A PAPER SUBMITTED TO BAROLOGIA - THE SOUTH AFRICAN SOCIETY FOR UNDERWATER SCIENCE
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ABSTRACT:

THE ADAPTATIONS FOR AND THE EFFECTS OF DEEP DIVING ON VARIOUS VERTEBRATES

Various physiological and anatomical features of diving vertebrates (mainly mammals) are cited, many of which are compared with those in man. The sperm whale can dive to 1134 m and remain submersed for up to 75 minutes. As in other diving vertebrates, the whales have important modifications of their blood systems, lungs and muscles, which enable them to stay submerged at depth for long periods of time. The advantages of an oblique diaphragm, small lung volume, pronounced Bohr shift, high muscle myoglobin content, depression of metabolic rate with circulation re-routing are some of the aspects discussed. The effects of high pressure are also mentioned.

INTRODUCTION

The aim of this paper is to bring to light some of the more important physiological and morphological features of diving forms and how these features come into operation during a dive. Comparisons are made with man and other terrestrial vertebrates.

Most of the mammal divers include the whales, dolphins, seals, dugong, manatee, walrus and sea-lions. Examples of diving birds are the penguins, puffins, ducks, cormorants and gannets, and of reptiles, the Galapagos iguana, turtle and crocodile.

Apart from the necessary prerequisites of general body form ie. the development of a torpedo-shaped body for reducing drag forces in dolphins, and a powerful fluke, or tail, for propulsion in whales and dolphins, three features are of prime importance to these diving forms. These are specialisations within the lungs the muscles and the blood. The cardiovascular and closely related respiratory adjustments have in fact extended the niches of all vertebrates, and in the case of those entering or leaving an aquatic environment, we find some incredible responses. Before elaboration on these responses, we should look first at just a few divers and the depths and times observed for their dives (Table I).

TABLE I
OBSERVED DURATION AND DEPTH OF DIVING IN SOME VERTEBRATES

	TIME (mins)	DEPTH (m)
Emperor Penguin	18	265
Grey Seal	18	128-146
Weddel Seal	43 (max 70)	600
Blue Whale	50	500
Sperm Whale	75	1,134
Bottle Nose Whale	120	300
Bottle Nose Porpoise	5	300
Most Men Resting	2	
Active	1	
Experienced skin divers	2.5	61
Record for man		73

After Gordon, MS, 1972
Harrison, RJ and Kooyman, GL, 1971

We can now consider adaptations of the lungs, muscles and blood separately. When these factors have been described, estimated dive times can be made, and compared with the observed dive times shown in Table I.

Discussion

1. LUNGS

One might well expect air breathing vertebrates to extend their dive times by having larger lung volumes per unit body weight compared with their terrestrial counterparts, so that an equivalently larger amount of oxygen is released to the tissues. This, however, is not the case - the lungs of some divers being the same proportional volume as non-divers, as in seals, or being half the volume of non-divers as in the case of whales. Scholander suggests that the lungs of whales may collapse during descent because they do not have a firm attachment to the thoracic wall - the air in them being forced into the dead air spaces (ie. a strengthened trachea), where gas exchange does not take place - the advantages of this will be discussed later.

Although the lungs are similar in size or smaller than those of man, the tidal volume and the percentage utilisation of oxygen is higher. See Table II.

TABLE II
LUNG VOLUME, TIDAL VOLUME AND PERCENTAGE OXYGEN UTILISATION IN SOME DIVING MAMMALS AND MAN

	LUNG VOL L/100 Kg	TIDAL VOL L/100 Kg	$\%O_2$ UTILISATION
Seal (Phoca)	5.0	1.8	5.0-7.0
Porpoise (Phocaena)	6.6	5.9	8.0-10.0
Bottle Nose Whale	2.5	2.2	8.0-10.0
Fin Whale	2.9	2.5	8.0-10.0
Man	5.0	0.8	4.0-5.0

2. Muscles

An important feature of diving vertebrates is the large quantity of myoglobin contained within their skeletal muscles. Compare for instance the myoglobin content of seal muscle with that of a cow, and we find the former contains 7715 mg myoglobin/ 100 g tissue whereas the latter has only 1084 mg myoglobin/100 g tissue.

Larger quantities of myoglobin are also fouled in birds such as grouse, which fly only short distances but do it very quick]y, the advantage as to these birds, and to diving forms, is that the increased myoglobin levels provide a very important oxygen reserve within the muscle - as will be seen in the next section.

3. Blood

There is a tendency for the blood volume and its oxygen carrying capacity to be greater in diving vertebrates than in man and other terrestrial vertebrates. As shown in Table III.

TABLE III

BLOOD VOLUME AND OXYGEN CARRYING CAPACITY OF THE BLOOD OF SOME DIVING AND NON DIVING SPECIES

	BLOOD VOL/% BODY Weight	O_2 CARRYING CAPACITY VOL%
Penguin	9.0	20.0
Seal (Phoca)	15.9	29.3
Porpoise (Phocaena)	15.0	20.5
Sperm Wale	-	29.1
Rabbit	6.5	15.6
Hen	3.9	11.2
Man	6.2 - 7.0	20.0

After Gordon, MS, 1972.

This obviously results in larger quantities of oxygen being taken down during the dive, and in a more rapid expulsion of CO_2, so that after emergence there will be a rapid recovery and the animal is ready to dive once again.

These diving forms also have a more pronounced Bohr shift. This means that the oxygen dissociation curve moves even further to the right than in the case of the terrestrial vertebrates. The advantage of this being that with the increased levels of carbon dioxide and the reduced pH during a dive, more oxygen is unloaded from the haemoglobin at the same O_2 tensions. This shifting to the right of the oxygen dissociation curve with the resulting straightening of the curve, means that the oxygen is made available to the blood at higher carbon dioxide concentrations. In effect, more use can be made of the O_2 that is available.

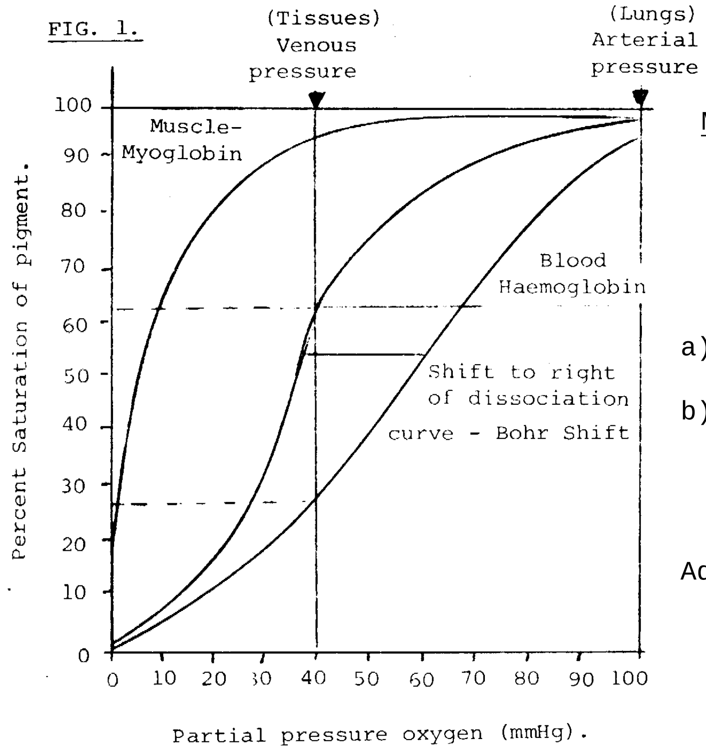


FIGURE I

OXYGEN DISSOCIATION CURVES FOR MAMMALIAN MYOGLOBIN AND HAEMOGLOBIN AT BODY TEMPERATURE

a) = 3mmHg PCO_2 & pH 7.6

b) = 40mmHg PCO_2 & pH 7.2

Adapted from Hoar WC, 1966.

The dissociation curve for myoglobin, unlike the sigmoid one for haemoglobin, is hyperbolic, and well to the left of the former.

This means that although oxygen is rapidly taken up from the blood, it is only released at very low oxygen tensions, or partial pressures, so that when the muscles are being exerted, as during a long dive, there is a good supply of oxygen available. Myoglobin, especially when at the high levels found in diving forms, therefore provides a very important, and quick, supply of oxygen when there is little available from the blood. See Figure I.

If we now look at Table IV, we find that the estimated dive times fall far short of the observed times, It can therefore easily be appreciated that diving mammals and birds can stay submerged far longer (up to 6 times as long in the penguin) than if they continued to consume oxygen at their normal pre-dive rate.

TABLE IV

COMPARISONS OF SOME OBSERVED DIVE TIMES WITH ESTIMATED DIVE TIMES

	OBSERVED DIVE TIME (Mins)	ESTIMATED DIVE TIME (Mins)
Penguin	18	3
Seal	18	6
Bottle Nose Porpoise	5	3
Bottle Nose Whale	120	36

The anatomical and physiological adaptations described clearly therefore do not give the full story. What further effects has evolution to an aquatic and diving existence had on these forms and how do these effects come into play?

The following will be considered:

- Bradycardia
- Lactic acid tolerance
- Circulation re-routing
- High pressure adaptations

Bradycardia

Non-diving vertebrates, such as man, have the necessary “equipment” to show a diving response, but it is nowhere near as specialised as in the diving forms.

It is generally accepted that there is a depression of the metabolic rate during a dive so that oxygen is conserved. Paul Bert (after Gordon MS, 1972) made one of the earliest observations of bradycardia, this being the lowering of the heart rate, during submergence experiments with ducks.

The Bradycardia response was soon afterwards shown to be of vagal origin, for when this nerve supply was sectioned the response was eliminated. Diving animals studied after this, have always shown the effect (Andersen, HT, 1961, 1964. Scholander, PF, 1940).

To demonstrate how much better at bradycardia the divers are than man we can use the Grey Seal as an example. This animal can reduce its heart beat from 130 bpm to 4 bpm after only one minute during a dive. Man, depending on such factors as age, diving experience, temperament of the individual, water temperature and so forth, can lower his heart rate by only a half.

Circulation re-routing

Another very important feature of the diving vertebrates mentioned, is the ability to circulate blood only to those tissues that are important during a dive, and reduce it or cut it off from those that are not.

Most work on the effects of diving on the vascular system has been done on pinnipeds (after Harrison, RJ, and Kooyman, GL, 1971), and circulation re-routing has been demonstrated by injections of a radioactive rubidium compound into the blood.

The pectoral, gastrocnemius and neck muscles, as well as the skin of all the body except the head, which must be kept warm, have the blood supply cut off. A cut-off of supply to the skin is important for conserving heat which is more readily lost to water than air, especially in the colder depths. There is also cessation of supply to the renal and gastro-intestinal regions. In the case of the latter, the oesophagus is supplied because it must function for the swallowing of food.

The adrenal and thyroid glands and brain, however, have an increased supply, and the liver, heart and eye muscles a normal supply.

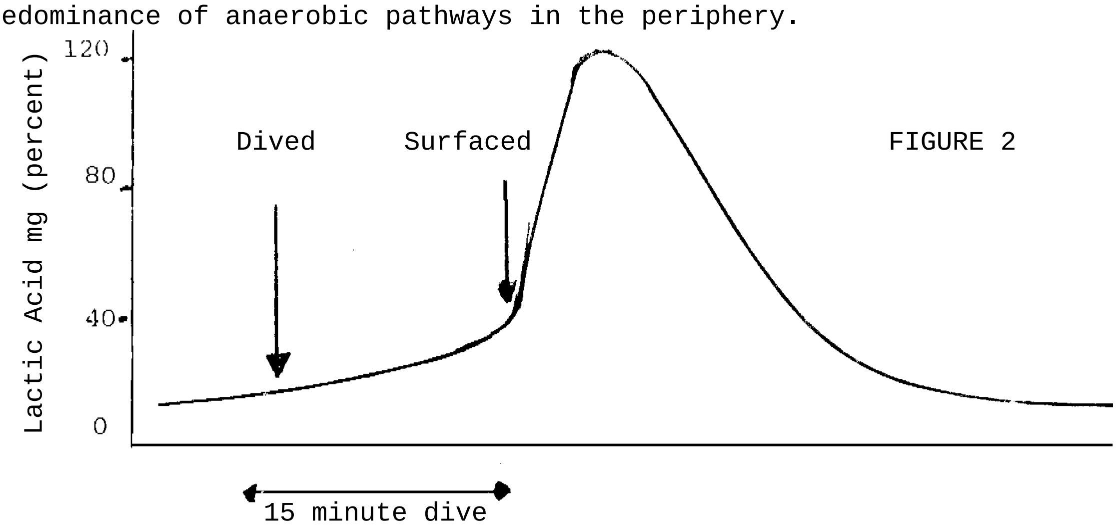
The site of vasoconstriction is unusual and characteristic in diving forms (eg. ducks and seals) for instead of the arteriolar constriction characteristic of non-divers, it is the larger arteries that constrict by innervation from the sympathetic nervous system. The advantage of this is that there can be no chance of peripheral dilation of vessels by the over-riding effects metabolic dilators can have on the sympathetic nervous system (ascending dilation), because the centre of control is further back than the site of production of the local dilator factors.

A change in blood pressure, which could be disastrous, does not take place, as Elsner et al. (1966) have shown with the sea-lion. The central arterial pressure does not change, because the high peripheral resistance is balanced by a low run-off rate of blood.

Lactic acid tolerance

Work done on the seal (Scholander, PF, 1940. Andersen, HT, 1969) has shown that the lactic acid level rises only slightly during the dive, but increases by nearly ten times after emergence (Figure II). This is almost certainly because the lactic acid is stored in the muscles in consequence of restriction of blood flow, and then released upon return to normal circulation. As well as tolerating low O_2 and high CO_2 levels, high lactic acid levels are also tolerated.

Clearly, oxidative metabolism is limited in most tissues because of vasoconstriction. It is also further restricted, and the vital oxygen conserved, because of the predominance of anaerobic pathways in the periphery.



Lactic acid level in arterial blood of a seal before, during, and after a 15-minute dive (after Andersen, 1969).

The Weddel seal can stay beneath the ice for well over 60 minutes. Kooyman (1969) and Peak et al. (1970) have shown that the lactate dehydrogenase isozyme complex of its muscles is involved with this anaerobic tolerance. The LDH5 is orientated towards pyruvate reduction, and its concentration is 30% higher in the muscles of the Weddel seal than in the less efficient diving, Cape Fur seal. Consequently, the greater amount of its present, the more oxygen will be spared by the muscles (the largest body tissue), and there will be an extended period of availability of this oxygen for aerobic respiration elsewhere.

High pressure adaptations

As depth increases, the hydrostatic pressure increases at a rate of approximately one atmosphere for every ten metres of sea water. Within the diving mammal therefore, air spaces such as the lungs and middle ear tend to collapse and there are modifications which permit these internal gas spaces to remain in equilibrium with ambient pressure. For instance, the thoracic wall is flexible and the diaphragm oblique, thus permitting abdominal blood and viscera to displace the diaphragm into the thorax. Also, the linings of the middle ear space contain sinuses, which become engorged so reducing the volume of the space when it is under pressure.

Finally, there is no danger of nitrogen narcosis upon the rapid decompression during a fast ascent, for the following reasons: when the lungs become compressed, air is forced into non-respiratory spaces so little nitrogen can enter the blood, next there is a low lung volume, and finally, because nitrogen is more soluble in fatty substances, it is thought that much of it enters the copious quantity of fatty tissue found for example, in the blubber of whales.

Conclusion

Diving appears therefore, to be a special case in which mechanisms of widespread occurrence have been elaborated to the extreme. Modifications of lungs, muscles and blood, with tolerance to high carbon dioxide and lactic acid concentrations, as well as a pronounced slowing of the heart beat, are some of the accomplishments that have resulted in the successful invasion, by air-breathing animals, of aquatic environments and have extended the vertical range of mammals to over 1000 metres below the surface of the ocean.

To quote Gordon:

> “Such adaptations also make possible the rather startling observations of SCUBA divers on the coasts of the Galapagos islands, where they encounter the rather improbable spectacle of marine iguanas, happily grazing on algae at depths in excess of 10 metres in the company of a host of fishes!”

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S W A L K

Brigitte Bardot has presented her pet 4 month old seal to the French Riviera's Marineland. She did this, she said, for the animal's own good. The seal was given her by Brittany fishermen who had found the deserted pup in Newfoundland. But the change to Marineland was followed by a severe psychological setback. Apparently the seal had become accustomed to a routine of bottled milk, fish soup and kisses from BB. Heaven preserve us from being done good with to such a set up!

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