwater river systems. Adapted to a completely aquatic existence, tied to the surface by the necessity to breathe air, and lured to the depths in search of rich food resources required for a high rate of metabolism, the whale family not surprisingly has produced the champions among mammalian divers.

Some cetaceans feed along the polar ice cap, even venturing inside pack ice and surfacing to breathe in polynyas or leads where pack ice is broken. Others swim near the equator over the deepest waters in the world, while still others hunt for food in the mangrove shallows of the tropics. With such diversity in their sizes and habitats, considerable ranges in any cetacean's diving capability might be expected.

DEPTHS OF DIVES

Historical background

Until recent years, the only information about deep diving cetaceans had been accumulated from observers attached to expeditions and whaling vessels. During the 19th century, William Scoresby (1820) studied diving by measuring the runout of the harpoon lines. He concluded that whales could dive at least to 50 fathoms (about 100 m). According to Scammon (1874), a whale could sometimes runout a mile of harpoon line, but dives were not likely this deep. He observed that harpooned bowhead whales often went to the bottom of the Arctic Ocean and Bering or Okhotsk seas in areas not over 100 fathoms (about 200 m) deep. Such whales sometimes stayed down for an hour or more (Scammon 1874).

From the 1940s through the mid-1960s widely differing opinions were expressed as to the diving depths of cetaceans. Ommanney (1932) thought that whales seldom dived deeper than 40 m. Laurie (1933) argued that the

depth limit for krill-eating species should be about 100 m, since krill is seldom found below that depth. Scholander (1940) attached tiny capillary pressure manometers to harpoon lines. The maximum dive recorded for a harpooned fin whale was to 355 meters. Others have concluded that dolphins and porpoises are not deep divers (Slijper 1962). Tomilin (1957) and Kleinenberg, Yablokov, Bel'kovich and Tarasevich (1964) deduced that belugas dive to depths no greater than 20 to 40 m. Cadenat (1959, from Norris, Baldwin, and Samson 1965), based on stomach contents, suggested that bottlenosed dolphins might dive to 200 m. Matthews (1952) expressed the view that there is theoretically no limit to the depth a cetacean could plumb.

Modern studies of diving depth

Even in 1986 there are published reports of diving depths in only a few species. We do know, however, that some marine dolphins and small toothed whales such as belugas and pilot whales are capable of deep dives, and, based on reports of their entanglement in deep sea cables (Heezen 1957), few cetologists doubt that the sperm whale is capable of diving deeper than 1000 m (see Table 3.1).

Recently, two methods have been employed to assess diving depth in small cetaceans. The first technique (Ridgway, Scronce, and Kanwisher 1969; Ridgway 1972) involves training a captive animal to dive to a test switch in the open ocean (Fig. 3.1). The second technique involves attaching a recorder or telemetry device to a dolphin at sea (Evans 1971).

In the first method, the dolphin is trained to dive on acoustic signal to a switch located at the end of a long marine cable. The switch is enclosed in a pressure housing containing the acoustic signal, a hydrophone, a pressure transducer, and a plunger that the dolphin can press to activate the switch. To earn food reward (typically, small fish such as Columbia River smelt, *Thaleichthys vetulus*, Pacific mackerel, *Scomber diego*, or herring, *Clupea harengus*), the dolphin must press the plunger at the end of the cable to turn off the signal, then return to the surface for a fish.

When the trainer sounds the acoustic dive signal, the dolphin usually blows several times. A stopwatch is started on the final blow (exhalation and inhalation cycle) as the animal dives. When the dolphin presses the plunger, thus turning the sound off, the elapsed time is recorded as descent time. When the animal reaches the surface, the stopwatch is stopped, and descent interval is subtracted from total dive time to yield ascent time. In one series of experiments (Fig. 3.2), a dolphin was trained to exhale into an underwater funnel so that its exhaled breath could be analysed (Ridgway *et al.* 1969). In another series, two bottlenosed dolphins were trained to slide onto a rubber couch after completing 25 dives in rapid succession (Ridgway and Howard

TABLE 3.1. Observed depth and duration of dives for some cetaceans

| | Depth (m) | Duration (min) | Method* | References |
|------------------------------------------------|--------------|-------------------|---------|---------------------------------------------------------|
| Sperm whale <i>Physeter</i> | 1136 2250 | 75 | E A | Heezen (1957) Whitney in Norris and Harvey (1972) |
| White whale <i>Delphinapterus</i> | 647 | 18 | T | Ridgway <i>et al.</i> (1984) |
| Pilot whale <i>Globicephala</i> | 610 | 15 | T | Bowers and Henderson (1972) |
| Bottlenose dolphin <i>Tursiops</i> | | | | |
| Pacific variety | 535 | 8 | T | McSheehy, personal communication (1981) |
| Atlantic variety | 390 | 8 | T | Ridgway and Scronce, unpublished observations (1980) |
| Fraser's dolphin <i>Lagenodelphis</i> | 500 | | F | Robinson and Craddock (1983) |
| Fin whale <i>Balaenoptera</i> | 355 | 20 | H | Scholander (1940) |
| Killer whale <i>Orcinus</i> | 265 | | T | Bowers and Henderson (1972) |
| Common dolphin <i>Delphinus</i> | 260 | 5 | R | Evans (1971) |
| White-striped dolphin <i>Lagenorhynchus</i> | 215 | 6 | T | Hall (1970) |

*Methods used to determine the depths were as follows: A = acoustic recording; T = trained free-swimming dives; R = recorder attached; E = entangled in submarine cable; H = pressure sensor attached to harpoon line; F = feeding habits.

1979). A mass spectrograph probe was inserted into their muscle through a hypodermic needle to measure partial pressure of nitrogen.

In the initial studies (Ridgway *et al.* 1969), a male *Tursiops* from the Gulf of Mexico reached a depth of 300 m. In subsequent tests (Ridgway and Scronce 1980, unpublished observations), a female of the same species (Atlantic variety) reached 390 m. In additional tests, McSheehy (personal communication 1981) dived a trained *Tursiops* to a depth of 535 m.

Hall (1970) induced a trained *Lagenorhynchus* that had been captured off Southern California to dive as deep as 215 m. Bowers and Henderson (1972) drilled a cooperative *Globicephala* that reached 610 m and an *Orcinus* that dived to 265 m. White whales trained to dive on command (Ridgway, Bowers, Miller, Schultz, Jacobs, and Dooley, 1984) in the open ocean remained submerged as long as 15 min and 50 sec and dived as deep as 647 m. Other than records of sperm whales (Table 3.1) entangled in deep sea cables

Kooyman and coworkers (Kooyman, Billups, and Farwell 1983) have developed recorders for monitoring diving activity—a time-depth recorder and a depth histogram recorder. These devices have been attached to pinnipeds and birds, but, to date, no cetacean studies have been done with such recorders.

HAZARDS OF DIVING

We know that dolphins dive to considerable depths. For an air-breathing mammal, diving poses potential problems and several questions immediately arise. How do dolphins cope with the crushing effects of pressure? How do they avoid the bends when making rapid, deep dives? How do they avoid the many additional problems that plague human divers, such as high pressure nervous syndrome (HPNS) and nitrogen narcosis?

We know a good deal about the answer to the first question and almost as much about the second one, but we are almost completely ignorant as to how they avoid HPNS and we know nothing about their susceptibility to nitrogen narcosis.

The effects of pressure

Although several authors have suggested that cetaceans exhale before descending and dive with lungs nearly empty or only partially full of air (Slijper 1962; Andersen 1966) and this assertion has often been repeated (cf. Clarke 1970; Eisenberg 1981), close observation of trained dolphins at the outset of many dives shows that such suggestions are unfounded. Norris *et al.* (1965) gave the following description: 'After the start command was given, "Pono" took one or two breaths, including a characteristic one just before submergence, a quick breath that often broke the normal breathing rhythm; then she dove with her lungs filled...' In the experiments of Ridgway *et al.* (1969) and Ridgway and Howard (1979), the dolphins also dived with lungs filled. Scholander (1940) states, 'It is a general observation that the whales dive after an inspiration.'

Full lungs, however, have only a slight effect on the compression of the dolphin's thorax as it dives. In accordance with Boyle's Law, the volume of a given quantity of gas varies inversely as the pressure on it. A dolphin diving with 10 litres (L) of air has only one L of gas in its lung at 100 m depth. The amount, in fact, is less than one L, because some of the oxygen and some of the nitrogen will have gone into the blood stream on the way down—the oxygen bound to haemoglobin and the nitrogen in solution. If the dolphin began the dive with lungs half filled (5 L), the gas volume at 100 m would be only 500 ml and less. The compression with respect to total lung volume would be 95 per cent rather than 90 per cent.

To compensate for the loss of 90 per cent of its gas volume the dolphin

thorax must collapse. The human diver is limited in his ability to expand and therefore to collapse his thorax. Even trained breathhold divers experience a condition called 'squeeze' at depths of 30 or 40 m and risk serious injury or death in diving deeper; however, by an almost superhuman effort one champion diver, Jacques Mayol, made a dive to 100 m. Morphological alterations in structure have made the dolphin immune to the effects of 'squeeze'. The dolphin diaphragm is positioned more obliquely than in other mammals. Many of the dolphin's ribs are floating, that is, they have no connection to the sternum and most of those that do connect make contact by long cartilages. The dolphin thorax is flexible; because of this flexibility lung and chest compliance are not limited, and no resistance is offered to the sea's pressure.

Thus, when the trained bottlenosed dolphin, 'Tuffy,' pressed a plunger on his diving test switch activating a camera to take his picture at 300 m depth, the collapse of the chest was apparent in the resulting photograph (Ridgway *et al.* 1969; Fig. 3.3).

Humans can have trouble clearing their ears or equalizing the pressure difference between that in the middle ear and in the water. This is especially difficult if the diver has a cold. Failure to clear properly on descent or ascent can result in severe pain, ear popping, tinnitus, and bleeding from the ear canal or nasal sinuses. The diving women of Japan, called Ama, often have



FIG. 3.3 A bottlenosed dolphin pushes the plunger on the test switch at a depth of 300 m. Thoracic collapse is evident, especially in the area behind the left flipper. The photograph was taken with an underwater camera that was triggered when the dolphin pressed the test switch plunger.

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sinusitis, rhinitis, hearing loss, opacity of the tympanic membranes, chronic otitis media, and stenosis of the Eustachian tubes (Strauss 1969).

Dolphins show some structural variations that may help them to cope with the problem of equalizing pressure in the ear, sinuses, and nasal system. A robust Eustachian tube leads from each side of the nasal cavity to the ipsilateral middle ear. The dolphin middle ear is invested in a massive venous plexus. The cranial bony sinuses are lined with venous plexuses that can probably expand to fill space in response to unequalized pressure changes (Reysenbach de Haan 1957).

Ridgway (1972) has listed four specialized characteristics that appear to vary among odontocete species, depending on their requirements for deep diving: (1) flexible thoracic structure that allows the thorax to collapse as hydrostatic pressure increases; (2) lungs containing large amounts of elastic tissue that stretches on inspiration, and at exhalation allows the lungs to become atelectic without separating from the chest wall; (3) a resilient trachea that permits the respiratory passages to collapse well beyond the limits of sea-level dead space volume (probably, in fact, to collapse completely); and (4) large distensible veins, venous sinuses, and retia mirabilia that can engorge with blood and fill space as respiratory air is compressed during a dive.

The rete mirabile

Early anatomists such as Edward Tyson (1680) and John Hunter (1787) dissected small cetaceans and hazarded their opinions that features such as the vascular plexuses called retia could function to equilibrate pressure during deep dives. In addition to pressure relief, Breschet (1836, cited by Wilson 1879) also thought the retia might function to store oxygenated blood, as did Ommanney (1932). Erikson (cited in Scholander 1940) suggested that the thoracic rete might serve as a shunt through which blood may flow while bypassing muscle and peripheral tissue during diving. No anatomical or physiological evidence has been obtained for Erikson's theory. Cunningham (1877) and Nakajima (1961) reasoned that the thoracic rete functioned to cushion the spinal cord and maintain a constant thermal environment for this part of the nervous system. Nakajima (1961) identified 12 different regions of retia in *Tursiops* and *Grampus* and suggested that a pressure adjustment function was more likely than one of oxygen storage.

Scholander (1940) rejected a working hypothesis that the large rete in the dorsal portion of the thorax could swell to take up space left by the compressing lung air during a dive. He argued that 'the intrathoracic plexuses are too small in capacity to be of any significance as swelling organs.' Hui (1975) experimented with a dead *Delphinus* in a pressure chamber. Based on the results of these experiments, Hui suggested that the thoracic rete might engorge slightly to reduce from 86 per cent to 79 per cent the percentage of pleural cavity volume temporarily displaced by thoracic

collapse, and displacement of abdominal viscera during a dive to 69.7 m (7 atmospheres).

In some mammals the internal carotid artery is the major supplier of blood to the brain. This is not the case in the dolphin which supplies its brain through the massive thoracico-spinal retia (Viamonte, Morgane, Galliano, Nagel, and McFarland 1968). In its course from heart to brain, blood passes through the retia. This arrangement is thought to have a pressure-damping function for the cerebral circulation (Nagel, Morgane, McFarland, and Galliano 1968).

McFarland, Jacobs, and Morgane (1979) noted the complete absence of any role of the internal carotid artery or vertebral arteries in supplying blood to the dolphin brain and the absence of a Circle of Willis. The entire cerebral blood supply comes through a thoracico-spinal rete, supplied by intercostal and posterior thoracic arteries. Vogl and Fisher (1981a), in a study of *Delphinapterus* and *Monodon*, concluded that the carotid artery is closed at a level just proximal to the carotid rete and has no direct involvement with the cerebral blood supply. Vogl and Fisher (1981b) summarize additional findings as follows: 'Circulation to the brain is effected by two pairs of arteries originating from intracranial retia. The rostral pair supplies most of the forebrain (prosencephalon) and hindbrain (rhombencephalon). The circulatory pattern is characterized by (1) complete independence of anterior cerebral arteries (no anastomoses); (2) extensive cortical supply by the anterior choroidal arteries; (3) absence of subdural communicating vessels between rostral and caudal trunks; (4) union of caudal trunks to form a small basilar artery; and (5) absence of vertebral arteries and hence of a vertebral basilar system.' In another paper, Vogl, Todd, and Fisher (1981) found that, despite the presence of large nerve trunks coursing through the rete, the rete mirabile is not under extensive nervous control in *Monodon*. They suggest that any vasomotor activity may be in response to catecholamines or other vasoactive agents in the circulation (Vogl *et al.* 1981).

Ridgway and Howard (1982) suggested that the rete might play some role in the dolphin's resistance to bends while making many repeated dives in the ocean. The large thoracico-spinal retia are dorsally positioned and well placed to trap bubbles that might be generated. Vogl and Fisher (1981b) have shown that the afferent vessels far outnumber the efferent ones. Temporary blockage of even half of these vessels might have little effect on circulation to spinal cord or brain. Krogh (1934) also thought the rete might play some role in protecting whales from bends: 'I suspect that the retia mirabilia of blood vessels present in all deep-diving mammals may have something to do with the mechanism for escaping caisson disease.'

Diving dolphins and the bends

Dolphins are breathhold divers. They do not breathe compressed gas as scuba and 'hard-hat' divers do. For a long time this was thought to be

sufficient explanation of why dolphins do not bend after making numerous dives at sea (cf. Slijper 1962). More recently, we have learned that a skin diver without equipment who repeatedly descends to depth is also in danger of the bends. Our understanding of this problem is due mainly to the studies of Paulev (1965, 1967). In one study, he made 60 dives to a depth of 20 m, spending about two minutes on the bottom each time, during a five hour period. He developed the symptoms of bends: pain in the joints, breathing difficulties, blurred vision, and abdominal pains. He was put in a recompression chamber at 6 atm. pressure and his symptoms rapidly disappeared. The treatment was continued according to U.S. Navy staging tables. He was brought to one atm. for 19 h 57 min.

Paulev's treatment was completely successful but there are other cases where this has not been so (Schmidt-Nielsen 1975). In another study, Paulev (1967) showed that nitrogen accumulated in the tissues when humans made repeated breathhold dives. The nitrogen tensions exceeded those allowable for 'no decompression dives'. The studies provide a possible explanation for Taravana, a syndrome of Polynesian divers of Tuamotu archipelago who show central nervous symptoms that appear to be bends (Strauss 1969).

Two series of experiments with trained dolphins in the open ocean have helped in the understanding of the problem with respect to diving dolphins (Ridgway *et al.* 1969; Ridgway and Howard 1979; also see Kanwisher and Ridgway 1983).

Scholander (1940) had proposed that alveolar collapse would occur in diving mammals at about 100 m. Such collapse prohibits gaseous exchange during deep dives and possibly protects the mammal against bends and nitrogen narcosis. Actually, this hypothesis was proposed six years earlier by Damant (1934) who stated the following: 'At 100 m the total pressure is about 11 atmospheres absolute, so, at that depth, the whale's lung is compressed until an average alveolus has only one eleventh of the volume it had when the whale left the surface and began to dive. This shrinking of the alveoli must greatly decrease the surface available for diffusion and, in addition, the epithelium of the alveolus must become thicker, still further hindering diffusion. The effect of these changes is to obstruct the entrance of excess nitrogen into the blood when the whale is at a considerable depth and to favor its discharge when the animal is breathing at the surface.'

To test the hypothesis, a trained dolphin, housed in a floating pen in the Pacific about 200 m off Point Mugu, California, was used. For diving tests, the dolphin was called from its pen to swim beside a small boat to a test buoy located in deep water about 8 km offshore. The dolphin usually positioned itself on the stern wave of the boat to get a free ride by 'surfing' most of the way. The dolphin, a male named Tuffy, was trained to dive to the end of a cable 308 m long and press the switch (see Fig. 3.1). When a high-frequency signal was turned on at a control box aboard the boat, Tuffy had to dive and press the switch turning off the sound. Immediately, a low-frequency cue

beckoned the dolphin to exhale into an inverted water-filled funnel 50 cm below the surface (see Fig. 3.2). The dolphin was also taught to remain just under the surface in response to a signal and then after a time, up to about six minutes, exhale into the funnel.

Tuffy had been trained to participate in the U.S. Navy Sealab II tests in 1965, delivering items to, and carrying lines between, divers on the sea floor. Ridgway *et al.* (1969) took advantage of Tuffy's experience and had him swim rapidly back and forth between two divers on the bottom at a depth of 20 m. After two to five minutes of such swimming, the low-frequency cue was sounded from the boat and the dolphin returned to exhale in the funnel.

With these methods, expired air was collected from deep dives, surface breathholds, and shallow dives that involved considerable exercise (swimming back and forth between divers). The analyses of oxygen and carbon dioxide after dives and breathholds requiring the same period of time showed that the most oxygen was taken from the lung air when Tuffy swam back and forth at shallow depths. Less oxygen was used on breathholds near the surface, and much less lung oxygen was used when the dolphin dived to depths greater than 100 m.

Although prolonged breathholding is essential for deep diving, this ability alone does not enable the animal to go to great depths. Structural adaptations, such as thoracic collapse (Fig. 3.3), resilient trachea and bronchi, highly elastic lungs, and expandable vasculature, permit air to be compressed away from the alveoli of the lung during the increasing pressure of the dive. When the diving dolphin reaches 100 m, the alveoli and respiratory bronchioles are probably collapsed, and this theoretically prevents more nitrogen from going into the blood and protects the animal from bends.

Open ocean diving studies with a trained dolphin have shown that when making a few very deep dives, a dolphin may be protected from bends by collapse of the respiratory portions of the lung (Ridgway *et al.* 1969). More recent studies have shown that the most common repetitive dive pattern of wild dolphins is to depths shallower than 100 m (Evans 1971). Considering Paulev's (1965, 1967) human studies, Ridgway and Howard (1979) used Workman's (1965) human decompression values to design a repetitive dive schedule for dolphins that would exceed the schedule necessary to produce bends in a human.

Two trained dolphins made 23 to 25 dives to 100 m depth in an hour. Mean dive time was about 90 sec and surface intervals were 1 min. After completion of the dive series, each dolphin slid onto a rubber couch and remained for an hour while a hypodermic needle probe connected to a mass spectrometer sampled muscle nitrogen. Based on these measures, nitrogen tensions as high as 1600 torr were observed (Ridgway and Howard 1979). Assuming no alveolar collapse, levels of 2400 to 2900 torr should have been reached. Therefore, in these two *Tursiops*, it was possible to pick 70 m as the point of respiratory surface collapse.

The study of Ridgway and Howard (1979) also showed that effective muscular circulation was maintained during free dives in the open ocean. This is in contrast to classical findings in seals restrained for submersion (Elsner, Franklin, Van Citters, and Kenney 1966b). Shunting of blood from the extremities to the great vessels during diving permits blood oxygen stores to be used almost exclusively to perfuse the heart and brain and thereby provides for long dive durations. The concept of a reflex-like circulatory redistribution for selective oxygenation of sensitive tissues at the expense of those having greater anaerobic capability has received considerable attention (Scholander 1963; Elsner *et al.* 1966b; Andersen 1966). *Tursiops* (Irving, Scholander, and Grinnell 1941; Elsner, Kenney, and Burgess 1966a; Kanwisher and Ridgway 1983) did not show so marked a circulatory adjustment to diving as did restrained seals. Even though marine mammals have the capability for peripheral vasoconstriction, they maintain an effective intramuscular circulation when diving free in an open ocean environment (Kooyman and Campbell 1972; Ridgway and Howard 1979). Bottlenosed dolphins are not protected by lung collapse from the decompression hazards of dives to depths shallower than 70 m, and the mechanism by which dolphins avoid decompression sickness on dive schedules known to produce the syndrome in man is not yet completely understood.

Lettvin, Gruberg, Rose, and Plotkin (1982) have suggested that the physiology and anatomy of dolphins is less generative of bubble nuclei than that of humans. Mackay (1982) suggests that repetitive diving crushes any bubble nuclei that might otherwise grow to symptomatic size during ascent, but Ridgway and Howard (1982) pointed out that this last suggestion seems to ignore the results of Paulev (1965).

As we mentioned previously, specialized anatomy such as the vascular networks and rete mirabile might make dolphins more resistant to bends. Differences in body chemistry such as a more potent heparin (Abe, Kazama, and Matsuda 1965) or lack of Hageman factor (Robinson, Kropatkin, and Aggeler 1969) might also be involved. Although Scholander (1940) found that bubbles formed just as readily in whale blood, the question of some dolphin biochemical or biophysical resistance to bends deserves further study with modern techniques.

Buoyancy regulation

With a few exceptions, cetaceans swim with a slightly negative buoyancy (Schevill, Ray, Kenyon, Orr, and Van Gelder 1967). If lung air is lost, they tend to sink. Ridgway *et al.* (1969) made some measurements on a freshly dead *Tursiops* weighing 200 kg. With deflated lungs, the animal weighed 10 kg just underwater. When the lungs were fully inflated with 11 L of air, the body was neutral or very slightly buoyant at the surface. As the dolphin dives and the air in its lungs compresses, the animal's body becomes heavier. This

is probably of little consequence to the dolphin, since normal swimming thrust is such that out-of-neutral buoyancy values of these small proportions (0.5 per cent of body weight) are unlikely to be very significant. Of course when a dolphin rests or sleeps at the surface, buoyancy provided by lung air may be quite important.

Clarke (1970, 1978) has given considerable thought to the problem of buoyancy regulation in the sperm whale and the function of the spermaceti organ. He suggested (1970) that the spermaceti organ serves as a buoyancy regulator by cooling as the whale dives. Ridgway (1971) opposed Clarke's theory on physiological grounds, and Norris and Harvey (1972) questioned the idea from several points of view including observed behaviour.

Although Clarke's (1970, 1978) hypothesis is intriguing, it might one day be tested if advances in microelectronics, telemetry, and remote sensing continue. Sensors might be placed in and around the nares and spermaceti organ of a captured whale. The animal could be released and its diving record monitored from a trailing boat. Values of temperature, pressure, and sound production could be transmitted while the whale is on the surface between dives.

RESPIRATION

The blow

Scholander (1940) pointed out that expiration begins just before the whale reaches the surface and before water is cleared off the nostrils (also see Kooyman, Norris, and Gentry 1975). It is this water together with water condensing from the breath that gives the visible blow of whales at sea. Gilmore (1960) has noted that the blow is hardly visible when grey whales exhale slowly. The dolphin blow is visible only at very short range or unusually cold, dry weather. Coulombe, Ridgway, and Evans (1965) showed that unlike most terrestrial mammals, dolphins exhale air that is not completely saturated with water vapour.

In man and most terrestrial mammals, 10 to 30 per cent of the body heat produced is lost in breathing. Because dolphins breathe less frequently, they conserve much of this body heat that would be lost by a faster breathing rate. Exhalation of drier air saves still more heat that might normally be lost in evaporative cooling.

Dolphins such as *Tursiops* breathe two or three times a minute during moderate swimming, but after a long dive they may blow 10 or even 15 times during the first minute on the surface. Sperm whales down for an hour may breathe 80 times in rapid succession before diving again. Scoresby (1820) observed a very regular diving and breathing pattern in a sperm whale he followed all day. The animal would dive for 50 min then surface for 50 or 60 blows in ten minutes before diving again.

Lawrence and Schevill (1956) have shown that *Tursiops* exhales and inhales in about 0.3 sec. Kooyman and Cornell (1981) studied the flow properties of expiration and inspiration of a trained *Tursiops* with a calibrated flow meter and came up with the same figure. Kooyman and Sinnott (1979) measured a peak expiratory flow rate of 10 vital capacities (VC) per sec in experiments with excised harbour porpoise lung. Kooyman and Cornell (1981) found 6 VC per sec peak expiratory flow in their trained *Tursiops*. Inspiratory flow rates in both species were much slower. Kooyman and Cornell (1981) summarize the implications of cetacean respiratory flow patterns as follows: 'The whale improves its utilization of time at the surface by initiating the blow just prior to surfacing (Kooyman *et al.* 1975). This early beginning and fast expiration not only leave more time while the blowhole is above the water's surface for the slower inspiration, but the explosive respiration also clears the upper airway completely of water. The short duration of the entire breathing maneuver reduces the time spent by the animal at or near the turbulent air/water interface and thus reduces swimming effort as well. Finally, the large VC and small residual volume of small whales (*Tursiops*, *Phocoena*, and *Globicephala*) (Irving *et al.* 1941; Olsen, Elsner, Hale, and Kenney 1969; Kooyman and Sinnott 1979) result in a somewhat more effective turnover of alveolar gas after a deep breath than in other mammals.'

Dolphins breathe less frequently than terrestrial mammals. They compensate by taking deeper breaths and they extract more oxygen from the air they breathe (Irving *et al.* 1941; Kanwisher and Sundnes 1965; Ridgway *et al.* 1969). They also exchange a greater percentage of lung air with each breath. Irving *et al.* (1941) reported 80 per cent tidal air in *Tursiops* while Olsen *et al.* (1969) found up to 88 per cent tidal air in the pilot whale. Laurie (1933) observed the collapsed lungs of dead whales and suggested that the lungs must be practically emptied by each expiration.

In terrestrial mammals, lung volume represents about 6 per cent of body volume irrespective of body weight (Schmidt-Nielsen 1975). Scholander (1940) concluded that whales have small lungs compared to terrestrial mammals and that the better diving whales have relatively smaller lungs. Goudappel and Slijper (1958) maintained that larger whales have a lung capacity of about 50 per cent of that of terrestrial mammals, whereas in the smaller toothed whales the lung capacity is about 150 per cent of that of land mammals.

Tidal air ranged from 5.5 to 10.0 L in *Tursiops* of 145 to 170 kg measured by Irving *et al.* (1941). Lung volume of these dolphins then ranged from 49 to 71 ml/kg. Ridgway *et al.* (1969) measured tidal air in a trained *Tursiops* by having the animal exhale into a calibrated underwater canister. Maximum exhalations by the 138 kg animal ranged from 5 to 6 L. Using the 80 per cent figure, lung volume would be about 7 L or 51 ml/kg. A 200 kg dolphin of the same species (Ridgway *et al.* 1969) had a measured lung volume of 55 ml/kg. According to these findings, tidal air in *Tursiops* is 5 or 6 times that of

humans but total lung volume is similar to that found in average terrestrial mammals.

Spencer, Gornall, and Poulter (1967) used a calibrated 'basket' pneumotachygraph to measure respiratory flows and tidal volume in a killer whale (*Orcinus*). Tidal volume averaged 46.2 L for a 1090 kg female. Olsen *et al.* (1969) measured tidal volume (39.5 L) and lung volume (45.1 L) in a 450 kg female pilot whale by helium dilution. The killer whale was beached during the measurements, and if we assume average tidal air was 70 per cent rather than 80 or 88 per cent, then its lung volume might be about 66 L or roughly 60 ml/kg compared to 100 ml/kg for the pilot whale.

In studies of Black Sea *Tursiops*, Kolchinskaya, Man'kovskaya, and Misyura (1980) found lower values for tidal air and similar values for total lung capacity. They argue that the tidal air values of Irving *et al.* (1941) were falsely elevated because the animals were breathing into a tube and thus making forced exhalations. They argued that subsequent investigators have simply duplicated the earlier results. Kooyman and Cornell (1981), on the other hand, found a VC of 26 L or 91 ml/kg on a 285 kg trained Pacific *Tursiops*, a value 50 per cent larger than previous investigators had found in Atlantic *Tursiops*. The Pacific *Tursiops* is a deeper diver (Table 3.1) and has a higher haemoglobin and higher haematocrit (Lenfant, Elsner, Kooyman and Drabek 1969, Duffield, Ridgway, and Cornell 1983) than the Atlantic variety of the same genus. There may be considerable variation in lung volume between different cetacean species and perhaps even between individuals of the same species from different geographical areas. At present, however, one can make the statement that cetacean lung volume is larger, smaller, or about the same as that of terrestrial mammals and find published findings to support the conclusion.

More studies with unrestrained, trained animals like that of Kooyman and Cornell (1981) or that of Ridgway *et al.* (1969) need to be done on a wider variety of individuals and species. It would be especially interesting to see how lung volume may relate to diving capability, body size, swimming speed, average respiratory rate, and ecology.

Sphincters in the respiratory bronchioles

Between the dolphin's alveoli and major bronchi there is a series of sphincters that can segment the lower bronchi into compartments. The sphincters (Fig. 3.4) are not present in the larger whales. When dolphins die in the water, subsequent histology often reveals many of these sphincters to be closed. In one case, a healthy *Tursiops* was caught in a net underwater and asphyxiated. Large numbers of contracted sphincters were seen on histologic examination (Simpson and Gardner 1972; Ridgway 1972). Kooyman and Sinnott (1979) observed contracted sphincters in *Stenella* that died in tuna seining nets.

In *Tursiops*, the expired breath may contain as little as 1.5 per cent oxygen

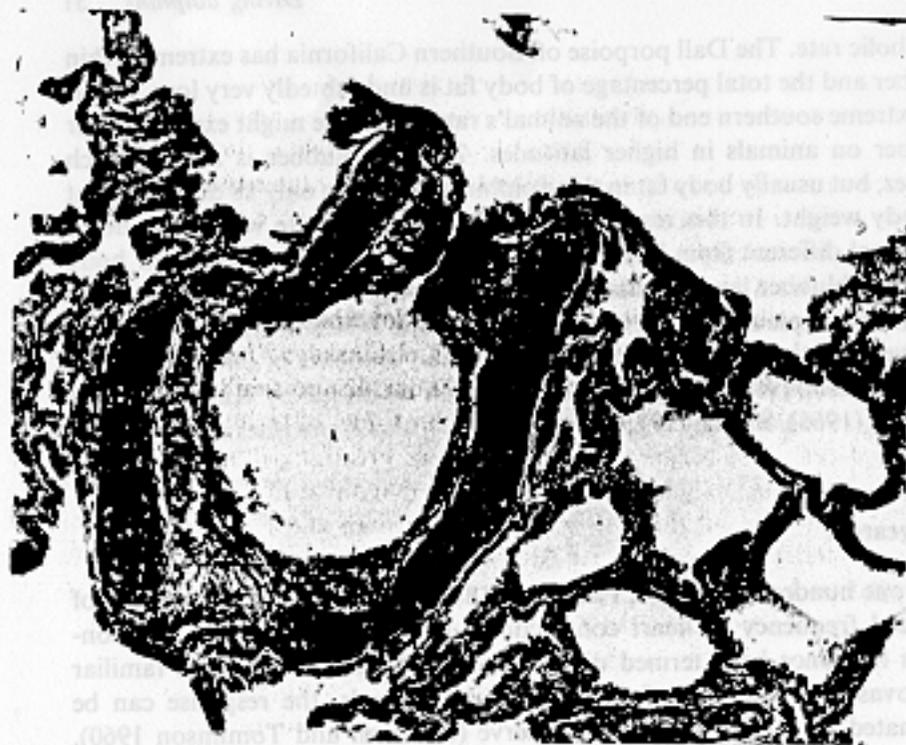


FIG. 3.4. Myoelastic sphincter in a microscopic section of dolphin lung tissue.

after prolonged breathholds (Ridgway 1972). To achieve such a low value, even with a small dead space, some mixing of lung air must occur. The smooth muscle sphincters may promote circulation of gas in the periphery of the respiratory tree and may function in emptying the lungs almost completely at the end of exhalation. Elephant seals and sea lions are diving mammals that do not have such sphincters and have never achieved such low oxygen values (never lower than 4.0 per cent) in exhaled air even after much longer breathholds. In addition, the pinniped exhaled air rarely contained more than 6.0 per cent carbon dioxide whereas dolphin values sometimes approached 8.0 per cent (Ridgway 1972, 1973).

Goudappel and Slijper (1958) speculated that 'the system of sphincters must be considered as an adaptation to fluctuations of the air-pressure in the lungs during quick and frequent diving and emerging, and especially during the violent inspiration and expiration of Cetacea with a very large lung capacity.' On deep dives, the sphincters may close as the alveoli collapse and remain closed during much of the ascent. Thus, the peripheral bronchi would be segmented into a series of small pressure gradients, which together make a large pressure gradient between the central airways and the alveoli (Goudappel and Slijper 1958).

METABOLISM

Many authors have found that small cetaceans have a higher metabolic rate than terrestrial mammals of similar size (Scholander 1940; Irving *et al.* 1941; Kanwisher and Sundnes 1965; Pierce 1970; Ridgway and Patton 1971; Hampton, Whittow, Szekercezes, and Rutherford 1971). The high protein diet (dolphins consume almost no carbohydrates) contributes considerably to a high metabolic rate. Those species studied have large thyroid glands (Harrison 1969) and a high level of circulating thyroid hormones (Ridgway and Patton 1971). Long term food consumption of captive animals correlates well with observed levels of oxygen consumption. The *Tursiops* studied by Ridgway and Patton (1971) required over 6000 kcal/day to maintain body weight. The feeding rates of several species of odontocetes have been summarized by Sergeant (1969).

Kanwisher and Sundnes (1965) showed that harbour porpoises had to maintain a metabolic rate about three times as large as a land mammal of a similar size to keep warm in cold waters. In their calorimetry experiments, *Phocoena* of 25–30 kg, in a water bath at 8 to 10°C, consumed 350 and 370 ml of oxygen per min. At 20 to 22°C these values only decreased to 305 and 340 ml/min.

Table 3.2 compares published values for oxygen consumption in small odontocetes with those from the Weddell seal (Kooyman, Kerem, Campbell, and Wright 1973). Weddell seals consumed 1.5 to 3.0 times that predicted for the mean standard metabolic rate based on land mammals (Kooyman *et al.* 1973) whilst California sea lions consumed 1.7 to 2.6 times the standard rate (Matsuura and Whittow 1973).

Based on its food consumption in captivity (about 15 kg of fish per day for a 120 kg animal, Ridgway 1966), the Dall porpoise (Fig. 5) has a very high

TABLE 3.2. Resting oxygen consumption in some small odontocetes compared with values from the Weddell seal

| Animal | Weight (kg) | Oxygen consumption (ml/kg/min) | Reference |
|----------------------|-------------|--------------------------------|------------------------------|
| <i>Phocoena</i> | 25 | 14.0 | Kanwisher and Sundnes (1965) |
| | 30 | 12.5 | Kanwisher and Sundnes (1965) |
| <i>Tursiops</i> | 170 | 6.0 | Irving <i>et al.</i> (1941) |
| | 156 | 6.1 | Hampton <i>et al.</i> (1971) |
| | 154 | 7.0 | Pierce (1970) |
| | | 5.5 | Pierce (1970) |
| | 128 | 7.0 | Ridgway and Patton (1971) |
| <i>Leptonychotes</i> | 425* | 5.0* | Kooyman <i>et al.</i> (1973) |

*Average of 5 animals.



metabolic rate. The Dall porpoise off Southern California has extremely thin blubber and the total percentage of body fat is undoubtedly very low. This is the extreme southern end of the animal's range and one might expect thicker blubber on animals in higher latitudes. *Tursiops* blubber is always much thicker, but usually body fat in this dolphin amounts to only 18 or 20 per cent of body weight. In this respect, dolphins from temperate waters are not a great deal different from humans. They just deposit nearly all of their body fat into a blubber layer around the body. There are no deposits of fat in the mesentery or pleural cavities or between muscle bundles. In larger whales, the liver and the bones may contain significant amounts of oil.

The metabolism of larger whales has been discussed by Kanwisher and Sundnes (1966), Brodie (1975), Gaskin (1982), and Kanwisher and Ridgway (1983).

Bradycardia

Over one hundred years ago, Paul Bert (1870) described the phenomenon of 'reduced frequency of heart contractions' in submerged ducks. This condition has since been termed diving bradycardia and is the most familiar cardiovascular response of diving animals. In seals, the response can be eliminated by section of the vagus nerve (Harrison and Tomlinson 1960). Many investigators have speculated that marine mammals may have sensors about the head or snout that trigger bradycardia.

Most early investigators used various methods of forcing the animal to dive. It is now recognized that restraint and fright may have been a primary component of many of the diving experiments reported (Kanwisher and Ridgway 1983). For this reason, more recent investigators have emphasized methods of inducing the animal to cooperate in the experiments (Ridgway *et al.* 1969; Ridgway 1972; Kooyman and Campbell 1972).

Kanwisher and Sundnes (1965) studied cardiac rhythm in *Phocoena*. They state: 'After every breath the heart rate increased in 1 or 2 seconds to 115–120/min. After 10 seconds this decreased rapidly and by 30 seconds was 50–60/min. It remained at this rate until the next breath.'

In *Tursiops*, the heart rate increases just after inspiration to a rate of 70–100 per min whether the dolphins are swimming or resting on a mat out of water. Within a few seconds the heart rate falls to 30 or 40 per min and remains at this rate until the next breath regardless of whether the breathhold

FIG. 3.5. (A) The Dall porpoise *Phocoenoides dalli* is a very fast swimmer and probably a deep diving animal. It has a large blood volume, and a high haemoglobin level that gives it an expanded oxygen transport and storage capability. This captive animal consumed about 15 kg of fish daily during its 20 months at Point Mugu, California. Small flippers help to reduce the animal's ratio of surface area to volume. (B) The Dall porpoise has an extremely large, muscular heart that may weigh as much as 1.34 per cent of body weight in animals at the extreme southern end of the range off Southern California, whose blubber is very thin (often 1 cm or less).

is for 20 sec or several minutes. Thus, when the dolphin is breathing two or three times per minute the heart rate is continually fluctuating between the upper and lower values in concert with breathing. A similar cardiac arrhythmia has been seen in *Orcinus*, *Globicephala*, *Lagenorhynchus*, *Phocoenoides*, and several other odontocetes (Ridgway 1972; Kanwisher and Ridgway 1983). This normal respiratory cardiac arrhythmia is obliterated by even the lightest levels of anaesthesia. The heart rate becomes very regular at a higher level (Ridgway 1972).

Kanwisher and Senft (1960) recorded a stranded fin whale 45 feet in length, finding a regular pulse of 27 beats per min (bpm) which they assumed to be the tachycardia rate. They thought a more normal rate for such a large whale might be 8 to 10 bpm.

A free-swimming bottlenosed dolphin with telemetry gear on a harness had a heart beat of 80–90 per min just after blowing which slowed in a few seconds to 33–45 bpm and remained at that rate until the next blow when the faster rate reappeared briefly. Longer breathholds did not result in a reduced number of bpm. The heart rate seemed to fall to a base level and remain there until the next blow. In fact, the lower rate seemed to be most characteristic of the animal and it might be more appropriate to speak of a respiratory tachycardia. The longer the breathhold, the more pronounced the tachycardia that followed when breathing resumed. Expired air collected after experimental breathholds showed that the tachycardia persisted until the exhaled carbon dioxide level had returned to normal. After a long breathhold, the breathing rate increased to about five times the resting rate and the heart rate increased from the apneic level of about 35 bpm to about 150 bpm and remained elevated, but steadily decreasing, until exhaled carbon dioxide returned to normal values (Ridgway 1972).

Anaerobic metabolism

During long dives, some tissues must be depleted of their oxygen stores and depend upon anaerobic metabolism (Hochachka and Storey 1975; Kooyman, Castellini, and Davis 1981). Ridgway *et al.* (1969) suggested that during the later portion of a deep dive there was barely enough oxygen remaining in the dolphin's system to maintain the heart and that even the brain might be capable of some anaerobic metabolism. Very little work has actually been done on the anaerobic capability of dolphins. Their diving times are not as long nor are they as easy to experiment with as are the seals. In any case it would appear most dives are aerobic, and a principal feature of the better divers is an increase in the capability for storage and transport of oxygen.

THE BLOOD

A relatively larger blood volume was one of the first diving adaptations

noticed. Bert (1870) found that blood volume was greater in ducks than in hens, and Bohr (1897) found higher blood volumes in guillemots and puffins than in non-diving birds. Since then numerous investigators have reported high blood volumes in diving mammals (Ridgway 1972).

Ridgway *et al.* (1984) found that blood volume in belugas (in ml/kg) was in the same range as that of much smaller odontocetes (1/8th to 1/4th as large) such as the Dall porpoise *Phocoenoides dalli* (about 100 kg body weight), and the white-striped dolphin *Lagenorhynchus obliquidens* (about 100 kg) (Ridgway 1972). The blood volume data do not support the idea that blood volume in cetaceans can be scaled to body weight as has been suggested for mammals in general (Prothero 1980) or that blood volume in mammals is uniformly 70 ml/kg of body weight (Stahl 1965). Nine different groups of investigators using four different techniques (Scholander 1940; Harrison and Tomlinson 1956; Wasserman and Mackenzie 1957; Ridgway and Johnston 1966; Bryden and Lim 1969; Lefant *et al.* 1969; Simpson, Gilmartin, and Ridgway 1970; Ridgway 1972; Ridgway *et al.* 1984) have reported high blood volumes (120 to 180 ml/kg) in hooded, harbour, elephant, and Weddell seals as well as California sea lions, the beluga, the harbour porpoise, and the Dall porpoise.

The significance of the increased blood volume in some small cetaceans seems to be in giving the animals increased oxygen storage and transport capacity, especially since the higher blood volume is often coupled with higher levels of haemoglobin and red blood cells (haematocrit or packed cell volume) (Table 3.3).

When trained dolphins (*Tursiops* and *Lagenorhynchus*) were kept in the open ocean and required to make frequent deep dives, a training effect was

TABLE 3.3. Comparison of blood measures that relate to total oxygen capacity in several odontocetes

| | N | Haematocrit % | N | Haemoglobin (g/100 ml) | N | Blood volume (ml/kg) |
|------------------------------------|------|------------------|----|---------------------------|----|-------------------------|
| <i>Phocoenoides</i> ¹ | 18 | 57.0 | 18 | 20.3 | 6 | 143.0 |
| <i>Monodon</i> ² | 8 | 57.5 | 8 | 22.5 | | |
| | 2 | 57.5 | 2 | 20.0 | | |
| <i>Delphinapterus</i> ³ | M 10 | 52.6 | 3 | 20.9 | 2 | 126.5 |
| | F 11 | 52.2 | 3 | 20.3 | 3 | 128.9 |
| <i>Lagenorhynchus</i> ⁴ | 29 | 53.0 | 29 | 17.0 | 13 | 108.0 |
| <i>Tursiops</i> ⁴ | | | | | | |
| Atlantic Coastal | 70 | 42.0 | 70 | 14.5 | 10 | 70 to 95 |
| Pacific Offshore | 6 | 52.0 | 6 | 18.4 | | |

All values are means. N = number of measurements.

References: ¹Ridgway and Johnston (1966); ²First: Vogl and Fisher (1982), second: MacNeill (1975); ³Ridgway *et al.* (1984); ⁴Duffield *et al.* (1983) and Ridgway (1972).

observed (Ridgway 1972). This was evidenced by increases in haemoglobin, haematocrit, and blood volume and a decrease in red blood cell diameter.

Vogl and Fisher (1982) compared the haematology and circulatory anatomy of beluga with that of narwhal (*Monodon monoceros*). Their haematocrit and haemoglobin values for narwhal are significantly higher than for any belugas measured and are in the same range as those reported for *Phocoenoides* (Ridgway and Johnston 1966). The thoracic retia were also larger in the narwhal. We agree with Vogl and Fisher (1982) that the narwhal is probably a deeper diver than the beluga, and considering that the latter has dived as deep as 647 m the former's capability must be considerable.

REFERENCES

- Abe, T., Kazama, M., and Matsuda, M. (1965). Anticoagulant activity of whale heparin and its characteristics. *Israel J. Med. Sci.* 1, 862.
- Andersen, H. T. (1966). Physiological adaptations in diving vertebrates. *Physiol. Rev.* 46, 212-43.
- Bert, P. (1870). *Leçons sur la Physiologie Comparée de la Respiration*. Paris, Baillière.
- Bohr, C. (1879). Didrag til Svømmefuglernes Fysiologi. *K. Danske Vidensk. Forh.* 2, 207.
- Bowers, C. A. and Henderson, R. S. (1972). Project Deep ops: deep object recovery with pilot and killer whales. *Naval Undersea Center Technical Paper* No. 306, San Diego, California. 86 pp.
- Brodie, P. F. (1975). Cetacean energetics, an overview of intraspecific size variation. *Ecology* 56, 152-61.
- Bryden, M. M. (1972). Growth and development of marine mammals. In *Functional anatomy of marine mammals* (ed. R. J. Harrison) Vol. 1, pp. 1-79. Academic Press, London.
- and Lim, G. (1969). Blood parameters of the Southern elephant seal (*Mirounga leonina*, Linn.) in relation to diving. *Comp. Biochem. Physiol.* 28, 139-48.
- Clarke, M. R. (1970). The function of the spermaceti organ of the sperm whale. *Nature, Lond.* 228, 873-4.
- (1978). Buoyancy control as a function of the spermaceti organ in the sperm whale. *J. Mar. Biol. Assn. U.K.* 58, 27-71.
- Coulombe, H. N., Ridgway, S. H., and Evans, W. E. (1965). Respiratory water exchange in two species of porpoise. *Science* 149, 86-8.
- Cunningham, D. J. (1877). The spinal nervous system of the porpoise and dolphin. *J. Anat. Physiol. Lond.* 11, 209-28.
- Damant, G. C. C. (1934). Physiology of deep diving in the whale. *Nature, Lond.* 133, 874.
- Duffield, D. A., Ridgway, S. H., and Cornell, L. H. (1983). Hematology distinguishes coastal and offshore forms of dolphins (*Tursiops*). *Can. J. Zool.* 61, 930-3.
- Eisenberg, J. F. (1981). *The mammalian radiations*. University of Chicago Press, Chicago. 610pp.
- Elsner, R. W., Kenney, D. W., and Burgess, K. (1966a). Diving bradycardia in a trained dolphin. *Nature, Lond.* 212, 407-8.
- , Franklin, D. L., Van Citters, R. L., and Kenney, D. W. (1966b). Cardiovascular defense against asphyxia. *Science* 153, 941-9.
- Evans, W. E. (1971). Orientation behavior of delphinids: radio telemetric studies. *Ann. N.Y. Acad. Sci.* 188, 142-60.
- Gaskin, D. E. (1982). *The ecology of whales and dolphins*. Heinemann, Exeter, New Hampshire. 459pp.
- Gilmore, R. M. (1960). Census and migration of California gray whales. *Norsk Hvalfangst-Tid.* 49, 409-31.
- Goudappel, J. R., and Slijper, E. J. (1958). Microscopic structure of the lungs of the bottlenose whale. *Nature, Lond.* 182, 479.
- Hall, J. D. (1970). Conditioning Pacific white-striped dolphins, *Lagenorhynchus obliquidens*, for open ocean release. *Naval Undersea Center Technical Publication* 200. San Diego, California.
- Hampton, I. F. G., Whittow, G. C., Szekercezes, J., and Rutherford, S. (1971). Heat transfer and body temperature in the Atlantic bottlenosed dolphin, *Tursiops truncatus*. *Int. J. Biometeor.* 15, 247-53.
- Harrison, R. J. (1969). Endocrine organs: hypophysis, thyroid and adrenal. In *The biology of marine mammals*. (ed. H. T. Andersen) p. 349. Academic Press, New York.
- and Tomlinson, J. (1956). Observations on the venous system in certain Pinnipedia and Cetacea. *Proc. Zool. Soc. Lond.* 126, 205-33.
- and — (1960). Normal and experimental diving in the common seal (*Phoca vitulina*). *Mammalia* 24, 386.
- and Ridgway, S. H. (1976). *Deep diving mammals*. Meadowfield Press, Durham, England. 51pp.
- Heezen, B. C. (1957). Whales entangled in deep-sea cables. *Deep Sea Res.* 4, 105-15.
- Hochachka, P. W. and Storey, K. B. (1975). Metabolic consequences of diving in animals and man. *Science* 187, 613-21.
- Hui, C. A. (1975). Thoracic collapse as affected by the retia thoracica in the dolphin. *Resp. Physiol.* 25, 63-70.
- Hunter, John (1787). Observations on the structure and economy of whales. *Phil. Trans. Roy. Soc. London., Ser. B.* 77, 371-450.
- Irvine, A. B. (1970). Conditioning marine mammals to work in the sea. *Marine Technical Society J.* 4, 47-52.
- Irving, L., Scholander, P. F., and Grinnell, S. W. (1941). The respiration of the porpoise, *Tursiops truncatus*. *J. Cell. Comp. Physiol.* 17, 145-68.
- Kanwisher, J., and Ridgway, S. H. (1983). The physiological ecology of whales and porpoises. *Sci. Am.* 248, 110-20.
- and Senft, A. (1960). Physiological measurements on a live whale. *Science* 133, 1379-80.
- and Sundnes, G. (1965). Physiology of a small cetacean. *Hvalradets Skr.* 48, 45-53.
- and — (1966). Thermal regulation in cetaceans. In *Whales, dolphins and porpoises* (ed. K. S. Norris) pp. 398-409. University of California Press, Los Angeles.
- Kleinenberg, S. E., Yablokov, A. V., Bel'kovich, V. M., and Tarasevich, M. N. (1964). *Beluga (Delphinapterus leucas) investigation of the species*. (English translation, Israel Program For Scientific Translation, Jerusalem, 1969) p. 131. Academy of Sciences of the USSR, Moscow.
- Kolchinskaya, A. Z., Man'kovskaya, I. N., and Misyura, A. G. (1980). Dykhaniye i kislorodnyye rezhimy organizma del'finov. *Naukova Dumka, Kiev.* 332p.
- Kooyman, G. L. (1966). Maximum diving capacities of the Weddell seal (*Leptonychotes weddelli*). *Science* 151, 1553-4.
- and Campbell, W. B. (1972). Heart rates in freely diving Weddell seals, *Leptonychotes weddelli*. *Comp. Biochem. Physiol. A* 43, 31-6.
- and Cornell, L. H. (1981). Flow properties of expiration and inspiration in a trained bottle-nosed porpoise. *Physiol. Zool.* 54, 55-61.

- and Sinnett, E. E. (1979). Mechanical Properties of the harbor porpoise lung. *Phocoena phocoena*. *Resp. Physiol.* **36**, 287–300.
- , Castellini, M. A., and Davis, R. W. (1981). Physiology of diving in marine mammals. *Ann. Rev. Physiol.* **43**, 343–56.
- , Kerem, D. H., Campbell, W. B., and Wright, J. J. (1973). Pulmonary gas exchange in freely diving weddell seals. *Resp. Physiol.* **17**, 283–90.
- , Norris, K. S., and Gentry, R. L. (1975). Spout of the gray whale: its physical characteristics. *Science* **190**, 908–10.
- , Billups, J. O., and Farwell, W. D. (1983). Two recently developed recorders for monitoring diving activity of marine birds and mammals. In *Experimental biology at sea*. (eds. A. G. Macdonald and I. G. Priede) pp. 197–214. Academic Press, London and New York.
- Krogh, A. (1934). Physiology of the blue whale. *Nature, Lond.* **133**, 635–7.
- Laurie, A. H. (1933). Some aspects of respiration in blue and fin whales. 'Discovery' Reports **7**, 363–407.
- Lawrence, B. and Schevill, W. E. (1956). The functional anatomy of the delphinid nose. *Bull. Mus. Comp. Anat. (Harvard)* **114**, 103–51.
- Lenfant, C., Elsner, R., Kooyman, G. L., and Drabek, C. M. (1969). Respiratory function of blood of the adult and fetus Weddell seal *Leptonychotes weddelli*. *Am. J. Physiol.* **216**, 1595–7.
- Lettvin, J. T., Gruberg, E. R., Rose, R. M., and Plotkin, G. (1982). Dolphins and the bends. *Science* **216**, 650–1.
- Lockyer, C. (1976). Body weights of some species of large whales. *J. Cons. int. Explor. Mer.* **36**, 259–73.
- Mackay, R. S. (1982). Dolphins and the bends. *Science* **216**, 650.
- McFarland, W. L., Jacobs, M. S., and Morgane, P. J. (1979). Blood supply to the brain of the dolphin, *Tursiops truncatus*, with comparative observations on special aspects of the cerebrovascular supply of other vertebrates. *Neurosci. Biobehav. Rev. Suppl.* **1**, 93p.
- MacNeill, A. C. (1975). Blood values for some captive cetaceans. *Can. Vet. J.* **16**, 187–93.
- Matsuura, D. T. and Whittow, G. C. (1973). Oxygen uptake of the California sea lion and harbor seal during exposure to heat. *Am. J. Physiol.* **225**, 711–5.
- Matthews, L. H. (1952). *British mammals*. London, Collins.
- Nagel, E. L., Morgane, P. J., McFarland, W. L., and Galliano, A. E. (1968). Rete mirabile of dolphin: Its pressure-damping effect on cerebral circulation. *Science* **161**, 898.
- Nakajima, M. (1961). In regard to the rete mirabile of the Cetacea with emphasis especially on *Grampidelphis griseus* and *Tursiops truncatus*. *Toho Igakkai Zasshi* **8**, 1611–23.
- Norris, K. S. and Harvey, G. W. (1972). A theory of the function of the spermaceti organ of the sperm whale (*Physeter catodon* L.) In *Animal orientation and navigation*. (eds. S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs, and R. E. Belleville), pp. 397–417. NASA, Washington D.C.
- , Baldwin, H. A., and Samson, D. J. (1965). Open ocean diving tests with a trained porpoise (*Steno bredanensis*). *Deep-Sea Res.* **12**, 505–9.
- Olsen, R. C., Elsner, R., Hale, F. C., and Kenney, D. W. (1969). "Blow" of the pilot whale. *Science* **163**, 953–5.
- Ommanney, F. D. (1932). The vascular networks (retia mirabilia) of the fin whale (*Balaenoptera physalus*). 'Discovery' Reports **5**, 327–62.
- Paulev, P. (1965). Decompression sickness following repeated breathhold dives. *J. Appl. Physiol.* **20**, 1028.
- (1967). Nitrogen tissue tension following repeated breath-hold dives. *J. Appl. Physiol.* **22**, 714–718.
- Pierce, R. W. (1970). Design and operation of a metabolic chamber for marine mammals. PhD Dissertation. University of California, Berkeley.
- Prothero, J. W. (1980). Scaling of blood parameters in mammals. *Comp. Biochem. Physiol.* **67A**, 649–57.
- Reysenbach de Haan, F. W. (1957). Hearing in whales *Acta Otolaryng.* **Suppl.** **134**, 1–114.
- Ridgway, S. H. (1965). Medical care of marine mammals. *J. Am. Vet. Med. Assoc.* **147**, 1077–86.
- (1966). Dall porpoise, *Phocoenoides dalli* (True): observations in captivity and at sea. *Norsk. Hvalfangst.-Tid.* **5**, 97–110.
- (1971). Buoyancy regulation in deep diving whales. *Nature, Lond.* **232**, 133–4.
- (1972). Homeostasis in the aquatic environment. In *Mammals of the sea*, pp. 590–747. (ed. S. H. Ridgway) Thomas, Springfield, Ill.
- (1973). Control mechanisms in diving dolphins and seals. PhD Dissertation. University of Cambridge.
- and Howard, R. (1979). Dolphin lung collapse and intramuscular circulation during free diving: evidence from nitrogen washout. *Science* **206**, 1182–3.
- and — (1982). Dolphins and the bends. *Science* **216**, 651.
- and Johnston, D. G. (1966). Blood oxygen and ecology of porpoises of three genera. *Science* **151**, 456–8.
- and Patton, G. S. (1971). Dolphin thyroid: some anatomical and physiological findings. *Z. Vergl. Physiol.* **71**, 129–41.
- , Bowers, C. A., Miller, D., Schultze, M. L., Jacobs, C. A., and Dooley, C. A. (1984). Diving and blood oxygen in the white whale. *Can. J. Zool.* (In press).
- , Scronce, B. L., and Kanwisher, J. (1969). Respiration and deep diving in a bottlenose porpoise. *Science* **166**, 1651–4.
- Robinson, B., and Craddock, J. (1983). Mesopelagic fishes eaten by Fraser's dolphin, *Lagenodelphis hosei*. *Fish. Bull.* **81**, 2.
- Robinson, A. J., Kropatkin, M., and Aggeler, P. M. (1969). Hagemann factor (Factor 12) deficiency in marine mammals. *Science* **166**, 1420.
- Scammon, C. M. (1874). *The marine mammals of the northwestern coast of North America*. Putnam's, New York.
- Schevill, W. E., Ray, C., Kenyon, K. W., Orr, R. T., and Van Gelder, R. G. (1967). Immobilizing drugs lethal to swimming mammals. *Science* **157**, 630–1.
- Schmidt-Nielsen, K. (1975). *Animal physiology*, p. 37. Cambridge University Press.
- Scholander, P. F. (1940). Experimental investigations on the respiratory function in diving mammals and birds. *Hvalrad. Skr.* **22**, 1–131.
- (1963). The master switch of life. *Sci. Am.* **209**, 92–106.
- Scoresby, W. (1820). An account of the Arctic regions with a history and description of the northern whale-fishery. 2 Vols. Constable, Edinburgh.
- Sergeant, D. E. (1969). Feeding rates of Cetacea. *FiskDir. Skr. Ser. HavUnders.* **15**, 246–58.
- Simpson, J. G. and Gardner, M. (1972). Comparative microscopic anatomy of selected marine mammals. In *Mammals of the sea* (ed. S. H. Ridgway) pp. 298–418. Thomas, Springfield, Ill.
- , Gilmartin, W. G., and Ridgway, S. H. (1970). Blood volume and other hematologic parameters in young elephant seals. *Mirounga angustirostris*. *Am. J. Vet. Res.* **31**, 1449–52.
- Slijper, E. J. (1962). *Whales*. Basic Books, New York.

- Spencer, M. P., Gornall, T. A. and Poulter, T. C. (1967). Respiratory and cardiac activity of killer whales. *J. Appl. Physiol.* **22**, 974-81.
- Stahl, W. R. (1965). Organ weights in primates and other mammals. *Science* **150**, 1039-42.
- Strauss, M. B. (1969). Mammalian adaptations to diving. U.S. Navy Submarine Medical Center, Groton, Conn., USA Rept. 562, 31pp.
- Tomilin, A. G. (1957). *Mammals of the U.S.S.R. and adjacent countries: Cetacea*. Academy of Sciences USSR, Moscow. (English translation, Israel Program for Scientific Translations, Jerusalem) p.686.
- Tyson, E. (1680). *Phocaena, or the Anatomy of a porpoise*. London, Benjamin Tooke.
- Viamonte, M., Morgane, P. J., Galliano, R. E., Nagel, E. L., and McFarland, W. L. (1968). Angiography in the living dolphin and observations on blood supply to the brain. *Am. J. Physiol.* **214**, 1225-49.
- Vogl, A. W. and Fisher, H. D. (1981a). The internal carotid artery does not directly supply the brain in Monodontidae (Order Cetacea). *J. Morph.* **170**, 207-14.
- and — (1981b). Arterial circulation of the spinal cord and brain in the Monodontidae (Order Cetacea). *J. Morph.* **170**, 171-80.
- and — (1982). Arterial retia related to supply of the central nervous system in two small toothed whales—narwhal (*Monodon monoceros*) and beluga (*Delphinapterus leucas*). *J. Morph.* **174**, 41-56.
- , Todd, M. E., and Fisher, H. D., (1981). An ultrastructural and fluorescence histochemical investigation of the innervation of retial arteries in *Monodon monoceros*. *J. Morph.* **168**, 109-20.
- Wasserman, K. and Mackenzie, A. (1957). Studies on the seal during the dive reflex. *Bull. Tulane. Fac. Med.* **16**, 105.
- Wilson, H. S. (1879). The rete mirabile of the narwhal. *J. Anat. Physiol. Lond.* **14**, 377-400.
- Wood, F. G. (1973). *Marine mammals and man*. R. B. Luce Inc., New York.
- Workman, R. (1965). *Calculation of decompression schedules for nitrogen-oxygen and helium-oxygen dives*. Rept. 6-65, U.S. Navy Experimental Diving Unit. Washington, D.C.
- Scammon, C. M. (1874). The marine mammals of the northwestern coast of North America. Putnam, New York.
- Schreivill, W. E., Ray, C., Kenyon, K., Orr, R. T., and Van Gelder, R. G. (1967). Immobilizing drugs lethal to swimming mammals. *Science* **157**, 630-1.
- Schmidt-Nielsen, K. (1973). *Animal physiology*, p. 37. Cambridge University Press.
- Scholander, A. F. (1940). Experimental investigations on the respiratory function in diving mammals and birds. *Wired. Ser.* **22**, 1-131.
- (1963). The master switch of life. *Sci. Am.* **208**, 93-106.
- Storöy, W. (1820). An account of the Arctic regions with a history and description of the northern whale-factory. 2 Vols. Constable, Edinburgh.
- Stewart, D. E. (1969). Feeding rates of Cetacea. *Fish. Res. Ser. Hav. Underw. 18*, 246-58.
- Simpson, J. G. and Gardner, M. (1973). Comparative nictipal anatomy of related marine mammals. *J. Morph.* **168**, 1-15.