Some Considerations on Diving of Whales

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(Tables 1–4)

INTRODUCTION

It has long been a recognized fact that whales can dive much longer and much deeper than other diving pulmonate animals. Especially, the sperm whale and the bottle-nosed whale are known to endure most prolonged and deepest submergence. Some experimental evidences and theories have been presented by a number of authors to elucidate the long apnoea of diving animals. It seems however, very interesting to the present author that the sperm whale and the bottle-nosed whale, both being the champions of all pulmonate divers, possess within their body a large quantity of wax, instead of usual fat. Moreover, the sperm whale has an enormous special organ, *spermaceti*, which is situated over the skull, the content of which is largely constituted of waxes. The physiological function of this organ however, has not yet been clarified. No other animals are known to possess *spermaceti* or any organ similar to it, except that the bottle-nosed whale has a small organ which is probably homologous to the *spermaceti*. As for the presence of large quantities of wax, similar instance is not known in any other animal than the two species named. Even in other whales, usual glycerides constitute the major part of the fatty substances together with a small amount of sterols and other unsaponified matters, as it is the case in other animals.

The problems to be considered in this article, are (1) what factors enable the whales particularly the sperm whale to endure apnoea so much longer than other animals and (2) how they can avoid getting the caison sickness, which may attack them when they emerge from a deep dive. Now we are to survey briefly the duration and the depth which whales can stand and reach.

DURATION AND DEPTH

Duration—. Table 1 shows the duration of dives of various mammals and birds which can anyhow endure diving apnoea. From this table, we can see that no other animals than the whale endure longer dives than 15 minutes. Only the seal and the manatee are tolerable for 15 minutes or little longer diving apnoea. Though many observations have been made on the duration of diving of whales, few informations are reliable. Descriptions based on the conversation of gunners are to be taken with some caution, because the estimations which are made by the gunners in

Table 1.   Duration of Dives of Mammals and Birds (after Irving and Scholander)

Animal	Time		Authority	
* Pigeon	1 min		Bohr	1897
* Hen	3 //		//	//
* Duck	4·¼—17 //		Richet	1899
* *Uria troile*	6—12 //		Bohr	1897
* White rat	2 //	6 sec	Bert	1870
* Water rat (*Arvicola amphibium*)	2 //	17 //	//	//
* Rabbit	3 //		//	//
* Cat	3 //		//	//
* Dog	4 //	25 //	//	//
Sea elephant (*Mirounga angustirostris*)	6 //	48 //	Harnisch	1937
* Muskrat (*Ondatra zibethica*)	12 //		Irving	1939
* Beaver (*Castor canadensis*)	15 //		Irving and Orr	1935
* Harbor seal (*Phoca vitulina*)	15 //		Millais	1906
* Gray seal (*Halichoerus grypus*)	15 //		//	//
Florida Manatee (*Trichechus latirostris*)	16 //	20 //	Parker	1922
New Zealand humbacked whale (*Megaptera nodosa*)	not over ½ hours		Lillie	1910
Fin whale (*Balaenoptera plupalus*)	20 min		Ommanney	1932
Blue whale (*Balaenoptera musculus*)	50 //		Andrews	1916
Finback whale (*Balaenoptera physalus*)	30 //		Allen	1916
Sperm whale (*Physeter catodon*)	1—1·½ hours		Millais	1906
Bottle-nosed whale (*Hyperoodon rostratus*)	2 hours		Gray	1822
Man, average swimmer	1 min		Irving	1932
Man, pearl and sponge divers	up to 2 min		Irving	1932

* average time to last movement by forced submersion.

the course of chase are often defective in exactness and sometimes exaggerated. The duration of diving differs naturally in different species of whales.   Within the same species, it is said that the larger the whale, the longer the duration.

LAURIE[1] observed that blue whales dive on being pursued, for 10 minutes or more and that the harpooned blue whales stay submerged as long as 25 minutes. He gathered from conversations with Norwegian gunners that the average time of dives of the blue whales which are not alarmed is about 10 minutes, and when being chased or harpooned, the submergence may last as long as half an hour.   According to OMMANNEY[2], although the usual duration of dives of the blue and fin whales is between 10 and 20 minutes, there are instances to be known of longer dives than this.   The Greenland right whale is said to be able to make dives lasting up to 45 minutes[3].

SCHOLANDER[4] observed how a swimming fin whale unfrightened and at liberty respires and dives, by means of a kymograph on board, on which the sounds of "spoutings" were recorded.   Diagrams taken from two different fin whales showed that the duration of each dive was within the range of 4 to 6 minutes.   However, he added that he himself had seen the longer dives of fin whales, lasting for 10 to

12 minutes. This author further cited the following particulars which were furnished by the experienced gunners at BRÖDRENE SÄBJÖRNSEN's whaling station at Steinshamn (Norway):

Fin whale (*Balaenoptera physalus*) 5–6 min. (10–12–15 min.)

Blue whale (*Balaenoptera musculus*) 7–8 min.

Piked whale (*Balaenoptera acutorostrata*) 6–7 min.

Bottle-nosed whale (*Hyperoodon rostratus*) 30–45 min.

Sperm whale (*Physeter catodon*) 30–45 min., 20–40 spoutings during the course of 7–8 minutes.

It is evident that the sperm whale and perhaps particularly the bottle-nosed whale are the best prolonged divers. There would be no doubt that the sperm whale is able to dive spontaneously for at least one hour and the bottle-nosed whale perhaps has still greater diving ability than the sperm whale. In contrast, the balaenopterids like the blue and fin whale show in general, far poorer diving ability. Their diving ability is not so surprising even when compared with that of other aquatic animals like the seal.

Depth—. OMMANNEY's opinion[2] which denies the deep dives of whales deeper than 130 feet (40 metres) on the ground of the risk of caison sickness, seems to have no reason, for the whales may have the sufficient reason for not being afraid of the caison disease. He said, "The limiting factor in any dive is the danger of caison disease upon returning suddenly from the depths where the excess hydrostatic pressure is greater than 1.25 atmospheres (2.25 atmosphers absolute pressure).·········· it seems improbable that any organism could withstand the effect of swift release from pressure greater than 5 atmospheres—corresponding to a depth of 132 feet." He continued further," It may be said then, that a whale probably does not descend to depths much greater than 130 feet, but can remain below for periods of up to half an hour." (pp. 357–8). Later, we will consider whether the danger of caison sickness is actually present when whales make a swift floating from the tremendously great depths.

LAURIE[1] assumed that a blue or fin whale does not go further down deeper than 100 metres, as the krill, food of these whales is not found in sufficiently large quantities below this depth. However he mentioned that he was informed of a dead sperm whale which was found off the Peruvian coast entangled in a submarine cable at a depth of 900 metres. Probably it was caught in the cable while it was in activity, and finally drowned.

As SCHOLANDER[4] pointed out, the depth estimated by length and the direction of run-out harpoon line, is uncertain and happens to contain a great error. He measured actually the depths up to which harpooned fin whales submerged, by means of a specially deviced manometer attached to the harpoon line, 75 metres behind the harpoon; to this length of 75 metres he assumed the depth of 25 metres. By this method, he measured the depths on five fin whales and the manometer readings were corresponding to 85, 105, 135, 230 and 355 metres respectively, every with the exception of 25 metres to be added.

A sperm and a bottle-nosed whale are known to live for a great part on the cephalopods belonging to deep sea species.   Therefore it may be very likely that these whales habitually go down to depths deeper than in the occasional deep dives of the fin whale.   Although direct evidence is still lacking, HEESEN's report[5] on the troubles caused to submarine cables by whales seems to provide some indirect evidences.   He inquired into the troubles caused by whales to the submarine cables belonging to the Western Union Telegraph Co. and four other agencies.   According to this report, the troubles so far recorded had amounted to 14 cases, of which the majority were caused by the sperm whales at great depths but a few were caused by balaenopterids in comparatively shallow waters.   Six out of the 14 cases took place at the depth of about 900 metres with the sperm whale as the culprit and the deepest record was 1130 metres.

The cables were hardly injured in almost all the cases, and the high correlation was held between the freshness of the carcass and the time-lapse from the time when the interruption of telegraph was found to the time when the cable was hauled up to the sea surface for repair and the carcass of the culprit discovered concurrently. It is very probable from these facts that whales were entangled in the cable when they were alive, perhaps while being engaged in pursuit of cephalopods.   It seems almost certain that the sperm whale, and perhaps the bottle-nosed whale go habitually down much deeper than so far imagined.

THE OXYGEN STORED AND CONSUMED

It will be unnecessary to say that a whale is in a state of complete apnoea during submergence.   A whale may expel the air but cannot inhale it, and the expelling the air means nothing but a loss of oxygen for a submerged whale.   It is inconceivable that a whale should be capable of taking oxygen from the surrounding sea water through any part of its body surface.   Therefore it is completely evident that the oxygen to be consumed during a dive must be stored within the whale's body, till the commencement of the dive.   We shall now consider how much oxygen can be stored in the whale's body and how much will be consumed in a single dive, in other words, we are going to inquire into the balance-sheet of oxygen within the whale's body during a submergence.

OMMANNEY[2] expressed his opinion that if whale's metabolism is in any way comparable with that of man, a whale will need to take down, when diving for half an hour, a store of oxygen at least twenty times greater than its lungs can contain. Certainly, the balance of oxygen storage and its consumption in whales seems at first sight, to be not coincident.   However the oxygen store cannot be restricted to the lungs.   Thus, such local consideration will serve little to elucidate this problem. Moreover, we must consider some special mechanism which would maintain the whale's metabolism in a condition of deficient oxygen. At any rate, we will consider in this chapter, the purely arithmetical relation between the oxygen store and its consumption.

Oxygen Stores

The lung air, blood and tissues should be considered to serve as the important oxygen depots. In addition to the absolute amount of oxygen in these depots, it should be important to know how completely these depots can be utilized.

Lung oxygen—. The direct measurement of the vital capacity* or the lung capacity of whales is impracticable. However, LAURIE[1] found that the lungs of a blue whale weighing 122 tons and 27.2 meters long, are in proportion to the body weight, lighter by about the half than those of man; the lungs of this whale weighed 1226 kg, or around 1% of its body weight, whereas human lungs average over 2 %. Assuming that the lung capacity is directly proportional to the lung weight in whales as in man, and taking the vital capacity as 3.5 litres in man of 70 kg body weight, he estimated the vital capacity of the whale under consideration at 3050 litres. This blue whale, by the way, the particulars of which were kindly supplied to the Discovery Committee by Capt. SÖRLLE in 1926, will be cited hereafter as the "SÖRLLE's blue whale" or merely as the "SÖRLLE's whale".

On the other hand, the measurements of lung capacity (maximum inflation capacity) of dead whales made by SCHOLANDER[4] by means of a specially big dry gasmeter gave the following results for three different fin whales:

Fin whale 50 feet, ca. 30 tons, lung capacity 800 litres (2.7 1/kg%)
——————— 68 // // 60 // ——————— 1500 // (2.5 //)
——————— 72 // // 70 // ——————— 2000 // (2.8 //)

From these figures, we can see that the LAURIE's assumption of the vital capacity of the SÖRLLE's whale is not too conservative; this is corresponding to just 2.5 1/kg% of the body weight. It would be closer to the lung capacity rather than the vital capacity.

Meanwhile, what should be thought about the ventilation efficiency of the whale lungs? Human tidal air (ventilating amount of air at each usual breath) is only 300 to 400 cc, or only 6 to 8% of the lung capacity of 5.3 litres. LAURIE[1] pointed out that the microscopic feature of the section of whale lung is characterized by the greater thickness of the walls of infundibula and alveoli as compared to those of man or pig. Such circumstances of lung tissues may effect more complete renewal of the alveoli air at each breath. As a further reason to suppose that a whale makes a more complete exchange of the lung air than any other animals, he referred to the forcible spoutings (blasts of expiration). According to his observations[1], a spouting of a whale in the Antarctic, is clearly visible as a column of condensed vapor of a height of 20 feet lasting for half a second and the noise is audible on a still day for a distance of at least half a mile.

SCHOLANDER[4] suggested from the results of the respiratory experiment, a high

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* Human vital capacity, i.e., the greatest amount of air which can be taken in, after the most forcible expiration, averages 3.5 litres in man of 70 kg body weight, that is, corresponding to 5 1/kg% of the body weight. The lung capacity, which is the vital capacity added by the residual air in the lungs, is about 3/2 times as great as the vital capacity, that is, it measures 5.3 litres in man of the same size—corresponding to 7.5 1/kg% of the body weight.

ventilation efficiency of a small porpoise (*Phocaena communis*) weighing 19 kg. The tidal air of this porpoise was surprisingly constant, amounting in every respiration to 1 litre.   From a certain experimental ground, he put the lung capacity of this *Phocaena* at 1400 cc at a high estimate.   From this results, it seems certain that the porpoise makes a very efficient renewal of the lung air and we might well presume that this is also the case in greater whales, though the actual evidence is not available.   It seems not to be strange to assume the great ability of renewal of the lung air for such animals like whales which must hold breath for a long time from their habit of life and during this time, must depend only upon the limited store of oxygen, instead of enjoying the continuous ventilation of the lung air as do land animals.

It is a general observation that the whale dives after inspiration.   There are two types of respiratory pause in general; the inspiratory and the expiratory one.   HARNISCH[6] observed in sea lions and sea elephants, that the respiratory pause is generally inspiratory but occasionally expiratory.   He frequently observed that the animals expelled air at the beginning of a dive.   According to SCHOLANDER[4], it was a constant occurrence in his respiratory experiments that a seal (*Halichoerus grypus*) expires strongly and dives with very little air in the lungs.   However, he noticed no such phenomenon in the porpoise (*Phocaena communis*).   He noted that *Phocaena* and the fin whale dive on an inspiration, as probably do all other whales.

As for the depletion of oxygen in the lungs, BOHR[7] found in *Uria troile* 1.5 to 4% oxygen in the lung air in suffocation.   RICHET[8] found that the lung air of ducks contains 1.3 to 2.9% oxygen at the premortal suffocation.   With whales however, no actual determination of this kind is available.

It may be well to regard the partial pressure of oxygen in the whale lungs as 150 mm Hg at the outset of submergence.   This is being decreased in the course of apnoea activity.   However, in considering the decrease in the oxygen partial pressure in the lungs, it may be necessary to take into account that whales make a deep dive.   If a whale stays submerged at a depth of 90 meters, the hydrostatic pressure exerting upon the whale body, will be 10 atmospheric pressures, and assuming that every part of the whale body undergoes this pressure uniformly, the air in the lungs must be compressed by the gas law, to 1/10 the volume that it has occupied at the sea surface.   This compression of the lung air may result in the more complete use of oxygen.   LAURIE[1] said that a partial pressure of 60 mm Hg is sufficient to keep the blood of most animals above 80% saturation with oxygen, and that, if the whale stays at the depth of 90 meters where the oxygen partial prssure in the whale lungs is assumed to have been decreased to 60 mm Hg, then, when the whale returns to the surface, the oxygen in this whale lungs would be at a partial pressure of only 6 mm Hg.

If the matter is as discussed by LAURIE, the residual oxygen is to be only 0.8% of the lung air, or 96% of the total amount of oxygen formerly inspired is to be utilized.   However, this discussion seems to be speculative.   Because, even if the oxygen partial pressure of 60 mm, at the total pressure of 760 mm Hg were suffici-

ent to keep the blood to 80% saturation with oxygen, the same oxygen partial pressure cannot be sure to effect the same degree of oxygen saturation of the blood when the total pressure is 10 times as great.

Blood oxygen—. The blood volume ranges from 7 to 10% of the body weight in most mammals and birds, and is somewhat greater in diving animals. According to Irving[9], the blood volume is about 10% in the duck and muskrat, i,e., a little greater than those found for land mammals. In two seals, the same author found about 10% blood volume. Scholander[4] also found that the blood volume is 9 to 10% in the seals. As for the whales, there is found little information. However, in the Sörlle's blue whale, it was estimated at 8000 litres*—corresponding to 6.5 % of the body weight. This value is smaller than that of man, 7-8%. However we may presume that the blood volume of whales would be at least, as much as that of man and more probably around 10%, in considering that the bleeding of such a gigantic animal as a whale is not easy to be carried out completely.

The oxygen capacity of the blood in diving animals is rather well known. Table 2 has mainly been based upon compilations by Irving[10] and Scholander[4]. In most mammals and birds, the oxygen capacity is between 15 and 20 v/v% of the blood, and in general, the diving animals have greater oxygen capacity than land animals.

Table 2. Oxygen Capacity of Blood in Equilibrium with Air

Animal	Oxygen capacity %	Authority	
Pigeon	21. 2	Wastl and Leiner	1931
Hen	11. 2	Winterstein	1921
Duck	16. 9	Wastl and Leiner	1931
Uria troile	26. 0	Bohr	1897
Dog	21. 8	Irving	1939
Beaver	17. 7	//	//
Muskrat	25. 0	//	//
Seal (Phoca vitulina)	29. 3	//	//
Sealion (Eumetopias stelleri)	19. 8	Florkin and Redfield	1931
Phocaena communis	20. 5	Green and Redfield	1933
Tursiops truncatus	31. 8	// //	//
Blue and fin whale	14. 1	Laurie	1933
Sperm whale	29. 1	Green and Redfield	1933
Man	20. 7	Irving	1939

A few informations are available as to the oxygen capacity of the whale blood. However, most of them are concerned with carcass' blood drawn up to many hours after death. As Scholander pointed out, the whale usually bleeds in the sea from the shot wounds for many hours and therefore there remains a suspicion that the

* This was supplied by Capt. Sörlle to the Discovery Committee in 1926, together with the other particulars of this whale.

sea water may enter the blood during towing, through the harpoon wounds and bel-
ly cuts.   In addition, there is another uncertainness to be not able to judge what
changes may have occurred in the blood as the result of bleeding and sedimentation.
However in whales, the oppotunity is almost rare to do with a alive individual.

SCHOLANDER[4] found the oxygen capacity of the blood in a living *Phocaena
communis* weighing 19 kg, to be 15.6%. LAURIE[1] obtained the result that the oxy-
gen capacity averages 14% in the blood from 7 fresh blue and fin whales.   SCHO-
LANDER[4] obtained the values of between 12 and 28% oxygen capacity in quite fresh
materials from greater whales.   He noted also that the carcass blood of some sperm
whale and that of some *Phocaena* showed both 24% oxygen capacity. He mention-
ed that a reasonable figure for the oxygen capacity of the fin whale blood would be
some 20 or 25% and that the sperm whale and the bottle-nosed whale bloods might
reasonably be assumed to have a higher oxygen capacity, about 30% or more than
in seal. This might be probable, but few evidences have been so far presented.

Tissue oxygen—. We will under this item, chiefly inspect the oxygen depots in
muscle pigments and in tissue fluids.   As will be seen later, the fat is capable to re-
tain much oxygen, but it is excluded here. The fat as an oxygen depot, will be dis-
cussed later in another chapter.

(1).   Muscle pigments.   In most mammals and birds, myoglobin and other re-
spiratory pigments in the muscle amount to about 15% of the blood hemoglobin.
The myoglobin as a store of oxygen, is characterized by the fact that it has a lower
oxygen tension of saturation than the hemoglobin and that its oxygen capacity is
much smaller as compared with hemoglobin.   TEORELL[11] demonstrated in a solu-
tion of the crystalline myoglobin from horse the myoglobin at pH 7.4 is already
half-saturated at the oxygen partial pressure of 3.26 mm Hg, whereas the hemoglo-
bin is not half-saturated until 20 mm.   VERZÁR[12] assumed a maximum oxygen ten-
sion in the resting muscle, of 19 mm, which would give 90% oxygen saturation of
the myoglobin.   MILLIKAN[13], by comparing the oxygen capacity of the myoglobin
in a normal mammalian heart and other red muscle, and its oxygen consumption,
deduced that the oxygen store of myoglobin could not last the tissue more than 10
or 15 seconds at rest and not more than 2 or 3 seconds at high activity.   He also
showed in cat that the myoglobin acts as a short time oxygen store to tide the mus-
cle over from one contraction to the next.

Thus, although it should be certain that the myoglobin serves as an oxygen
store, it seems that we cannot expect much from it. However, muscle pigments are
known to be more plenty in the whale's muscle, especially in the muscle of the sperm
and the bottle-nosed whale.   TAWARA[14] determined the amount of the myoglobin
and cytochromes in the muscle of sperm and sei whale, and found that the amount
of myoglobin is twice as much in the muscle of sei whale, and 8 to 9 times as much
in the sperm whale, as in beef.   But no remarkable difference was found to exist in
the content of the cytochromes between the muscles of the named three and that of
the blue whale.   From these result, we may well presume that myoglobin serves as
more important oxygen store in the sperm whale and perhaps in the bottle-nosed

whale.   Nevertheless, the oxygen stored in these depots cannot be expected to last the muscle more than 1 minute at the moderate activity.

(2).   Tissue fluid oxygen.   Excepting the blood, the tissue fluid of the whale may be estimated at 60% of the body Weight.   As the fat content is considerably high in the whale body, this may be rather a high estimate.   On the other hand, the solubility of oxygen in water is 2.44 cc (reduced to standard state) per 100 cc of water, at 35°C and at the oxygen partial pressure of 760 mm Hg.   Therefore, when the water is brought into contact with the atmospheric air in which the oxygen partial pressure is about 150 mm Hg, the water will dissolve about 0.5 v/v% oxygen at 35°C.   Accordingly, the tissue fluid of the whale body may be also able to dissolve some 0.5 v/v% oxygen when the whale is at the surface.   IRVING[10] and SCHOLANDER[4] adopted this value of 0.5%.

At first sight, this estimation seems to be the very truth, if disregarding some discrepancy due to the fact that the tissue fluid is a solution in which various substances are already dissolved.   However, it will prove that it is not the case, when we take into account that the tissue fluid does not come into contact with the atmospheric air but comes into contact with the blood.   The blood can retain much oxygen owing to its chemical combining power of oxygen; its oxygen capacity is usually over 15%, when it is brought in equilibrium with 150 mm oxygen partial pressure of the atmospheric air.   In other words, we can regard the blood as a concentrated aqueous solution of oxygen, though it is heterogeneous.   Thus, when the tissue fluid is brought into contact with blood whose oxygen concentration is over 15 %, it is evident that the tissue fluid will dissolve oxygen more than 0.5% of its volume.   If the solubility of oxygen in the tissue fluid is sufficiently great and the blood is so constructed that the equilibrium is established when the oxygen concentration of the blood comes to equal to that of the tissue fluid, then the tissue fluid can finally dissolve oxygen up to 15 v/v%.   However, this will be far from the truth.   It will be only right to say that the amount of oxygen which should dissolve in the tissue fluid is determined by the actual oxygen partial pressure of the blood.

Energy Requirement during Submergence

There are found a few informations related to this problem about whales.   Indeed, how much energy is consumed during submergence of a whale, it would be hard to estimate.   However, we are to enumerate at least, as the dissipation sources of energy, the energy consumption for basal metabolism, that for the translational movement of the whale body and that for the vertical motion against the buoyant or gravitational forces.   Beside these kinds of energy dissipation, the balaenopterids will consume their energy in collecting a large amount of the krill, and the sperm and bottle-nosed whale, for struggling with the great cephalopods.   The harpooned whale, which immediately dives deeply with full speed, pulling the harpoon line, must use a considerably large amount of energy.   The net dissipation of energy of these kinds is very hard or almost impracticable to compute.   Thus for the moment, we will consider only the first named three, that is, the energy requirement

for basal metabolism, that for translation and that for the vertical motion.

Energy for basal metabolism—. LAURIE[1] assumed a very little energy for the basal metabolism (b. m.) of the whale. Assuming that the energy requirement for b. m. of a warm-blooded animal is a function of the body surface alone, and that it is 1000 Calories per day per square metre of the body surface, and taking the body surface of the SÖRLLE's blue whale as 275 m², he calculated the energy requirement for b. m. of this whale at 275000 Cal/day. If we reduce this value to per body weight, it amounts only to 0.0016 Cal/kg, min—corresponding to about 0.3 cc/kg, min of oxygen consumed, as the oxygen consumption is 200 cc per Calorie produced. While the oxygen requirement for b. m. is 4.3 cc/kg, min, in man of 70 kg body weight.

The present author wonders, however, whether LUBNER's surface law which LAURIE applied to the estimation of energy for b. m., is so universal as to be applicable to any warm-blooded animal regardless of the species and the living environment. Surely we may feel to go too far with this law, when LAURIE applied it to such an aquatic homoiotherms as a whale. The medium in which the whale lives is much different in physical properties from that for land animals. The heat capacity of water is some 3200 times as great as that for the same volume of air, at ordinary temperatures and pressures. It would be partly for this reason that warm-blooded animals are not suitable to live in water. On the other hand, we must certainly remember that the whale is enveloped in the thick blubber which undoubtedly constitutes a good insulating wall. If it is the case that, owing to the insulating capability of the blubber, the energy consumption for b. m. is kept at the same level, for a whale in its water life and for a land animal in its land life, LAURIE's estimate will be right, although it seems doubtful to the author. Nevertheless, the author will tentatively adopt the value given by LAURIE, for our later calculations.

Work for submergence—. A whale must at first, sink its body against buoyancy of the water. Now we will consider the quasi-static work which must be done by the whale (or the potential energy aquired by the whale), when it submerges vertically against the buoyancy. If we write w and v for the weight and volume of a whale and ρ and ρ' for the specific gravity (sp. G.) of the whale body and the sea water respectively, the buoyancy which acts upon the whale body, is

$$B = v\rho' = w\frac{\rho'}{\rho} . \quad \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots (1)$$

Accordingly, the whale body undergoes an upward force $B-w$. So that, quasi-static work which must be done against this force for a vertical submergence through the length l, is

$$A = w(\frac{\rho'}{\rho} - 1)l, \cdots\cdots\cdots\cdots\cdots\cdots\cdots (2)$$

where A denotes the work. In Equation 2, if $\rho' > \rho$, the work is positive and if inverse, the work is negative, that is, work is necessary for floating, not for sinking.

In our calculations, it may be sufficient to assume that the sp. G. of the sea water

is 1.025. As for the sp. G. of the whale body, there is found no description but only one. In this old description, W. SCORESBY[15] mentioned that the Greenland right whale is very nearly of the same sp. G. as sea water, some individuals sinking and others barely floating when dead. In the modern whaling as we know, it is the usual practice that the whale after death, is inflated with the compressed air in order to prevent from sinking, but this procedure occasionally can be omitted in the sperm whale.

Therefore we may well regard the sp. G. of the whale body when it is dead, as a little greater or little smaller than that of the sea water. However, we must pay attention to the fact that this statement is concerned with the sp. G. of the whale *when dead*. When the whale is dead, the respiratory muscle being relaxed, it would not be strange to suppose that only a part of the air remains in the lungs of the carcass, the other part having escaped through the respiratory ducts.

We will now proceed to the numerical consideration of this problem, taking the example of the SÖRLLE's blue whale weighing 122000 kg, whose lung capacity being 3050 litres according to LAURIE. If we assume that, when this whale is dead, 2000 litres of air escaped from its lungs and therefore, 1050 litres remained, and that, in such circumstances, the sp. G. of this whale is 1.028 (a little greater than the sp. G. of sea water), then the sp. G. of this whale must have been 1.011, when with a lungful air of 3050 litres, ignoring the weight of the air. Whereas, the air in the lungs must decrease in volume, in accordance with the depths up to which the whale dives. If the decrease in volume results according to the gas law, we can easily find the depth where the sp. G. of this whale becomes identical with that of the sea water. Thus, it may be advisable to find at first, the depth at which the sp. G. of the both comes to be equal. Because, work is needed only to this depth and beyond this point deeper, no work is necessary to be done by the whale; the vertical sinking must be a spontaneous process. As a result of calculation, we find this point, at the depth of 12 meters from the surface, in the afore-mentioned conditions.

On the other hand, starting from the assumption that the sp. G. of the carcass is 1.022 (a little smaller than that of sea water) and the others are all the same as before, we obtain the equilibrium point to be 34 meters in depth.

These calculations were carried out on the assumption that the solid and the liquid parts of the body undergo no compression and the hydrostatic pressures increase at the rate of 1 atmospheric pressure for every 10 meters of water depth.

The above-mentioned calculations suggest that a whale need not make so much effort to dive. In divings, whales have parhaps a native skill to render the buoyancy minimized, by exposing a part of their body out of the water; by doing so, they can make the work of submergence minimized or negative. In fact, they habitually bow their back and then dive. The depth of 12 or 34 metres will be a trifle for a whale as long as 27 metres. It seems therefore that the work of submergence need not be considered as an important source of energy dissipation.

Work for emergence—. As has been mentioned in the preceding section, the

buoyant force comes to in equilibrium with the gravitational force, at the depth of about 34 metres, on the second assumption that the sp. G. of the whale is 1.022 when it is dead.   So that, at the depths below, the gravitational must overcome the buoyant force, in other words, the work must be done for floating not for sinking. Let us now consider the work that the SÖRLLE's whale must do for floating.   It is a matter of course that Equation 2 is valid for this calculation, but the opposite form is more convenient for use, that is,

$$A = w(1 - \frac{\rho'}{\rho})l, \quad \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots (3)$$

where A denotes the work for floating, w, the weight of the whale, and ρ and ρ', are the sp. G. of the whale body and the sea water respectively.

Assumptions and other particulars to be used in the calculation are as follows:

(1)   that the whale weighing 122000 kg begins to float from the depth of 1000 metres; this assumption may be true for the sperm whale;

(2)   that the sp. G. of the carcass with 1050 litres lung air is 1.022; hence, the sp. G. of the same whale with no lung air amounts to 1.031;

(3)   that this value of 1.031 is taken for the sp. G. of the solid-liquid portion of the whale body as a whole and this value of the sp. G. does not change with changing hydrostatic pressures; that is, the sp. G. of the whale body excluding the lung air is regarded as a constant throughout our floating process; this assumption may be true, because of the very small compressibility of the solid and liquid;

(4)   that the total mass of the lung gases remains unchanged throughout the process and it takes the volume of 3000 litres at the temperature of the whale body and at 1 atm.; this assumption is made with the intention that nitrogen gas is hardly affected by metabolism and the loss of oxygen will be compensated by the production of carbon dioxide.

To simplify the calculations, the work of floating is divided into two parts; namely, the work of lifting the solid-liquid portion of the whale body (A_1) and the work of lifting the gaseous portion (A_2), that is,

$$A = A_1 + A_2 . \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots (4)$$

A_1 is obtained by the simple numerical calculation of Equation 3, where $w = 122000$ kg (neglecting the weight of the lung air), $\rho = 1.031$, $\rho' = 1.025$ and $l = 1000$ m, and we find the work, $A_1 = 707600$ kg-m.

Next, let us calculate, A_2, the work for lifting the gas in the lungs. If we write w', for the weight of the gas in the lungs, ρ_0 and ρ' for the sp. G. of the gas and the sea water respectively and dl for the distance through which the gas is lifted, the infinitesimal work for lifting the gas, is

$$dA_2 = w'(1 - \frac{\rho'}{\rho_0})dl. \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots (5)$$

In Equation 5, since the sp. G. of the gas, ρ_0 is a function of the water depth, l, we

must give the relation between ρ_0 and l. At the first, we write as our definition,

$$\rho_0 = \frac{w'}{v'}, \quad \dots\dots\dots\dots\dots\dots\dots\dots (6)$$

where v' denotes the volume of the gas in the lungs. Furthermore we obtain from the preceding assumption (4), ignoring the effect of the temperature change,

$$pv' = 3000 \ (1, \ \text{atm}), \dots\dots\dots\dots\dots\dots\dots (7)$$

where p is the hydrostatic pressure which must be equal to the lung air tension. Finally the relation between the hydrostatic pressures and the water depths can be approximately stated as

$$p = \frac{l}{10} + 1. \quad \dots\dots\dots\dots\dots\dots\dots\dots (8)$$

For combining Equation 5, 6, 7 and 8, we obtain

$$\mathrm{d}A_2 = w'\Big[1 - \frac{30000\,\rho'}{w'\,(l+10)}\Big]\mathrm{d}l. \dots\dots\dots\dots\dots (9)$$

Integlation of Equation 9 gives

$$A_2 = w'l\big]_0^{1000} - 30000\,\rho'\ln(l+10)\big]_0^{1000}, \quad \dots\dots\dots\dots (10)$$

and by the the numerical calculation of Equation 10, taking $w' = 3.6$ kg (as the sp. G. of the lung air is 0.0012), we find $A_2 = -209120$ kg-m, for the work of lifting the air in the lungs. Thus, we have the total amount of the work for floating the whale

$$A = A_1 + A_2 = 498480 \ \text{kg-m}$$

This is the quasi-static work which must be done by the SÖRLLE's whale, for floating through 1000 metres; around 500000 kg-m—corresponding to 1167 Calories (as 1 kg-m=1/427 Cal).

Meanwhile, we can hardly find the way to estimate the efficiency, or the conversion factor of the muscle engine of the whale. SCHOLANDER[4] estimated it at 20 %. However, the present author was told that the efficiency of the muscle in ordinary sportsmen averages 22% and in well-trained experts, it reachs about 30% for their familiar exercise.* A whale must be an expert in divings. Therefore, we may be less erroneous to regard the efficiency of the muscle of whales as 30%, than to regard it as 20%.

Assuming it to be 30%, 3890 Calories is necessary for the work under consideration—corresponding to 778 litres of oxygen consumption (0.2 1/Cal). This amount of oxygen is greater than the oxygen stored in the lungs, namely, 610 litres

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* From the conversation of Dr. Prof. H. HAGIWARA (Sports Physiology), Department of Sportings, Faculty of Education, Hiroshima University.

with respect to the SÖRLLE's whale. In summary, we can see from the above calcu-
lations that the amount of oxygen consumed for floating may be not a trifle for the
sperm whale, which must preserve this amount for the last travel of emergence.

Towing resistance—. HANSSEN calculated the towing resistance of the SÖRLLE's
whale (cit. SCHOLANDER) and obtained the results that the towing resistance is e-
quivalent to 1.5 horse powers (Hp.) at a speed of 3 knots, 6.5 Hps. at 5 knots and
46.8 Hps. at 10 knots.

As for the swimming speed of whales, it may be said that the blue and fin
whales can swim at the sea surface with repeated shallow dives, at the speed of 15 to
20 knots, when they are on a long voyage or being chased. However, it is difficult to
tell at what speed they swim under the water. We have no evidence as to whether
whales swim at less speeds under the water than at the surface. However, they dis-
play only a part of their body out of the water, even when swimming at the sur-
face. Hence, it seems reasonably to be presumed that they could swim under the
water at nearly the same speed as at the surface.

On the other hand, in view of the energy economy, it is improbable that the
whales swim under the water at an unnecessarily high speed and thus they consume
energy for useless work. Then, it appears most probable that they swim under the
water, at the speed of 5 to 10 knots, taking account of the collecting a large mass
of the krill (for the balaenopterids) and of the pursuing the great cephalopods (for
the sperm and bottle-nosed whale). On the basis of this reasoning, we estimate con-
servatively that the average power for swimming of a submerged whale is 10 Hps.
If assumed so, 10 Hps. is 45000 kg-m/min, or 105 Cal/min, as 1 Hp. $=75$ kg-m/
sec and 1 kg-m $= 1/427$ Cal. Taking the efficiency of the muscle engine as 30% as
before, the energy consumption for swimming under the water averages 350 Cal/
min, or the oxygen required for this work comes to 70 1/min, in average.

The Balance of Oxygen

In the preceding section, we have attempted to give the total amount of oxy-
gen which a whale must carry with them in diving, and have found that several
factors which would constitute the basis of our quantitative considerations remain
still unknown. Indeed, there is still much to be learnt until we can strictly speak of
the maximum oxygen content of the whale body and further, how completely this
amount could be used up during submergence.

For the present, we can merely estimate from discussed above as follows, tak-
ing the example of the SÖRLIE's whale:

(1). The lung oxygen amounts to 610 litres, because the total lung air is 3050
litres, according to the LAURIE's estimate. Then, the utilizable oxygen at high esti-
mate, can be 550 litres, taking the depletion as 90%.

(2). The maximum estimate of the blood oxygen amounts to 2440 litres, tak-
ing the blood volume as 10% of the body weight, and the oxygen capacity as 20%
of the blood. As for the sperm or bottle-nosed whale, it would amount to 3660
litres, if they are of the same size as the SÖRLLE's whale (as the oxygen capacity is as-

sumed to be 30%). However, these estimated values may be considerably far from the truth, for we have not taken into account the degree of arterialisation of the blood. Therefore, when considering various depressing factors, the blood oxygen available during diving might be far less; the present author will estimate it at 70 % of the amount estimated above.

(3). The oxygen store ascribable to the muscle pigments may be negligible, as has been mentioned in the corresponding section.

(4). The tissue fluid oxygen is hardly to be estimated as has been already discussed. However, the present author is strongly inclined to believe that the tissue flluid is reasonably considered to dissolve oxygen up to the solubility at the oxygen partial pressure of 760 mm Hg, when it is brought into contact with blood. On the other hand, it may be also improbable that the whole amount of the fluids becomes saturated with oxygen within a comparatively short time. At the same time, we must take into account that the tissue fluid is a solution in which various substances are already dissolved. Thus under favorable conditions, if the tissue fluid has dissolved 1% oxygen at the onset of diving, then the total amount of the tissue fluid oxygen amounts to 730 litres, as the tissue fluid is assumed to be 60% of the body weight. Taking the depletion as 90%, the utilizable oxygen is estimated at 660 litres.

Thus, the total amount of oxygen which would be available for the metabolism during submergence of a whale sums up as follows:

	For SÖRLLE's whale	For sperm whale of the same size
Lung oxygen	550 litres	550 litres
Blood oxygen	1700	2560
Tissue fluid oxygen	660	660
Sum	2910 litres	3770 litres

We must now recall that a whale must reserve the oxygen necessary for the floating. This will be at least, 780 litres, if the whale emerges from the depth of 1000 metres, as calculated in the preceding section, and about 160 litres, if it emerges from 200 metres. Subtracting these amounts from the total available oxygen, the remainder will be 2750 litres for the SÖRLLE's whale (assuming from 200 m), and 3000 litres for the sperm whale of the same size as the SÖRLLE's whale.

On the other hand, the oxygen consumption rate during submergence will sum up to about 110 litres per minute; 38 litres for basal metabolism and 70 litres for swimming. At this consumption rate, the SÖRLLE's whale could last for 25 minutes dive with this depot, and the sperm whale endures 27 minutes dive. However, we must remember that this oxygen consumption rate is the minimum to be calculated. With this rate, whales cannot even change their swimming direction. The work for towing resistance contains no other energy dissipation than the translational motion at constant velocity. Concerning the energy for basal metabolism, the said figure is probably fairly underestimated, as has been noted in the preceding section.

Nevertheless, it seems interesting to us that the calculated and the experienced

diving durations are of the same order, for the balaenopterids. Thus it may be possible to consider that a dive lasting for several or ten and several minutes may be not severe for the balaenopterids, if viewed merely from the point of oxygen economy, disregarding the sensitivity to the excess of carbon dioxide. On the contrary, for the sperm and bottle-nosed whale, it is evident that their long diving duration cannot be explained from the estimated oxygen depot alone.

THE MECHANISMS WHICH WOULD REDUCE THE
OXYGEN CONSUMPTION DURING DIVING

Diving bradycardia—. Since P. BERT[16] first discovered it in ducks in 1870, the bradycardia (heart beat slowing) during submergence has been recorded by many authors in a variety of mammals and birds, and even in essentially non-diving animals including man. SCHOLANDER[4] observed the pronounced and reflective bradycardia in the submergence of seals; the decrease in heat frequency from 150 to 10 per minute. However, the same author could not detect the bradycardia in the artificial apnoea experiment of a porpoise (*Phocaena communis*). He said, "Palpatory and auscultatory there was some respiratory arrhythmia of the heart during apnoea, but no apnoea bradycardia could be induced, nor was this possible in a previous real submersion experiment on another porpoise. This is in sharp contrast to the immediate occurrence of bradycardia in seals during such experiments."

There is yet no proof as to whether bradycardia is induced in the greater whales, but it may probably be not, if inferred from the SCHOLANDER's observation on *Phocaena*. The direct consequence of the bradycardia will be, of course the retardation of the blood flow, and therefore it may lead to the general shortage of oxygen in every tissue and organ.

In connection with this problem, IRVING and his school suported the hypothesis of "the differential distribution of oxygen during diving". He said, "The storage of oxygen is inadequate to provide for its indiscriminate use by all of the tissues. No shift of metabolism can compensate for the lack of oxygen, but differential control of oxygen might reasonably serve to maintain the brain, allowing less sensitive tissues or those with fair capacity for anaerobic metabolism to do without oxygen." OMMANNEY[2] also called attention to the fact that, provided the brain and nervous system are kept supplied with oxygen, a man may incur a dept of oxygen in his tissues equal to ten times the amount of oxygen in his lnugs.

Some experiments speaking for this hypothesis are also known. However, the observations which apparently offer the decided evidence for this hypothesis were made by IRVING himself. The measurements were carried out in anaesthetized beavers, on the blood circulation both in brain and in muscles by insufflation apnoea and apnoea by clamping the trachea. He found in this case, that the apnoea bradycardia is accompanied with the reduced blood circulation in the muscle but increased blood circulation in the brain. They ascribed this effect to the peripheral vasoconstriction.

Retia mirabilia—. The retia mirabilia are the most remarkable anatomical feature in whales. These vascular networks, of which HUNTER[18] mentioned for the first time, have been noticed by many anatomists and have caused much speculation. However, in this connection, we may be referred to the study of OMMANNEY[2]. He gave the detailed description of the thoracic, basicranial and other retia, in the anatomical investigation of two fin whales' foetuses.

The thoracic rete is the vast and long-extended mass of networks of the vascular capillaries, located along the vertibral column from the 1st cervical to the 6th dorsal vertebra. These networks moreover, pass between the transverse processes into the neural canal where they are in connection with the intraspinal retia. The basicranial rete lies at the base of the skull.

The fundamental features of these retia are given by OMMANNEY[2]. The rete is the dense mass of networks of vascular capillaries which are in open communication everywhere with certain arteries and veins, embedded in its capillary system. This capillary system of the rete is supplied with blood by its own arteries from the main arterial system and drained through its own veins into the main venous system. The rete does not impede the blood flow on the course of main blood vessels, but intervenes between the main arteries and veins. In this respect, it gives an impression of the arterio-venous shunt, but it is not merely the constrictor mechanism. The rete is as a whole, embedded in a large quantity of fat and enveloped in stout connective tissues. Thus it has no relation with any surrounding organ or tissues, and therefore it appears to be an independent organ.

The retia mirabilia or structures similar to these, are found in all mammals which are capable of diving and of staying submerged for long periods, that is, in seals, porpoises, dolphins and whales. The sirenia which do not have the habit of remaining submerged so long, do not possess these vascular networks.

OMMANNEY[2] is of the opinion that these vascular networks are most likely to be concerned in some way with gaseous exchange. He said, "In this connection, the situation of the networks near the respiratory centre and on the course of main blood vessels and also around the brain and nerve chord is extremely suggestive. It has already been mentioned that the masses of the rete are abundantly charged with fat. Oxygen is very soluble in fats. It may be imagined that some chemical mechanism exists for a more speedy transfer of oxygen from the blood to the fatty masses of the retia, which may thus act as an oxygen storage mechanism. The retia may in fact be capable of forming a sort of accessory lung. Since the vascular networks are under the control of the somatic nervous system, they may possibly be engorged with blood at will from the posterior thoracic artery, and this blood may perhaps be discharged at will again into the posterior thoracic vein."

THE POSSIBLE MEANING OF EXISTENCE OF FAT IN WHALES

As for the solubility of oxygen in fat, OMMANNEY[2] made reference, in connection with the probable functions of retia, to the book of LEWKOWITSCH[19], in which the solubility is given as follows:

After 3 days' exposure at normal temperatures and pressures.

100 parts of cod liver oil absorb 6. 382 O_2

    //   whale oil   //   8. 266

    //   sperm oil   //   1. 629

    //   Japan fish oil //   8. 194

From these figures, we can see that the whale oil is of the highest solubility of oxygen, while the fish oil is also capable of dissolving almost the same amount of oxygen. Remarkable is the fact that the sperm oil can absorb far less oxygen when compared with the other samples. In this connection, OMMANNEY[2] expressed his opinion as follows: if the sperm whale makes a longer dive than the fin whale, as is usually said by whalers and accepted by some writers (he did not believe in this tendency of the sperm whale, at that time), one should expect to find in the sperm oil a high oxygen solubility; the results tabulated above however, show that the solubility is decidedly lower in the sperm oil than in other oils; the retia of the sperm whale were not yet examined in detail, but a superficial inspection indicates that they are of even greater extent than in the fin whale; this might be possible, if the oxygen solubility of the sperm oil is less than that of the fin whale.

ISHIKAWA[20][21][22] measured not only the solubility but also the absorption rate of oxygen and other respiratory gases in a variety of oily substances and water at 35°C and at various pressures. Thus, he ascertained that (1) the solubility of oxygen does not differ so much among the sperm waxes, whale oil and usual glycerides at each given pressure, but among all the samples employed, sperm waxes show the highest oxygen solubility; (2) for all the solvents investigated, HENRY-RAOULT's law on the dilute solution of the gas is valid; (3) in every material used, the absorption rate of a gas can be expressed by the formula, $y = A(1 - e^{-\alpha t})$, where y is the amount

Table 3. Solubility of gases in oily substances and water

Material	Solubility (cc/100g, atm)*		
	CO_2	O_2	N_2
Sperm whale head oil	130. 0	14. 4	9. 12
Sperm whale body oil	122. 0	14. 6	8. 82
Fin whale oil	118. 0	—	—
Blue whale oil	—	13. 0	7. 41
Olive oil	124. 0	13. 3	8. 21
Camellia oil	121. 0	12. 7	6. 92
Castor oil	106. 0	8. 8	5. 59
Oleic acid	127. 0	—	—
Oleyl alcohol	103. 0	—	—
Liquid paraffin	85. 0	13. 6	7. 27
Dist. water	61. 0	2. 4	1. 24
1% saline water	60. 0	—	—

* The solubility is expressed in terms of cc (reduced to standard state) of a gas per 100 g of a material and per 1 atmospheric pressure of the gas.

Table 4. Absorption rate of gases in oily substances and in water

Material	Initial absorption rate (cc/100 g, atm, min)*		
	CO_2	O_2	N_2
Sperm whale head oil	32. 5	1. 40	1. 40
Sperm whale body oil	27. 0	1. 19	1. 01
Fin whale oil	18. 2	—	—
Blue whale oil	—	0. 49	0. 60
Olive oil	8. 4	0. 55	0. 46
Camellia oil	6. 7	0. 46	0. 24
Liquid paraffin	4. 9	0. 26	0. 15
Castor oil	3. 0	0. 088	0. 043
Dist. water	36. 8	0. 20	0. 19
1% saline water	32. 6	—	—
Oleic acid	14. 1	—	—
Oleyl alcohol	10. 7	—	—

* The absorption rate is expressed in terms of cc (reduced to standard state) of a gas per 100 g of a material, per 1 atmospheric pressure of the gas, and per minute.

of gas absorbed up to the time t, A, the saturated amount at given temperature and pressure, α, a constant disregarding the pressures applied but characteristic of the kinds of solvent and (4) absorption rate thus calculated from the said formula is very different with different kinds of material used (see Table 3 and 4).

The solubility of oxygen in the sperm wax is 14.5 cc (reduced to standard state) per 100 g of solvent and per 1 atm. of the oxygen partial pressures, in contrast to the solubility in water of 2.4 cc, that is, about 6 times as great in the sperm wax as in water. While, the solubility of oxygen in the whale oil is 13.0 cc by the same unit. As for the absorption rate, the initial absorption rate is 7 times as great in the sperm head wax as in water, and some 2.5 times as great in the blue whale oil as in water.

Here must be noted that the result obtained by ISHIKAWA is inconsistent with that of LEWKOWITSCH, with respect to the oxygen solubility of sperm wax. However, we must call to mind that the former is obtained at 35°C (near the body temperature of the whale) and the latter is at the "normal temperatures." The sperm wax as we know, is the crystalline soft solid at room temperatures and on the contrary, is the liquid of high fluidity; the viscosity of the sperm wax at 35°C, measured by ISHIKAWA[20] is lower than all the oily materials employed. Then, it is possible that the sperm wax at the normal temperatures, is of the low solubility of oxygen, or more probably, of so slow rate to absorb oxygen, that the saturation cannot be reached by far, by the 3 days' exposure to the atmosphere. To all intents and purposes however, it may be sufficient to say that the wax should act at the body temperatures of the whale, not at the normal temperatures.

It will be clearly seen from the aforementioned, that the solubility of oxygen in oils particularly in the whale wax, is much higher than that in water, and that the absorption rate is especially greater for the wax than for the whale oils and other

glycerides. It might then, the next problem, whether oxygen can be really dissolved in oils or wax in the living whales.   No direct information is available about this problem.   However, the present author would refer to the fact which was found by the post-mortem examinations of patients of the caison sickness.   LAURIE[1], discussing the possibility of getting this disease in whales, made reference to the book of HILL[23], who gave the detailed description of this disease.   According to HILL, the nitrogen bubbles are found in various parts of the corpses, but most frequently in the fat.   The fat in all cases of decompression is honey-combed like whisked egg white.

Then, it may be unreasonable to consider that oxygen does not dissolve in fat, in spite of the foregoing fact that nitrogen is actually dissolved in fat of living individuals.   It may be probably that the oxygen partial pressure is far predominant over that of nitrogen within the whale body, when the whale respires on the surface.   Because the physical solubility of oxygen is about twice as great as that of nitrogen, at the same partial pressure and temperature, in both aqueous tissue fluids and fats.   Moreover, the blood may be regarded as a concentrated aqueous solution of oxygen, on account of its chemical combining power for oxygen; it is usually 15–20% oxygen solution in equilibrium with air.   On the contrary, nitrogen can be dissolved in the blood, as far as only 1% at the same atmospheric air.   In a word, the blood can carry 15–20% oxygen and some 1% nitrogen.   If the blood should transfer the oxygen and nitrogen to the fats in the whale body, this transfer would occur according to their own solubilities and their partial pressures.   Thus it may be possible to expect that the ratio of oxygen to nitrogen which are given up from the blood to the fat, is 15–20: 0.5.

The solubility of oxygen in fat as seen from Table 3, is 14.5 v/w% in the sperm wax, and 13.0% in the blue whale oil, at the oxygen partial pressure of 760 mm. Hg and at 35°.   So that, at the partial pressure of 150 mm Hg (under the atmospheric air), the solubility comes to about 3%.   However, as has been already discussed in the foregoing chapter (see p. 359), the dissolution of oxygen in fat does not occur in equilibrium with the oxygen partial pressure of the air, but would occur in equilibrium with the oxygen concentration of the blood.   Thus, it appears reasonable to the author that the fat can dissolve oxygen as far as the solubility at the oxygen partial pressure of 760 mm Hg.   If that is the case, this value of 14.5 or 13 % is that which is comparable to the oxygen capacity of the usual blood.

While, the fat content of the whale is in general, 25 to 30% of the body weight. Hence, for a moment, if the fat content is taken as 20% and this amount of fat could dissolve *in vivo*, oxygen as far as 10%, we will have 2440 litres of oxygen for the SÖRLLE's whale weighing 122000 kg.   That is just the same amount as the blood might store at high estimate.   This arithmetic answer may be of course, far from the truth.   Because, the fatty system is in general, not so abundantly supplied with blood vessels that the system can take much oxygen from the blood during a short period.   However we can not avoid the conclusion that the fat would dissolve more or less, oxygen from the blood or from the lymph.   Especially it is hardly supposed

that the retia and any system like these, which contain much fat and at the same time, are supplied with rich circulation, do not store any oxygen from the blood.

In reference to the problem in question, the result obtained by SCHOLANDER[4] in the artificial apnoea experiment of a porpoise (*Phocaena communis*), is very suggestive. He summarized as follows: the oxygen intake of this little *Phocaena* weighing 19 kg, was exceedingly high, between 400 and 500 cc per minute, this amount is more than for a man of 70 kg body weight, or twice the consumption per kg body weight of a seal; during whole of the experiment, the whale lay immoval and the high oxygen "consumption" remained unchanged for 33 minutes. The present author cannot but inquire whether this great amount of oxygen (13–15 litres for 33 min) was really consumed by the 33 minutes metabolism at rest, of this 19 kg porpoise. Certainly, this reminds me of some phenomena like the latent heat.

At the end of this chapter, it may be of interest to see the peculiar habit of respiration of the whale. As the whale comes up to the surface, it expires forcibly with half opened nostrils (by the way, the sperm whale has only one nostril), and then immediately inspires with nostrils wide opened. According to LAURIE[1], the total time from the commencement of the expiratory blast (spouting) to the closing of the blow holes, averages 1.5 sec; 0.6 sec for expiration and 0.9 sec for inspiration. Now after this inspiration, follows an immediate dive. But this dive is not long nor deep. In general, between two succesive deep dives (sounding) intervene 5–6 times shallow dives in the balaenopterids, and 20–40 times, occasionally 80 times shallow dives in the sperm whale. It is the point to which the author will refer, why the whale inevitably takes a respiratory pause after every inspirations, by means of the shallow dive. This shallow dive seems to be of no effect but rendering the inspiration effective. Indeed by this procedure, the oxygen inspired in the lungs must be made more soluble in the tissue fluid and in the fat, as a result of the increased hydrostatic pressures.

DEEP DIVING AND CAISON DISEASE

One of the problems which arises from the deep diving of the whales, is how the whales avoid getting the caison sickness, when they emerge from the deep submersion. During diving, the nitrogen gas goes into solution in the blood and distributes itself in the liquid parts of the body by the diffusion. The solubility of nitrogen in the aqueous fluid or fat is proportional to the hydrostatic pressures which the whales undergo, and the hydrostatic pressures are increased at the rate of 1 atmospheric pressure for every 10 metres of water depths. Then the amount of nitrogen soluble in the body fluid of the whale is to be determined by the depth and the time of submergence. If the whale should rise too quickly to the surface, there would not be time enough to emit for the nitrogen out of the blood or fluid, then it would form bubbles in the blood vessels and other tissues; it is the cause of the gas embolism. By the way, the oxygen and carbon dioxide dissolved in the body fluids cannot in ordinary cases, give rise to the caison disease. Because the former is soon consumed and the latter is of greater solubility. Thus the nitrogen and other innert

gases (but these latters being the minor importance) remain to be the object of the considerations.

Human divers can descend to a depth where the hydrostatic pressure is 2.25 atm. (all our expressions being by the absolute pressure), i.e., to the depth of 12.5 metres, and return to the surface with no care, but at the greater depths than this, precautions for prevention of the gas embolism must be taken depending on the duration of the exposure to the increased pressures.

Many authors have been hitherto engaged in searching this problem. However it seems to have proved that this question is a kind of the bugbear. OMMANNEY[2] denied the deep divings of the whale to avoid this difficulty (see p. 353), and LAURIE[1] answered this question by finding the "X-organism", which is according to him, living in the blood of the whale and eliminates the nitrogen. It may be however improbable that any microbe inhabits in the blood of healthy animals. Moreover, the results of the same author indicate that this small creature expends a considerable amount of oxygen, together with the nitrogen. So that the existence of these organisms in the whale blood becomes more and more doubtful, partly because of the said reasonings and partly because of the more decided fact that these organisms are again found by no other investigator.

In considering the possibility of getting caison sickness in whales, it may be advantageous to divide the diving into two categories, in order to avoid confusion; that is, diving with a lungful air (mono-breath dive) and diving with the respiratory apparatus (poly-breath dive).   In the poly-breath dive, the source of nitrogen is practically unlimited and the nitrogen is continued to be supplied without limitation. On the contrary, in the mono-breath dive, it is limited and the amount of nitrogen is evidently that which is already dissolved in the body at the normal atmosphere, plus that in the lung air. Thus it is evident that, in the poly-breath dive, the amount of nitrogen soluble in the body fluids is a function of the depth and duration of submergence, but in the mono-breath dive, the maximum amount of nitrogen soluble in the body fluids is only dependent upon the limited amount aforementioned. Thus, the question whether the whale can get caison sickness, is to be answered by the fact whether the amount of nitrogen in a lungful air of this whale is sufficient to give rise to this disease.

Let us now, proceed to the numerical consideration of this problem, taking the SÖRLLE's whale as an example.   At a starting point, let the aqueous fluid of this whale be 70% including the blood, and fat be 25% (the oil produced from this whale was 22.75% by SÖRLLE) of the body weight.   The solubility of nitrogen in water and in the whale oil is from Table 3, 1% and 6% respectively in round numbers, under the atmosphere.   Then the maximum amount of nitrogen soluble in the whale body sums up to 2680 litres.   On the other hand, the nitrogen in the lungs (the lung capacity being 3050 litres by LAURIE) is 2440 litres. This amount of 2440 litres is that which will be already soluble in the whale body before this whale reaches the depth of 10 metres.

Thus when the whale rises quickly from the great depths, it cannot undergo

more effect than that which would be exerted upon the whale on emerging from the depth of 10 metres, with respect to the gas embolism. The present author at least, cannot believe that the mono-breath dive might be accompanied by the caison disease.

SUMMARY

In this article, two problems are mainly argued namely, (i) what mechanisms enable the whale to endure submergence so much longer than other animals, and (ii) how it can avoid getting caison disease when it makes the swift rising from the great depths.

(1). The duration and depth of submergence in whales are surveyed by making reference to the reliable informations.

(2). The balance of the oxygen store and its consumption is considered. As oxygen depots, the lung air, the blood and tissue fluids are enumerated, and as the oxygen consumption sources, basal metabolism, translational movement and vertical motion are taken into account. Thus, it is almost certain that the storage of oxygen cannot cancel the oxygen consumption during a long dive of the sperm whale or the bottle-nosed whale.

(3). The mechanisms which would reduce the oxygen consumption during apnoea are considered. The retia mirabilia are the most remarkable structures which may serve as the control mechanisms of oxygen distribution, preventing the brain and nervous system from the oxygen deficiency.

(4). The author discussed the problem as to whether the fat in the whale body is possible to act as the oxygen storage or to be concerned with gaseous exchange.

(5). It was argued whether the whale can get caison disease, when it makes a swift rising from the great depths. The present author was strongly inclined to conclude that any animal cannot get caison disease in its "mono-breath dive."

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