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Physiology of Diving of Birds and Mammals

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Butler, Patrick J., and David R. Jones. Physiology of Diving of Birds and Mammals. *Physiol. Rev.* 77: 837–899, 1997.—This review concentrates on the physiological responses, and their control, in freely diving birds and mammals that enable them to remain submerged and sometimes quite active for extended periods of time. Recent developments in technology have provided much detailed information on the behavior of these fascinating animals. Unfortunately, the advances in technology have been insufficient to enable physiologists to obtain anything like the same level of detail on the metabolic rate and physiological adjustments that occur during natural diving. This has led to much speculation and calculations based on many assumptions concerning usable oxygen stores and metabolic rate during diving, in an attempt to explain the observed behavior. Despite their shortcomings, these calculations have provided useful insights into the degree of adaptations of various species of aquatic birds and mammals. Many of them, e.g., ducks, smaller penguins, fur seals, and Weddell seals, seem able to metabolize aerobically, when diving, at approximately the same (if not greater) rate as they do at the surface. Their enhanced oxygen stores are able to support aerobic metabolism, at what would not be considered unusually low levels, for the duration of the dives, although there are probably circulatory readjustments to ensure that the oxygen stores are managed judiciously. For other species, such as the larger penguins, South Georgian shag, and female elephant seals, there is a general consensus that they must either be reducing their aerobic metabolic rate when diving, possibly by way of regional hypothermia, and/or producing ATP, at least partly, by anaerobiosis and metabolizing the lactic acid when at the surface (although this is hardly likely in the case of the female elephant seals). Circulation is the proximate regulator of metabolism during aerobic diving, and heart rate is the best single indicator of circulatory adjustment. During voluntary dives, heart rates range from extreme bradycardia to well above resting, reflecting metabolic performance. Efferent cardiac control is largely parasympathetic. Reflex cardiorespiratory responses are modulated by conditioning and habituation, but reflexes predominate during extended dives and during recovery, when gas exchange is maximized.

I. INTRODUCTION

Diving birds and mammals remain submerged underwater for differing durations, from several seconds to many minutes, and, in general terms, these differing durations relate to the depth to which the animals routinely dive in the water column, from a meter or so to many hundreds of meters. There are, therefore, two major problems confronting many species of aquatic birds and mammals: relating to their limited oxygen stores and to the large hydrostatic pressures to which they are exposed. With an increase of 1 atmosphere for approximately every 10-m descent into the water column, an animal at a depth of 200 m will experience a pressure of 21 atmospheres.

The problems facing these animals are all related to the fact that they have air-filled cavities in their bodies and that air is compressible. There are a number of anatomic features in marine mammals that enable them to overcome many of these problems, and these were all discussed by Butler and Jones (53) and Kooyman (218). Because there has been little research on this topic during the past 10 years, we do not intend to discuss this aspect of diving to any great extent in this review.

Regarding their limited oxygen stores, the central question is: What physiological and metabolic processes enable these air-breathing, homeothermic endotherms to remain submerged and, maybe, active for extended periods? Two very important aspects of the answer to this question relate to the amount of oxygen that can be stored in the body for use underwater (and, conversely, the amount of carbon dioxide that can be stored during submersion for removal at the surface) and the rate at which that oxygen is used during the period of submersion. Related to the latter is how the stored oxygen is distributed to the various organs and tissues to meet their different requirements and to what extent living and/or diving in cold (maybe around 0°C) water and eating cold food affects the metabolic rate of these endothermic homeotherms. Although temperature regulation and adaptations to low temperature were also discussed in some detail in Reference 53 and are not covered to any great extent in the current review, we intend to highlight some exciting recent observations that indicate that regional hypothermia may be an important factor in reducing overall oxygen requirements during diving, in at least some species of marine birds and mammals. Another important aspect, particularly as far as foraging is concerned, is the rapidity with which the oxygen stores can be replaced (and the carbon dioxide removed) when the animals are at the surface.

It is possible to identify three distinct phases in the evolution of the answer to the above question. Initially, data were obtained from restrained animals that were forcibly submerged. These studies go back well over 100 years, but perhaps the most influential publications were those of Irving (195, 196) and Scholander (346). These and subsequent publications by the same authors and others using restrained animals have been reviewed many times (3, 28, 45, 53, 69, 135, 218), so it is not the intention here to produce another review of this material.

The model that emerged from these studies is that, although the oxygen stored in the body is greater in diving than in nondiving species (Table 1), it is insufficient to enable aquatic birds and mammals to maintain aerobic metabolism and remain submerged for the durations obtained during the experiments. Consequently, there is an overall reduction in the level of aerobic metabolism so that the oxygen stores are conserved for those tissues that cannot survive hypoxia. This is achieved by selective peripheral vasoconstriction causing a reduction in the perfusion of all parts of the body except the oxygen-sensitive tissues, the central nervous system, and heart [note, there is no reduction in coronary flow in forcibly submerged ducks (204), whereas in seals it does decrease in proportion to the reduction in cardiac output (27, 30, 424)].

Thus, in the underperfused tissues, which includes the skeletal muscles in these restrained animals, there is a net accumulation of lactic acid that is flushed into the blood soon after the animal is surfaced. As well as the

TABLE 1. *Sites of oxygen storage in diving and nondiving homeotherms*

	Myoglobin, g/100 g tissue		
Muscles			
Hummingbird (pectoralis)	0.47		
Tufted duck (gastrocnemius)	0.98		
Tufted duck (pectoralis)	0.73		
Gentoo penguin (pectoralis)	4.4		
Thoroughbred horse (psoas)	0.88		
Beaver	1.2		
Ribbon seal	8.1		
Weddell seal	5.4		
Elephant seal	5.1		
Bottlenose dolphin	3.2		
Porpoise (psoas)	4.1		
Sperm whale	5.7		
Bottlenose whale	6.3		
	Volume, ml BTPS/kg		
Respiratory System			
Mallard duck	112		
Tufted duck (lesser scaup)	180 (355)		
Adélie penguin	165		
Dog	61		
Human	74		
Beaver	60		
Weddell seal	48		
Harbor porpoise	59		
Bottlenose whale	25		
	Volume, ml/100 g body mass	Hb, g/100 ml blood	Oxygen Capacity, ml O_2/100 ml blood
Circulatory System			
Pigeon	9.2	15.3	21.2
Mallard	9.1	17.1	22.9
Tufted duck	11.4	18.4	24.6
Chinstrap penguin		19.6	26.3
Emperor penguin		16.8	23.0
Human	7.7	14.8	20.2
Beaver	6.5	11.9	16.1
Weddell seal	21.0	25.9	34.7
Bladdernose seal		26.4	36.0
Elephant seal	21.7	23.3	31.2
Bottlenose porpoise	7.1	14.4	19.7
Dall porpoise	14.3	20.3	26.5
Sperm whale		14.7	18.5

Hb, hemoglobin; BTPS, body temperature and pressure, saturated. Data are from the following sources: Ref. 49; lesser scaup, Ref. 364; elephant seal, Ref. 218; Weddell seal, Ref. 324.

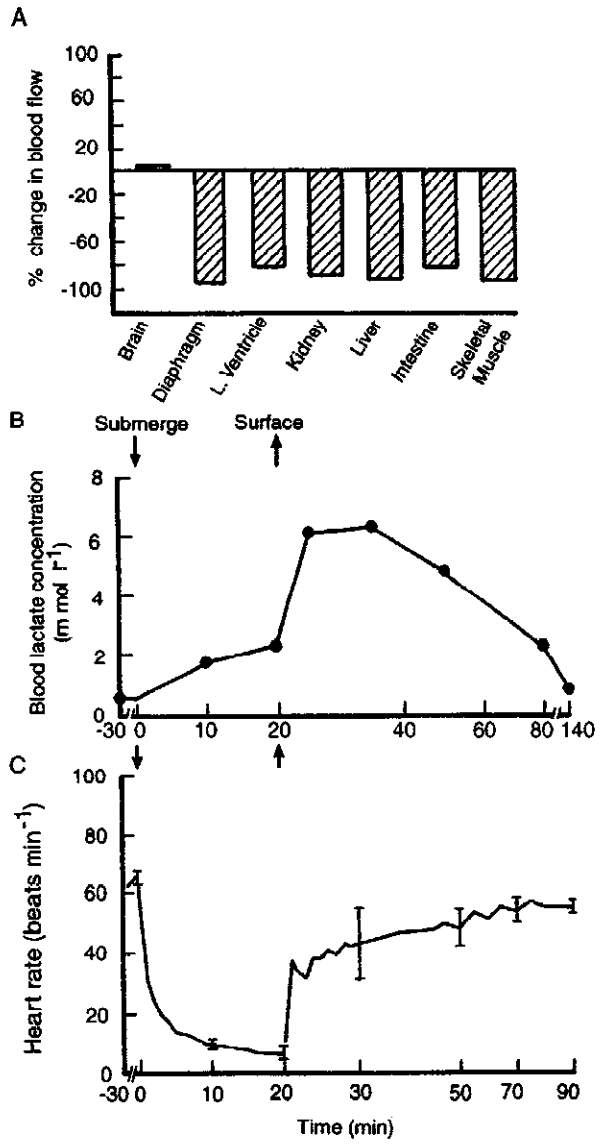


FIG. 1. Cardiovascular and metabolic changes that occur during and after a period of involuntary submersion of Weddell seals. *A*: percentage change in blood flow to various organs after 8–12 min of involuntary submersion of up to 6 seals. [Modified from Zapol et al. (424).]. *B*: concentration of lactate in whole arterial blood during involuntary submersion and subsequent recovery of 1 seal. [Modified from Murphy et al. (300).] *C*: mean ± SD of heart rate of 4 maternal seals during and after involuntary submersion. [Modified from Liggins et al. (257).]

selective peripheral vasoconstriction, there is also a reduction in heart rate during submersion. Because cardiac stroke volume does not change in most birds and mammals (see Ref. 53 for details), this diving bradycardia causes a reduction in cardiac output of similar magnitude. The increase in peripheral resistance and decrease in cardiac output tend to offset one another, so there is no change in central blood pressure. The bradycardia is often taken as being indicative of the other physiological and metabolic events taking place during submersion. Some of the components of this "classic" response to diving are shown in Figure 1. Of particular importance is the fact that it takes approximately six times the duration of the forced submersion for the concentration of blood lactate to return to the predive level (see also Ref. 53).

This hypothesis of large-scale peripheral vasoconstriction, reduced aerobic metabolism, and a substantial increase in anaerobic metabolism during voluntary submersion was challenged during the late 1970s and early 1980s, initially as a result of studies on two species, the tufted duck, *Aythya fuligula*, and the Weddell seal, *Leptonychotes weddellii* (59, 235, 414), although it must be said that Scholander, himself, was not too certain of the universality of the Irving-Scholander hypothesis. In his 1940 paper (346), he says that it would "be of great interest to compare the circulation in a relaxed muscle during a dive with that of a working muscle during a dive and corresponding conditions when the animal is not diving." He goes on to write that even if "reduced metabolism might be thought possible during a quiet dive this cannot be the case in an ordinary dive. It is during submersion that a seal does most of its exercise in hunting fish and by distance swimming."

Two years later, Scholander and colleagues (348) noted that harbor (common) seals, *Phoca vitulina*, rarely dive for longer than 4–5 min "and thus usually dive under a comfortable aerobic muscular condition without need for acid formation." Similarly, for the two species of penguins that he studied in 1940, macaroni, *Eudyptes chrysolopus*, and gentoo, *Pygoscelis papua*, Scholander noted that most natural dives were of <1 min in duration. He concluded that the feature of these birds is not so much prolonged diving as their ability to dive repeatedly with only a few or single breaths between each dive. These comments and observations on some naturally diving birds and mammals are not at all consistent with the idea of the accumulation of lactate and long recovery periods at the surface to remove this lactate.

It was the initial observations and studies on freely diving birds and mammals that led to the second stage in the evolution of the answer to the question, i.e., that most, if not all, dives performed naturally are aerobic in nature. Attempting to study the physiological processes, and their control, that are associated with a particular type of behavior of an animal is fraught with difficulties. Scholander clearly yearned, on occasions, to be able to make physiological measurements on freely diving birds and mammals, but this was not to be. Nonetheless, a compatriot of his, Eliassen, published in 1960 what turned out to be a very perceptive paper (129).

Using largely his own observations on the durations of natural dives of a number of marine birds, calculations of oxygen stores in these birds, and data on oxygen usage during such dives of normal duration (which incorporated his own laboratory experiments on the drag of the birds at a range of underwater speeds), he refuted the idea that

vasoconstriction and anaerobiosis occur in the locomotor muscles of birds during natural diving. In fact, he compared normally exercising and diving animals, suggesting that the circulatory events are the same in both cases, with blood being preferentially distributed "in favour of the working organs." He went on to say, "Considering the diving animals, the peripheral constriction during diving should, therefore, not take place in the muscles, but in the viscera alone." He did not support the idea of a reduction in (aerobic) metabolism during diving. At the time, his methodology was criticized (197) and his proposals were rejected (2).

The first real hint that data obtained from birds undergoing involuntary submersion might be different from those obtained during voluntary dives was provided by Millard et al. (285). They used radiotransmitters to record heart rate from freely exercising and diving Adélie and gentoo penguins (*P. adeliae* and *P. papua*, respectively). They noted that "The cardiovascular adjustments recorded during voluntary diving in penguins are. . .not readily compared with earlier reported results in diving birds. Such comparison is difficult because previous studies have been performed on restrained birds forcefully dived. . . . Our data have been obtained on penguins performing normal swimming and diving, which will give results as a composite of (involuntary) diving and exercise responses." It was the further use of radiotransmitters, with pochards (*Aythya ferina*) and tufted ducks (59, 413), and the introduction and use of time-depth recorders (TDRs) with freely diving Weddell seals (214, 215), both in conjunction with more conventional physiological techniques, that gave rise to the idea that most, if not all, natural dives are aerobic in nature.

As is often the case in biology, it can be folly to make generalizations on the basis of studies on one or two species. Tufted ducks and Weddell seals were chosen for particular reasons. The former can be used relatively easily in laboratory and semi-laboratory situations, while the natural habitat of the latter enables a laboratory to be created in the field. Thus it has been possible to obtain more conventional physiological data from these animals, together with the information obtained from the transmitters or TDRs. However, more recent field studies on other species of diving birds and mammals, which have relied entirely on transmitters, data storage devices, and/or TDRs, have taken us to the third stage in the evolution of the answer to the question, and about full circle. Evidence from species such as thick-billed murres (Brünnich's guillemots, *Uria lomvia*) (96), king and emperor penguins (*Aptenodytes patagonicus* and *Aptenodytes forsteri*, respectively) (221, 232), northern and southern elephant seals (*Mirounga angustirostris* and *Mirounga leonina*, respectively) (179, 248), and gray seals (*Halichoerus grypus*) (378) indicates that some species, maybe only at some time during the annual cycle, either have a very low rate of aerobic metabolism during diving and/or metabolize anaerobically and accumulate lactate during some dives.

This review concentrates on the physiological responses, and their control, that occur in freely diving birds and mammals. Although some of the data presented are behavioral, the emphasis is on their physiological implications. Similarly, some of the data discussed here have been obtained from experiments on restrained animals, but they are discussed in the context of their implications for freely diving animals.

Before one embarks on this review, it is important to understand the terminology used to describe the natural, and unnatural, diving of birds and mammals. Three broad categories, natural, forced, and trained, encompass virtually all types of dives, but these categories are somewhat arbitrary and, consequently, not exclusive. Natural or voluntary dives are performed by unrestrained animals and are most frequently (>90%) within the animal's capability to provide energy requirements aerobically. Natural dives can be performed in the wild or simulated habitats to which animals are acclimated. Extended dives are a subset of natural diving and are dives that are temporally extended by the animal's own volition and may involve a switch to anaerobic energy production.

Dives in which the animal is restrained and submerged, confined and submerged, is encouraged to dive by presentation of a threatening stimulus (escape dives), or is prevented from surfacing ("trapped dives") all fall into the category of forced or involuntary dives. An unusual circumstance is when an animal is trained to dive, submerging only the head or the whole body, or trained to change natural diving behavior. Training implies some psychological restraint, so in one sense these are forced dives, but for reasons that will become clear, these dives will be termed trained dives, with the added qualifier that the animal is either active or passive.

II. DIVING BEHAVIOR

The diving behavior of an animal will inevitably be related to the extent to which the animal is adapted to an aquatic existence. The methods of locomotion on land, in the air, and in water have different mechanical requirements. Most aquatic birds are still able to fly, so even if the wings are used for underwater propulsion, they and the density of the body must be consistent with flight in both media. Only the penguins have abandoned aerial flight altogether, but they still retain their legs for terrestrial locomotion. Similarly, among the aquatic mammals, the four limbs of mink, muskrats, and otters have become only marginally adapted for an aquatic existence, whereas in otariids (fur seals and seal lions) and even more so in phocid (true) seals, the limbs have become more adapted

for aquatic propulsion and the animals are, thus, more cumbersome on land. In terms of locomotion, the cetaceans are completely adapted to an aquatic life-style. The hindlimbs have disappeared altogether, and the animals never come ashore. Thus, for these animals, all of their activity occurs in water.

All of these factors, together with the buoyancy of the animals, will contribute to the rate at which oxygen will need to be consumed to swim a given distance underwater, i.e., to the efficiency of underwater swimming. At one extreme, diving ducks and mink are relatively buoyant, use webbed feet for generating thrust, and have relatively high drag coefficients (363, 364, 405). At the other extreme, penguins and dolphins are close to neutral buoyancy, use flippers or tail flukes as hydrofoils, and have relatively low drag coefficients (11, 149). Whether or not dolphins possess special mechanisms for reducing drag, or whether body shape is the major factor, is still a contentious issue (149, 342), although Barnasch (11, 12) has proposed such mechanisms for penguins. All of these facts should be borne in mind when studying the behavior and metabolism associated with diving in aquatic birds and mammals. Although there may be similarities between different species, we should not be surprised to find differences.

A relatively simple way of describing diving behavior in a number of different species of birds and mammals is to present a table of mean and extreme values of dive duration and depth. It is clear, from recent studies, however, that diving behavior is influenced by a number of factors, many of which, such as light levels and food availability, are variable. Also, the frequency of particular dive depths or durations may not be normally distributed, so to give mean values without an indication of the factors that may influence those means, or whether "mean" is appropriate, can be misleading. In fact, some authors (35) give median values rather than means.

There have been recent attempts to model diving behavior in terms of optimal foraging because a number of dives, if not most for some species, are feeding dives. An interesting feature, from a physiological point of view, is that the rate at which oxygen can be loaded when an animal is at the surface may strongly influence the time it remains feeding at a given depth. Houston and Carbone (192) predict that, for animals that remain aerobic during diving, time in the foraging area at first increases and then decreases as travel time from the surface to the foraging area (i.e., depth of dive) increases. This, they argue, is because at relatively shallow depths the animals should operate over the steep part of the oxygen-loading curve and thus neither unload nor load the oxygen stores toward their extreme levels. At relatively greater depths, however, it is more efficient for the animal to spend longer at the food source and to operate over a greater range of the oxygen-loading curve. Beyond a certain depth, and when

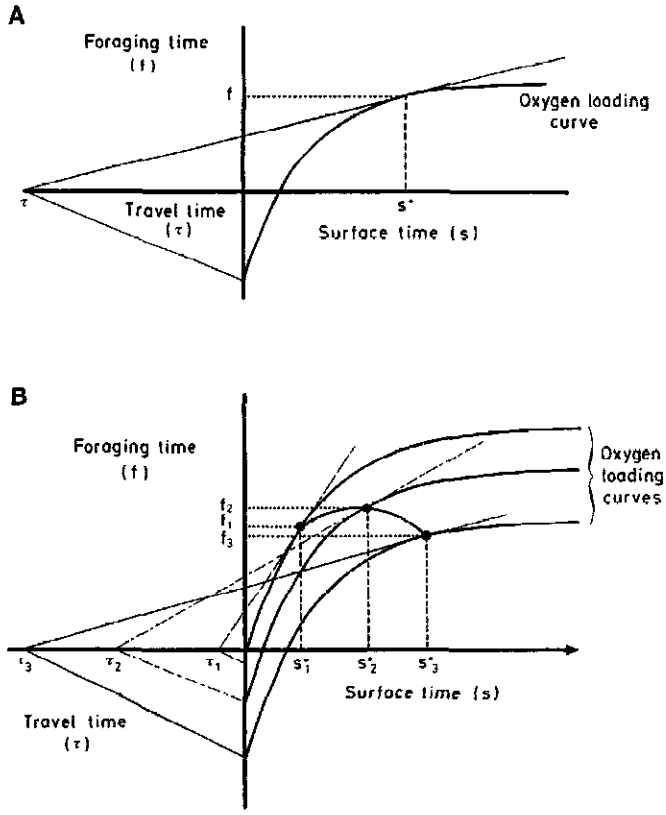


FIG. 2. *A*: graphical representation illustrating amount of time that a diving bird or mammal should spend at surface (s^*) loading its oxygen stores to maximize ratio of foraging time (f) to travel time (τ) plus time at surface (s) [$f/(\tau + s)$]. *B*: graph illustrating optimal solution for 3 values of travel time, τ_1, τ_2, and τ_3, indicating that corresponding optimal times at surface, s_1^*, s_2^*, and s_3^* should increase, whereas resulting foraging durations, f_1, f_2, and f_3 should first increase and then decrease. [Modified from Houston and Carbone (192).]

a critically greater proportion of the oxygen is used for traveling to and from the food, the time at the food patch begins to decrease (Fig. 2). This prediction is corroborated by some independent studies (96, 411) but not by others (81).

Recent evidence from gray seals (334) indicates that the oxygen-loading curve used by Houston and Carbone (192) may not be strictly correct for all aquatic birds and mammals. Certainly, the introduction of a 10- to 20-s delay into their model representing the time before oxygen is extracted from the inhaled air after surfacing more accurately predicts the diving behavior of Antarctic fur seals (37).

Thompson et al. (380) have discussed, among other things, the speed at which a diving animal should swim to its food supply from consideration of the cost of transport (amount of energy required to transport a given mass over a given distance) as well as the oxygen-loading curve. It appears that, if an animal wishes to maximize its gross energy intake, it should swim slower to reach greater depths (Fig. 3). When the animal has reached the food, its swim

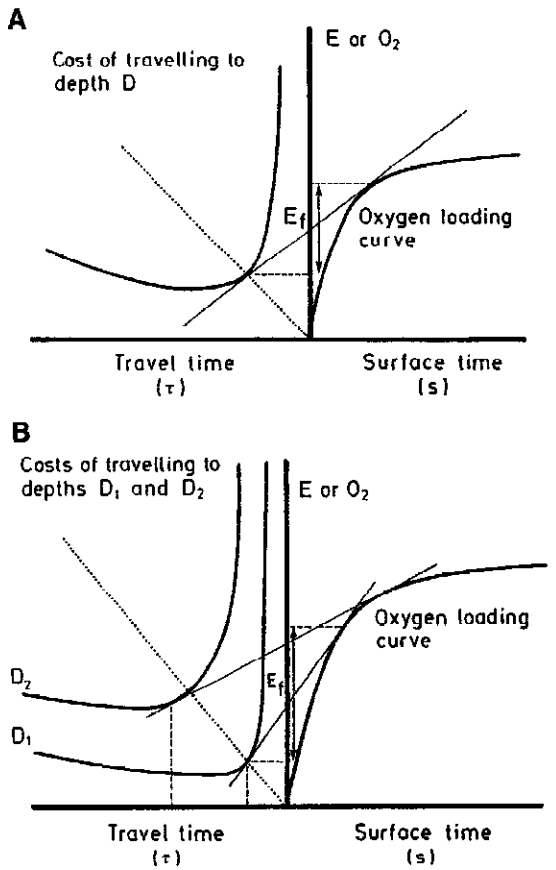


FIG. 3. *A*: graphical representation of relationship, for a diving bird or mammal, between time traveling to its foraging area (τ), energy (or oxygen) used during foraging (E_f), and time at surface loading its oxygen store (s). Vertical distance between intersections of common tangent with curve representing energy cost of traveling to a particular depth, *D*, and oxygen loading curve represents amount of energy (or oxygen) available for foraging at depth *D*. Dotted line passing through intersection of common tangent with cost of traveling curve represents τ and hence swimming speed (u), which maximizes rate of delivery of oxygen to foraging area at depth *D*. In *B*, this optimal condition is illustrated by shallower of 2 depths, D_1. If animal dives to a greater depth, D_2, common tangent with oxygen loading curve touches cost of traveling curve to left of intersection with dotted line, indicating that u, which maximizes rate of oxygen delivery to foraging area, decreases as depth increases. [Modified from Thompson et al. (380).]

speed will depend on the density of the prey and the rate at which they are moving. For low-density, rapidly moving prey, it may be energetically advantageous for the diving animal to remain stationary. When searching for prey, it should swim at the minimum cost of transport speed.

It is proposed to summarize, where possible, the diving behavior of those species that are mentioned in subsequent sections, in tabular form (Tables 2 and 3) and briefly to describe the behavior of these and other species where the influence(s) of variable factors is known.

A. Birds

As Jones and Furilla (206) point out, diving birds foraging in nature may spend a large proportion of their time underwater. For example, the tufted duck may spend as much as 25% of a day underwater, and most of this foraging behavior occurs during a 14-h period that spans nighttime (321). Foraging behavior of birds can be divided into bouts during which a number of dives follow one another in relatively quick succession; the pause between dives is relatively short (~30 s), and the animals spend more time underwater than at the surface. Most diving ducks spend ~63% of a diving bout underwater, i.e., they have a dive-to-pause ratio of 1.7. Such behavior (i.e., relatively short periods at the surface between dives) is taken to indicate that the dives are aerobic in nature with little or no accumulation of anaerobic by-products, although termination of a bout could be the result of a progressive accumulation of such by-products.

The duration of dives performed by most birds is relatively short. For many birds that feed on benthic organisms, dive duration is related to the depth of the water (64, 117, 124, 421). At a depth of 2 m, tufted ducks dive, on average, for 20–25 s, with a maximum duration of 46 s (124, 367). They swim at a speed of 0.6 m/s during descent (60). It appears from a detailed study on eider ducks, *Somateria mollissima*, that, for benthic feeding ducks, the surface period increases with dive duration (i.e., the dive-to-pause ratio is constant). Ydenberg and Guillemette (421) interpret this to indicate that these birds complete their recovery between each dive.

A number of birds, such as grebes, divers, cormorants, and auks are, to a greater or lesser extent, active predators of fish. These species, therefore, may have to employ different behavior patterns to exploit their mobile prey (420). From the latter study, the dive-to-pause ratio for western grebes, *Aechmophorus occidentalis*, increases from ~2 for dives of 20-s duration to >3 for dives of 60-s duration. This is taken to indicate that there may not be full recovery between each dive. Observations of a number of species of cormorant (*Phalacrocorax sp.*) indicate mean dive durations from 7 to 70 s and dive-to-pause ratios from 1 to >4 (87, 181, 381, 411). Mean swimming speed during diving varies between 0.8 and 1.2 m/s (411). Dive duration is clearly related to the depth of the dives (381, 411), and larger animals tend to remain submerged longer than smaller ones, even at the same depth (87, 381). The latter authors also noted that the frequency distribution of dive durations is positively skewed. However, studies on the Antarctic blue-eyed shag (Imperial cormorant, *Phalacrocorax atriceps*), using back-mounted transmitting or recording devices (100, 386), indicate that the diving behavior of these birds is strongly bimodal (Fig. 4, Table 2), with long dives being twice as common as short dives, but not confined to any particular time of day (100).

It is assumed that shallow dives do not involve benthic foraging, and it has been suggested that they may be a more economic way of moving foraging location than

TABLE 2. *Diving behavior of a number of species of birds*

Species	Mean (and Maximum) Dive Duration, s	Mean (and Maximum) Dive Depth, m	Mean (and Maximum) Surface Time, s	Conditions	Reference No.
Tufted duck (*Aythya fuligula*)	22.4 (46.3)	2 (3)		Experimental pond	367
Blue-eyed shag (*Phalacrocorax atriceps*)	34 (78) 196 (312)	7 (21) 85 (116)		Male, freely diving at sea with time-depth recorder	100
Common guillemot (common murre) (*Uria aalge*)	67 (202)		44	Freely diving at sea with radio transmitter	387
Brunnich's guillemot (thick-billed murre) (*Uria lomvia*)	55 (224)	18 (210)		Freely diving at sea with dive recorders	96
Little penguin (*Eudyptula minor*)	22 21	2.1 March (20) 1.3 December (50)		Freely diving at sea with dive and speed recorders	158
Gentoo penguin (*Pygoscelis papua*)	46 166 (>300)	6.9 (<21 m) 81 (>30 m) (156)	128 100	Freely diving at sea with time-depth recorders	403, 404
Adélie penguin (*Pygoscelis adeliae*)	102 (240)* 73 (160)†	9.4 (26.8)* 26 (98)† (>150 <180)‡		Free diving at sea with time-depth recorders	307* 81† 400‡
King penguin (*Aptenodytes patagonicus*)	(7.5 min)	(304)		Freely diving at sea with time-depth recorders	221
Emperor penguin (*Aptenodytes forsteri*)	4–5 (15.8 min) (mode for foraging dives)	20–40 (534) (mode for foraging dives)		Freely diving at sea with time-depth recorders	228

flying or swimming, although it is also accepted that they may be used to target prey visible from the surface (100). For both long and short dives, the dive-to-pause ratio is 0.3–0.4, i.e., overall surface times are 2–3 times greater than the preceding dive duration, although this does not seem to be the case for some shorter dives (see Fig. 16). Both groups of authors (100, 386) conclude that most of the long, deep dives performed by blue-eyed shags are longer than would be expected in terms of calculated oxygen stores and rate of oxygen consumption, based on data from other species. Thus the blue-eyed shag could, routinely, be engaging in anaerobic metabolism while foraging. Mean swim speed during the descent phase of the long dives was between 1.7 and 2.2 m/s. The maximum descent rate quoted was a staggering 5 m/s!

A study on the shag (*Phalacrocorax aristolelis*) has

TABLE 3. *Diving behavior of a number of species of mammals*

Species	Mean (and Maximum) Dive Duration, min	Mean (and Maximum) Dive Depth, m	Mean (and Maximum) Surface Time, min	Conditions	Reference No.
Northern fur seal (*Callorhinus ursinus*)	2.2 (7.6)	68 (256)		Breeding female at sea with time-depth recorder	163 323
Antarctic fur seal (*Arctocephalus gazella*)	0.95 (10) Median	12.6 (181) Median	0.57 (0.75) Median	Breeding female at sea with time-depth recorder	35
Weddell seal (*Leptonychotes weddellii*)	11.5 (82)	118 (626)		Diving from an artificial hole in shelf ice with time-depth recorders	74
Common (harbor) seal (*Phoca vitulina*)	2 (6)		0.5	Adult males at sea with radiotransmitters	142
Gray seal (*Halichoerus grypus*)	5.2		0.83	Adults at sea with radiotransmitters	379
Northern elephant seal (*Mirounga angustirostris*)	19.9 (62)	504 (1,581)	2.4	Adult female at sea between lactation and molt with time-depth recorder	246 374
Southern elephant seal (*Mirounga leonina*)	24.5 (120)	423 (1,430/1,595)	2.7	Adults at sea with time-depth recorders	178 354 and M. A. Fedak, personal communication
Sperm whale (*Physeter catadon*)	35 (73)	600 (1,185 >2,000?)	18	Diving in open seas with acoustic tags	390

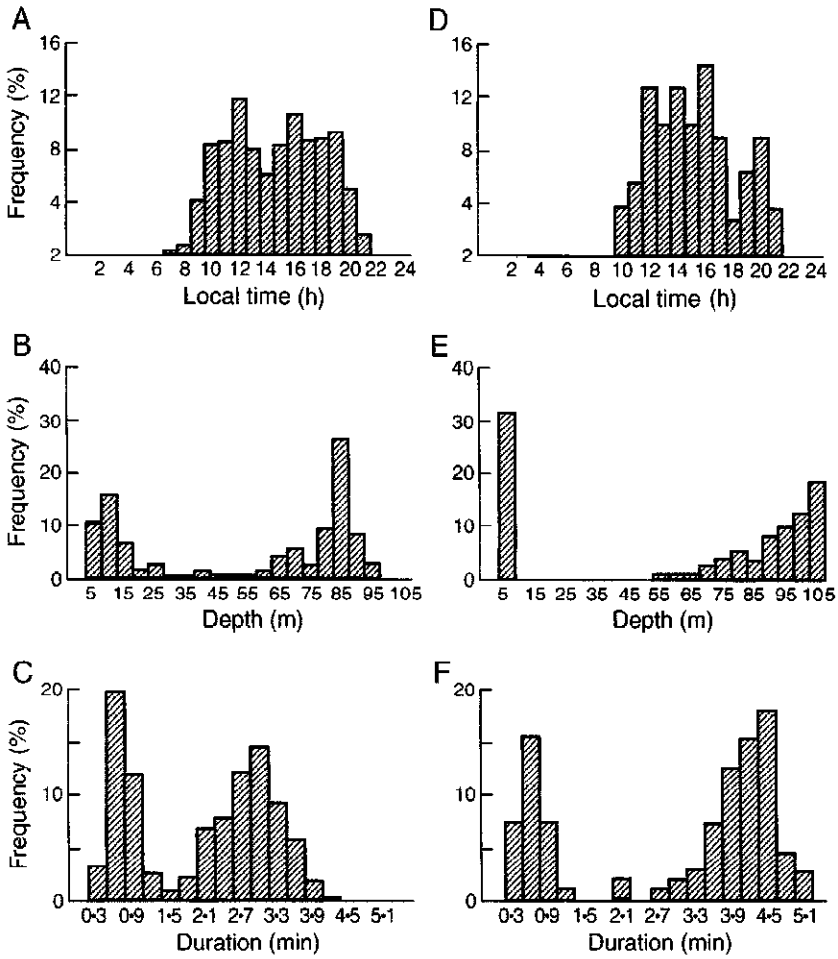


FIG. 4. Frequency histograms indicating time of day, depth, and duration of natural dives performed by 2 male, Antarctic blue-eyed shags. For one, of mass 2.55 kg (*A–C*), 564 dives were recorded during 11 days; for the other, of mass 2.80 kg (*D–F*), 110 dives were recorded during 3 days. [Modified from Croxall et al. (100).]

demonstrated how characteristics of the prey may influence diving behavior (385). The study was performed over three seasons (1987, 1988, and 1989), and during 1989, the size of the prey (sand eels) was significantly smaller than during 1987 and 1988. The authors estimated that both prey capture rates and the time spent submerged at any depth were greater in 1989.

Thick-billed murres (Brünnich's guillemots) illustrate another influence of prey on diving behavior (96). Most (67%) of the dives occur between 20.00 and 04.00 h and are generally <20 m deep. As the sun rises, there are fewer but deeper (>40 m) dives, which suggests that the birds are following the diurnal migration of their prey (the amphipod, *Parathemisto*). The frequency distributions of both dive depth and dive duration are positively skewed. Mean descent speed is 0.9 m/s.

Little penguins (*Eudyptula minor*) are, as their name suggests, the smallest of the penguins, and their diving behavior is more like that of ducks than of auks and other penguins (Table 2), except that their mean swimming speed is impressively high at 2.4 m/s (158). Foraging activity of nonbreeding gentoo penguins during winter is similar to that of chick-rearing birds, when the behavior is distinctly bimodal (403, 404). The birds spend ~20% of their total diving time engaged in shallow (<21 m) dives and ~75% of their diving time is spent on deeper (>30 m) dives. These deeper dives are thought to be feeding dives and are to mean depths of 30–40 m at dawn and dusk and to mean depths 80–90 m at midday (Fig. 5), which is consistent with the behavior of their main prey, krill. Availability of prey also influences the diving behav-

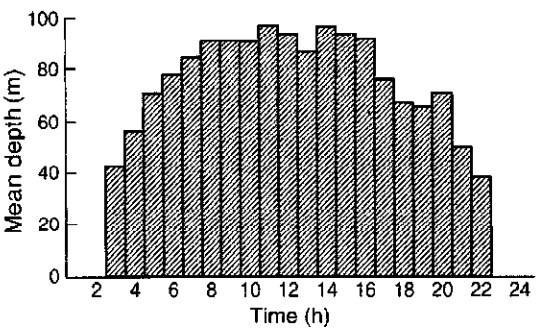


FIG. 5. Histograms relating depths of dives (>30 m) performed by 7 free-ranging gentoo penguins with time of day. [Modified from Williams et al. (403).]

ior of penguins. A study on the Adélie penguin during the Antarctic summers of 1990 and 1991 (389) indicates that, in 1991 when food availability was comparatively poor, the mean dive depths (12.3 m) and dive durations (1.9 min) were greater than those in 1990 (7.1 m and 1.5 min, respectively). It is also clear from the studies of Naito et al. (307) and Chappell et al. (81) that diving behavior of a species may vary between locations and/or with the type of TDR used (Table 2).

Average underwater swim speed of chinstrap, Adélie, and gentoo penguins is ~2.2 m/s (410), although it has to be noted that externally attached devices may affect the behavior of these animals (103; see also Ref. 403). The former authors found that instrumented Adélie penguins in a 21-m-long water channel have a bimodal speed distribution of 1.8 and 2.4 m/s. The preferred speed of uninstrumented birds is 2.0 m/s.

It is the larger penguins, the kings and emperors, that are the most impressive avian divers. A detailed study on the behavior and energetics of diving in king penguins indicate that they, like the gentoo penguins, dive in response to the vertical movements of their prey (221). It has even been postulated that king penguins may be constrained at night, because of low light levels, to feed at depths where prey densities are lower (330), At night, dives are never deeper than 30 m, whereas during the day they are to >100 m (Fig. 6). There may be a number of shallow dives between some of the longer deeper dives (Fig. 7). Preferred swim speed is 2.1–2.2 m/s. This compares with a mean descent rate during dives of 0.6 m/s. In emperor penguins, the majority of dives are to <200 m in depth and these occur at any time during the 24-h cycle, whereas those to >300 m tend to occur between 04.00 and 20.00 h (228). Rates of descent and ascent were between 1.0 and 2.0 m/s for dives to >100 m and never exceeded 2.5 m/s. In another study, Kooyman et al. (232) recorded a maximum (burst) swim speed of 7.1 m/s for this species. It is interesting to note that surface time increases progressively following dives in excess of 7- to 8-min duration (228).

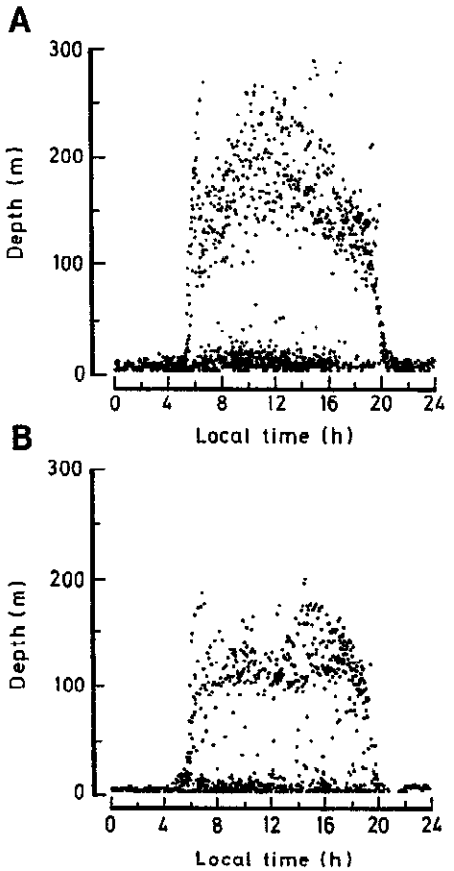


FIG. 6. Scatter plots of dive depths with time of day for 2 free-ranging king penguins. [Modified from Kooyman et al. (221).]

B. Mammals

A similar progression, from smaller species, which tend to perform shorter and shallower dives, to larger species, which tend to perform longer and deeper dives, as seen in birds, is also apparent among the aquatic mammals, although cetaceans may be an exception to this generalization. For otters, *Lutra lutra*, feeding at sea, mean dive duration is related to whether or not prey are caught (86), with successful dives (13.3 s) being significantly shorter than unsuccessful ones (22.7 s). Maximum dive duration recorded is 96 s (309). Although otters will dive to depths over 10 m, their preference seems to be to dive in relatively shallow (<3 m) water (309). Details of the dive behavior of some other species of aquatic mammals are given in Table 3.

Of the pinnipeds, it is the female otariids that have been most extensively studied. Breeding female otariids, unlike the phocids, periodically go to sea to feed during the lactating period, returning to suckle their pups. Thus it is relatively easy to deploy and retrieve archival recorders with these animals, in much the same way as it is with breeding aquatic birds.

In both northern and Antarctic fur seals (*Callorhinus ursinus, Arctocephalus gazella*, respectively), most dives occur at night, and these are shallower than those that occur during the day. This pattern of behavior suggests that the seals follow the vertical movements of their major food items, krill for the Antarctic fur seal, fish and cephalopods for the northern fur seal (99, 163). When prey abundance is low, Antarctic fur seals spend proportionately longer time diving and feeding at night (34). A closer analysis of deep and shallow dives in the northern fur seal (323) indicates that, although swim velocity is similar between the two (1.65 vs. 1.35 m/s, respectively), duration is substantially different, being 3.2 min for the former and 1.2 min for the latter. The proportion of time spent at the

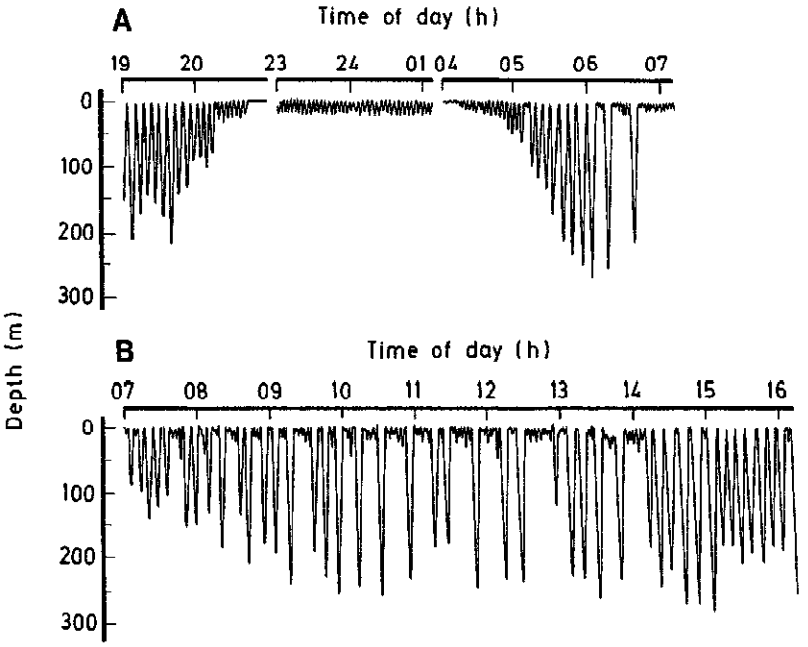


FIG. 7. Time-depth records from 2 free-ranging king penguins. *A*: transition from day to night types of diving and back to day-type dives. *B*: a series of deep dives during day, most of which are separated by a few shallow dives. [Modified from Kooyman et al. (221).]

surface is 1.5–3 times greater during deep diving behavior, and these authors conclude that the deeper, longer dives must involve substantial anaerobic metabolism.

For the larger lactating female California sea lions, *Zalophus californianus*, the pattern of diving is similar to that of fur seals (145). Mean dive duration is 2.1 min (maximum, 9.9 min), mean surface interval is 1.3 min, and mean dive depth is 61.8 m (maximum estimated depth, 274 m). As indicated previously for other species, there is a tendency for dives during daylight hours to be deeper and for those at night to be shallower. The swimming speed at which cost of transport is minimum for this species is ~2 m/s (144), which is similar to the mean value for the Galapagos sea lion, *Zalophus californianus wollebaeki*, when at sea (328).

The most intensively studied phocid seal is the Weddell seal, and although much of the behavior of this animal has been reported in many of the previous reviews on diving cited in section I, because of the central importance of these data in the development of our ideas on the physiology of freely diving mammals, a brief account of the diving behavior of this seal is given here.

As long ago as 1965, Kooyman (214) published a paper indicating how it was possible to deploy and retrieve mechanical recording devices with Weddell seals, because these animals dive under Antarctic ice and have to surface at specific places where natural cracks in the ice exist. Thus, by transporting the seals long distances from natural cracks, boring an artificial hole in the ice and releasing the seal(s) at this hole, Kooyman and co-workers had a field situation where it was possible to obtain behavioral and physiological data from a freely diving phocid.

Under these conditions, mean dive duration was 11.5 min (maximum 82 min), and mean depth was 118 m (maximum 626 m) (74). As these authors point out, there are, as with other species, many factors that can influence the diving behavior of Weddell seals such as season, geography, and location of prey, and merely giving mean and maximum values hides this variability. From Kooyman et al. (235), it is clear that these seals, during the austral summer at least, perform a number of dives in relatively quick succession for 10–12 h around midday and rest for the remainder of the time (Fig. 8). The surface interval between each of these dives is only of 2- to 4-min duration. When Kooyman et al. (235) examined the frequency distribution of dive durations (Fig. 9), they found that only 8% of the dives from an artifi-

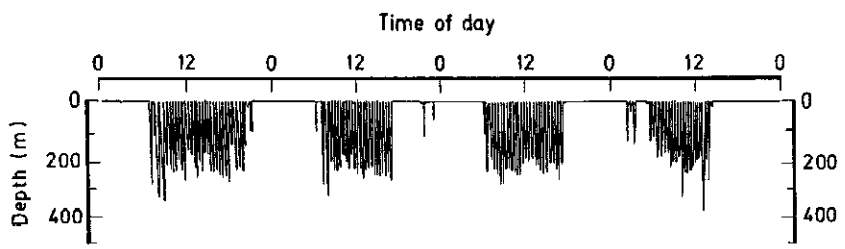


FIG. 8. Time-depth record of a free-ranging Weddell seal over a 4-day period. [Modified from Kooyman et al. (235).]

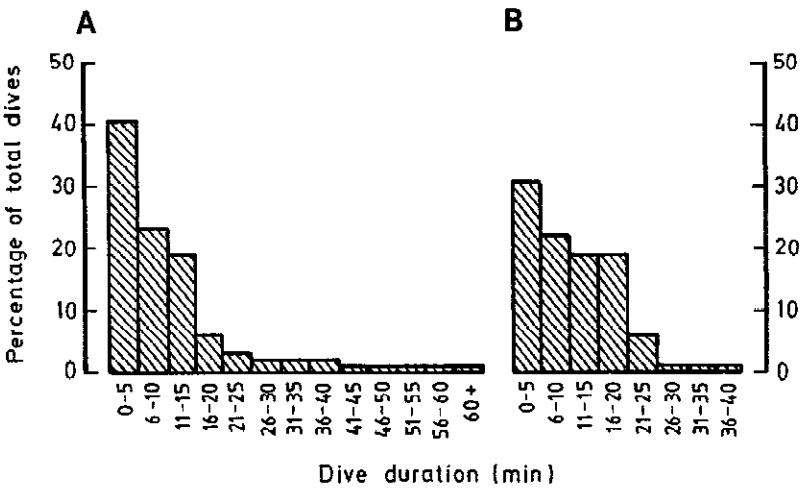


FIG. 9. Frequency distribution of dive duration for Weddell seals. *A*: 1,057 dives from 6 seals diving from a hole cut in Antarctic ice and to which they had to return to breathe. *B*: 4,601 dives from 22 completely free-ranging seals. Maximum dive duration recorded during these observations was 73 min. [Modified from Kooyman et al. (235).]

cial hole exceeded 26-min duration and only 2.7% of those from seals using natural breathing holes were longer than 26-min duration. For the few dives that were longer than 20–26 min in duration, the recovery time increased progressively more with dive duration so that when returning from a 60-min dive, the seals "were exhausted and usually slept for several hours or more in the ice hole before making any more dives." These data are important because they relate to metabolic data, some of which were obtained from the same seals, which are discussed in section III and have given rise to a concept, the aerobic dive limit, that is frequently used in diving physiology.

Despite the difficulty of recovering data from most freely diving phocids, success has been achieved with some species. By attaching very high frequency (VHF) radiotransmitters to the animals, Fedak et al. (142) were able to locate harbor (common) seals in the field and monitor their diving behavior. Mean dive duration was 2 min, and the maximum recorded dive was ~6 min in duration. Most surface intervals were ~30 s long. Time-depth recorders have been used with northern and southern elephant seals. The female northern elephant seal, at least, returns to the rookery to moult after being at sea for 10 wk after the nursing of her pup.

The astonishing fact to emerge from a study of these animals (246, 248) is that they, unlike the Weddell seal, dive more or less continuously for the whole 10-wk period (Fig. 10). There is a marked diurnal pattern to their diving. Only rarely is the continuous diving pattern interrupted. Less than 0.5% of the dives are followed by extended surface intervals, of mean duration 51.9 min. In fact, there is usually little variation in surface interval with dive duration, even after the longest dives (Fig. 11), which, in southern elephant seals at least, may be followed by further long dives, with short surface intervals (Fig. 12). The result is that during the 10 wk at sea between breeding and moult, female northern elephant seals spend 83–90% of the time underwater. Average swim speed during diving is ~1.3 m/s, and descent swim speed is greater for deeper dives (247). This is counter to the prediction of Thompson et al. (380).

Similar studies have been performed on both male and

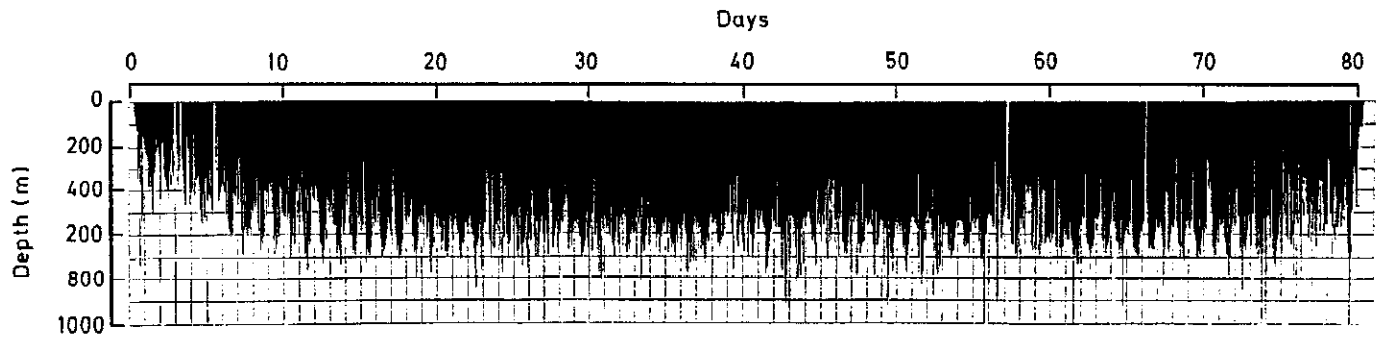


FIG. 10. Compressed diving record of a female northern elephant seal during whole of her period at sea between lactation and moult. Her initial mass was 291 kg, and during 81 days at sea she performed 5,657 dives, the longest of which was 44.4 min and the deepest was to 1,093 m. It is not possible to discern normal surface periods, but those of an hour or more appear as white vertical lines. Note their paucity and irregularity. Regular variations in depth reflect diel pattern of diving, with deepest dives occurring at midday. [Modified from Le Boeuf et al. (248).]

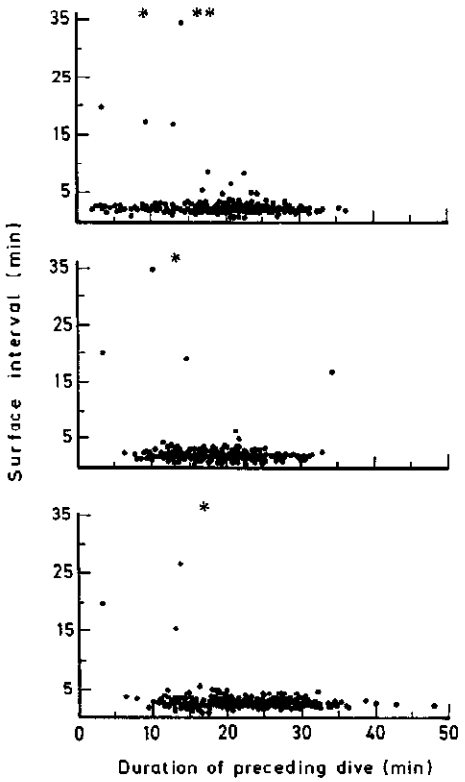


FIG. 11. Scatter plots of surface interval in relation to duration of preceding dive for 3 free-ranging female northern elephant seals. Asterisks indicate surface intervals that exceeded 35 min. [Modified from Le Boeuf et al. (246).]

female southern elephant seals, but also extending between moult and the next breeding season (178). Attachment of radiotransmitters as well as TDRs aided the location of the animals. The diving behavior of the southern elephant seals is similar to that of the northern species (Table 3), although the maximum recorded duration is substantially longer. From this study, it is clear that the relentless diving behavior of elephant seals continues for the whole of the 8 mo they are at sea between molt and the next breeding season and, on average, 89% of this time is spent underwater. Although these seals, like the northern species, do occasionally remain at the surface for an hour or two, the maximum surface interval recorded for one female was only 5 min during 40 days at sea! Elephant seals are not divers, they are surfacers (236).

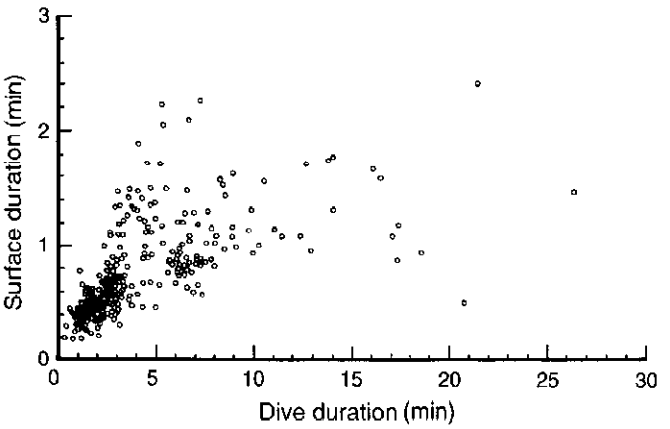


FIG. 13. Relationship between time at surface and duration of preceding dive for 3 free-ranging grey seals during traveling and foraging dives. [Modified from Thompson and Fedak (378).]

So, elephant seals may illustrate the extreme of phocid diving behavior. However, recent studies on gray seals, *H. grypus* (378, 379), indicate that there are similarities between elephant seals and other phocid species. With the use of radiotransmitters to locate the animals, depth and velocity meters could be attached to and retrieved from the seals from an ocean-going yacht. These seals did not remain at sea continuously, but hauled out periodically. However, when at sea, they spent a large proportion of their time underwater. Even when resting in water next to the haul-out sites, they were submerged for almost 85% of the time (379). Although there is an increase in surface interval with increasing dive duration for relatively short dives, this is not so for dives in excess of 7-min duration (Fig. 13). When traveling, the seals have V-shaped depth versus time dive profiles and swim at 1–2 m/s, but when feeding, the depth versus time dive profiles have a square shape and, when at the bottom, the animals swim very slowly, if at all. Similar conclusions were reached by Crocker et al. (95) studying a single female northern elephant seal. The minimum cost of transport speed of gray seals is ~1.5 m/s (380).

Although cetaceans are the best-adapted mammals to an aquatic existence, there is, unfortunately, little information on their behavior and physiology (218). What data there are indicate that at least some of these species are not outstanding divers. For example, a group of humpback

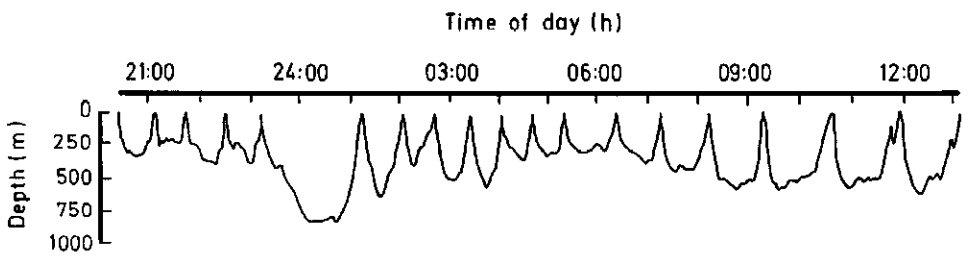


FIG. 12. Selected trace from dive record of a free-ranging southern female elephant seal (320 kg) showing a dive of 120-min duration that was followed by continuous diving activity, with no extended surface periods. [Modified from Hindell et al. (179).]

whales, *Megaptera novaeangliae*, performed most of their dives (85%) to <60 m, with few (<39%) exceeding 120 m. Mean dive duration was 2.8 min, and maximum duration was 21.1 min. Average speed during descent was 1.7 m/s, and that during ascent was 1.9 m/s (120–122). Mean dive duration of bowhead whales in the Beaufort Sea varied between years. In 1980 and 1981, the values were similar and averaged 3.4 min (maximum 17.4 min), whereas in 1982, the mean and maximum values were 12.1 min and >30 min, respectively (417). For gray whales, *Eschrichtius robustus*, mean dive duration was 3.2 min with a maximum of ~7 min (275, 418).

Further examples of the fact that the natural behavior of an animal may not always be an indication of its full potential are the white or beluga whales (*Delphinapterus leucas*). These are benthic feeders and, because they often swim into shallow water, they have been considered not to be very deep divers, with maximum depths reported to be only 20 m (see Ref. 336). These authors, however, were able to train a pair of beluga whales to dive to much deeper levels. They were capable of diving to 400 m with apparent ease, although dives of 400–600 m appeared to be more difficult. Nonetheless, the deepest trained dive was to 647 m, and the longest was 15.8 min. In deeper water, Martin and Smith (278) recorded natural dives to a maximum depth of 350 m and for a maximum duration of 13.7 min. Also, the deepest dives, to 251 m, recorded from three narwhales (*Monodon monoceros*) off northern Baffin Island are thought to represent the depth of the water column in which these animals routinely dove (277). The maximum dive duration of 15.1 min is close to the mode of the frequency distribution of dive duration of 12–13 min.

The most accomplished diver among the cetaceans appears to be the sperm whale, *Physeter catadon*. By attaching acoustic transponder tags to these animals, Watkins et al. (390) were able to monitor their diving behavior (see Table 3). Average underwater swim speed was between 0.75 and 1.2 m/s, but in one whale, speeds of 2 m/s and even up to 4 m/s were recorded.

An exciting recent development has been the deployment of a small (30 cm long, 13 cm diameter, 2.2 kg in water), self-contained video system and data logger with northern elephant seals and bottlenose dolphins, *Tursiops truncatus* (T. M. Williams, B. Le Boeuf, R. Davis, D. Crocker, and R. Skrovan, unpublished data). The data indicate that, when moving horizontally underwater, the animals engage in burst and glide swimming, which may be energy efficient (cf. Ref. 25 for review of studies on fish). Of much more significance is that, during descent, both species ceased active propulsive strokes below certain depths (73 ± 22 m for elephant seals, 64 ± 12 m for the dolphins) and glided passively down. The compression of gas stores, thus reducing buoyancy as hydrostatic pressure increases, is, no doubt, an important factor in this behavior. Whether or not other deep-diving birds and mammals adopt this behavior has yet to be determined, but the implications of this discovery are very important.

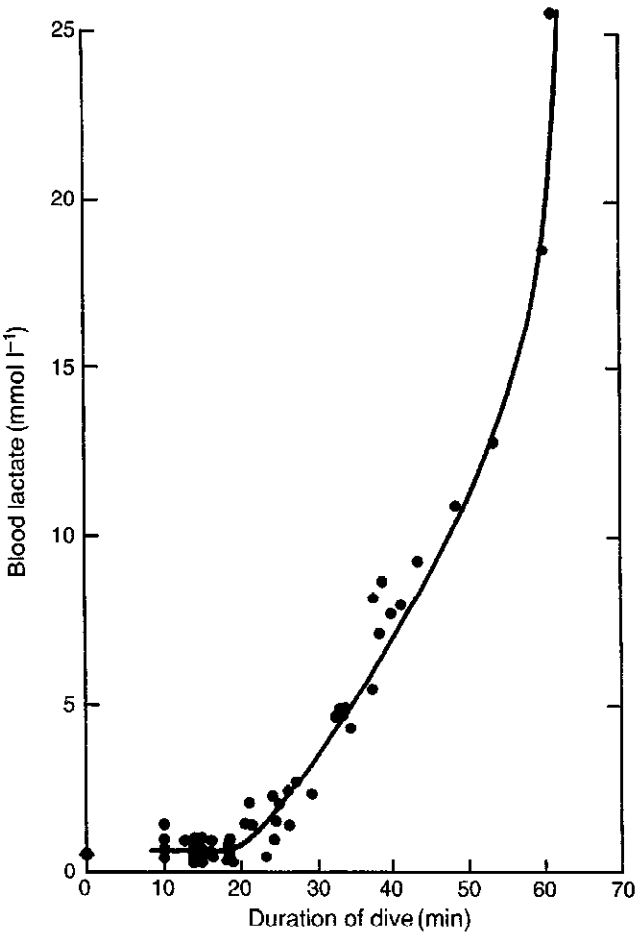


FIG. 14. Plot of peak concentration of lactate in arterial blood against duration of preceding dive for 3 Weddell seals diving from and returning to a hole cut in Antarctic ice. Diamond on abscissa represents average concentration of lactate in 3 seals when at rest. [Modified from Kooyman et al. (235).]

III. METABOLIC RATE AND METABOLISM

A. Aerobic Dive Limit

It is clear from the previous section that the diving performance of an aquatic bird or mammal is not always determined by its own physiological limitations. Often, environmental factors such as light level and/or the behavior of the prey influence the behavior of the diver. However, there is evidence from adult Weddell seals that ~90% of dives (feeding dives) are of <20-min duration (Fig. 9) and for those few that are longer (exploratory dives), there is a long recovery period (235). These authors also

found that, after the majority of shorter (<20 min) dives, there was no accumulation of blood lactate, whereas after the longer (>20 min) ones there was (Fig. 14). Peak postdive blood lactate concentration was greater with longer dives, and after a dive of 60-min duration, it was 50 times the resting value. Thus the shorter dives, which constituted the vast majority of those performed by the seals, were aerobic in nature, whereas during the relatively infrequent, longer dives, a proportion of ATP production was by anaerobiosis. Based on these data, Kooyman et al. (220) coined the term *aerobic dive limit* (ADL), which in this context denotes the dive duration up to which there is no increase in postdive blood lactate concentration. From Figure 14, this is ~20 min for fully grown adult Weddell seals [note, Kooyman et al. (235) quote 26 min as the critical time].

Although until very recently the only information on postdive blood lactate concentrations was from studies on Weddell seals, many authors, studying other species of aquatic birds or mammals, have calculated the theoretical ADL for those species. This is done on the basis of calculated or, in only one instance, measured oxygen stores. Packer et al. (312) used $^{18}O_2$ to measure the oxygen stores of harbor seals on land. All other values come from calculating the oxygen content of various oxygen storage compartments in the body. Calculated oxygen stores divided by calculated or measured rate of oxygen consumption during diving yields the calculated ADL. Clearly, if both of these variables are calculated, there will be a number of assumptions which give rise to "risks of embarrassment" (218). If not measured in some way, oxygen consumption during diving may be extrapolated from exercise studies performed in a laboratory or determined as some multiple of resting metabolic rate, usually from an allometric relationship of body mass versus resting metabolic rate. Methods of determining the volume of the respiratory system which involve restraint of the animal in any way may yield values that are significantly less than those obtained from unrestrained animals of the same species (364, Table 1).

Even if the amount of oxygen stored in the various compartments of the body is assessed accurately, assumptions still have to be made as to what extent they can be used by the animal when determining usable oxygen stores (211). In birds, for example, a substantial proportion of the available oxygen is in the respiratory system (~50% in the tufted duck), and there is clear evidence, from the low oxygen content of the first exhalation upon surfacing of the Humboldt penguin (62), that at least some of this oxygen is used during shallow, voluntary dives. Eliassen (129) suggested that movements of the limbs during underwater locomotion could cause movement of air between the anterior and posterior groups of air sacs and, therefore, through the gas exchange regions of the lungs. Measurements of pressures in these air sacs of the tufted duck while diving indicate that this is a possibility (31). Also, for the oxygen bound to the myoglobin to be of use, the P_{O_2} in the blood would have to be exceptionally low or, maybe, the muscles have to become ischemic, because the P_{O_2} at which myoglobin is half-saturated (P_{50}) is very low.

To illustrate the general problem, earlier calculations of the usable oxygen stores for Weddell seals give a value of 59 ml/kg (75, 218). Thus a 450 kg animal has 2.5 l of usable oxygen. Castellini et al. (75) found that the mean rate of oxygen consumption (oxygen consumption measured during the surface period, averaged over the duration of the previous dive and the time at the surface) for all dives was 4.5 $ml \cdot min^{-1} \cdot kg^{-1}$. These authors divided the dives into relatively short (<14 min) and relatively long (>14 min) ones. For the former, mean rate of oxygen consumption was 5 $ml \cdot min^{-1} \cdot kg^{-1}$ (see Fig. 19), and this would give a calculated ADL for a 450 kg seal of only 11.8 min. This would mean that there is a substantial discrepancy (−40%) between it and that obtained from the determination of postdive blood lactate concentrations (20 min). However, Ponganis et al. (324) have more recently themselves measured plasma and blood volumes and hemoglobin and myoglobin concentrations in Weddell seals. From the values obtained, they calculate the usable oxygen stores to be 86.2 ml/kg and, with the use of an oxygen consumption value of 4.5 $ml \cdot min^{-1} \cdot kg^{-1}$, calculate an ADL of 19.1 min. This is almost identical to the value (~20 min) determined from Figure 14. Even if an oxygen consumption value of 5 $ml\ min^{-1}\ kg^{-1}$ is used, a calculated ADL of 17.2 min is obtained, which is only 14% less than that determined from postdive lactate concentrations. If the critical dive duration based on blood lactate concentration is taken as 26 min (235), the discrepancy is somewhat greater (−34%). Furthermore, there appears to be a reversal of the relationship between ADL calculated from O_2 stores and during diving and that determined from postdive lactate concentration in younger, smaller Weddell seals, with the calculated value being ~60% greater than that determined from postdive lactate concentrations in pups (44).

Another aspect of the calculated ADL is that it implies that all of the usable oxygen stores are consumed. However, it is clear from Figure 14 that Weddell seals can and sometimes do remain submerged for longer durations than the ADL based on postdive blood lactate concentration. It is assumed, therefore, that during such extended dives there is sufficient oxygen remaining in the stores at least for the central nervous system and heart. This, of course, further exaggerates the discrepancy between ADL obtained by the two different methods. Possible explanations for the discrepancy will be discussed later, but the reason for mentioning ADL at this stage is to highlight the likely imprecision of many of the calculated values quoted later in the review, particularly in the context of the original definition of Kooyman et al. (220).

B. Methods for Determining Metabolic Rate of Diving Animals

There are two major methods for determining the metabolic rate of a freely diving bird or mammal: one is direct respirometry and the other is to use doubly labeled water, DLW, ($HT^{18}O$, $D_2{}^{18}O$) to determine the rate of CO_2 production (256). This is then converted to oxygen consumption either by knowing or assuming the respiratory exchange ratio, which in the long term is equivalent to the respiratory quotient (RQ). Apart from the latter (359), there are a number of assumptions associated with this technique that have been discussed by Nagy (304) and Tatner and Bryant (376), among others. An even less direct method is to use tritiated water (HTO) to determine water turnover, use this to estimate food intake and convert this to energy expenditure (225). All of these methods have their limitations with free-ranging animals. With a very few exceptions, direct respirometry is not feasible. Even when it is used, it can only measure rate of oxygen consumption between dives and not the rate at which O_2 is being metabolized during dives. With labeled water, it is necessary to recapture the animal after a sufficient delay following injection of the isotopes and release, to enable a reasonable decline in the enrichment of ^{18}O (a minimum of one biological half-life), but before the enrichment is too low (a maximum of three biological half-lives) (305). What is more, biological half-life varies, depending on the mass of the animal and between the major taxa (305, 376). It also, of course, depends on the level of activity of the animal. The other problem is that the technique only gives an average value for energy expenditure between the two sampling points.

A new method that is being tested in the field is to use heart rate as an indicator of oxygen uptake. Laboratory studies have demonstrated that there is a good relationship between these two variables in a number of species, including aquatic birds and mammals (22, 63, 141, 308, 414), and validation studies, both in the laboratory and in the field, indicate that heart rate is at least as accurate as DLW for determining oxygen consumption (20, 23, 38). In fact, the study by Boyd et al. (38) indicates that the DLW may overestimate field metabolic rate in marine mammals (or at least in otariid seals) by as much as 40%. Thus, with the use of a data-logging system (415), heart rate can be monitored and oxygen consumption estimated for at least some species of aquatic birds and mammals when at sea for several weeks. It is also possible with this technique to estimate metabolic rate associated with particular types of behavior (21). Unfortunately, it will only enable metabolic rate during a diving bout (i.e., including surface periods) to be determined and not that of diving itself.

Metabolic rate should be given as the rate of energy expenditure, i.e., power (W = 1 J/s). The conversion of rate of oxygen consumption to W depends on the metabolic substrate; for pure carbohydrate metabolism, i.e., with an RQ of 1, 1 ml O_2/s = 21.1 W, whereas for pure fat metabolism, i.e., with an RQ of 0.71, 1 ml O_2/s = 19.6 W (41, 263).

C. Birds

Respirometry has been used to estimate oxygen consumption during voluntary diving by tufted ducks (414). The birds dove from an open-circuit respirometer positioned at the water surface of a 1.7-m-deep tank. Oxygen consumption between dives was measured by a fast-responding mass spectrometer, and a linear multiple regression analysis was performed between dive duration, the succeeding duration at the surface, and the rate of oxygen uptake during the surface period. The regression coefficients represent the mean rate of oxygen consumption at mean dive duration and at mean duration at the surface. So, for six tufted ducks, mean oxygen consumption at a mean dive duration of 14.4 s in water at 13.5°C was estimated at 57 $ml \cdot kg^{-1} \cdot min^{-1}$ at standard temperature and pressure, dry (STPD). This is 3.5 times the resting value and not significantly different from that obtained from the same birds when swimming at their maximum sustainable speed at the surface (63 $ml \cdot kg^{-1} \cdot min^{-1}$ STPD). Thus, for tufted ducks, feeding underwater is a very costly activity. However, on the basis of usable oxygen stores (45 ml/kg; Refs. 211, 414), this species should be able to remain submerged and metabolize aerobically at the level given above for ~50 s. This is some 2.5 times longer than the preferred dive duration of these animals on a 1.9- to 2.8-m-deep pond (367) and 4 s longer than the maximum recorded dive duration. This would suggest that these ducks metabolize completely aerobically during most, if not all, voluntary dives, using oxygen stored in the body and rapidly replacing it upon surfacing.

In two thorough studies, Stephenson (363, 364) measured buoyancy and volumes of the respiratory system and plumage of lesser scaup, *Aythya affinis*, actively swimming to a depth of 1.5 m for their food. He found that buoyancy accounts for 62% of the mechanical cost of descent and 87% of the cost of remaining at the food patch under these conditions. The birds remained submerged for an average of 11.9–13.5 s and, during this time, buoyancy fell by ~20% as a result of loss of air from the plumage and compression by the hydrostatic pressure. The relative importance of these two factors will vary with dive depth and duration. In Stephenson's (364) experiments, the respiratory system contributed 52% of the initial buoyancy and 65% of the minimum value. This increase was the result of a loss of almost 50% of the air from the plumage during diving. Wilson et al. (409)

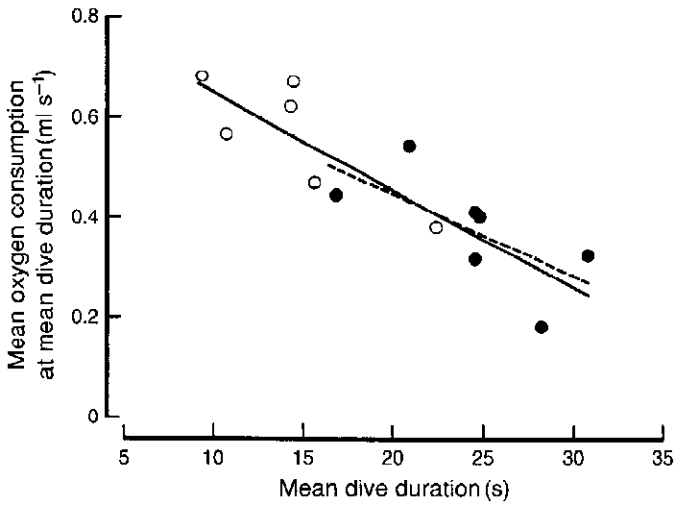


FIG. 15. Relationship between mean rate of oxygen consumption at mean dive duration ($\dot{V}O_{2d}$) and mean dive duration (t_d) of tufted ducks. Solid circles are from 7 birds trained to dive for different durations (22). Regression equation for these data, represented by dashed line, is $y = 0.80 - 0.017x$ ($r^2 = 0.47$), where y is $\dot{V}O_{2d}$ and x is t_d. Open circles are values from 6 ducks diving spontaneously to a depth of 1.7 m (414). Regression equation for all of data, represented by solid line, is $y = 0.838 - 0.019x$ ($r^2 = 0.87$). [From Bevan et al. (22). Copyright is held by Company of Biologists Ltd.]

found that the volume of air trapped in the feathers is lower and body density is greater in deeper diving birds. Less air in the feathers would reduce insulation and increase heat loss, so deep diving birds require more fat for insulation which, by increasing body mass, increases the energetic cost of flight. Such are the conflicting selective pressures acting on volant, aquatic birds, which have been avoided by penguins.

Regulation of the volume of the respiratory system could also have large (>40%) effects on buoyancy. Certainly, tufted ducks that had been trained to swim long distances (mean distance 6 m, mean duration 25 s) underwater for their food had a smaller end-expiratory respiratory volume [165 ml/kg at body temperature and pressure, saturated (BTPS)] than that (232 ml/kg BTPS) in ducks that performed shorter dives (mean distance, 0.6 m; mean duration, 11 s) (373). Blood volume was greater in those ducks that had to travel farther for their food, so that total usable oxygen stores were the same in both groups. The conclusion was that the reduced volume of the respiratory system, by reducing the buoyancy of the ducks, caused a decrease in the aerobic cost of underwater swimming in those that had to travel further for their food.

It is not easy to test the effect of dive duration on the energy cost of diving in these birds because, in the wild, dive duration is related to depth (117, 124). However, a method has been devised, using a computer-controlled system of lights, whereby tufted ducks have been trained to dive for up to 45-s duration in 0.6 m of water (22). With the use of data from this study and from that of Woakes and Butler (414), there is a clear negative relationship between mean rate of oxygen consumption at mean dive duration and mean dive duration (Fig. 15). The different energy costs of descent, bottom time, and ascent (262, 363) cannot completely explain this phenomenon because of the very small descent distance. With the importance of buoyancy on the energy cost of diving kept in mind, this could mean that those birds that are less buoyant and thus have a lower energy cost during diving are able to remain submerged longer; it could also mean that for any individual duck, the rate of oxygen consumption decreases with dive duration as buoyancy decreases during a dive. The latter could result from loss of air from the feathers (364) because, even during shallow dives, air can be seen leaving the plumage.

During deeper dives, compression would also be a contributing factor (261, 409) but, as mentioned earlier, this could also cause an increase in heat loss across the body (which could, in turn, result in a reduction of tissue metabolism; see below). However, in the experiments of Bevan et al. (22), buoyancy was still sufficient to allow passive surfacing, even after long dives. Another possibility is that during longer dives, aerobic metabolism may decrease as part of the "classic dive response" with, perhaps, increasing anacrobiosis.

The counteraction between air trapped in feathers acting as an insulator and as a substantial contributor to the buoyancy of diving ducks may be exacerbated during winter. For the same group of tufted ducks when at rest on water, rate of oxygen consumption during winter (air temperature 6°C, water temperature 7.5°C) was 90% greater than that during summer (air temperature 26°C, water temperature 23°C); however, mean rate of oxygen consumption at mean dive duration was similar under the two conditions (18). Although mean rate of oxygen consumption at mean surface duration was 50% greater during winter, there was only a 43% greater rate of oxygen consumption over a total dive cycle (dive plus subsequent surface interval) during winter than during summer. It was concluded that, when actually diving, the "wasted" energy of locomotion contributed to thermoregulation. Although this may not have been completely adequate, as deep body temperature was 1°C lower after a diving bout in winter compared with that in summer, it does mean that the energy cost of diving in winter is not as great as might be expected from the elevated oxygen consumption of ducks at rest on the water surface. These experiments were performed with ducks trained to dive in shallow (0.6 m) water, so the effect of compression of the air trapped in the feathers during deeper diving in winter has yet to be determined. Even so, its potential effect may be partly offset by increased tissue insulation as a result of peripheral vasoconstriction (201). Resting in cold water also causes a substantial increase in metabolic rate in other birds (see Ref. 18 for references).

Tufted ducks and eider ducks feed on benthic organisms, whereas other species, such as grebes, cormorants, and auks, are active predators of fish. It has been suggested that the western grebe alternates periods of search for schools of fish during which they recover fully from each dive with periods of more intense diving while they exploit a newly discovered school (420). During the latter periods, the birds may not spend sufficient time at the surface between dives to repay fully the oxygen stores and may, therefore, become increasingly reliant upon anaerobiosis. Ydenberg and Clark (419) argue that, for such aquatic predators, anaerobic diving may allow better exploitation of a group of mobile prey. A study on forcibly submerged Pekin ducks indicates that, as well as glycolysis, hydrolysis of phosphocreatine (PCr) is also a substantial anaerobic source of ATP, at least in the pectoral muscle (370). Turnover of ATP of the (inactive) pectoral muscle did not decline during 6.5 min of forced submersion in these ducks. However, it should be noted that, in response to electrical stimulation, the muscles of the hindlimb of a Pekin duck are unable to maintain strength of contraction for more than 30 s after blood flow was stopped by occlusion of the ischiadic artery and that a similar situation occurred once extreme bradycardia was apparent during forced submersion (207).

Thus the locomotory (leg) muscles of a diving duck appear unable to contract for more than several seconds in the absence of oxygen. Also of possible relevance in this context is the fact that, if temporarily unable to surface from a voluntary dive, tufted ducks, upon becoming aware of the situation, exhibit an immediate and profound bradycardia of similar magnitude to that seen during forcible submersion, when there is also peripheral vasoconstriction and anaerobiosis. They do not perform another dive for an hour or more (54, 367). On the other hand, tufted ducks can perform a number of successive dives when having to swim long horizontal distances (13 m) to and from food, even though they remain submerged for longer than usual (average 35 s) and develop a progressive but mild bradycardia during the dives, indicating a partial switch to the classic dive response (367). It is suggested here, therefore, that if western grebes do resort to anaerobiosis when feeding on a school of fish (see above, Ref. 419), this is minimal during any one dive, but may well be cumulative during the bout and that diving is terminated before the oxygen stores are depleted to such an extent that the bird is unable to maintain an adequate supply of oxygen to the locomotory muscles. If this is the case, then appropriate cardiovascular adjustments (bradycardia) would be expected to occur during such dives.

A detailed study of thick-billed murres (Brünnich's guillemots) suggests that they behave similarly to western grebes (96). The murres also feed on schooling fish that rise to the surface at night. The authors estimated oxygen storage capacity of the birds using similar assumptions to those employed by Stephenson et al. (373), which used a low value for the volume of the respiratory system, and, on the basis of this, calculated a usable oxygen store of 45 ml/kg. A more accurate value may be 55 ml/kg (364). It is reported that, when inactive in water at 5°C, the metabolic rate of thick-billed and common murres is approximately twice the value of that when they are resting at 15–20°C (97). The average rate of oxygen uptake for thick-billed murres over complete dive cycles (dive plus surface interval) in water at 20°C is 1.03 ml $O_2 \cdot s^{-1} \cdot kg^{-1}$ (2.6 times the resting value) which is slightly greater than that for tufted ducks diving for a mean duration of 15 s (414). Mean dive duration of the murres used in the above experiments was 41 s, which compares with 55 s for murres in the field (96).

It is clear from Bevan et al. (22) that, for tufted ducks diving in shallow water, mean rate of oxygen consumption at mean dive duration declines as mean dive duration increases, so that at a mean dive duration of 30 s, mean rate of oxygen consumption is approximately half of the value determined at a mean dive duration of 15 s (Fig. 15). However, mean rate of oxygen uptake over the complete dive cycle is <10% lower for dives of 30-s duration compared with that for dives of 15-s duration. If a similar situation exists for murres, then it is likely that the value of oxygen consumption during diving used by Croll et al. (96) for their birds is too high, perhaps 100% too high, particularly if the effect of depth on buoyancy is taken into account (262, 409). However, on the basis of the above value (1.03 ml $O_2 \cdot s^{-1} \cdot kg^{-1}$), ADL for these birds works out at 45–55 s but, only just over 50% of recorded dives of the murres when foraging at sea were within this duration. Croll et al. (96) seem to favor the idea that these murres may accumulate lactate during a series of feeding dives (i.e., when prey have been located) and metabolize it once the bout has terminated (see also above for western grebes). It is quite feasible, however, that most of the dives are completely aerobic. Clearly, further physiological data are required from these birds during their natural diving activity.

The energy cost of the complete dive cycle in the common murre is less than that in thick-billed murres, at 0.64 ml $O_2 \cdot s^{-1} \cdot kg^{-1}$ (1.6 times the resting value; see Ref. 97). With the assumption that the usable oxygen store is similar in the two species, the calculated ADL for the common murre, on the basis of these values, is 70 s and again, ~50% of recorded dives exceed this duration (387). The argument concerning mean rate of oxygen consumption at mean dive duration being 50% of that used by Croll and McLaren (97) (see above) is even more relevant for the common murre, because the mean dive duration in the experiments of Croll and McLaren (97) was 23 s, whereas mean dive duration in the field is 67 s (387). Thus, if the ADL is actually in excess of 140 s, the duration of all of the dives recorded by Wanless et al. (387) was within

the aerobic limit of this species. On the basis of their biochemical study of the pectoral muscles of common murres, pigeons, and pheasants, Davis and Guderley (107, 108) conclude that the common murre does not rely on glycolysis to any great extent during diving, and the latter calculation and comments would support this.

Some physiological data are available for other diving birds, notably the penguins, and are currently being obtained for the South Georgian shag, *Phalacrocorax georgianus*. Heart rate of South Georgian shags when resting on its nest is, on average, 104 beats/min, and abdominal cavity temperature is ~39°C (16). When diving, there is a progressive fall in abdominal cavity temperature by an average of 5°C (Fig. 16*A*), and after a relatively slow decline, heart rate reaches an average minimum of 65 beats/min during relatively short (<3 min) dives and 43 beats/min during relatively long (>3 min) dives. The combination of reduced temperature, in at least part of the body, and a subresting heart rate during diving indicate that overall aerobic metabolic rate may be lower than for an equivalent level of activity in air and/or there may be an increase in anaerobiosis. The latter is certainly thought to be the case by Croxall et al. (100) and Wanless et al. (386), especially for the longer dives.

The decline in abdominal cavity temperature during diving could be the result of ingestion of cold food and, maybe, water (330, 408), but also the result of increased heat loss to the water (52) and/or reduced blood flow to the viscera during diving (17). The important point is that the animal does not expend energy to maintain the temperature of the abdominal cavity at its "normal" value. The extent to which this hypothermia affects other parts of the body has yet to be determined. The locomotor muscles (either those of the legs or of the wings) will, presumably be at normal body temperature, as will the central nervous system and heart. Nonetheless, reduced temperature in part of the body will undoubtedly lead to a reduction in the metabolic rate of that region. However, the return of abdominal cavity temperature to its normal value after a diving bout (which may be related to the heat increment of feeding) may result in a substantial rise in oxygen consumption above its resting level (408). Smaller rises in rate of oxygen consumption may also occur between individual dives, because abdominal temperature may increase by up to 5°C, particularly between longer dives (Fig. 16*B*). On the other hand, the wasted heat of any exercise at the surface may be used to return body termperature to normal.

Penguins have been the most intensively studied group of aquatic birds, and the most widely used technique to determine the energy cost of foraging is DLW. As indicated in section III*B*, this technique only gives an average value of CO_2 production over the experimental period, so to determine the energy cost of a specific activity, time budgets must also be determined. Even so, with one exception, it has only been possible to determine average metabolic rate while the birds were at sea.

For the little penguin, the rate of energy expenditure when at sea varies between 21 W/kg in winter to 35 W/kg during the late chick-rearing period (3.1 and 5.2 times the resting, or inactive, value, respectively). This presumably reflects the more intense foraging activity as the chicks grow (157). According to these authors, little penguins spend ~95% of their time at sea swimming and diving, so the above values are close to the energetic costs of these activities. However, because these birds dive for relatively short durations (158), such a high level of aerobic metabolism during diving would not pose a problem and is consistent with the basically aerobic nature of their pectoral muscles (284). By incorporating information on time budgets, Nagy et al. (306) estimated that, when swimming underwater at sea at an average speed of ~1.75 m/s, energy expenditure of jackass (African) penguins, *Spheniscus demersus*, is 27 W/kg (5.9 times the value when it is resting on land). Similarly, Chappell et al. (82) estimated that the cost of swimming for Adélie penguins is 26.5 W/kg.

To calculate ADL for these, and any other penguins, an estimate of usable oxygen stores is required. From Table 4.5 of Kooyman and Davis (223), a value of ~45 ml O_2/kg is given for Adélie and gentoo penguins, although this appears to have been obtained only from O_2 bound to myoglobin and hemoglobin. Keijer and Butler (211) calculated that 20 ml/kg of usable oxygen resided in the respiratory system of tufted ducks. In a later paper, however, Kooyman and Ponganis (230) quote the available oxygen store of emperor penguins to be 58 ml O_2/kg and state that this large store "is due mainly to the relatively large gas volume of the air sacs, which we assumed to be similar to that determined for gentoo and Adélie penguins . . ." Because blood oxygen capacity, blood volume, and myoglobin concentration are also similar in these three species of penguins, a usable oxygen store of 58 ml O_2/kg for all three species may seem reasonable. A smaller amount of oxygen stored in the respiratory system than in that of ducks (on a mass-specific basis) is certainly consistent with a lower buoyancy in the penguins. However, the values for the volumes of the respiratory systems of gentoo and Adélie penguins were obtained from restrained birds (233) and could, therefore, be substantially different from those in unrestrained, naturally diving penguins (cf. Ref. 364). How much of the oxygen in the respiratory system of birds is really available when birds dive to great depths remains to be seen (230). During shallow dives of Humboldt penguins, *S. demersus*, there is no doubt that gas exchange does take place during the submersion period (62).

So, with the assumption of a usable oxygen store of 58 ml/kg and if 1 ml O_2/s = 20.1 W, the calculated ADL of jackass penguins, if metabolizing at the above rate, is 43 s.

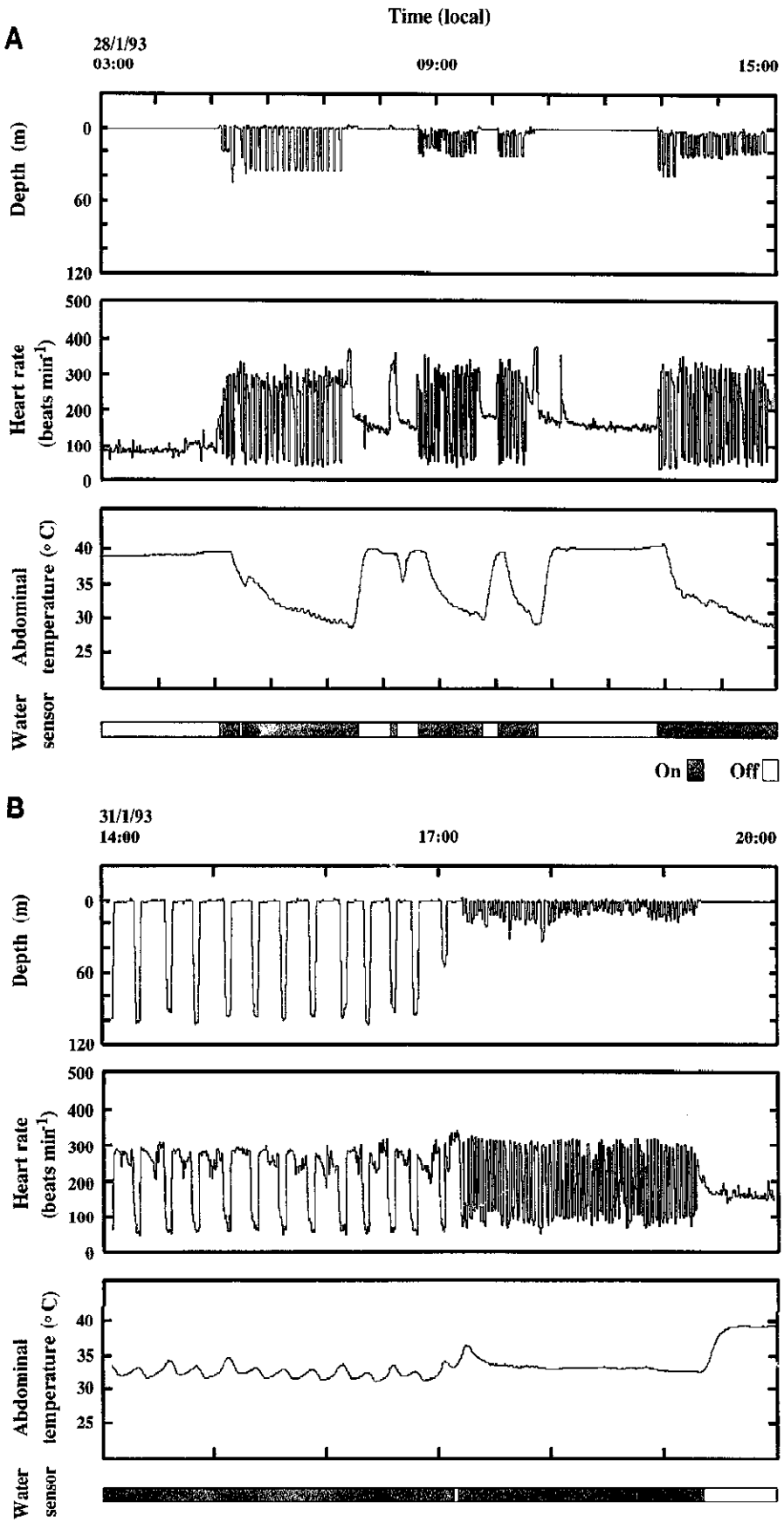


FIG. 16. Traces of diving depth, heart rate, abdominal temperature, and time on water of a female South Georgian shag (2.1 kg) performing relatively shallow dives over a 12 h period (*A*) and a male shag (2.5 kg) performing a series of relatively deep dives followed by a series of shallower dives over a 6-h period (*B*). [From Bevan and Butler (19). Copyright is held by Springer-Verlag.]

Mean dive duration of this species is ~70 s (maximum 180 s), and only 35% of dives recorded are of <43-s duration (412). At-sea metabolic rates of macaroni and gentoo penguins are slightly lower than that for swimming jackass penguins, at 22.2 W/kg and 14–19 W/kg, respectively (111). In the field, the average swimming speed of Adélie and gentoo penguins is ~2.2 and 1.8 m/s, respectively (104). These authors found that, when swimming at ~1.8 m/s in a static water canal, the metabolic rate of gentoo penguins was 16.1 W/kg. Culik et al. (104) point out that, in their experiments the penguins had to accelerate and decelerate, at least once, as they swam from one end of the canal to the other. By making allowances for this, they calculated the metabolic cost of swimming at 1.8 m/s for gentoo penguins to be 13.7 W/kg, which is very similar to the lower at-sea metabolic rate for this species determined by Davis et al. (111). However, Culik et al. (104) do point out that even their correct estimate may be too high, because of the "wall effects" of the water canal. With the use of the above values for usable oxygen store and at-sea metabolic rates, the calculated ADLs of macaroni and gentoo penguins are 53 and 61–83 s, respectively. For gentoos, these are much shorter than the mean dive duration of 2.5 min for their longer dives and 45–55% of recorded dives exceeded 83 s (403). However, these data should be treated with some caution because, as already indicated, these mean values of energy expenditure for the duration of time at sea, or even for swimming and diving at sea, may be substantially greater than the energy cost of diving itself, and usable oxygen stores may be 20% or more greater than those used to calculate ADL.

As for the South Georgian shag, there is a decline in abdominal cavity temperature in gentoo penguins when at sea (52), and for seven birds this averaged over 5°C. With the use of heart rate as an indicator of rate of oxygen consumption (23), the average value of oxygen consumption for the whole of the diving period was 26.5 $ml \cdot min^{-1} \cdot kg^{-1}$ (9.0 W/kg), which is 2.2 times the value recorded when they were sitting on their nests and only 18% greater than that obtained from the same birds resting on water at 5°C. This gives a calculated ADL of 2.2 min. Even so, ~40% of recorded dives exceed this duration (403). Gentoo penguins do not dive continuously when at sea and when they are not diving, heart rate and, therefore, oxygen consumption are elevated. This may reflect surface swimming and/or thermogenesis (perhaps by way of heat increment of feeding) and the return of abdominal temperature toward normal. It appears that, when gentoo penguins are resting on water (at 5°C), there is a substantial increase in metabolic rate, presumably to maintain body temperature (52). However, the metabolic rate during diving itself may be lower than expected as a result of the fall in abdominal temperature (assuming a Q_{10} of 2, a 10°C drop in temperature would reflect a 50% fall in metabolic rate in these tissues/organs), whereas metabolic rate between bouts and at the end of diving activity may be higher than expected as abdominal temperature is returned to normal. This could, at least in part, explain the discrepancy between dive durations and estimates of energy expenditure during diving based on the average energy expenditure during total time at sea. Because dive duration scales to body surface area in gentoo penguins and South Georgian shags, Boyd and Croxall (36) suggest that these birds reduce metabolic rate during diving, possibly by reducing body temperature. We await further, more detailed, analysis of the field heart rate and body temperature data to see if this is the case.

Kooyman et al. (221) determined the energetic cost of foraging of the king penguin to be 10 W/kg (30 $ml \cdot min^{-1} \cdot kg^{-1}$), and this is similar to the energy cost of swimming in a static water canal at 2.2 m/s (102). With usable O_2 stores of 58 ml/kg, the calculated ADL is, therefore, ~2 min. If this is the case, then 40–45% of all dives, and this includes all deep, feeding dives, exceed the ADL. Pütz and Bost (330) report that there are large reductions in stomach temperature of foraging king penguins. Recent studies have indicated that there is also a substantial reduction in abdominal temperature of king penguins during diving activity (51) and that it may fall to as low as 11°C (171a). Thus the energetic cost of diving could be some 60% of the total cost of foraging. If this is so, ADL would be 3.5 min. This would still place ~25% of all dives of king penguins in excess of this duration. Although there are no comparable data available for emperor penguins, their relatively long dive durations and high underwater swim speeds led Kooyman et al. (232) to conclude that many of the dives performed by this species require a significant contribution from anaerobic glycolysis.

When swimming in a water channel in water at 2–4°C, three emperor penguins reached an average maximum oxygen uptake of ~45 ml $O_2 \cdot kg^{-1} \cdot min^{-1}$ (231), although, on the basis of wing beat frequency, these authors conclude that when diving freely in the sea, oxygen consumption would be between 7 and 20 $ml \cdot kg^{-1} \cdot min^{-1}$ (2.2–6.7 W/kg). This would give an ADL of ~3–4.5 min, which again is less than the duration of >40% of their natural dives (228). The latter authors conclude, from the relationship of surface interval to duration of the previous dive in these birds (see sect. IIA), that the true ADL is ~7–8 min (the point at which surface interval begins substantially to increase). If so, this would mean that only 4% of foraging dives exceed the ADL and that most of these are to depths of >300 m.

In an important study, Ponganis et al. (327) have managed to determine postdive lactate concentrations for emperor penguins, which indicate that the true ADL, as per the original definition by Kooyman et al. (220), is between 5.5 and 6.5 min. Thus, for the second species (in addition to the Weddell seal), a discrepancy between the ADL de-

termined from postdive lactate concentrations and the calculated ADL is apparent, but the true ADL indicates that most of the dives performed by the animals are aerobic. As well as regional hypothermia and a low drag coefficient, gliding during descent, as recently reported for elephant seals and dolphins (see sect. IIB) may be an important factor in keeping the energy costs of diving at a minimal level.

D. Mammals

Those aquatic mammals that use fur as a form of insulation have similar problems to birds, in as much as the air trapped in the fur increases the buoyancy of the animal, and if the air layer is reduced for any reason, e.g., loss and/or compression, conductive heat loss will increase. Regardless of the insulative properties of their fur, being in water, even at 29–30°C, causes a 1.9 times increase in resting oxygen consumption of muskrats, *Ondatra zibethicus*, above that in air (1.5 vs. 0.8 ml $O_2 \cdot g^{-1} \cdot h^{-1}$; Ref. 274). The energy cost of diving under these conditions is 2.2 ml $O_2 \cdot g^{-1} \cdot h^{-1}$ (2.75 times the resting value in air). As the usable oxygen store (not the total O_2 store) in muskrats in summer is ~21 ml O_2 STPD/kg (270), the calculated ADL is 33.7 s. In winter, mainly as a result of a 32% increase in blood volume, the usable oxygen store increases to 30 ml O_2 STPD/kg (270), thus giving rise to an increase in the calculated ADL.

It is known that, under laboratory conditions, voluntary immersion in cold water causes a reduction in abdominal temperature, and increased postdive oxygen consumption in muskrats (268). Rate of oxygen consumption remains elevated after the animals leave the water, and it is during this period that abdominal temperature returns to normal. It is likely, therefore, that because of the reduced abdominal temperature and the fact that nonshivering thermogenesis appears to be inhibited when the animals are diving in cold water (269), the energy cost of diving in cold water may be no greater than that in warm water, which would give a minimum ADL in winter of 49 s. When at the surface, and particularly after leaving the water, oxygen consumption is elevated as a result of nonshivering thermogenesis in the brown adipose tissue.

In winter, all foraging movements of these animals may occur under ice between shelters and from the shelters to the feeding areas. Movements between shelters may account for the longest dives routinely encountered by muskrats, and MacArthur (271) found that for the shelters located in emergent vegetation, virtually all of the transit dives were within the calculated winter ADL (49 s). However, for those shelters constructed in open bays, 20% of them required transit times in excess of the ADL, and dives of 60- to 95-s duration were documented in four muskrats swimming from distant shelters. Maximum recorded dive duration was just over 120 s. One possible explanation for these dives of long duration is that, when under ice, the animals are able to recover previously expelled gas (272). It is interesting to note also that during all dives, regardless of duration or temperature of the water, heart rate fell below the value recorded when the animals were resting in air (273 beats/min) or resting in water (283 beats/min; Ref. 273). During foraging dives it averaged 111 beats/min, whereas during escape dives it was 73 beats/min. Diving heart rate was lower in animals with reduced abdominal temperature. So, it appears that whether dives are aerobic or not, there is, unlike the situation in most birds, a clear bradycardia during voluntary submersion in this aquatic mammal.

At-sea metabolic rate has been determined for three species of otariid seals using the DLW technique, and for one of these species, the heart rate method is also being deployed. These studies have indicated how these different species respond to differences in prey availability. Rate of energy expenditure while at sea varied between years in lactating northern fur seals (91). In 1981, energy expenditure was 6.6 W/kg (1.4 times the resting value), whereas in 1982, it was 9.8 W/kg (twice the resting value). Duration of the foraging trips was similar for the 2 years, so the conclusion is that foraging effort was greater in 1982, perhaps in response to changes in prey abundance or distribution (88). The increased energy expenditure in 1982 was matched by increased energy intake so that net energy gain was similar in both years (1.77 and 1.83 W/kg). It could be that in 1982 there was a relatively low abundance of high-energy prey, such as pollock, which occur at depth so that the females had to perform a greater number of relatively shallow dives to obtain the low-energy prey, squid (88).

There is evidence to indicate that deep-diving females make fewer dives and expend less energy than those that perform shallow dives (91, 163). During normal years, northern fur seals spend 57% of their time at sea being active at the surface, 26% diving, and 17% resting (163), so there is scope for increasing their energy expenditure while at sea. However, during the El Niño of 1983, there was a significant (30%) increase in the duration of foraging trips of lactating northern fur seals compared with the preceding and following years (113).

Lactating Antarctic fur seals spend 60% of their time at sea swimming, 35% diving, and only 5% of their time resting (224). This species, therefore, has much less scope for increasing its foraging effort, and in fact, when prey was scarce in 1984, the average duration of their foraging trips was 85% greater (8.4 days) than it was in 1985 (90, see also Ref. 34 for the seasons 1988/89 to 1993/94), whereas at-sea energy expenditure was similar (9.2 and 9.8 W/kg, respectively, which was approximately twice the resting value). From these two data sets, it would appear that the energy cost of diving and swimming in

these two species of fur seal is ~9.5 W/kg (28.3 ml $O_2 \cdot min^{-1} \cdot kg^{-1}$). If the usable oxygen stores of otariids are ~40 ml/kg (163, 218), this gives an estimated ADL of 1.4 min. Taken at face value, this would indicate that ~80% of the dives performed by the Antarctic fur seal (35) are within the ADL and that the shorter, shallower dives performed by the northern fur seal (mean duration, 1.2 min) are also within the ADL. However, the longer, deeper dives performed by this species (mean duration, 3.2 min) are well in excess of the ADL, thus supporting the proposal by Ponganis et al. (323) that they must involve substantial anaerobic metabolism.

With the use of the heart rate method, estimated rate of oxygen consumption of lactating Antarctic fur seals resting on shore (52) is similar to the values quoted by Costa and Gentry (91) for northern fur seals and by Costa and Trillmich (92) for Antarctic fur seals. Both the latter authors used the DLW method. However, when estimated from the heart rate method, rate of oxygen consumption of Antarctic fur seals foraging at sea is some 75% of the values obtained by the above authors using the DLW method. This should be viewed in the context of the results of Boyd et al. (38), which indicate that the DLW method may overestimate at-sea energy expenditure by as much as 40% in otariids. Taking this lower value of the energy cost of foraging gives an ADL of 1.9 min. This would mean that 90% of the dives performed by Antarctic fur seals are within their ADL. Another interesting feature of the study using the heart rate method is that the measured metabolic rate of Antarctic fur seals resting in water at 6.8°C (6.1 W/kg) is not significantly different from that estimated while they were traveling to and from their foraging area (6.5 W/kg). Thus it appears that these animals may as well be active when in water, since it costs just as much to be inactive (see also Ref. 93). For dives of <100-s duration, heart rate during submersion of Antarctic fur seals is similar to that for animals resting in air. For dives of longer duration, heart rate falls below the resting value, which may be indicative of a reduction in aerobic metabolism. Thus it appears that most of the dives of these animals are well within their ADL.

California sea lions adopt a foraging strategy that is intermediate between those of the northern and Antarctic fur seals. During the El Niño of 1983, the mean duration of each trip was 7.3 days, and the corresponding mean energy expenditure was 7.8 W/kg, whereas in the more normal year of 1984, the values were 4.2 days and 5.4 W/kg, respectively (89). Consistent with these data are the facts that in 1983, dive bouts and dives themselves were of longer duration than those in 1984 (146). The value of 7.8 W/kg (23 ml $O_2 \cdot min^{-1} \cdot kg^{-1}$) is close to maximum rate of energy expenditure (25–30 ml $O_2 \cdot min^{-1} \cdot kg^{-1}$) measured in California sea lions swimming at ~3 m/s in a water channel (63, 144, 407). The value of 5.4 W/kg (16.12 ml $O_2 \cdot min^{-1} \cdot kg^{-1}$) is achieved at a swimming speed of ~2 m/s (144, 407), which is at the top end of the range of average speeds determined for four species of otariid (329). With a usable O_2 store of 40 ml/kg, the above rate of energy expenditure during diving would give an estimated ADL of 2.5 min, which would mean that ~40% of the dives are in excess of this (145). However, if, as with Antarctic fur seals, the ADL as estimated above is 75% of its real value, and it should be 3.3 min, then only 20% of the dives are in excess of this.

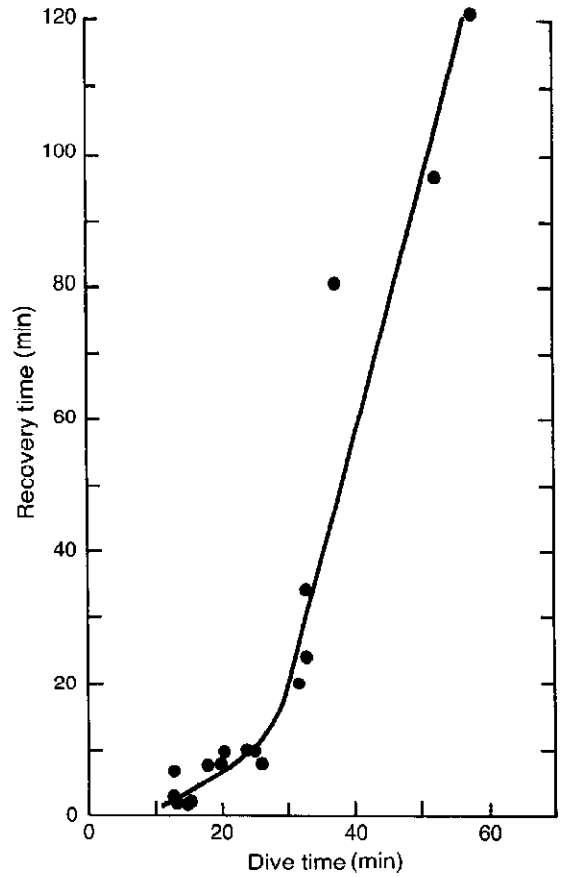


FIG. 17. Plot of time taken for concentration of lactate in arterial blood of Weddell seals to return to a value of 0.55 mM (or when recovery curve was extropolated as a straight line to resting level) after dives of various durations (see Fig. 14 for further details). [Modified from Kooyman et al. (235).]

As already indicated, the most complete set of data on the metabolism of a diving mammal has been obtained from the Weddell seal. For adult Weddell seals, ADL, based on postdive lactate measurements, is 20–26 min (235), but it is shorter for smaller animals (44, 220). The greater the length of time the dive exceeds the ADL, the greater is the postdive concentration of blood lactate (Fig. 14) and, not unexpectedly, the longer it takes for the blood lactate concentration to return to its resting level (Fig. 17). On very rare occasions, Weddell seals may perform a series of short dives (i.e., within the ADL) following a dive exceeding the ADL and the lactate accumulated dur-

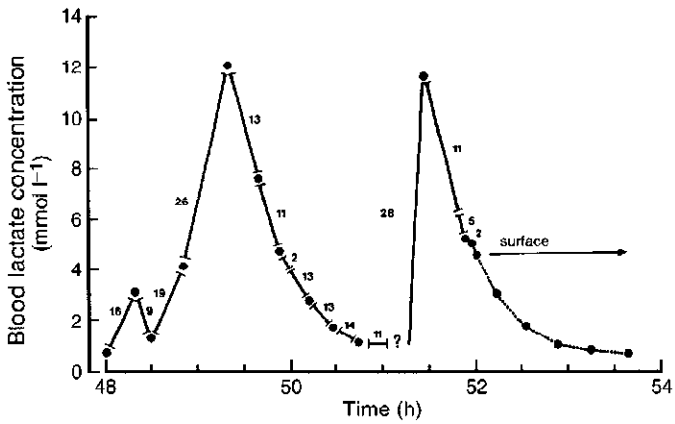


FIG. 18. Sample of data (from *hour 48* to *hour 54* of 75-h sampling period) indicating concentration of lactate in venous blood of a young Weddell seal (205 kg) following dives, from a hole cut in ice, of various durations (in min; given against lines drawn between dots). Note that, after a 26-min dive at ~49 h and a 28-min dive at ~51 h, seal continued to perform dives, despite elevated concentrations of lactate in blood. These subsequent dives were of relatively short duration, and concentration of lactate in blood progressively decreased. [Modified from Castellini et al. (73).]

ing the latter is metabolized during the former (Fig. 18; Ref. 73). More often than not, however, there is no diving activity following dives exceeding the ADL until the blood lactate concentration has been restored to its resting value.

There are a number of aspects of lactate production and removal from studies on terrestrial mammals that may be relevant to mention here. One important observation is that lactate is produced in fully oxygenated contracting muscles (202). However, during moderate hypoxia, even if muscle oxygen consumption and developed tension remain unaltered, lactate production increases (190). It has been concluded that the level of lactate production by active skeletal muscle may not always be a suitable indicator of oxygen lack (362). In terms of the concentration of lactate in the blood, its rate of production by the skeletal muscles is only one side of the story. The other side is its rate of removal, and an increase in the rate of production may be matched by an increase in the rate of removal.

There is evidence that in dogs, approximately one-half of the lactate produced at rest is removed by oxidation and, although turnover rate of lactate increases during exercise, the proportion removed by oxidation increases to ~75% (116). Thus there is evidence that oxidative skeletal muscle fibers use lactate as a substrate for oxidative metabolism during exercise (42). It has also been suggested the high level of lactate dehydrogenase activity in the heart of the Weddell seal is more related to its ability to metabolize lactate rather than to produce it (80). Thus both oxidative skeletal muscle fibers and the heart could be important in removing excess lactate from the blood during dives within the ADL, following one which exceeded the ADL and led to the accumulation of the lactate. It should be stated, however, that Davis et al. (110) found in the resting common seal that only 27% of lactate turnover was oxidized and that this fell to 21% when the seals were swimming at 50% of maximum oxygen consumption.

It is clear from Figures 14, 17, and 18 that the rate of lactate removal in Weddell seals is similar whether or not the animal continues to dive following a long, natural dive. After the long (26 min) dive depicted in Figure 18, blood lactate concentration was 12 mM, and it took ~90 min to return to its normal level. From Figures 14 and 17, a lactate concentration of 12 mM was reached after a dive of ~50-min duration, and it took ~100 min to recover from such a dive. However, after forcible submersion, it took slightly longer (120 min) for blood lactate to return to its resting value from a lower concentration (6 mM; see Fig. 1). Fedak and Thompson (143) discuss the implications of oxidizing lactate after an excessively long dive for subsequent diving behavior. They point out that only one molecule of ATP is produced for each molecule of lactate produced by glycolysis, yet 17 molecules of ATP are produced by the subsequent oxidation of one molecule of lactate. Thus, if an animal metabolized anaerobically for 5 min during one dive, it would take ~85 min (17 × 5) of aerobic diving activity, using lactate as a substrate, until the level of blood lactate had returned to normal. For an animal with an ADL of 15 min, that would require approximately six dives within the ADL (cf. Fig. 18).

As with the Antarctic fur seal, the rate of energy expenditure during diving of the Weddell seal is not substantially greater than when it is resting in water (75). For

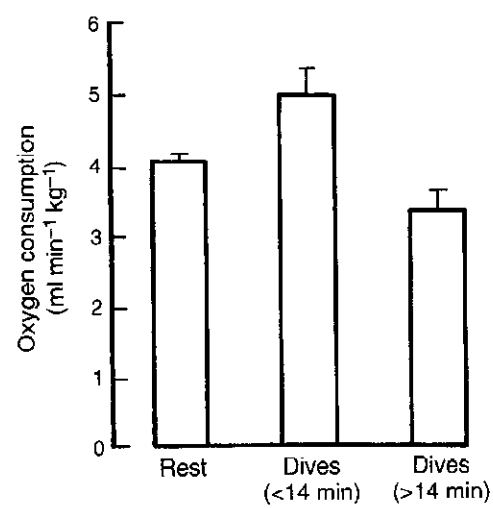


FIG. 19. Mean ± SD values of oxygen uptake of 5 adult Weddell seals (mean mass 355 kg) at rest and after dives, from a hole cut in ice, of <14-min duration and of >14-min duration. Oxygen uptake measured after dives was averaged over duration of dive plus subsequent time at surface. [Data from Castellini et al. (75).]

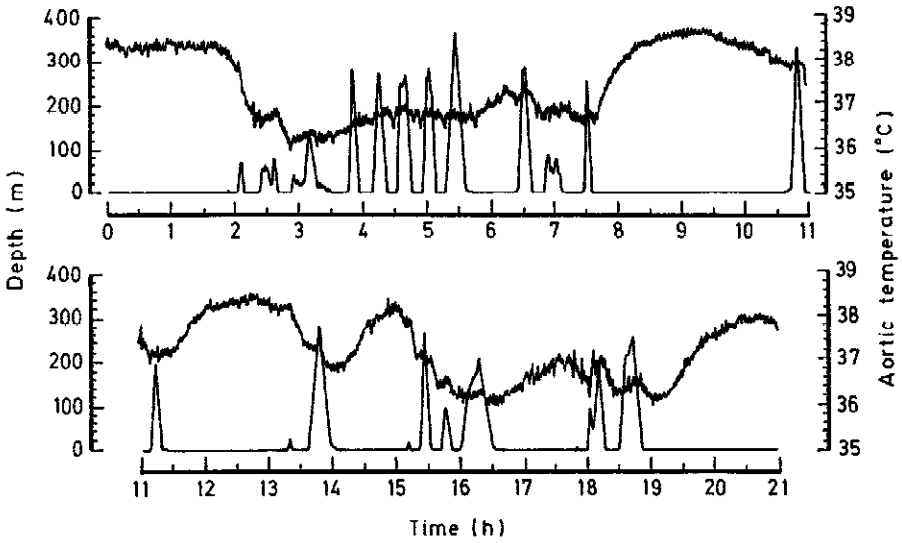


FIG. 20. Selected period of 21 h (from a total of 118 h) of continuous recording of temperature in aortic blood and diving behavior (depth) of an adult male Weddell seal diving from a hole cut in ice. [Modified from Hill et al. (177).]

relatively short dives (<14 min for 355-kg seals), average rate of oxygen consumption over a dive/surface cycle is only 25% above the resting level, whereas for longer dives, it is not significantly different from the resting value (Fig. 19). It is possible also that the energy cost of diving itself may be even lower than these values indicate. Hill et al. (177), using a data-logging system (176), found from one seal that often during natural dives, there is a reduction in the temperature of aortic blood (Fig. 20), which is maintained for as long as diving continues. There may be as much as a 2°C drop in temperature when longer (>30 min) dives are performed. When diving activity has ceased, temperature increases quite rapidly. Thus a similar argument could be used here as was expounded earlier for birds that, when averaging over complete dive/surface cycles, the energy expended during diving may be overestimated, since "excess" oxygen is consumed during the surface period when body temperature is returned to normal. This could be a partial explanation for the discrepancy between ADL determined by postdive lactate levels and that determined by measured oxygen uptake and calculated usable oxygen stores. It has recently been reported that there was no change in the temperature of locomotory muscles in one Weddell seal during long dives (325), but perhaps this is not surprising, since these muscles would have been generating heat. The fact that the temperature did not increase could be the result of the muscle having been perfused with blood during submersion.

On the basis of measurements of the O_2 content of arterial blood before and after natural dives, Guppy et al. (168) performed simple calculations to gain some idea of the rate of O_2 consumption during such dives. Unfortunately, there are some fundamental errors in the calculations, e.g., the total blood O_2 content of a seal before a dive is not likely to be the O_2 content of the arterial blood times the total blood volume, since approximately two-thirds of the blood is in the venous system and its content is likely to be ~5 vol% below that of the arterial blood (see Ref. 324). Also, if the total oxygen consumed during a 30-min dive is 19,900 ml, then the average rate of consumption is 663 ml/min and not 863 ml/min. Despite these errors, the general conclusion is probably valid, i.e., that during diving, the rate of O_2 utilization is substantially less than that in an animal resting at the surface. Hochachka and Foreman (187) come to a similar conclusion, but again their calculation is flawed. They seem to assume that, because surface heart rate between natural dives is twice the resting heart rate, oxygen consumption at the surface must also be twice the resting value. They appear to ignore the basic fact that much of the oxygen "consumed" during the surface interval is used to replenish the oxygen stores and, in fact, represents oxygen metabolized during the diving period.

Rates of muscle metabolism in diving Weddell seals have been estimated to be ~4.5 mmol ATP · kg^{-1} · min^{-1} (75). If there is no muscle blood flow during the dive, then energy can be supplied aerobically from the utilization of myoglobin-bound oxygen or anaerobically from breakdown of high energy phosphate stores (PCr) and through lactate production. However, the sequence in which the myoglobin oxygen store, the PCr reserves, or lactate production is utilized to provide for muscle metabolism during diving is unknown. In forced dived seals, lactate concentration does not increase until the muscle oxygen stores are completely exhausted (348). This observation prompted Guyton et al. (169) to attempt to determine the amount of utilization of the muscle myoglobin oxygen store using a submersible dual-wavelength near-infrared spectrophotometer (753–754 and 812–814 nm) attached to a naturally diving Weddell seal. Data were collected by an on-board data logger. The probe was implanted on the

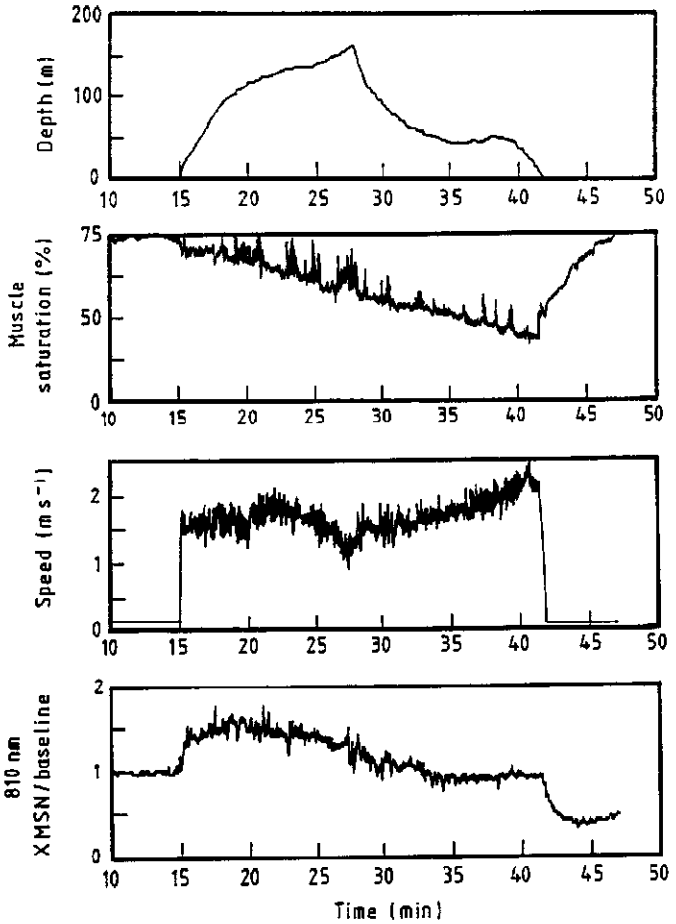


FIG. 21. Dive depth, muscle oxygen saturation, swimming velocity, and 810-nm transmission (relative blood volume) during a 27-min dive by a Weddell seal. Muscle oxygen sturation decreased monotonically during dive. The 810-nm transmission signal suggests early vasoconstriction that returned to baseline late in dive and was followed by hyperemia during recovery. Swimming velocity remained relatively constant. [From Guyton et al. (169).]

surface of the latissimus dorsi muscle. Four seals had a monotonic decline in O_2 saturation during diving with slopes of $-7.33\%\ min^{-1}$ during relatively short dives (<17 min) and $-2.93\%\ min^{-1}$ during relatively long dives (>17 min) (Fig. 21). Aside from the fact that Weddell seals utilize their muscle oxygen stores, it is difficult to determine what these results tell us about the actual energy obtained from the myoglobin oxygen store during submergence.

A complicating factor with the technique is that the hemoglobin signal interferes with that from myoglobin and may even dominate the myoglobin signal at high flows. Because partial pressure of oxygen in the blood will never fall below the P_{50} of myoglobin even during the longest dives (331), myoglobin should either be saturated (flow condition) or desaturated (no-flow condition). This was not the case, and muscle saturation during dives occupied intermediate values (169). There would seem to be three explanations for this. *1*) Flow continues and the hemoglobin signal dominates the myoglobin signal. Interestingly, hemoglobin saturation during long dives declines at one-half the rate of that during short dives, qualitatively but not quantitatively similar to myoglobin desaturation during long and short dives. *2*) Flow continues, but its distribution is uneven and may be shunted away from exchange regions so the muscle saturation signal is a compromise between hemoglobin saturation and saturated and unsaturated myoglobin. *3*) There is a dynamic equilibrium established between the rate at which the muscle oxygen store is utilized and oxygen is supplied by blood flow, and this equilibrium changes as dives progress (169).

In any event, even when all the myoglobin store is utilized, it would only be sufficient to power metabolism for 5 min at a muscle utilization rate of 4.5 mmol ATP/kg. In contrast, if muscle PCr stores are in the same range as those of terrestrial mammals (~30 mmol PCr/kg), then PCr will provide about one-third more ATP than myoglobin-bound oxygen. Hence, the aerobic and anaerobic stores are capable of maintaining diving muscle metabolism for ~12 min. Due to the much higher affinity of myoglobin for oxygen compared with hemoglobin, both aerobic and anaerobic energy stores will not be depleted until perfusion stops. If muscle perfusion is maintained, it means that the muscle stores of oxygen bound to myoglobin as well as high-energy phosphates in the form of PCr must be viewed as only an emergency supply.

Unfortunately, PCr stores of diving mammals have not been reported, but available evidence suggests that they are in the same range as those of their terrestrial counterparts. Blix (26) measured creatine in the brain, heart, and skeletal muscle of the hooded seal (*Cystophora cristata*), eider duck, and sheep and found no differences between them. Unfortunately, not all the creatine in muscle and heart, for instance, is available to form PCr, since it is either bound or stored in discrete and inaccessible intracellular compartments (343). Nevertheless, the creatine level reported by Blix (26) for the eider duck is similar to the PCr concentration obtained by Stephenson and Jones (370) for the Pekin duck, using nuclear magnetic resonance technology.

An added advantage of utilizing the PCr store is that each millimole of PCr broken down removes an almost equivalent quantity of H^+, which is derived from lactate metabolism. Hence, 30 mmol PCr will effectively remove 30 mmol H^+, which is more than enough to ameliorate the acidifying effects of all but the most severe bout of anaerobic glycolysis. Unfortunately, muscle lactate levels at the end of dives are unknown. In an immature harbor seal, Scholander et al. (348) recorded a muscle lactate concentration of 44 mmol/kg after 15 min of forced diving. Muscle lactate levels during natural or extended diving are a matter for speculation. Postdiving blood levels fall in the range of 8–26 mM lactate after 30- to 60-min diving,

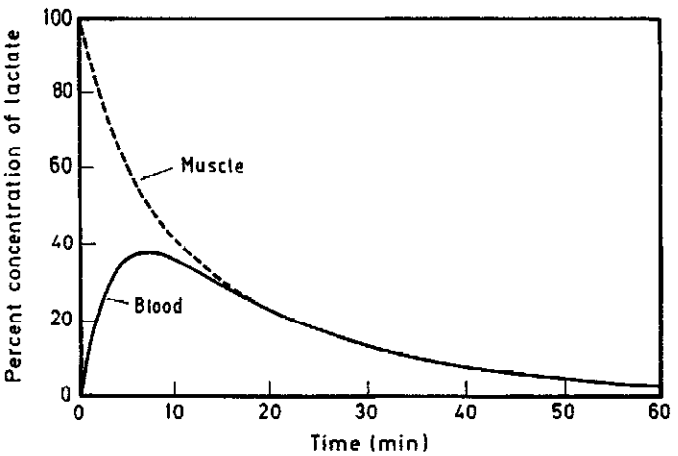


FIG. 22. Estimation of lactate concentration in muscle from blood values at end of a 42.6-min dive by a Weddell seal of body mass ~400 kg (235). A curve-fitting program was used, and best fit to blood data of Kooyman et al. (235) was obtained when exponential wash out from muscle to blood was 5 times faster than lactate loss from blood. Muscle mass was assumed to be 120 kg, and blood volume was 50 l. Lactate concentration in muscle at end of dive was 2.5 times peak blood concentration.

respectively (168, 235). Kooyman (217) estimated that muscle lactate concentration would approach, or slightly exceed, 40 mM after the longest dives.

Figure 22 shows an estimate of muscle lactate concentration based on a blood wash-out curve of a Weddell seal after a 42-min extended dive. It was assumed that total muscle mass was 120 kg and blood volume 50 l. The exchange between the tissues and blood and the time course for removal of lactate from the bloodstream were set to reproduce the observed wash-out curve (235). The result is that muscle lactate concentration must be 2–2.5 times peak blood levels, in this case 34–42 mM. Hence, PCr breakdown, allied to the considerable buffering properties of seal muscle (79), will greatly ameliorate acidification caused by anaerobic glycolysis.

The relatively low aerobic requirements of underwater activity mean that the rate at which oxygen is used is not excessively high. Usually, the animal surfaces while there is still sufficient oxygen for aerobic metabolism and quickly replenishes the stores (hyperventilation, tachycardia, vasodilatation). Thus, at the tissue level, the animal is in a steady state. The discontinuous nature of lung ventilation and uptake of oxygen from the atmosphere, compared with the situation in terrestrial mammals, causes associated fluctuations in circulatory performance, but this does not necessarily reflect similar oscillations in the supply of oxygen to the tissues. If these animals exceed their true ADL, then, as we have seen, postdive lactate concentration increases as does postdive recovery time.

Although there are data on oxygen consumption of harbor (common) seals at rest and at different levels of swimming activity (110, 112, 407), there is only one determination of daily energy expenditure (DEE) in free-living common seals (335). These authors used the DLW method with one male during the mating season, and they estimated DEE to be 52.5 MJ. They do not give the body mass of this seal, but from the details of how DEE was estimated, an average mass of 90 kg is assumed. Neither is there any indication of what proportion of time was spent at sea. With the assumption that 1 ml O_2 ~20.1 J, this male had an average oxygen consumption of 20.1 ml $O_2 \cdot min^{-1} \cdot kg^{-1}$, which is ~50% of maximum oxygen consumption (110). If this is the rate at which oxygen is consumed during normal diving activity in these seals, then with oxygen stores of 56 ml/kg (110), ADL would be 2.8 min. Approximately 80% of the dives are of shorter duration than this (142). Thus common seals also seem to dive within their ADL, most of the time, as do gray seals. Reed et al. (334) directly measured breath by breath gas exchange in freely diving, captive gray seals and found that, as with Weddell seals (75), oxygen consumption averaged over the dive and surface period decreases with increasing dive duration. Using the average oxygen consumption for all dives (5.2 ml $O_2 \cdot min^{-1} \cdot kg^{-1}$, STPD) and calculated usable oxygen stores of 50 ml/kg, the average value for ADL would be 9.6 min. Only 6% of dives monitored from freely diving gray seals in the open sea exceeded 10-min duration (378), and for dives of that duration, measured oxygen consumption was only 3.5 ml $O_2 \cdot min^{-1} \cdot kg^{-1}$ (334).

The most enigmatic of all the diving mammals are the elephant seals, which dive more or less continuously while at sea and for which there is no relationship between dive duration and subsequent time at the surface (Fig. 11). Le Boeuf et al. (246) conclude that there cannot be any net accumulation of lactate in diving northern elephant seals, and Hindell et al. (179) state that if southern elephant seals do accumulate high levels of lactate, then they must have developed unique mechanisms for dealing with it while continuing to dive, often for relatively long durations. Both groups of authors came to the inevitable conclusion that the metabolic rate of these animals during long dives must be substantially, maybe 60%, below what would be considered as their resting metabolic rate. However, for juveniles and females, making short repetitive dives of 15-min duration, with 1.7-min surface intervals, metabolic rate is 10% above that of an animal resting on the beach and 1.7 times the metabolic rate predicted for resting animals. Hence, it seems likely that in elephant seals, metabolic rate declines with dive duration (4).

Hindell et al. (179) used the allometric equation quoted in Schmidt-Nielsen (345) for resting metabolic rate in terrestrial mammals on the basis that it applies equally well to marine mammals (244). They calculated rate of oxygen consumption for the lean body mass of their animals and took it to be the diving oxygen consumption.

They used the value of usable O_2 stores (79 ml O_2/kg) quoted in Kooyman (218) to calculate the ADL for all the seals they had studied in an earlier paper (178). Calculated in this way, ADL averaged 28.9 min for the females and 44.9 min for the larger males. It should be noted that, if total body mass is used instead of lean body mass, the mean ADL values are 30.8 and 48.3 min, respectively. On the basis of their calculations, Hindell et al. (179) report that only a very small percentage (0.6%) of the dives performed by the males exceeded the calculated ADL, whereas the corresponding values for postbreeding and postmoult females were 7 and 44%, respectively. So, even with an already low resting oxygen consumption (i.e., based on that for terrestrial mammals), many of the dives performed by the females exceed the calculated ADL. However, Hindell et al. (179) state that if a value of 40% of the calculated resting metabolic rate is taken as the diving oxygen consumption, then only nine of the dives that they monitored would exceed the calculated ADL. On the other hand, if the metabolic rate of female southern elephant seals during moult is used as the diving oxygen consumption (6.4 ml $min^{-1} \cdot kg^{-1}$; Ref. 33), then even with the usable O_2 stores recently determined for Weddell seals (86.2 ml/kg; see Ref. 324), the ADL of the postmoult females would only be 13.5 min.

Le Boeuf et al. (246) discuss ways in which low diving metabolic rates may be achieved in elephant seals. One is that the animals may spend part of their time underwater asleep. Another is that, as already mentioned for birds, the muskrat, and Weddell seals, being in cold water and ingesting cold prey may cause a reduction of body temperature and thus a fall in metabolic rate. Certainly it appears that inactivity on land leads to a fall of 2–3°C in deep body temperature, even of an adult bull (281), so inactivity in water may have an even greater effect. In juvenile elephant seals making short dives (15 min), subcutaneous temperature fell to within 1°C of water temperature, and the thermal gradient across the blubber layer averaged only 14°C. Core body temperature decreased 1–2°C at the onset of deep diving, whereas temperature in nonactive muscle fell by as much as 8°C (4). Even so, the impact of these temperature changes is not intuitively obvious. The fall in subcutaneous temperature will restrict surface heat loss and reduce the metabolic costs of thermoregulation. On the other hand, a fall in core temperature of 1–2°C might be expected to reduce metabolism by a Q_{10} effect. The analysis by Boyd and Croxall (36) indicates that female elephant seals, like gentoo penguins and South Georgian shags, have dive durations that scale to body surface area. As for the birds, they conclude that female elephant seals reduce metabolic rate during dives, possibly by reducing body temperature, which enables them to perform many dives in excess of their calculated ADL.

Another possible mechanism of metabolic rate reduction is that during unusually long dives (whatever they may be for these animals), organs such as the liver and kidneys may not be perfused, and it is during the rest dives and extended surface periods (~70 min a day for southern elephant seals) that these organs "catch up on the backlog" (179). Certainly there is evidence that the liver cells of seals can tolerate hypoxic (hypoperfused) conditions by means of the mitochondria entering a "reversible functionally protected" state, with reductions in both aerobic and anaerobic metabolism (186). Such a state appears possible, because the mitochondrial membranes have low permeabilities to K^+ and Ca^{2+} and thus have reduced needs for ATP. Whether or not the kidneys of diving mammals are able to withstand periods of hypoperfusion by similar mechanisms remains to be seen, but it is interesting to note that one of the major differences between the ectothermic reptiles and the endothermic (terrestrial) mammals is the low ionic permeability of the cell membranes of the former (130).

Hochachka (185) continues to speculate on the mechanisms(s) responsible for a low metabolic rate during diving and argues that a reduction in the demand for ATP in response to a reduction in the supply of oxygen, rather than an increase in the anaerobic production of ATP, is the more likely during diving in a number of marine mammals (see Refs. 9 and 189 for detailed discussions). Thus a reduction in perfusion of some tissues would lead to a fall in their metabolic rate (cf. Ref. 397). In this context, though, it is worth noting that Hogan and Welch (190) report hypoxia having no effect on oxygen uptake in resting or working gastrocnemius muscle of dogs. Hochachka and Foreman (187) point out that, as well as metabolism being relatively low during diving, its efficiency may be optimized by there being a high ratio of pyruvate kinase-to-lactate dehydrogenase, thus maximizing the ratio of aerobic/anaerobic metabolism.

In the absence of physiological data, particularly postdive levels of blood lactate, it is not possible to determine how different the two species of elephant seals are from the Weddell seal in their metabolic adjustments during diving. We do, however, have some physiological data from gray seals, which in some respects behave similarly to elephant seals when they are at sea (see sect. II*B*). Diving heart rate is lower during longer dives in gray seals (378), and during some long dives, it may fall to as low as 4 beats/min, and these authors suggest that gray seals, to conserve energy during long foraging dives, may employ wait and ambush tactics rather than active pursuit. Nonetheless, calculations similar to those used for other phocid seals indicate that, to remain aerobic during the longer dives, metabolic rate would have had to be below the calculated resting levels and below that measured in resting common seals (112).

Thompson and Fedak (378) point out that when traveling to and from the deepest part of the dive, metabolic rate would be expected to be two to three times above

the resting level (112, 407). However, like elephant seals, this species may passively glide below certain depths (see sect. IIB). Regional hypothermia may be at least a partial answer to the problem, but the low (sometimes very low) heart rates during the longer dives do indicate much reduced tissue perfusion and hence oxygen supply to parts of the body. So, we are back either to anaerobiosis, which on the basis of the behavior of these animals and the activity of glycolytic enzymes in marine mammals as a whole (80) is unlikely, or to an unusually low metabolic rate, the nature and mechanism of which are unclear. A pointer to the latter may be that the aerobic capacity of a locomotor muscle in gray seals (as indicated by the mass-specific activity of citrate synthase) is ~30% of that in the harbor seal (and even 50% of that in the rat) and yet the myoglobin concentration is 30% greater in gray seals than it is in harbor seals (333). Whether or not hydrostatic pressure affects the function of oxidative enzymes remains to be seen, although it appears to have no influence on Michaelis constant of cofactor binding of NADH of muscle M_4 lactate dehydrogenase from emperor penguins, elephant seals, and sperm whales (98).

Although, unlike Weddell seals, gray seals do not spend extended times at the surface following long dives, at least one of those studied by Thompson and Fedak (378) performed a series of relatively short dives after each excessively long dive and may, therefore, have been oxidizing any accumulated lactate during the series of shorter dives. It appears that this species and perhaps some others have a number of options available to them.

Few metabolic studies have been performed on exercising cetaceans. Williams et al. (406) used the heart rate method to estimate rate of oxygen consumption of bottlenose dolphins, *Tursiops truncatus*, swimming next to a boat in the open sea. If mean swimming speed when they dive is 2 m/s (and this seems to be the case) and it is the speed at which the cost of transport is at its lowest, then during diving, oxygen consumption will be ~8 $ml \cdot kg^{-1} \cdot min^{-1}$, which is not significantly different from the value measured for animals resting in water at 25°C and may be a reflection of their hydrodynamic efficiency, as much as anything else. If usable oxygen stores are 33 ml/kg (see also Ref. 218), the ADL for this species is 4.1 min. Maximum dive duration recorded for a juvenile male bottlenose dolphin off the coast of Wales was <2.5 min (259). Thus, in the absence of further field data, all of the dives of this species seem to be well within the ADL. With the exception of the sperm whale, cetaceans as a whole appear to have rather short dive durations, at least compared with the phocid seals, and may all, therefore, operate within their ADL.

Whether or not sperm whales dive aerobically or not remains to be seen but, if a 355-kg Weddell seal has an oxygen consumption of 5 $ml \cdot min^{-1} \cdot kg^{-1}$ when diving aerobically (75) and if oxygen consumption scales to (body mass)$^{0.75}$ (244), oxygen consumption during diving of a 20,000-kg sperm whale will be 1.8 $ml \cdot min^{-1} \cdot kg^{-1}$. If we take the highest usable O_2 store quoted for a marine mammal, i.e., 86 ml/kg for Weddell seals (324), then the ADL for sperm whales would be 48 min, which is some 13 min longer than mean dive duration and 25 min less than the maximum recorded dive duration for this species (390). It should be noted that there are no data on the masses of the sperm whales that have been studied in the field. If they were substantially larger than 20,000 kg, their metabolic rate would be less than the 1.8 $ml \cdot min^{-1} \cdot kg^{-1}$ mentioned above. By recording respiratory frequency and making assumptions about tidal volume and oxygen extraction, Blix and Folkow (29) estimated that a 4,000-kg minke whale (*Balaenoptera acutorostrata*) at sea consumes oxygen at a rate of 10.9 l/min (~2.73 $ml \cdot kg^{-1} \cdot min^{-1}$). This, coincidentally, is exactly the same as the value obtained if the above assumptions are applied to a 4,000-kg marine mammal.

IV. CONTROLLING METABOLISM: CARDIORESPIRATORY RELATIONSHIPS DURING DIVING

It would appear from the preceding sections that voluntary diving is usually aerobic, with oxygen stores and their utilization governing aerobic dive times. The preference for aerobic metabolic pathways shown by most diving animals avoids deleterious effects of accumulating anaerobic end products. Consequently, it follows that modulation of the aerobic metabolic rate will influence diving performance so that the higher the rate of aerobic metabolism ($\dot{M}$), the shorter will be the dive time (DT), hence

$$DT \propto \frac{1}{\dot{M}}$$

In terrestrial animals, a close relationship exists between perfusion and cellular metabolism. At the whole body level, the relation between cardiac output ($\dot{V}_b$) and rate of oxygen consumption begins at resting levels and moves up toward maximum aerobic metabolic rates (388). Even though cardiac output drives tissue blood flow, the relationship between the change in cardiac output with change in metabolic rate is seldom 1:1 due to variations in perfusion as well as oxygen extraction at the tissues [arterial (a) minus mixed venous ($\bar{v}$) oxygen content (C_{O_2}); ($Ca_{O_2} - C\bar{v}_{O_2}$)]. Nevertheless, there can be no doubt that during exercise, for example, changes in flow and metabolism are well matched. In diving birds and mammals, maintenance and tight regulation of aerobic metabolism is even more crucial than in terrestrial animals, not only to avoid significant anaerobic contributions to diving metabolism but also to ensure that, when submerged, suf-

ficient oxygen remains in the oxygen stores to maintain physiological integrity of those tissues (i.e., heart and brain) that cannot survive without it. Hence, cardiac output and tissue perfusion will be important regulators of aerobic metabolism and metabolic rate and perfusion rate can be considered to be indicative of oxygen flux under both reduced and enhanced metabolic conditions (184). Therefore, during diving, circulation becomes the proximate regulator of metabolism, modulating dive time

$$\dot{V}_b[Ca_{O_2} - C\bar{v}_{O_2}] \propto \dot{M} \propto \frac{1}{DT}$$

Changes in heart rate and stroke volume contribute to changes in cardiac output unequally. Heart rate can vary one and, sometimes, even two orders of magnitude between diving and surfacing in both birds and mammals. In contrast, stroke volume is usually unchanged or reduced by one-half (16, 328). The difference in arteriovenous oxygen content could change by three to five times, but the fairly rapid fall in oxygen content during natural dives will limit achievement of that level of increase. Hence, for divers, heart rate (f_H) provides the most reasonable estimate of aerobic metabolism in the absence of recordings of stroke volume and tissue oxygen extraction so that

$$f_H \propto \dot{M} \propto \frac{1}{DT}$$

This relation implies that heart rate is variable, depending on dive time, so tissue perfusion must also be variable in intensity. It seems plausible that, in highly active species, the locomotor muscles would be perfused in preference to visceral vascular beds, but in more lethargic animals, the situation is less clear. Nevertheless, if it is assumed that tissue perfusion does indeed regulate metabolism, then it follows that

$$f_H \propto \dot{M} \propto \frac{1}{TPR}$$

where TPR is total peripheral resistance and is indicative of the degree of vasoconstriction that occurs during submersion.

The above relations imply that, if they can be substantiated, an analysis of voluntary diving performance can be achieved by monitoring dive time, metabolic rate, and heart rate. In fact, it is the substantiation of these relations with respect to cardiorespiratory function that forms the basis for what follows. In addition, the control of circulatory adjustments is important because of the role that the circulation plays as the proximate controller of metabolism.

Furthermore, cardiorespiratory adjustments upon surfacing cannot be ignored. Fedak et al. (142) characterized the surface interval as an "unproductive but necessary state," suggesting that surface time should be reduced to the bare minimum to improve foraging success. This can be done in two ways: *1*) to enhance ventilation and gas exchange to reduce the interval necessary for repaying oxygen deficits and *2*) to increase dive time by ensuring that aerobic (in the form of oxygen) and anaerobic (in the form of PCr) sources of energy production are fully in place before the dive. Hence, circulatory work normally required for exercise is completed before the dive, thereby reducing energy costs during the dive (142). In this respect, it has been suggested that variation in the dive time-to-surface time ratio (see sect. IIA) is the major regulator of metabolism in diving animals (94, 160).

This does not necessarily hold, however, for recovery from dives that have been extended into the anaerobic metabolic domain, beyond the ADL, for

$$EDT \propto [Lac^-]$$

where EDT is extended dive time and $[Lac^-]$ is lactate concentration. Lactate is the end product of anaerobic metabolism. Recovery from extended dives therefore represents not only preparation for the dive ahead but "payback time" for costs incurred during the preceding dive.

A. Circulatory Adjustments to Diving

1. Heart rate

During natural diving, virtually all divers show changes in heart rate, occurring not only during the dive per se but also during the predive and postdive periods. Exceptions would appear to be Humboldt penguins submerging in an artificial pond (62); Adélie penguins submerging in a still-water canal after spending at least 50 s at the surface between dives (101); rhinoceros auklets (*Cerorhinca monocerata*) making feeding dives in a tank (368); harbor seals making short feeding dives, also in a tank (205); and dolphins submerging while swimming at high, but not low, swimming speeds at sea (406). In diving ducks, heart rate is usually above the resting rate during natural dives (59). A similar response has also been observed in cormorants, dippers (*Cinclus mexicanus*), and even dabbling ducks (mallards, *Anas platyrhynchos*) that have been trained to dive for food (153, 210, 301). In contrast, heart rate in both large and small mammals during natural dives is usually well below eupneic resting rates (6, 162, 219, 273, 279, 378) or at least the resting rates derived from the allometric scaling curve of Stahl (361). Hence, if any relationship holds between diving metabolism and heart rate, then avian diving metabolic

TABLE 4. *Heart rate ranges of selected diving mammals and birds during natural and forced diving*

Common Name*	Body Mass, kg	Eupneic Heart Rate, beats/min	Natural Dive Heart Rate, beats/min			Forced Dive Heart Rate,§ beats/min	Reference No.
			Predive	Dive†	Lowest‡		
			Mammals				
Weddell seal (*L. weddellii*)	300–450	65	70–85	25–30	15–20	5	219, 331, 424
Elephant seal (*M. angustirostris*)	150–350	50–70	100–120	20–40	<5	5–10	4, 5, 383
Gray seal (*H. grypus*)	90–270	80–120	120	20–25	<5	5–10	141, 346, 378
Harbor seal (*P. vitulina*)	30–120	80–150	80–150	35–55	15–30	10–20	126, 142, 205, 320, 328
California sea lion (*Z. californianus*)	20–25	55–65	90–120	30–80	25	10	123, 131, 134, 407
Dolphins (*T. truncatus, T. gilli*)	145		80–120	40–60		45	137, 198, 406
Manatees (*T. inunguis, T. manatus*)	80–155	30–40		30–40		30	162, 347
Muskrat (*O. zibethicus*)	0.7–1.8	260–300	300	110–115	40	50	125, 167, 273, 279, 351
Mink (*M. vison*)	0.65–1	200–260	230	100–200	55–80	20–40	167, 366, 396
			Birds				
Diving ducks (*A. fuligula, A. affinis, A. americana*)	0.6–0.8	110–125	300–500	120–200	50	35–50	46, 55, 59, 151, 367
Dabbling duck (*A. platyrhynchos*)	2–3		150–500	250		20	153, 193, 276
Cormorant/shag (*P. georgianus, P. auritus*)	2	100	250–300	100	65	60	19, 276
Rhinoceros auklet (*C. monocerata*)	0.3–0.6	180	440	397		45	368
Penguins (*A. forsteri, P. papua, Eudpytes chrysolophus, P. adeliae, Sphenicus demersus*)	5–25	70–105	100–220	60–155	30–95	20–60	62, 230, 232, 285, 346, P. J. Butler, R. M. Bevan, and A. J. Woakes, unpublished data

* Several species may be grouped under one common name. † Heart rate was usually observed during natural dives (includes trained dives). ‡ Lowest heart rates were often seen during extended dives (not including "trapped" dives). § Forced dive heart rate refers to restrained or confined animals.

rates should be well above those of mammals, which appears to be the case (48, 75).

An inspection of Table 4 reveals that for birds and mammals the heart rate observed during natural dives is above that seen during forced dives. Dolphins, manatees, and cormorants are perhaps the most obvious exceptions. During forced dives, heart rate may be up to an order of magnitude lower than that during natural diving but, more usually, the difference is less, being of the order of two to five times. During forced dives, the actual length of the dive is relatively unimportant in governing heart rate, once a full bradycardia is established. The full extent of bradycardia can take a couple of minutes or more to be achieved in elephant seal pups (170) and manatees (347), but is usually completed in under a minute in most diving birds and mammals. During natural dives, heart rate attains a stable rate, which may or may not be a bradycardia, in the first few seconds of the dive and even, in some diving birds and seals, before the dive commences (anticipation of submergence).

Anticipation of submergence, in terms of heart rate, has only been convincingly recorded from diving ducks (60) as well as harbor and harp seals (66, 205) diving in artificial ponds. Typically, the longest cardiac interval during a dive occurs at or just before submergence. The coarse time resolution of most remote heart rate-monitoring devices (i.e., data loggers) precludes analysis of cardiac responses to free diving in such detail but, in harbor seals diving in a tidal stream, there is no doubt that the lowest heart rates are associated with the immediate dive period (142). That the lowest heart rate occurs early in the dive also appears to be the case in ringed seals (*Phoca hispida*) voluntarily diving under ice on the end of an electrocardiogram (ECG) tether (139) and in captive gray seals submerging in a swim mill (141). However, Weddell seals monitored using the tether technique do not show extended cardiac intervals during the early dive period (219). Also, naturally diving elephant seals carrying Holter monitors do not usually show this initial cardiac response (6).

In contrast to cardiac anticipation of diving, anticipation of surfacing, in which heart rates increase and may even reach predive levels before emersion, is a usual feature of the cardiac response to voluntary diving in both birds and mammals. The smallest change in heart rate in anticipation of surfacing occurs in those animals in which diving heart rate is high (muskrats, Ref. 273; ducks, Ref. 367). Fedak et al. (142) suggest that the duration of the period of rapid heart beats before surfacing is related to the length of time it takes the animal to reach the surface. In fact, even in ducks swimming long horizontal distances for food, there is a sustained increase in heart rate for about the last 16% of the diving period as the animal swims back to the surface. However, there is notable bradycardia

in these extended dives and heart rate only returns to the resting, but not to the predive, rate (367).

It has been postulated for harbor and elephant seals that decompression may be important in causing these anticipatory increases in heart rate (173, 219), although harbor and harp seals surfacing from shallow depths still show the response (66, 205). Visual orientation appears to be an important component in anticipatory increases in heart rate in ringed seals, because a blindfolded animal did not display any anticipatory cardiac increase when approaching an artificial breathing hole in the ice cover of a lake (139).

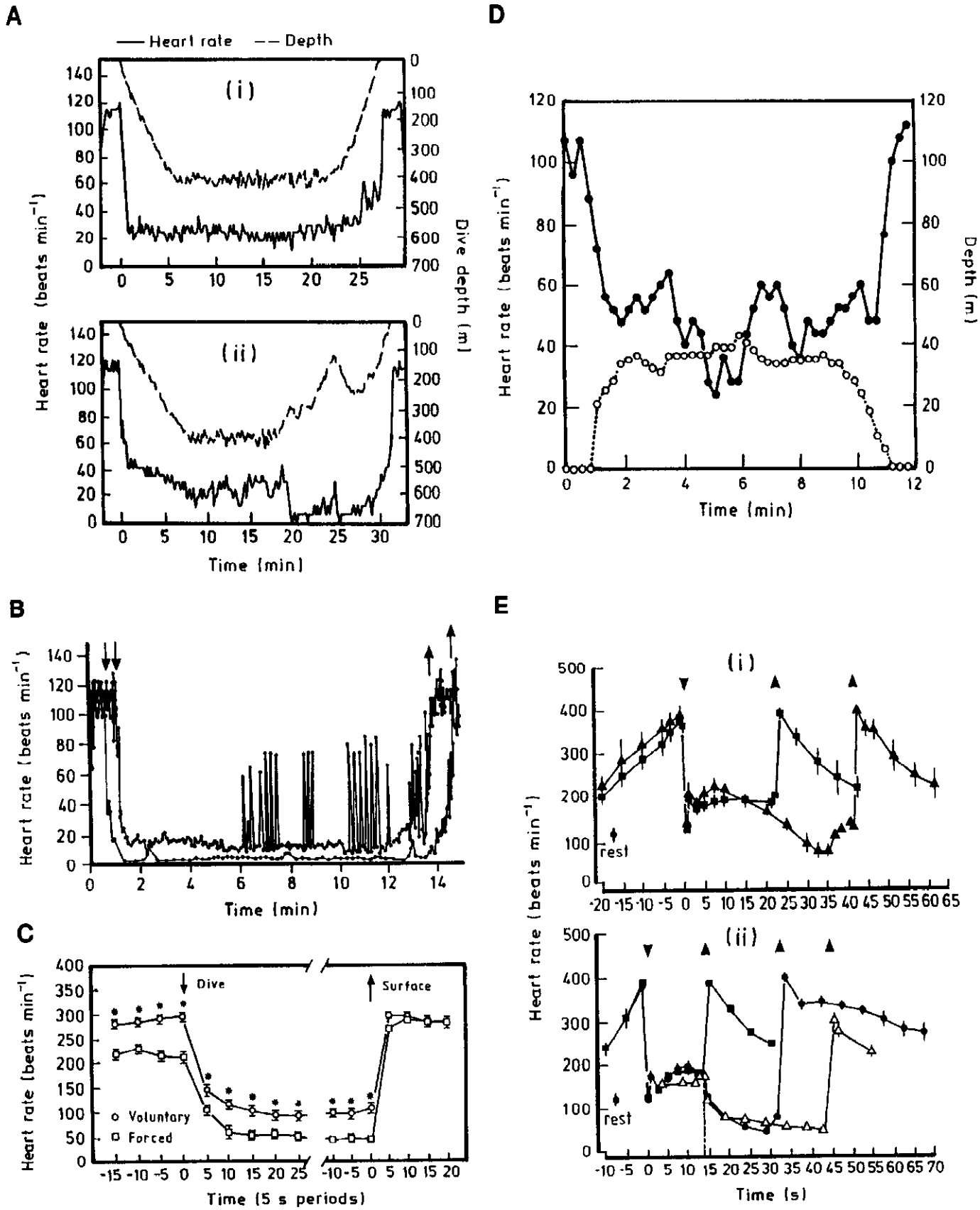
If time spent at the surface is truly an "unproductive but necessary state" for marine mammals (142), then anything that prepares the animal and its circulatory physiology for emergence might serve to shorten the surface interval. Thompson and Fedak (378) have suggested that an increased heart rate before surfacing will circulate blood around the musculature and other organs so that oxygen-depleted tissues and myoglobin in muscle could remove residual oxygen from the blood, reducing P_{O_2}, which would maximize oxygen at the start of breathing and reduce the time needed at the surface. For animals whose brains are crucially dependent on oxygen, this seems a dangerous exercise, particularly in view of the fact that anticipatory increases in heart rate revert to diving bradycardia if the animal returns to depth without actually surfacing (5, 299).

Aside from the initial and terminal variations, heart rate during natural dives seems virtually stable during any one dive (Fig. 23). However, for elephant, gray, and harbor seals and muskrats during natural dives and ducks during dives extended by training, bradycardia increases with dive time (Fig. 24). In fact, Kooyman and Campbell (219) believed it was possible to predict dive time from monitoring heart rates early in a dive by Weddell seals. In contrast, Hill et al. (177) found it impossible to predict long dives from the early dive heart rate. Only short dives (<5 min) could be predicted from high heart rates (>50 beats/min) in the early dive period. The preponderance of short dives biased the relation between early dive heart rate and ensuing dive time; if dives of 4 min or less were excluded, then no significant relationship was observed. Nevertheless, as in other seals, Weddell seals displayed a strong tendency toward greater bradycardia as dive time was prolonged (177). The inverse relation between heart rate and dive time led Thompson and Fedak (378) to suggest that 220 heart beats are rationed throughout any dive longer than 7 min in gray seals. They find it difficult to think of a plausible rationale for heart beat rationing and, from their data, so do gray seals. For instance, in dives of 14- to 18-min duration, the total number of heart beats varied from 87 to nearly 240.

It is apparent from Table 4 that the lowest heart rates that occur during natural dives are similar to those more usually associated with forced dives. In the gray seal, heart rates of 4 beats/min may be sustained for long periods while the animal sits on the bottom (378). Thompson and Fedak (378) claim that this is part of a seal's usual cardiac repertoire during submergence, but they followed their seals by boat, which may have disturbed them. Extremely low diving heart rates have been obtained from swimming harbor seals when tethered to a boat (299) or ringed seals, tethered to an ECG recording device, submerging on ice-covered ponds (139). In fact, Fedak (141) reports that for gray seals swimming in a flume, a forced-dive type of cardiac response (heart rate <10 beats/min) is provoked by any "surprising" stimulus, such as the appearance of an inflated weather balloon in the window on the side of the flume. On the other hand, extreme bradycardia has also been recorded in elephant seals diving far from, and long after, intervention by the experimenters. Heart rates of 3–5 beats/min were recorded on occasion; in the example shown in Figure 23*Aii*, this occurred as the seal began to swim toward the surface (4). Whether or not these seals were disturbed by potential predators or boats passing overhead is not known.

For mink (*Mustela vison*), muskrat, and platypus (*Ornithorhynchus anatinus*), extremely low heart rates occur when the animal is motionless underwater. In muskrats, this behavior occurs during escape dives induced by contact with the experimenters (273, 279, 351). In mink, extreme bradycardia occurred after the animal entered an underwater pipe (366). The platypus just seems to "like" wedging itself under tree roots on the bottom of a pond and remaining motionless with a heart rate of 4 beats/min (140). Only recently have heart rates been monitored from birds foraging in nature. Both emperor penguins (232) and South Georgian shags (16) display heart rates in the same range as those seen in forced dives (Table 4). Otherwise, for birds, low heart rates have only been observed in diving ducks trained to make extended dives (367) or when access to the surface was prevented at the end of a natural dive (Fig. 23*Eii*; Refs. 151, 367). This latter cardiac response is akin to that displayed by gray seals in a flume, when access to the breathing hole is prevented (77, 141).

Both seals and ducks continue to swim after being denied access to the surface, so physical activity has little influence on the low diving heart rates that occur after "trapping" them underwater. Diving heart rate in a number of seals is likewise unaffected by physical exertion. Harbor seals swimming in a flume exhibit a bimodal heart rate pattern (high rate, surface; low rate, submerged) even at high levels of exercise (estimated at 4–5 times resting rate of oxygen consumption; Ref. 407). Similarly, Kooyman and Campbell (219) report that a young Weddell seal vigorously swimming while diving showed the same cardiac response as adults making "leisurely" shallow dives. Also, heart rates of naturally diving elephant seals (4) and gray seals (378) appear not to be influenced by swimming up to speeds of 1–2 m/s.


A
Heart rate
Depth
(i)
(ii)
Heart rate (beats min⁻¹)
Dive depth (m)
Time (min)
B
Heart rate (beats min⁻¹)
Time (min)
C
Heart rate (beats min⁻¹)
Dive
Surface
Voluntary
Forced
Time (5 s periods)
D
Heart rate (beats min⁻¹)
Depth (m)
Time (min)
E
(i)
(ii)
rest
Heart rate (beats min⁻¹)
Time (s)

On the other hand, high levels of physical activity appear to have an effect on diving heart rates in dolphins (406), seal lions (407), muskrats (273, 352), platypus (140), and diving ducks with unimpeded access to the surface (45, 59). Butler (45, 48) has hypothesized that for diving ducks at least, there is a conflict between the exercise and diving cardiovascular responses. This antagonism is flexible and the balance can be tipped toward exercise or diving-type responses depending on conditions, such as the length of the dive. For instance, during natural dives, the heart rate of diving ducks is above resting rates (59, 151), whereas during dives that are extended by training, heart rate falls well below resting rates toward the end of the dive (367). In these situations, exercise intensity is "similar" throughout both extended and natural dives (262, 363, 372), so it is the factors related to diving per se that modulate the exercise response. β-Adrenoceptor blockade with nadolol prevents the interdive heart rate from increasing above ~300 beats/min, although there is no effect of β-adrenoceptor blockade on heart rate during natural diving (151). In contrast, muskrats forced to swim against water currents in a flume show an increase in diving heart rate with increases in water flow. At flows of 1 m/s, heart rate is almost twice that observed when diving in still water (352). Hence, in this situation, exercise intensity is increasing (see Refs. 147, 148) and overruling the diving response. β-Adrenoceptor blockade with nadolol has no effect on the increase in heart rate with exercise intensity. This contrasts to the situation when the muskrat is exercising in air, for much of the increase in heart rate with increased running speed is prevented by β-adrenoceptor blockade (352).

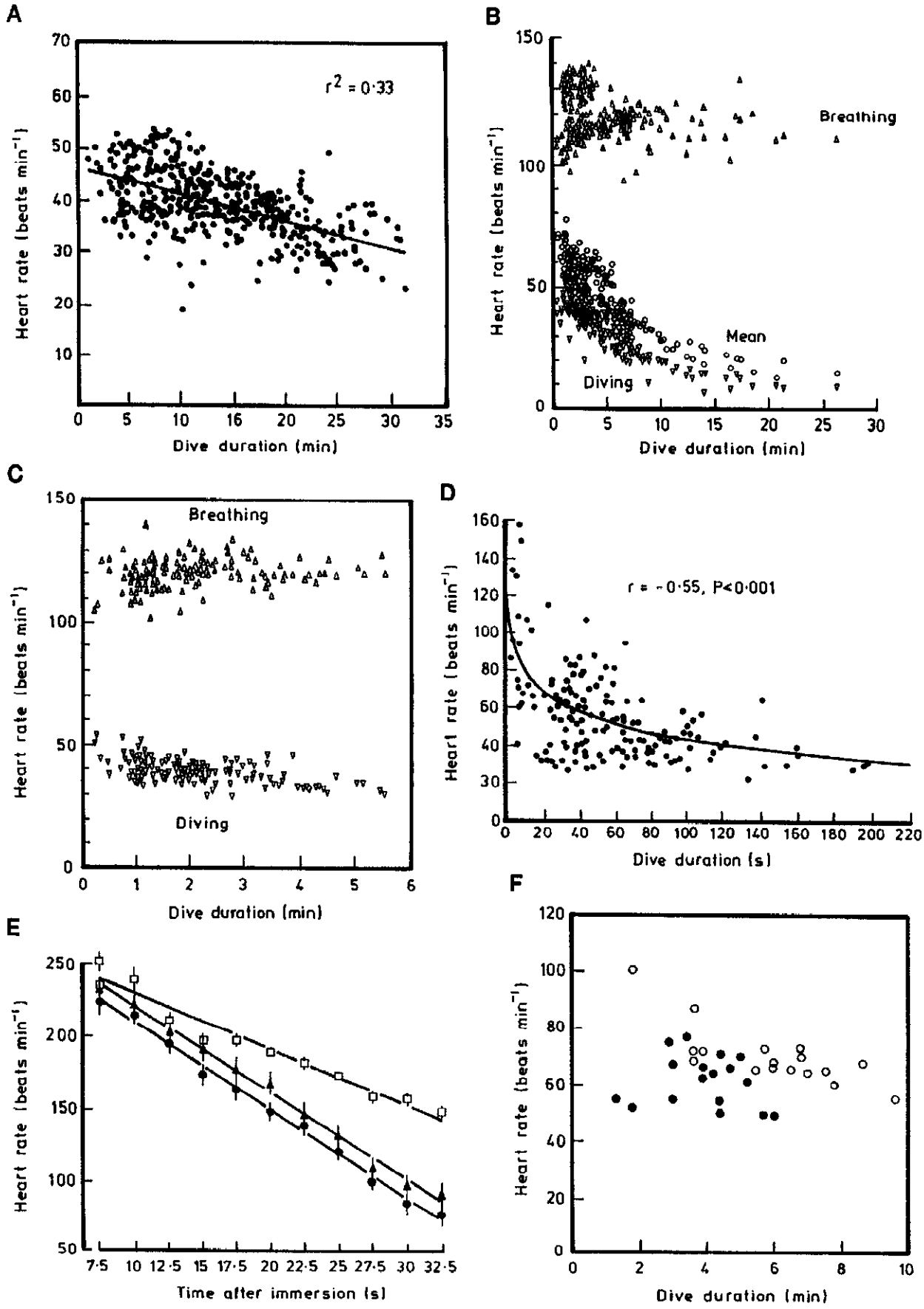
2. *Stroke volume and arterial blood pressure*

During forced dives, stroke volume is either unchanged or decreases in both birds and mammals (27, 30, 150, 208, 297, 353, 424). Bradycardia would, by itself, be expected to cause an increase in stroke volume, so the decrease in stroke volume is usually attributed to a fall in myocardial inotropic state and, in seals with a caval sphincter, decreased venous return [although the evidence for such a role for the caval sphincter is not good (136, 191, 295)]. Only three studies have measured stroke volume in unrestrained divers, and all animals were trained. In sea lions, stroke volume is unchanged (134), whereas in tufted ducks, stroke volume doubled at the start of the dive and then declined, being around resting stroke volume by the end of the dive (17). In the harbor seal, however, stroke volume decreased (328). Hence, the emerging picture for unrestrained animals during trained dives is similar to that for restrained animals during forced submersions.

Unvarying or decreasing stroke volume, allied to the marked changes in heart rate that accompany submergence in many diving animals, means that circulatory adjustments must be occurring, especially if there is a requirement to maintain arterial blood pressure. Some variability in blood pressure might be expected due to changes in "set point" of the barostatic control system induced by activity or asphyxia (355) or by different time courses of the cardiac output and arterial constrictor responses, but over all, one would expect blood pressure to be closely regulated. Unfortunately, there is little information about blood pressure in freely diving birds and none for freely diving mammals.

Tufted and redhead ducks making trained or escape dives show little change in arterial blood pressure (19, 371). Even trapping animals underwater, sometimes inducing a marked bradycardia, has little effect on peak ventricular or mean arterial pressures (371). However, Bevan and Butler (19) report that the long cardiac interval that occurs upon submergence in tufted ducks is associated with a fall in diastolic pressure, indicating that pe-

FIG. 23. *A*: heart rate and dive depth of an elephant seal performing natural dives at sea. *i*: Typical profile for heart rate and dive depth. *ii*: atypical profile in which heart rate fell to extremely low levels as seal swam toward surface (R. D. Andrews, D. R. Jones, J. D. Williams, P. H. Thorson, G. W. Oliver, D. P. Costa, and B. J. Le Boeuf, unpublished data). *B*: heart rate during 2 natural dives by a gray seal on one feeding trip. Each dot represents a single heart beat. A downward pointing arrowhead marks start of a dive, and an upward pointing arrowhead represents surfacing. In a typical foraging dive, heart rate was extremely arrhythmic, with occasional pairs of beats close together. Heart rate averaged 16 beats/min for entire submergence, including anticipatory tachycardia before surfacing. Other trace shows a dive from same foraging trip exhibiting most extreme bradycardia recorded in this seal. For entire dive, heart rate averaged 6.5 beats/min and was below 4 beats/min for 90% of time. [Modified from Thompson and Fedak (378).] *C*: heart rate profiles before, during, and after natural and forced dives of muskrats. Time was set to zero when animal's nose entered water (↓ dive) and then reset to zero at end of dive when nose broke surface (↑ surface). Asterisk indicates values significantly different from heart rate during corresponding period in forced dives. [From Signore and Jones (351).] *D*: heart rate (●) and depth profile (○) during a 10-min natural dive by an emperor penguin (232). *E*, *i*: mean heart rate (±SE) of tufted ducks before, during, and after natural dives (■) and extended dives (▲). Downward pointing arrowhead (*time 0*) represents point of immersion, and upward pointing arrowheads represent mean points of emersion for natural dives (22.4 s) and extended dives (41.4 s). *ii*: mean heart rate (±SE) of tufted ducks before, during, and after natural dives (■), natural dives from which ducks were temporarily unable to surface, "trapped" (●) and forced dives (△). [Data from Butler and Woakes (61).] Downward pointing arrowhead represents point of immersion during natural dives and "trapped" dives (but not forced dives). Upward pointing arrowheads represent points of emersion for all dives. Vertical dashed line represents point at which ducks apparently became aware that they were temporarily unable to surfce during "trapped" dives (after 13.8-s mean duration of submersion), and it also represents point of head immersion in case of forced dives. [Modified from Stephenson et al. (367).]


A
Heart rate (beats min⁻¹)
Dive duration (min)
r² = 0·33
B
Heart rate (beats min⁻¹)
Dive duration (min)
Breathing
Mean
Diving
C
Heart rate (beats min⁻¹)
Dive duration (min)
Breathing
Diving
D
Heart rate (beats min⁻¹)
Dive duration (s)
r = -0·55, P<0·001
E
Heart rate (beats min⁻¹)
Time after immersion (s)
F
Heart rate (beats min⁻¹)
Dive duration (min)

ripheral vasoconstriction lags behind the cardiac response. Mean arterial blood pressure increased during the dive as heart rate rose in anticipation of surfacing, but fell on emergence despite the marked increase in heart rate accompanying that event. In contrast, rhinoceros auklets showed no changes in heart rate or blood pressure before, during, or after escape dives (368).

3. *Blood flow distribution*

Cardiac output increased by 33% in the transition from rest to diving in tufted ducks, yet blood flow to the legs increased five times, indicating massive vasodilation of this vascular bed (17). The amount of blood flow to the legs during diving was similar to that observed in ducks swimming at the surface at 0.75 m/s. Interestingly, blood flow to the leg measured directly by Bevan and Butler (17) in surface-swimming ducks was a similar proportion of cardiac output as that assessed indirectly using radiological imaging techniques by Stephenson and Jones (371). Flow in the brachiocephalic arteries increased by 20% while carotid flow doubled during diving, compared with rest. In contrast, in animals swimming at the surface, brachiocephalic and carotid flows were significantly less than or the same as those at rest. Obviously, there was a substantial redistribution of blood flow between resting, swimming, and diving (17), with the "rest of the body" (i.e., that not supplied by the ischiadic and brachiocephalic arteries) receiving substantially less blood during diving than during surface swimming or than in resting animals. This selective distribution of blood during natural diving must be viewed in the context that tufted ducks appear to dive well within their ADL and may indicate a mechanism by which regional hypothermia could be achieved in other species of birds, such as shags and penguins (see sect. III*C*).

Bevan and Butler (19) used their blood pressure data along with the above flow data (17) to assess changes in TPR during trained dives (Fig. 25). Total peripheral resistance increased by 35% after 5-s submergence, and this increase was maintained at least through 12 s of diving. Peripheral resistances of the ischiadic and carotid

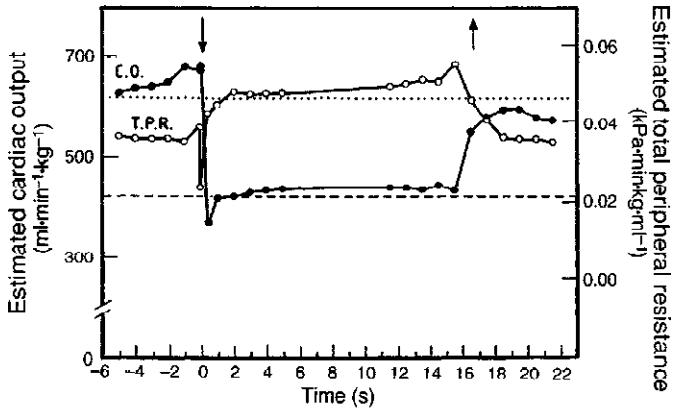


FIG. 25. Estimated mean cardiac output (CO; ●) and total peripheral resistance (TPR; ○) during trained dives in 3 tufted ducks. Estimates were made from heart rate, blood flow, and mean arterial pressure measurements of Bevan and Butler (17, 19). Horizontal dotted and dashed lines represent levels of TPR and CO, respectively, in interdive intervals. [From Bevan and Butler (18). Copyright is held by Company of Biologists Ltd.]

vascular beds were effectively unchanged by diving, thereby making no contribution to the increase in TPR. On the other hand, brachiocephalic flow resistance increased by 20% due to an estimated two to three times increase in resistance of the vascular beds supplied by the brachial artery, after 12-s submergence. Toward the end of the dive, blood flow was being directed away from the largely inactive breast muscles. Cardiac output and stroke volume were strongly correlated to heart rate (17). That is not to say, however, that heart rate is necessarily a good indicator of regional blood flow changes in birds. Using radiological imaging techniques, Stephenson and Jones (371) showed that flow distribution in ducks swimming at the surface was qualitatively similar to flow distribution in ducks making escape dives [in agreement with the quantitative data of Bevan and Butler (17) for trained dives]. However, when ducks were trapped underwater, only one in four showed a blood flow pattern characteristic of the forced dived animal, i.e., preferential distribution of blood flow to the heart and brain in association with pronounced bradycardia, even though heart rate was

FIG. 24. Relationship between heart rate and dive duration in birds and mammals. *A*: elephant seals; 486 dives from 7 seals, $r = 0.33$ and probability that slope = 0 is <0.0001. Coefficient of determination for individual seals ranged from 0.32 to 0.75 (R. D. Andrews, D. R. Jones, J. D. Williams, P. H. Thorson, G. W. Oliver, D. P. Costa, and B. J. Le Boeuf, unpublished data). *B*: gray seals; heart rates when making natural dives (▽), during surface breathing periods (△), and mean for complete dive/surface cycles (○). Note that heart rate for complete dive cycles declines as a function of dive duration, despite surface heart rates being similar. [From Thompson and Fedak (378). Copyright is held by Company of Biologists Ltd.] *C*: harbor seals; natural dives at sea encompassing full range of apparent activity levels are represented. There is no relation betweeen breathing heart rate and dive length. Diving heart rate decreases slightly with dive length (least squares linear regression model, probability that slope = 0 is <0.01). [From Fedak et al. (142).] *D*: muskrats; 149 escape dives from 5 animals. [From MacArthur and Karpan (273).] *E*: tufted ducks; mean values of heart rate during extended dives in intact (●, $n = 12$), sham-operated (▲, $n = 4$), and carotid body-denervated (□, $n = 6$) ducks. [From Butler and Stephenson (55).] *F*: emperor penguins; over 600 natural dives made by two animals (●, ○). Each point is average for heart rate measured at indicated time interval. For ○, $r^2 = 0.13$, and for ●, $r^2 = 0.03$. [From Kooyman et al. (232). Copyright is held by Company of Biologists Ltd.]

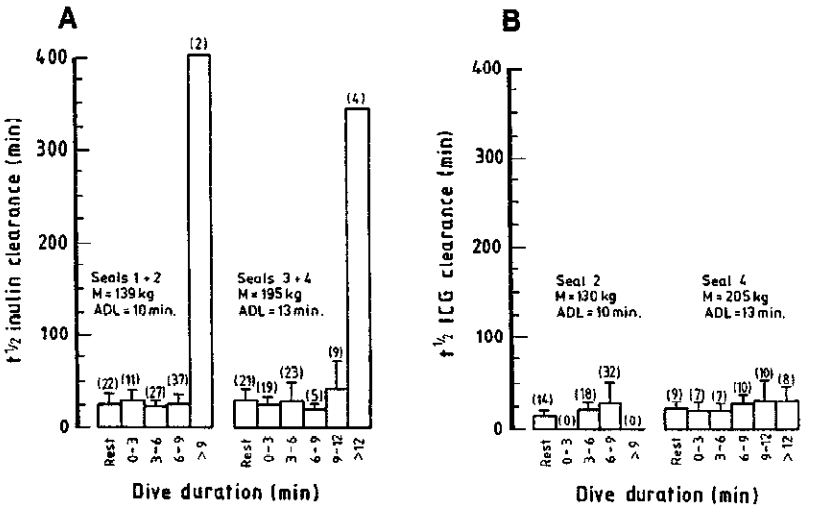


FIG. 26. Relationship of half time ($t_{1/2}$) for inulin (*A*) and indocyanine green (ICG; *B*) clearance at rest and during natural dives. M, body mass; ADL, aerobic dive limit. Number of dives for each column is shown in parentheses. [From Davis et al. (109).]

equally as low in another trapped bird. In fact, no correlation could be established between heart rate and relative blood flow to the hindlimbs, heart, and brain in ducks that were "trapped" underwater.

Ducks use their leg muscles for propulsion during diving, whereas penguins use their wings, so it is perhaps not surprising that leg blood flow in Adélie and gentoo penguins declined during diving (285). In penguins submerging voluntarily, heart rate fell to one-half or one-third the predive value (~200 beats/min), which was in the same range as changes in leg and carotid blood flow. In the absence of data on arterial blood pressure, it is difficult to assess the nature of these flow changes, but it is possible that cardiac output, blood pressure, and flows may all decline together.

Hence, the picture that emerges for birds is one of subtle rather than massive redistribution of blood flow during diving, compared with the predive period. In fact, on a somewhat more extended time course, a similar view could be taken of circulatory adjustments to natural diving in mammals. Heart rates, and perhaps cardiac outputs, are frequently at one-half to one-third of resting, if not predive, levels. Hence, if maintenance of arterial blood pressure is a priority then, as in birds, large changes in TPR are unnecessary. The 10 times changes in TPR seen in forced dives might only be expected in those animals showing unusually low heart rates, e.g., gray seals sitting on the bottom or elephant seals swimming with heart rates of 3–5 beats/min (5, 143).

Unfortunately, not much information on blood flow in voluntarily diving mammals is available, whereas much of what is available is contradictory. In resting humans, renal and hepatic flows can account for 50% of cardiac output, and if this is also the case in divers, then any restriction in these regional flows could partially compensate for changes in cardiac output consequent upon submergence. In a sea lion trained to immerse its head on command, Stone et al. (375) found only a 33% decrease in renal artery blood flow, yet in a trained harbor seal, diving caused an immediate and complete cessation of urine production (298). Similarly, using the clearance rate of inulin, either after a single injection or after equilibration of inulin distribution, Davis et al. (109) found that, in Weddell seals, glomerular filtration rate was unchanged from resting levels in most natural dives, but fell dramatically if the dive exceeded the ADL (Fig. 26*A*). Hence, a massive increase in resistance of the renal vascular bed is not an initial part of the circulatory arsenal of cardiovascular adjustments in diving Weddell seals. Support for the notion that there is little renal function during extended dives comes from clearance studies using *p*-[^{3}H]aminohippurate and inulin (168). During a 24-min dive, there was no evidence for kidney clearance of these tracers. In fact, their equilibration within the vascular compartment was considerably delayed, indicating marked vasoconstriction throughout the dive.

Hepatic function tests using indocyanine green (ICG) (109), cholic acid, or galactose clearance (168) again gave contradictory results. Davis et al. (109) found that, even during extended dives, hepatic flow was maintained (Fig. 26*B*), whereas Guppy et al. (168) found no hepatic clearance of metabolites even during short natural dives. However, during one short dive, Davis et al. (109) found that ICG clearance dropped by 25 times. Davis et al. (109) suggest that fright or other forms of stress may initiate a profound dive response, similar to that in forced dives, which would cause a marked reduction or even elimination of glomerular filtration rate and hepatic blood flow. This seems a reasonable explanation for the discrepancies between the two data sets.

A range of indicators (Evans blue) and radiolabeled metabolites (glucose, palmitate, and lactate) have also been used to assess metabolic function in unrestrained dives by

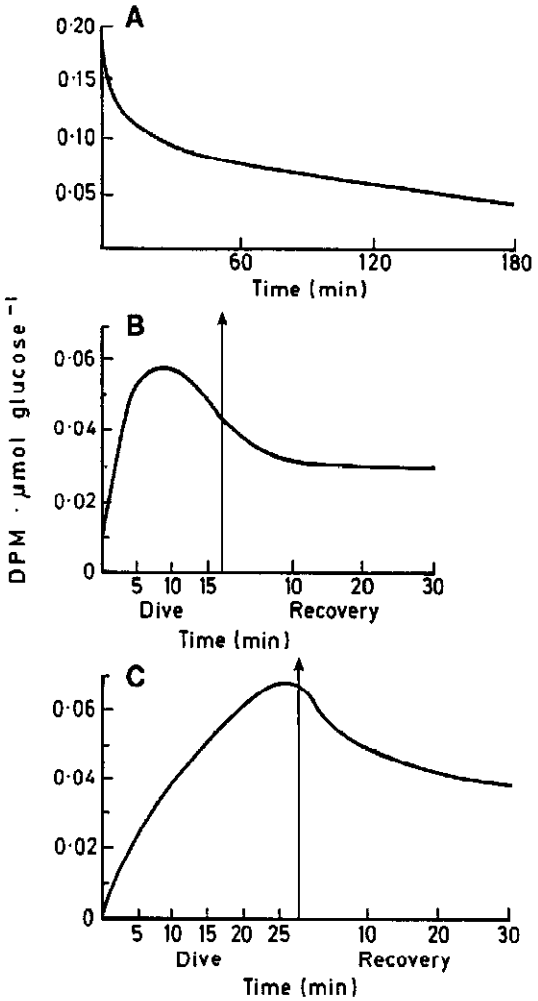


FIG. 27. Clearance of [^{14}C]glucose from plasma of Weddell seals at rest (*A*), during a relatively short (17 min) "feeding" dive (*B*), and during a longer (28 min) "exploratory" dive (*C*). Seals were diving from a hole cut in ice. Vertical lines in *B* and *C* indicate when animal surfaced. Note difference between curve in *A* and curves in *B* and *C*. The fact that radiolabeled glucose took some time to reach peak activity during dives is taken to indicate a slow circulation time resulting from peripheral vasoconstriction. DPM, disintegrations per minute (1 DPM = 0.0167 Bq). [From Butler (47) after modification from Guppy et al. (168).]

Weddell and gray seals (68, 77, 168). Unfortunately, the resulting decay curves are difficult to analyze and interpret. For instance, the label may be diluted by endogenous products, e.g., lactate during long dives, and it is also possible that lactate label could come from another source, such as glucose or palmitate, when these are injected along with labeled lactate. Furthermore, the label may be metabolized, e.g., free fatty acids or glucose, depending on the state of the circulation. Hence, it is not surprising that these studies contributed little to our understanding of the metabolic biochemistry of seals and instead have been used solely as indicators of circulatory restriction during diving. In Weddell seals, wash-in and equilibration times are far slower during diving than at rest (Fig. 27). Furthermore, wash-in times for glucose, for instance, were 66% slower during a 28-min "exploratory" dive (Fig. 27*C*) than during a 17-min "feeding" dive (Fig. 27*B*), despite the fact that heart rate during the feeding dive was, on average, one-half that in the exploratory dive (168). However, there was a "break" in the bradycardia during the shorter dive after 5 min, which lasted for a minute, and may have considerably speeded up the mixing process. In gray seals, diving with a heart rate of <10 beats/min, a complex specific activity decay curve was observed that differed markedly from the exponential decay seen at rest or during surface swimming (77). In reality, these curves represent entirely different things. The exponentially declining curves at rest or during exercise describe metabolism of the label, whereas during diving, the curve solely describes wash-in kinetics into a circulatory compartment in which flow must be greatly slowed (175).

Muscle circulation during natural diving has been indirectly estimated from measurement of temperature (325) and partial pressures of nitrogen in the muscles (340). Both of these methods suggest that muscle circulation remains open during natural diving. In Weddell seals making a 40-min dive, muscle temperature should increase by 0.3–2.2°C, depending on the metabolic rate, if there is no blood flow (325). Because this did not occur in the single Weddell seal in which temperature was recorded, then one of two postulates must hold: *1*) exercising seal muscle is extremely hypometabolic or *2*) the circulation remained patent even during long dives. Likewise, muscle circulation in dolphins making 1.5-min dives also remained patent as judged from nitrogen accumulation. However, it is interesting to note that perfusion of the blubber layer was not maintained as effectively as that of muscle, since the partial pressure of nitrogen was much lower than that in muscle (340).

Muscle circulation is stopped during forced dives due to extreme vasoconstriction. Some lactate appears in the blood during the dive, but there is a large blood lactate peak during recovery as circulation is restored to the previously hypoperfused tissues (Fig. 1; Ref. 346). A similar pronounced lactate peak during recovery occurred in the blood of Weddell seals after extended dives (Fig. 14; Ref. 235), implying that muscle blood flow was shut down for a considerable portion of the dive (217). It does not follow, however, that muscle blood flow continues during natural dives within the ADL, for the muscle oxygen and high-energy phosphate stores can serve to power the energy requirements (see sect. III*D*).

One way to use muscle oxygen and fuel stores more effectively is to perfuse muscles intermittently so that oxygen can be stripped from the myoglobin during the no-flow condition. Kooyman (217, 218) has proposed an intermittent flow model based on ideas obtained from studies of forced dive animals. During the initial stages of the dive, muscle flow ceases, but after the myoglobin stores have been depleted, accumulation of anaerobic end

products causes local vasodilation, and the muscle store is recharged. Vasoconstriction would then occur, thus cutting off the muscle circulation again. These cycles could repeat over and over. Certainly, the fact that heart rate may cycle up and down during long dives has led others to suggest an intermittent perfusion model for muscle circulation (168, 378). If, during extended dives, the worst came to the worst, then arterial vasoconstriction, beyond the reach of vasodilator metabolites, would eliminate muscle blood flow, saving blood oxygen for the crucially oxygen-dependent heart and brain. This restriction in flow could be effected neurally or via the agency of circulating catecholamines. Hence, in this model, the fall in cardiac output on submersion due to bradycardia could be compensated by an immediate restriction in muscle blood flow (232).

Guyton et al. (169) claim that their recording of myoglobin/hemoglobin saturation and relative blood volume in the muscle of diving Weddell seals gives no support to the pulsatile flow hypothesis (Fig. 21). Relative muscle blood volume declined immediately on diving and during short dives remained low throughout. During long dives (>17 min), muscle blood volume returned to normal levels on ascent and indicated hyperemia 1–2 min after surfacing. On occasion, muscle resaturation occurred before surfacing at the end of dives, but this must have been due to restoration of a normal muscle flow pattern when the heart rate increased in anticipation of surfacing. Bursts of resaturation throughout dives were not observed.

To summarize, the picture that emerges of blood flow redistribution in freely diving mammals is either profound circulatory restriction throughout the dive (77, 168) or moderate initial changes in flow distribution that become more pronounced as the ADL is approached or exceeded (109, 218). It is possible for the animal to move rapidly from the latter to the former type of response depending on prevailing conditions. A third type of circulatory adjustment, or more correctly nonadjustment, involving little or no change in flow during diving is also possible. At present, however, there is no direct evidence that this lack of response occurs in natural diving, and little support can be inferred from published data.

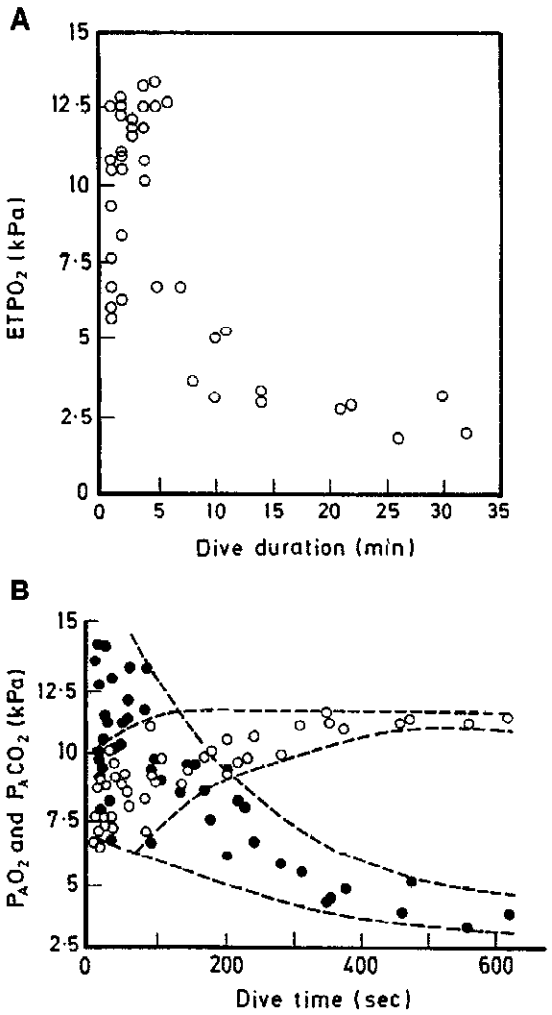


FIG. 28. *A*: first postdive exhalation end-tidal P_{O_2} (ETP_{O_2}) as a function of dive time in a Weddell seal. [From Ponganis et al. (324).] *B*: alveolar P_{O_2} ($P_{A_{O_2}}$, ●) and P_{CO_2} ($P_{A_{CO_2}}$, ○), sampled from single postdive breath, in relation to dive time in 2 Amazonian manatees. Results from both manatees did not differ significantly and have therefore been combined. [Modified from Gallivan et al. (162).]

B. Efficacy of Cardiorespiratory Responses to Diving

Oxygen is crucial for diving birds and mammals, so the levels of oxygen maintained in arterial blood during breath-holding are a measure of the efficacy of cardiorespiratory responses to diving. That depletion of oxygen stores limits diving performance and metabolism was challenged by Hochachka (182), who suggested that depletion of glucose stores was the crucial factor. Hochachka's (182) view was based on the fact that whole blood glucose levels decreased in diving Weddell seals, presumably due to increased glycolytic metabolism. In recent years, Hochachka's view has been criticized on both theoretical (218) and empirical grounds (71). Seal red blood cells (RBCs) have a much lower glucose concentration than the surrounding plasma, so hematocrit changes during a dive can severely affect whole blood glucose levels. In fact, although all changes in whole blood glucose concentrations are not due to hematocrit variations alone, there is no doubt that plasma levels of glucose are unaffected by breath-holding (71).

In tufted ducks making 18-s trained dives, there was little effect of diving on arterial P_{O_2} (Pa_{O_2}), arterial P_{CO_2} (Pa_{CO_2}), or arterial pH (pH_a). The Pa_{O_2} values fell by 2.4 kPa, Pa_{CO_2} effectively did not change, whereas pH_a fell from 7.55 to 7.48 due to an increase in blood lactate from 1.7 mM (at rest) to 3.0 mM (49). Only minor changes in

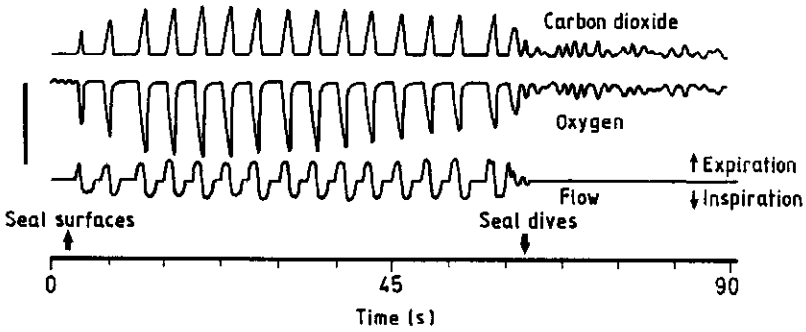


FIG. 29. Instantaneous measures of carbon dioxide, oxygen, and air flow during a single surface period after a natural dive by a gray seal. Scale bar (on *left*) represents a 10% change in oxygen and carbon dioxide traces and 0 to +40 l/s (expiration for flow trace). Maximum tidal volume, peak levels for carbon dioxide, and lowest oxygen levels are not attained until 3rd to 5th breath postdive. [Redrawn from Reed et al. (334).]

flow distribution occur in diving ducks, with the blood gases indicating that more profound adjustments are unnecessary. Similarly, in rhinoceros auklets, in which no cardiac adjustments occur upon diving, Pa_{O_2} only fell to 7 kPa, whereas Pa_{CO_2} was unchanged. Interestingly, hematocrits of blood samples taken during diving (25%) were considerably below predive levels (37%) (368).

For diving mammals, data for Weddell seals (227, 324), manatees (161, 162), and the bottlenosed porpoise (341) support the reasonable notion that the longer the dive, the lower will be the Pa_{O_2} at the end. The Pa_{O_2} values were assessed indirectly from end-tidal P_{O_2} of the first breath, or in the case of manatees the only breath, terminating the dive (Fig. 28). All these data point to the extreme tolerance to hypoxia displayed by diving mammals with alveolar oxygen levels of 2% not being unusual. In fact, arterial levels may be even lower than this. Hence, it is possible that in Weddell seals returning to the blow hole after a long dive, Pa_{O_2} could be as low as 1.33 kPa. These field data showing extreme insensitivity to hypoxia complement observations made many years earlier on Weddell seals subjected to simulated dives or nitrogen breathing (138).

Recently, Reed et al. (334) have shown that the lowest end-tidal oxygen is not reached for several breaths after surfacing in gray seals (Fig. 29) and that end-tidal P_{O_2} of the first breath upon surfacing (12.0 ± 0.23 kPa) is similar to that of the last breath before submerging (12.9 ± 0.21 kPa). Assuming that end-tidal P_{O_2} in this study is representative of alveolar P_{O_2}, these data indicate that there is little removal of O_2 from the lungs during submersion. This either means that there are effective pulmonary shunts, thus maintaining alveolar P_{O_2}, and that O_2 has been preferentially removed from the blood and, possibly, from the muscles, or that effective tissue shunts occur, whereby tissues are not perfused and rely entirely on the oxygen and PCr stored within them, thus maintaining Pa_{O_2} as well as alveolar P_{O_2}. It must be assumed, however, that the tissues that have small O_2 stores, such as the central nervous system and heart, are perfused and that they consume sufficient oxygen to reduce Pa_{O_2}. Thus, although the mechanisms are not clear, it would seem more likely that there are effective pulmonary shunts during submersion and that alveolar gas equilibrates with that in the blood only after surfacing.

Partial pressures of blood gases have been recorded from freely diving Weddell seals (331, 423), and the picture that emerged was more complex than the inverse propor-

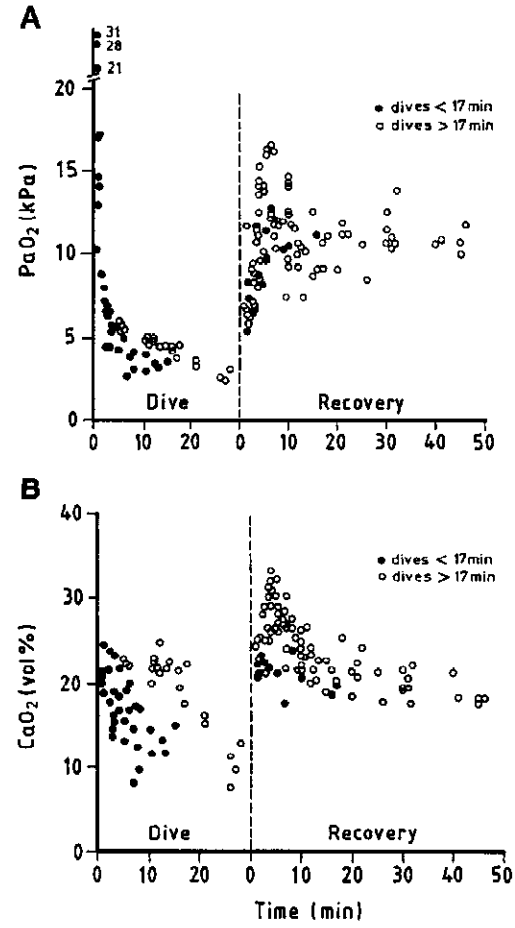


FIG. 30. Oxygen partial pressure (Pa_{O_2}) (*A*) and content (Ca_{O_2}) of arterial blood (*B*) in Weddell seals during natural diving and after resurfacing. Early diving compression hyperoxia is apparent. Lowest Pa_{O_2} recorded was 2.4 kPa at end of 27-min dive. Similar low Pa_{O_2} values were recorded at end of short dives (i.e., dives that ended <17 min). During long dives, Ca_{O_2} remained above resting values (18–19 vol%) for 15–17 min. Rate of decrease thereafter was not significantly different from that measured during short dives. [From Qvist et al. (331).]

tionality of Pa_{O_2} and dive time assessed from measuring solely end-tidal P_{O_2}. Values of arterial oxygen content (Ca_{O_2}) and Pa_{O_2} recorded close to the end of short dives (<17 min) were higher but not significantly different from those recorded at the end of extended dives (>17 min) (Fig. 30, *A* and *B*). Hence, Pa_{O_2} fell slower during long than during short dives, indicating greater circulatory restriction during long dives right from the start (Fig. 30*A*), confirming the conclusions of Guppy et al. (168). Compression hyperoxia was apparent at the beginning of a number of relatively short dives, but in spite of this, Ca_{O_2} fell throughout the dive (331). In contrast, during long dives, Ca_{O_2} remained normal or elevated for the first 15 min or so despite a fall in Pa_{O_2} from 10.5 to 4.25 kPa. Ca_{O_2} was elevated due to an influx of oxygenated RBCs, with blood hemoglobin reaching 25 g/100 ml blood and hematocrit approaching 60%. Hematocrit also increased during short dives, but this was insufficient to prevent a fall in Ca_{O_2}. At the end of a dive, RBC concentration returned to resting levels within 10–12 min (423). Similar RBC dynamics were also observed in elephant seals pups during periods of apnea and breathing (72).

Hematocrit variations during diving were first attributed to venous pooling of RBCs as the circulation slowed during submergence (235). However, Qvist et al. (331) showed that not only venous but also arterial hematocrits increased during diving and suggested that the spleen was the source of the RBCs. Bryden and Lim's (43) postulate that the spleen might serve as a reservoir for RBCs in seals was considerably embellished as a result of the research of Qvist et al. (331). The spleen was envisaged as a "scuba tank," injecting oxygenated RBCs into the circulation to promote aerobic metabolism while, at the same time, assuaging the impact of CO_2 retention on blood chemistry and diluting N_2 tensions (183, 422, 423).

Because blood viscosity is proportional to hematocrit, the former increasing exponentially with hematocrit then, in the absence of change in arterial blood pressure, an increase in hematocrit of some 50% (from 40 to 60%) will almost halve blood flow, purely passively (174, 282, 401). This passive flow restriction may be ameliorated to some extent in the smallest blood vessels, due to the anomalous viscous properties of blood. Passive flow changes may also be offset due to increases in blood pressure, consequent to increases in blood volume, unless the venous storage vessels can accommodate all the increased circulating volume.

Measured and estimated splenic masses of pinnipeds support the idea that the splenic reservoir is large enough to function as a scuba tank (67, 71, 331, 326). In fact, it has been argued that, because splenic mass as a proportion of body mass is highly correlated ($r^2 = 0.9$) to mass specific blood volume then, as diving mammals have such large blood volumes, it follows that they have large spleens (Fig. 31; Ref. 67). Hence, splenic contraction or relaxation

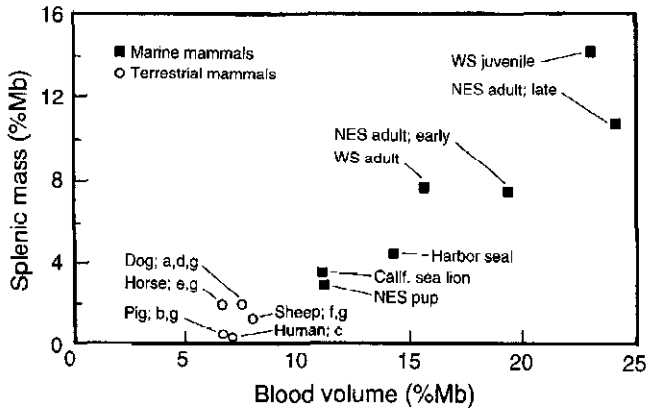


FIG. 31. Relationship between splenic mass and blood volume, both as a percentage of body mass (%M_b), for several species of marine and terrestrial mammals. Marine mammal vaules were calculated from measured M_b values and hematocrit (Hct) ranges, known plasma volumes, and calculated maximum blood volumes (based on maximum Hct) and include values for northern elephant seal (NES) adults during early and late fasting. Values for adult Weddell seals (WS) were obtained from calculations of Qvist et al. (331). Values for terrestrial mammals were obtained from published studies as indicated: *a*, Ref. 65; *b*, Ref. 172; *c*, Ref. 286; *d*, Ref. 291; *e*, Ref. 322; *f*, Ref. 382; and *g*, Ref. 395. [From Castellini and Castellini (67).]

will contribute to hematocrit change during diving, but the frequency and efficacy of such contractions is speculative. On the other hand, the Weddell seal spleen has the requisite equipment with many smooth muscle cells in the capsule and trabeculae, which are extensively innervated (349). Spleen size is reduced immediately after injection of epinephrine (194).

A caveat to the idea of the spleen functioning as a scuba tank in large marine mammals is provided by the diving behavior of many of these animals. Most marine mammals do not spend long periods at the surface between dives. Dives occur in bouts in Weddell seals, with surface intervals of <5 min between each dive of a bout (74), whereas in both northern and southern elephant seals, surface periods of longer than 3 min are unusual, even when the animal is diving continuously for 24 h or more (178, 246). Hence, hematocrit will rise on the first dive of a bout and, in the case of elephant seals, could remain elevated for months. If this is the case, then it is not unexpected that the viscosity of northern elephant seal blood is lower than that of Weddell seals at all flow rates (282).

So, the question must be asked as to what is the effect on oxygen stores and ADLs of splenic contraction in the first dive of a bout compared with maintained high hematocrit in all the ensuing dives. Ponganis et al. (326) examined this question in Weddell seals using the splenic size and blood volume estimates of Qvist et al. (331) and the ADL assumptions and calculations of Kooyman et al. (220, 227, 235). The RBCs in the spleen were assumed to be fully oxygenated. During the first dive of a bout, splenic

contraction provides the major proportion of the blood oxygen (67%) during the dive. However, during the next dive, RBCs continue to circulate if the spleen remains contracted, so the total blood oxygen store is only reduced by 10% (1.9 l), which is enough oxygen for 1.2 min of diving time (326). The slight reduction in the blood oxygen stores comes about because RBCs from the spleen are fully oxygenated, whereas when mixed in the circulation, 67% of the RBCs are on the venous side (326). Similar calculations for harbor seals yield an even smaller difference in oxygen stores between the first and subsequent dives in a bout (326).

A direct measure of the efficacy of oxygen conservation would appear to be provided by a comparison of blood gas data obtained from Weddell seals during forced dives (257, 424), natural dives (331), and spontaneous apneas on land or in water (235). Unfortunately, a comparison of blood gas data is not straightforward, because it is not known how hematocrit changes during forced dives and apnea. If hematocrit increases during apnea, as occurs in elephant seal pups (72), then a comparison between Pa_{O_2} during voluntary dives and apnea is justified. After 4–8 min of apnea, Pa_{O_2} declined to ~3 kPa (235), with these levels not being reached in free dives for over 20 min or so (331). Hence, given the caveats mentioned above, oxygen would appear to be conserved less well during apnea than during voluntary diving.

The extreme circulatory restriction during forced dives (424) means that oxygen uptake will be greatly reduced compared with that during voluntary dives. Qvist et al. (332) estimate that ~6 ml $O_2 \cdot l^{-1} \cdot min^{-1}$ was provided from the blood in the forced dived animals studied by Liggins et al. (257) which, for a 450-kg animal, gives an aerobic metabolic rate of somewhat <1 $ml \cdot kg^{-1} \cdot min^{-1}$. This value for oxygen uptake during forced dives is one-third to one-fifth that estimated for natural diving (75). Nevertheless, during forced dives by pregnant and nonpregnant Weddell seals, Pa_{O_2} appeared to fall more rapidly than that during voluntary dives. In pregnant seals, Pa_{O_2} fell to 4 kPa after a 4-min submergence and to 3 kPa after a 20-min submergence (257). In nonpregnant animals, Pa_{O_2} fell more slowly, reaching 4.25 kPa after 8–12 min of diving (424). Heart rate fell in the range of 8–15 beats/min during the forced dives, being 12–25% of the predive rate. In contrast, heart rate during voluntary dives only halved, yet Pa_{O_2} was 4.25 kPa after 15 min of submergence (331).

Acid-base disturbances are much more striking than Pa_{O_2} differences between natural diving and spontaneous apnea on the one hand and forced diving on the other. During natural diving and apnea, Pa_{CO_2} rose by <20%, whereas pH_a was effectively unchanged or fell by 0.5 units, at most (235, 331). In contrast, during forced dives, Pa_{CO_2} increased by 25–60% and pH_a declined by at least 0.5–1 unit (257, 424). Hence, despite the fact that Weddell seal blood is well buffered, the large acid-base disturbance during forced diving will mean that equivalent partial pressures of oxygen in arterial blood during forced and voluntary dives will represent very different oxygen contents due to the prominent Bohr effect of the blood (332, 358, 394). Addition of oxygenated RBCs to the blood notwithstanding, there seems little doubt that forced diving in Weddell seals does not appear to result in the parsimony of oxygen use from the blood that might be expected.

The properties of the blood in loading and unloading oxygen, at the lungs and tissues, respectively, are important to underwater survival. Blood with a high affinity for oxygen would favor full utilization of oxygen in the lung, whereas a low affinity would be advantageous in allowing more effective oxygen unloading at the tissues (241). A complicating factor here is that there may be an inverse relation between P_{50} and body mass, either intraspecifically or interspecifically, and many diving mammals and birds are relatively large (14, 265). However, Dhindsa et al. (118), summarizing data for 12 cetaceans and 7 pinnipeds, found no relation between P_{50} and body mass. In fact, Snyder (358) argues that oxygen affinity in mammalian divers relates to whether they use the lung as an oxygen store or not. Hence, affinity is high in small cetaceans, manatees, and rodents, in which the lungs represent an oxygen store (85, 251, 399), and low in large cetaceans and pinnipeds (242).

Almost all vertebrates have multiple hemoglobins that have different properties with respect to oxygen equilibria, so it is possible that the predominant hemoglobin type and oxygen affinity could change with exposure to the diving habit. Most seals, however, only appear to have two hemoglobins (251, 303, 393). In Weddell seals, "fast" and "slow" hemoglobins were designated according to their relative mobilities (394). The oxygen affinity of the fast hemoglobin is higher than that of the slow hemoglobin, whereas the Bohr shift is greater for the slow hemoglobin (394). In contrast to the work of Wells and Brennan (394), Qvist et al. (332) report four hemoglobins in both fetal and adult Weddell seal blood, with the two major components exhibiting practically identical P_{50} values and Bohr shifts. The P_{50} of fetal blood, however, is lower than that for adult blood (252, 332), which results from different 2,3-diphosphoglycerate (2,3-DPG) concentrations in the fetal and adult erythrocytes. Concentrations of 2,3-DPG are almost three times higher in adult than fetal RBCs, and the rise in concentration, and subsequent fall in oxygen affinity, is complete 4–5 wk after birth (332).

Lapennas (240) has argued that, in the steady state, Bohr factors of about one-half the RQ will maximize oxygen delivery to the tissues, rather than buffering pH changes caused by the addition of CO_2 to the blood in the tissues. On the other hand, much larger Bohr shifts, approaching unity, would be optimal to reduce P_{CO_2} and acidosis (39). Large Bohr shifts may also indicate that the

lung is not used as an oxygen store during diving because CO_2 cannot be eliminated during a breath-hold dive. Large Bohr shifts may also reflect a dependence on anaerobic metabolism, in that lactic acid added to the blood during dives will contribute to maintenance of a high Pa_{O_2} (203, 254, 288). The minke or lesser roqual whale (*Balaenoptera acutorostrata*) seems to be an extreme example, in that lactate plays an important role as a specific allosteric ligand facilitating oxygen unloading (40). Finally, if the Bohr factor is not constant but declines with oxygen saturation, then oxygen extraction from the lung might be favored. This seems to be the case in both adult and fetal blood of Weddell seals (332) but not in gray seals (242) or ducks (283). However, in harbor seals, the Bohr effect is largest around 50% saturation and declines at both low and high saturations (402).

The buffering capacities of the blood and tissues prevent large reductions in pH as a result of the accumulation of respiratory and metabolic acids. However, high buffering capacities would tend to reduce pH fluctuations and thus oppose the Bohr effect (358). Increased protein concentrations and high hemoglobin levels in penguin blood increase its buffering characteristics compared with the blood of most birds (302). The buffer value ($\Delta HCO_3/\Delta pH$) of true plasma for the Adélie penguin is 33 $meq^{-1} \cdot pH^{-1}$, which is some 50% higher than that of the muscovy duck (254, 344). In gray and bladdernose seals, the high hemoglobin concentration is solely responsible for elevated blood buffer values (85, 242), whereas in harbor, northern elephant, ribbon, and especially Weddell seals, other factors such as plasma proteins contribute to the buffer capacity (251–253). Furthermore, the Bohr and Haldane effects are linked so that the Haldane effect (H^+ binding by hemoglobin on deoxygenation) will also buffer pH changes. Hence, the adaptive feature of a high Bohr effect may be to counter the high buffering capacity of the blood and ensure an appropriate swing in blood oxygen affinity between the lungs and tissues (358).

Similar to the role of hemoglobin in the blood, myoglobin contributes to the buffering capacity of tissues, especially muscle (79). For the diving birds and mammals investigated by Castellini and Somero (1981), the tissue buffering capacity (β) is related to myoglobin concentration ([Mb], g/100 g tissue) as follows

$$\beta = 3.9[\text{Mb}] + 58.1 \quad (r^2 = 0.25)$$

The low r^2 indicates that myoglobin, however, is not a major contributor to muscle β in diving animals. Castellini and Somero (79) reached the same conclusion using both empirical and theoretical arguments (Fig. 32).

The shape of the oxygen equilibrium curve (Hill's number) is also important because oxygen extraction from the lungs will be favored if the curve is steep (Hill's number is low) at low saturations, whereas unloading at the tissues will be favored by a more markedly sigmoidal curve (Hill's number is high). Birds seem to have somewhat higher cooperativity than diving pinnipeds (242, 243, 402), which could be viewed as a disadvantage in diving birds which access the lung oxygen store during submergence (62). However, in virtually all bird species, cooperativity declines at low oxygen saturations, thereby facilitating oxygen extraction from the lung (180, 243, 344, 392).

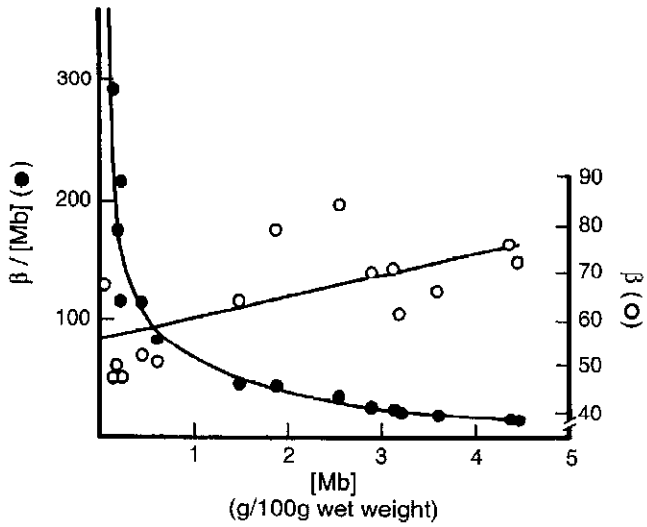


FIG. 32. Relationship between buffering capacity (β) expressed as μmol base (NaOH) required to raise pH of 1 g (wet wt) of muscle by 1 pH unit (titrations were made between approximately pH 6 and pH 7), and muscle myoglobin concentration [Mb] for the following diving birds and mammals: spotter porpoise (*Stenella attenuata*), northern fur seal, harbor seal, Weddell seal, sea otter adult and pup (*Enhydra lutris*), elephant seal pup, Adélie penguin, California sea lion, and a California gray whale calf (*Eschrichtius robustus*). Ratio of β to [Mb] is also plotted for these species to illustrate that correlation between β and [Mb] does not imply a strongly causal relationship between these 2 variables. [Derived from Castellini and Somero (79).]

Many divers experience regional hypothermia (see sect. III, *C* and *D*). Temperature has a dual action on the oxygen affinity of blood, a direct effect, which is a function of the intrinsic heat of oxygenation (ΔH) and an indirect effect caused by temperature-induced changes in blood pH (416). A fall in blood temperature increases oxygen affinity directly, as well as indirectly, by making the blood more alkaline. These complementary effects on oxygen affinity will tend to compromise both oxygen unloading at the tissues and cellular oxygenation. However, oxygen binding in many diving animals has a reduced exothermic oxygenation enthalpy (smaller ΔH), which will offset effects of temperature per se on oxygen affinity. In the harbor seal, for instance, Willford et al. (402) report a ΔH (kcal/mol) almost one-half that of humans. This low thermal sensitivity has been attributed to endothermic, oxygen-linked reactions such as 2,3-DPG release (391). In fact, 2,3-DPG in harbor seal blood is twice the concentration necessary to bind hemoglobin fully (350) and probably plays an important role in decreasing

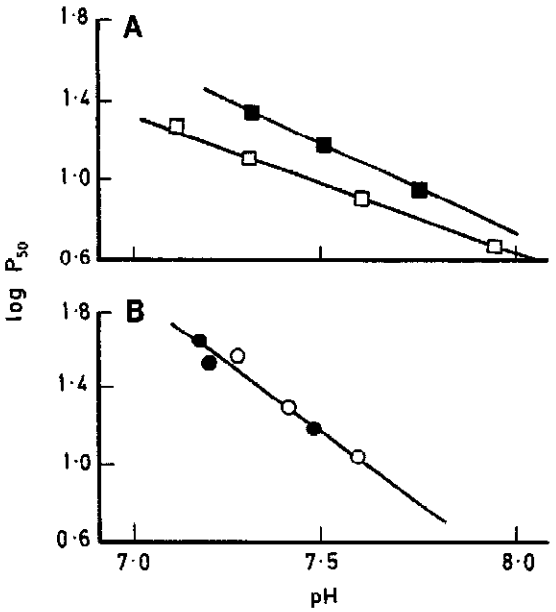


FIG. 33. Effect of CO_2, as a function of pH, on oxygen affinity of whale hemoglobin at 20°C (*A*) and 37°C (*B*). Assay conditions were 0.1 M Tris·HCl buffer plus 0.1 M NaCl and 30 mM inositol hexaphosphate, in absence (open symbols) and in presence (closed symbols) of 20% CO_2. [From Di Prisco et al. (119).]

the sensitivity of the oxygen dissociation curve to temperature. In this respect, the tripling of 2,3-DPG concentration in the blood of adult compared with that of fetal Weddell seals also suggests that 2,3-DPG might play a role in reducing ΔH as well as decreasing oxygen affinity in adult blood. Physiologically this makes a lot of sense, because the fetus is protected from large temperature variations. However, 2,3-DPG and hemoglobin only occur in equimolar concentrations in adult RBCs (332). There is not an excess of 2,3-DPG as is found in the harbor seal.

In the lesser roqual (minke) whale, the functional properties of hemoglobin are regulated by organic phosphate, CO_2, and temperature in a highly sophisticated manner (119, 165). There is a strong effect of temperature on oxygen binding in the absence of CO_2 and organic phosphate. The value of ΔH drops by two-thirds in the presence of the latter and halves again when CO_2 is added to the hemoglobin (Fig. 33). This minor enthalpy change means that, in the presence of organic phosphates and CO_2, oxygen binding is virtually independent of temperature. Furthermore, the CO_2 effect is, in itself, temperature dependent. There is no CO_2-induced release of oxygen from hemoglobin at 37°C, but there is a marked release at 20°C (165). Also, if the animal is breathing extremely cold air, then the allosteric behavior of CO_2 may promote oxygen uptake at the lungs. Elimination of CO_2 will increase the oxygen affinity of hemoglobin provided the lung surface is cold (165).

In birds, inositol phosphates are the principal allosteric modulators of oxygen affinity, and there is some evidence that the effect of saturating concentrations of organic phosphates on the blood of two divers, blacked necked grebe (*Podiceps nigricollis*) and cormorant (*Phalacrocorax carbosinensis*), is markedly less than it is in the blood of the chicken and turkey (164, 384). However, unlike the situation with respect to 2,3-DPG in mammals, inositol pentaphosphate (IP_5) is synthesized at the time of cell differentiation and remains constant throughout the life span of the cell (199, 264). Hence, modulatory effects of changing concentrations of organic phosphates that occur in mammalian blood are not paralleled in bird blood. Giardina et al. (164) hypothesize that other adaptive mechanisms may be important in diving birds, such as competition between IP_5 and CO_2. In view of the situation in the blood of the lesser roqual whale, this might prove to be a fruitful area of investigation.

The properties of hemoglobin and its interactions with allosteric modifiers, allied to subtle regional variations in blood flow that can occur during diving, suggest that it would be futile to describe the metabolic character of a dive in terms of variations in a single physiological variable, such as heart rate. Nevertheless, averaged over whole dive cycles (submergence plus recovery at the surface), diving animals may be in a steady state (50), and heart rate, independent of changes in tissue oxygen extraction and changes in stroke volume can, with certain provisos, provide an excellent and accurate measure of overall aerobic metabolism (23, 38). In this respect, Fedak (141) demonstrated a linear relationship between heart rate and oxygen consumption of swimming gray seals when heart rate and oxygen uptake were averaged over complete dive cycles. Having now reviewed the complexity of the interaction between the relevant variables, then advocating the use of heart rate as a global measure of diving performance may seem too simplistic, but nevertheless, it is such a convenient simplicity that it is sure to be pursued, at least in terms of the relation between aerobic metabolism and heart rate.

V. RECOVERY FROM DIVING: CARDIORESPIRATORY RESPONSES TO SURFACING

Gas exchange in diving animals is markedly uneven as the animal switches between a closed system during dives to an open system during recovery. During recovery, the potential exists to achieve a steady state in gas exchange, although this potential is modulated by the metabolic rate, the "nature" of the oxygen deficit, the level of ventilation, and the state of the circulation. The oxygen deficit may be aerobic, requiring only replenishment of oxygen stores, or have anaerobic components (143). When a pronounced anaerobic contribution has been made to dive metabolism, then recovery is prolonged and can even be stretched out over several dive/surface cycles (73, 227, 331).

It is not unreasonable to suppose that surface times

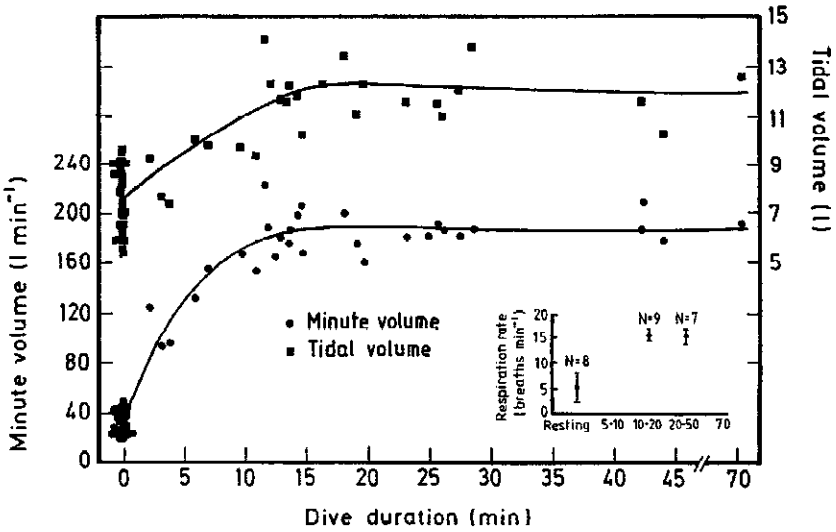


FIG. 34. Minute volume (l/min), tidal volume, and respiratory frequency averaged over first 2 min after surfacing against durations of natural dives by 5 Weddell seals varying in mass from 370 to 450 kg. Minute volume and tidal volume curves were drawn by eye. All volumes are in liters, BTPS. [From Kooyman et al. (226). Reprinted with kind permission of Elsevier Science-NL, Sara Burgerhartstraat 25, 1065 KV Amsterdam, The Netherlands.]

will be proportional to the preceding dive time. Certainly, in Weddell seals, dives exceeding the ADL are followed by extended recovery periods (235). A 35-min dive was followed by ~10 min of recovery, whereas a dive in excess of 60 min required 120 min for recovery (Fig. 17). Blood lactate concentration was ~5 mM at the end of the 35-min dive and 25 mM at the end of a 61.4-min dive (Fig. 14). Hence, surface interval increases exponentially with dive time (143). In rare instances, diving may continue, but the subsequent dives are short (73). However, long dives are rare in Weddell seals (Fig. 9) and usually the surface interval varies from 2 to 5 min (Fig. 17; Ref. 235). In contrast, gray seals show a direct proportionality between surface time and dive time only up to 7 min of diving (Fig. 13). Above 7 min of submergence, surface time is independent of dive time (378). Obviously, there is a major change in the diving physiology and metabolism of gray seals after 7 min of diving. In this respect, Gallivan (160) noted that in unrestrained harp seals, short dives, usually associated with high metabolic rates, required relatively longer surface times than long dives, in which metabolic rates were low.

Both birds and mammals hyperventilate, not only before, but also after natural diving (59, 94, 226, 235, 341). Even animals that usually take single breaths will increase the frequency of individual breaths after a dive, i.e., whales and dolphins (83, 222, 340, 341). Ventilation is the product of tidal volume (V_T) and respiratory frequency (f_{resp}), but there is often a reciprocal relation between these two variables during hyperventilation, the limits being set by lung mechanics. Tidal volume as a proportion of total lung capacity (TLC) is exceptionally large in many of the single or low-frequency breathers. In animals with breathing frequencies of <20 breaths/min, V_T may vary from 40 to 90% of TLC during postdiving hyperpnea (334, 341). Kooyman et al. (226) found that hyperventilation in the Weddell seal was due to an increase in V_T of 1.5–2 times while f_{resp} increased 3 times (Fig. 34). Tidal volume could approach 75% of TLC, which would promote rapid and complete exchange of alveolar gas. In contrast, when f_{resp} is >20 min^{-1}, postdive V_T seems to be closer to that of terrestrial mammals of the same size. Both Gallivan (160) and Craig and Påsche (94) reported that, at f_{resp} of ~27 breaths/min in harp seals and over 35 min^{-1} in harbor seals, V_T was between 20 and 30% of estimated TLC. In fact, Påsche (318) had remarked earlier that the ability to increase V_T and f_{resp} above resting levels by harbor seals, in response to hypoxia, was less than that in terrestrial mammals.

Birds have an exceptional volume of air in their lung-air sac system; this volume is three to seven times greater than that of most diving animals on a unit weight basis (Table 1). The only diving mammal that comes close to the TLC of birds is the sea otter (249, 250, 253). Hence, in birds, V_T is probably only a small proportion of TLC during postdive hyperpnea. Breathing frequency increased in both pochard (58) and tufted ducks (59) during the interdive intervals of a diving bout.

Northern elephant seals at sea make extremely long dives, frequently in excess of the calculated ADL (see sect. IIID), with only short surface intervals between them (Fig. 11). On land, awake and sleeping seals show prolonged periods of apnea interspersed with short bouts of breathing. In northern elephant seals, respiratory variations in heart rate are pronounced, with heart rate increasing on inspiration and falling during expiration (13, 69, 70, 76). Surprisingly, respiratory variations in heart rate were not observed in beached southern elephant seals (213). In a study with beached subadult northern elephant seals, spectral analysis of cardiac intervals and breathing patterns showed maximum power at frequencies of between 0.1 and 0.2 Hz for both breathing and heart rates

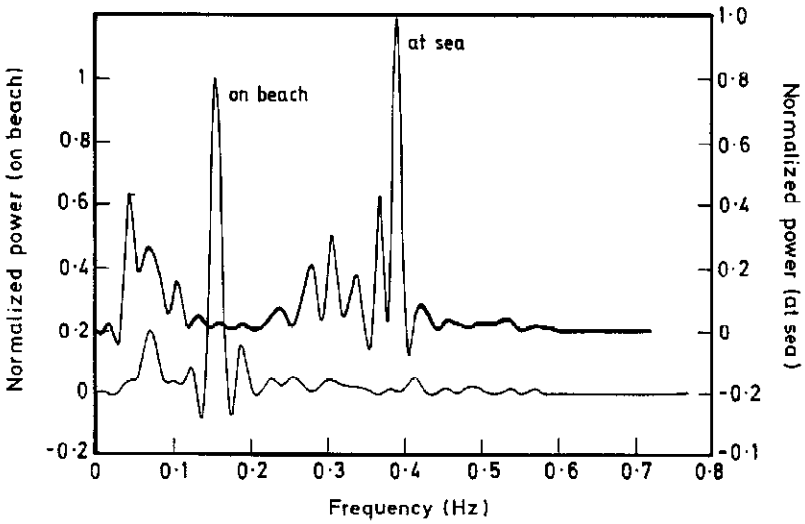


FIG. 35. Spectral analysis of heart rate variability in an elephant seal breathing on beach and breathing at sea between dives. On beach, frequency of maximum power (0.15 Hz) was identical to breathing frequency. Frequency of maximum power at sea (~0.4 Hz) gives a breathing frequency of 24 min^{-1} between dives. A nonlinear bandpass filter was used to remove baseline trend and very low frequency components. (R. D. Andrews, Y. Yeh, D. R. Jones, J. D. Williams, P. H. Thorson, D. P. Costa, and B. J. Le Boeuf, unpublished data).

(Fig. 35; R. D. Andrews, Y. Yeh, D. R. Jones, J. D. Williams, P. H. Thorson, D. P. Costa, and B. J. Le Boeuf, unpublished data). Hence, spectral analysis of cardiac intervals alone can be used to give breathing rates of animals at sea. When breathing at sea, maximum power occurred at 0.4 Hz (Fig. 35; Andrews et al., unpublished data). This breathing rate is three times the maximum rate observed in beached juvenile seals (13, 24).

The time taken for a single breathing cycle in marine mammals is usually short, which is advantageous in reducing surface time. The extreme case is the dolphin, *Tursiops*, which exhales and inhales in ~0.33 s (222, 245). Expiration in marine mammals is usually briefer than inhalation, with expiratory air flow rates being higher than inspiratory rates (229, 311, 334, 360). The hydrostatic pressure head when the animal approaches the surface, allied to extremely compliant chest walls, means that the driving pressure for exhalation will be very high (15, 249). To take advantage of this large driving pressure, many marine mammals exhale through constricted airways ("pursed-lips" breathing; Refs. 216, 229), and the airways themselves are strongly reinforced to prevent collapse (15, 114, 115, 234). Nevertheless, peak expiratory flow rates in marine mammals are not exceptional in comparison to those for terrestrial mammals (250), but what is exceptional is the ability of marine mammals to maintain high flow rates at extremely low lung volumes (15, 222, 234). Hence, reinforced airways prevent lung collapse at high diving pressures and permit high flows at all lung volumes, thereby shortening expiratory time. This allows V_T to be extremely large and end-expiratory volume to be low so that there is a high turnover of alveolar gases (250). Reinforced airways also have an additional role in ensuring orderly collapse of the lungs from the smallest to the largest airways during hydrostatic compression, thereby removing potentially hazardous nitrogen from the exchange surface during deep dives (216, 338, 346).

Any circulatory changes initiated in anticipation of, or coincident with, the start of diving are usually reversed before the end of the dive, in anticipation of surfacing. Thompson and Fedak (378) suggest that during anticipatory tachycardia, blood flow may be restored to previously hypoperfused areas of the body so that the blood will be further deoxygenated and maximum oxygen uptake on surfacing will be ensured. Certainly, gray seals showing no anticipatory increase in heart rate did not achieve maximum rate of oxygen uptake with the first few breaths (334). This may be analogous to the situation at the start of exercise in humans when ventilation runs ahead of circulatory changes (398). Heart rates and, presumably, cardiac outputs are quickly restored to predive levels and are usually well above resting levels in both birds and mammals at the end of a dive (6, 17, 66, 101, 142, 177, 205, 232, 331, 378). In harbor seals, there is no relation between heart rate during breathing and the length of the preceding dive (142). This suggests that in seals, heart rates in the range of 80–150 beats/min observed in the early postdive recovery period may be maximal. Seals contrast with birds, in which interdive heart rate increases with each succeeding dive in a bout, up to rates approaching 500 beats/min (59). If the surface interval is prolonged, then heart rates usually decline in both birds and mammals.

Hyperpnea combined with increased circulation leads to a rapid restoration of the partial pressure of blood gases. The Pa_{O_2} value is usually elevated somewhat during the early postdive recovery period in Weddell seals, reaching values well above those at rest (Fig. 30*A*). Changes in Pa_{CO_2} are more complex depending on whether the dive exceeded the ADL, in which case a large lactate load is added to the blood during the recovery period. After natural dives, Pa_{CO_2} falls rapidly, usually within 1–2 min, whereas after extended dives, it may take 5–10 min for Pa_{CO_2} to be reduced to or below predive values (235, 331).

Acid-base balance is little disturbed by natural diving but, after extended dives, when large concentrations of lactate appear in the blood markedly reducing base excess, pH_a falls and usually takes 30–45 min to regain predive values (235, 331). Body temperature of seals may drop during diving, particularly during extended dives, so the initial blood gas values could be overestimated (331). In birds, there is little information about blood gas tensions in the postdive recovery period, although in diving bouts by ducks, pH_a declines due to a doubling of blood lactate (48, 49). In contrast, although lactate also increased in rhinoceros auklets making escape dives, the acidosis was partially compensated by lung ventilation between dives, because Pa_{CO_2} did not increase progressively throughout the diving bout (368). Only minor changes in partial pressure of oxygen in the blood and in blood pH were observed after voluntary diving in penguins (285).

Due to the increased hematocrit and Pa_{O_2} in Weddell seals after diving, Ca_{O_2} can attain the remarkable value of 33 vol% (Fig. 30*B*). But Ca_{O_2} falls as RBCs are removed from the circulation. Obviously, it is advantageous if RBCs are stored early in recovery, when Pa_{O_2} is highest. Also, the metabolic acidosis after a long dive could reduce 2,3-DPG content of the RBCs, thereby increasing blood oxygen affinity, although there was no evidence for this from the in vivo oxygen equilibrium curve (331). However, the time course for restoration of resting hematocrit levels is controversial. Recent data suggest that hematocrit is elevated throughout a diving bout in Weddell seals (73) and also during apnea-eupnea cycles in elephant seals (70). Hence, only if the interdive interval is prolonged (>5 min) will hematocrit return to resting levels between dives.

Elevated hematocrit, rapid circulation, low oxygen levels in arterial and venous blood, combined with hyperpnea, mean that oxygen consumption during the recovery phase will be high. This will allow rapid repayment of oxygen deficits if no anaerobic debt has been incurred. In fact, oxygen consumption during the postdive recovery phase may represent the highest rate of oxygen consumption ever recorded for seals and dolphins.

Even after forced dives with restrained animals out of water, maximum oxygen consumption of gray seals approached 24 ml $O_2 \cdot min^{-1} \cdot kg^{-1}$ (346), which is higher than maximum values reported for exercise (141), but not as high as the oxygen consumption of unrestrained gray seals, which approaches 40–45 ml $O_2 \cdot min^{-1} \cdot kg^{-1}$ for breaths associated with the lowest end-tidal P_{O_2} values during the recovery period (calculated from Ref. 334). Unfortunately, the current proclivity for presenting recovery as a function of a dive and surface cycle means such values do not represent maximum during the surface period. However, this was not the case with data from harbor seals (94). Oxygen uptake in the short surface intervals (0.25–0.5 min) reached values between 30 and 50 ml $\cdot min^{-1} \cdot kg^{-1}$. This is within the range of estimated and recorded maximum for this species (132, 407).

After dives of 5–20 min, Weddell seals had a maximum oxygen consumption of >40 ml $O_2 \cdot min^{-1} \cdot kg^{-1}$ (227). This was 2.5 times oxygen consumption after short (<5 min) dives and, surprisingly, 25% greater than maximum oxygen consumption after extended dives (20–70 min). The rate of oxygen consumption fell to the resting rate (5.15 ml $O_2 \cdot min^{-1} \cdot kg^{-1}$) 5 min after surfacing, although hyperventilation persisted for at least 20 min after extended dives (226). These values can be compared with estimated rate of oxygen consumption from data averaged over a dive and surface cycle (75). After 15-min dives, with 2.5–5 min of recovery, oxygen consumption was within the range of 16–36 ml $O_2 \cdot min^{-1} \cdot kg^{-1}$, which falls within the range of values given by Kooyman et al. (227).

For diving ducks, the situation appears to be somewhat different. The rate of oxygen consumption during the recovery period is around six times resting oxygen consumption (414), which is probably half the minimum oxygen consumption that occurs during flight (48). This may reflect the much higher levels of Pa_{O_2} at the end of a dive in ducks as well as lower V_T, as a proportion of total lung/air sac volume, during the recovery period.

The above discussion has been about divers that take multiple breaths during the recovery period. Manatees, on the other hand, only take a single breath on surfacing, so there is no possibility that manatees will ever attain a steady state (161). In fact, large imbalances in oxygen stores have to be corrected over several dive-surface cycles. Hence, maximum oxygen consumption values recorded in manatees are much lower than those of seals, being in the range of 8.0 ml $O_2 \cdot min^{-1} \cdot kg^{-1}$. Tidal volumes in manatees are only ~40% of TLC (162).

In both birds and mammals, hyperventilation before a dive is usually associated with respiratory exchange ratios (RE) greater than one, because oxygen stores are loaded and CO_2 is blown off (94, 227, 414). Hyperventilation, after short dives by seals, does not usually cause much of a change in RE, compared with that at rest (94, 160, 227), whereas during recovery from longer dives, RE increases and may exceed unity after 5–6 min of hyperventilation (227, 235). During the early phase of recovery, oxygen consumption and carbon dioxide consumption must increase in step but, even without addition of lactate to the blood, it is possible for RE to increase due to different time constants for loading and unloading O_2 and CO_2 stores, respectively. In contrast to seals, ducks recovering from dives shorter than their ADL have an RE in excess of unity (414). Because lactate increases during a diving bout, CO_2 will be blown off to preserve acid-base homeostasis (49).

During recovery, increases in ventilation and circulation should be matched, although there is some evidence to suggest that circulation during recovery may be selec-

tively altered as it is during diving. Scholander et al. (348) remarked on the mosaic appearance of muscle during recovery from forced dives, indicating that peripheral vasodilatation was modulated. This observation was confirmed and extended to include other hypoxia-resistant tissues (e.g., liver, kidney, and stomach) in a detailed microsphere study by Blix et al. (27). In fact, even during recovery from free dives, there is evidence that restoration of kidney and liver function may be delayed. The half-time values for indicators of kidney and liver function during recovery from diving in Weddell seals were much longer than those obtained from resting animals (168). Clearances of the kidney function indicators, *p*-aminohippurate and inulin, during recovery from a 24-min dive were, respectively, two and approximately five times slower than those at rest (168). Similarly, cholic acid clearance by the liver was over three times faster at rest than during recovery following a natural dive that was well within the ADL (168).

VI. CONTROL OF CARDIORESPIRATORY RESPONSES

In response to forced diving, both birds and mammals display the same suite of responses: apnea, profound bradycardia, and marked increase in peripheral resistance. Similar afferent and efferent neural pathways control the circulation in forcibly submerged birds and mammals. The responses are reflex, being little altered by decerebration (2, 125) or even brain transection at the pontomedullary level (155). Nasal or other upper respiratory tract receptors initiate the cardiac responses in diving birds and mammals (125, 127, 151, 313–315), and these receptors may even play a role in dabbling ducks, such as the mallard, when predive heart rate is high, well above resting. This initial response in dabbling birds is subject to habituation (156). Collapse of the lungs or cessation of activity in central respiratory neurons may have provocative, permissive, or facilitory effects on the diving cardiovascular responses (8, 57, 125, 126, 207, 260, 396).

Both central and peripheral chemoreceptors will be stimulated by the progressively developing hypoxia and hypercapnia during apnea, and their output causes the majority of the cardiovascular response in dabbling ducks (209), whereas chemoreceptors reinforce the response in forcibly submerged birds and mammals (61, 106, 133). The nasal and chemoreceptor components can be habituated in both diving and dabbling birds (154) and, in dabbling ducks, habituation even occurs after decerebration (G. R. J. Gabbott and D. R. Jones, unpublished data). The role played by baroreceptors in the circulatory adjustments to forced submersion in ducks is disputed (356, 357, 369), but baroreceptors may be important in seals, due to an increase in gain of the baroreceptor reflex (7). These afferents and their interactions have been reviewed often, and at length (28, 45, 53, 105, 365, 369).

Changes in heart rate in anticipation of natural diving, or surfacing, in birds and mammals suggest that suprabulbar or even cortical influences may modulate the reflexogenic response. That is not to say, however, that the same mechanisms are involved in birds and mammals. A hint that the mechanisms are different may be gleaned from the fact that bradycardia can be conditioned in sea lions (337) but in birds the cardiac response has only ever been overruled, not accentuated, by habituation (154). On the other hand, heart rate is lower when birds and small mammals make "escape" dives compared with heart rates during natural dives, suggesting similar responses to arousal (151, 279).

In muskrats, there was a marked difference in bradycardia during natural (115 beats/min), escape (95 beats/min), and forced (60 beats/min) dives (279). A similar pattern of cardiac response as in the muskrat was displayed by the beaver (166, 167). Physical removal of ~50% of the cortex in muskrats eliminated any differentiation in cardiac response to the type of dive, with all heart rates being similar to those during natural dives (279). Interestingly, sham operation had no effect on heart rate during natural dives but accentuated the cardiac response to escape and forced dives. Hence, it is tempting to suggest that upper respiratory or pulmonary afferents initiate the bradycardia, which is then modulated by cortical influences. The extent of this modulation in muskrats seems quite small but, in harbor seals, the "reflex" response to submergence can be completely overruled (205). The expression of an extreme reflex-type cardiac response occurs during natural dives (6, 378, Table 4) and, in captive animals, when they are presented with unusual stimuli during submergence (141). The rapidity with which seals can switch from one level of heart rate to another led Fedak (141) to suggest that marine mammals have incorporated autonomic function into the realm of behavior. In this respect, it is interesting that Elsner et al. (139) found no anticipation of surfacing in a blindfolded ringed seal.

It seems unlikely that the reflex expression of the cardiac response is modulated by higher nervous centers in diving birds, because pronounced reflex controls on heart rate during natural submergence have never been demonstrated. [A rider should be added here, because cardiac responses to exhalation per se on submergence have never been investigated during voluntary diving (207). However, with respect to pulmonary afferents, their effect may be minimal because cardiac responses to voluntary diving are unaffected by breathing hypercapnic gases before a dive (55). In birds, pulmonary receptors are silenced by high levels of CO_2 in the airway.] Abolition of nasal receptor input by local anesthesia of the internal nares, but not the glottis, only reduced heart rate by 10–

30% during natural submergence in redhead ducks compared with untreated animals diving naturally (151). During forced dives, anesthetizing the internal nares eliminated up to 80% of the bradycardia (151).

Carotid body chemoreceptor denervation (61) or breathing hyperoxic gas mixtures before diving (55, 151) had no effect on heart rate during natural dives of normal duration in redhead and tufted ducks. However, carotid chemoreceptors were involved in the gradual development of bradycardia during extended dives by the tufted duck (Fig. 24*E*; Ref. 55). Chronic barodenervation had no effect on heart rate during natural dives of redhead ducks (152). Interestingly, however, arterial baroreceptors play the major role in the cardiac adjustments to whole body submergence in the mallard duck, trained to dive rather than to dabble for food (153). In intact ducks, heart rate was adjusted to ~250 beats/min during dives. If predive heart rate was <250 beats/min, then heart rate increased on submergence; if >250 beats/min, then heart rate fell on submergence. Cardiac adjustments to trained dives were virtually eliminated by chronic barodenervation; heart rate remained unchanged throughout the diving maneuver (153).

Many diving birds make the whole gamut of cardiac adjustments to diving (predive tachycardia followed by a rapid decline in heart rate) even when no dive is performed (414). On the other hand, the full, forced dive type bradycardia occurs in both ducks and penguins if the normal diving routine is interrupted, usually by trapping the animal underwater and preventing access to the surface (62, 151, 367). These observations, together, suggest that the initial cardiac response in ducks may be conditioned and that the full bradycardia after trapping results from dishabituation of the conditioned response. Because trapping is usually done sometime after submergence, then it is the chemoreceptor input that will dominate in this phase. Hence, denervation of chemoreceptors should greatly affect the evolution of the profound bradycardia. As was the case with both nasal and baroreceptors (152), the cardiac response to natural diving was unaffected, but subsequent reinforcement and maintenance of bradycardia during trapped and extended dives were slowed after long-standing bilateral denervation of carotid body chemoreceptors in the tufted duck (55). Therefore, the suggestion that dishabituation after trapping allows the full chemoreflex response to be played out is supported. On the other hand, this cannot be the explanation for the fact that bradycardia during extended dives attained the same level as after trapping (55). Gabbott and Jones (154) showed that intense chemoreceptor input could not be habituated during forced dives of restrained ducks, and this is probably the case during extended dives.

Cardiac responses to the first dives ever made by ducklings were similar enough to the adult response to argue against conditioning of cardiac adjustments (212). The ducklings had been on the water an average of 1.2 days before their first whole body dives. The average initial cardiac responses to beak and head submersions (performed before any dives), first-ever dives, and subsequent dives were similar to those seen in adult tufted ducks upon natural submersion (59, 367). Although it is clear that the cardiac response to natural diving is not a habituated forced dive response, as suggested by Gabbott and Jones (154), it is uncertain whether the response is ultimately conditioned on nasal receptor input, because there can be no expectation that the reflex response to submergence should be different from the conditioned response; in fact, they would be the same. Support that some form of "learning" may be involved in cardiac control during natural diving is given by recent work on elephant seal neonates and pups (78). Heart rate does not cycle up and down with breathing (sinus arrhythmia index; Fig. 36*D*) in young pups and during apnea their heart rate can be in excess of 100 beats/min (Fig. 36*B*). In contrast, in older pups, sinus arrhythmia is prominent and heart rate during apnea is considerably lower, close to the minimum seen during breathing (Fig. 36*C*). Durations of apnea increased with age (Fig. 36*A*). Obviously, tight cardiorespiratory control is crucial for long-duration apnea, and this control matures over time (78).

That the vagus is the primary efferent neural pathway for cardiac adjustments to diving in ducks was shown by Butler and Woakes (60). After pretreatment with atropine, heart rate of tufted ducks was high and did not change during escape dives. Similar observations have been made on atropinized muskrats diving on an artificial pond (273, 351) and harbor seals, diving at sea (299). A point of interest is that atropinized muskrats dive voluntarily beyond their ADL and can withstand forced submergence for over 7 min (351). This contrasts with an atropinized seal diving at sea, which succumbed in 3 min (299).

Furilla and Jones (152) speculated about the efferent neural control of heart rate responses during forced, trapped, and natural diving in ducks. They observed a strong correlation between predive (or pretrapped) heart rate and heart rate some 2–5 s after diving (or trapping) in redhead ducks and lesser scaup (*A. affinis*). The relation encompassed natural diving, forced diving in restrained ducks, and even ducks forced to dive while exercising on a treadmill (Fig. 37*B*). Furthermore, the relation also described predive-dive heart rate relations in tufted ducks (*A. fuligula*) studied by Butler and Woakes (59). Finally, the relation even applied to diving ducks when they were dabbling (Fig. 37*A*). This last observation is significant, because metabolic rate of diving ducks during dabbling must be well below that when diving, indicating that the level of exercise in ducks diving voluntarily has, per se, little influence on diving heart rate.

Furilla and Jones (152) were able to identify regions

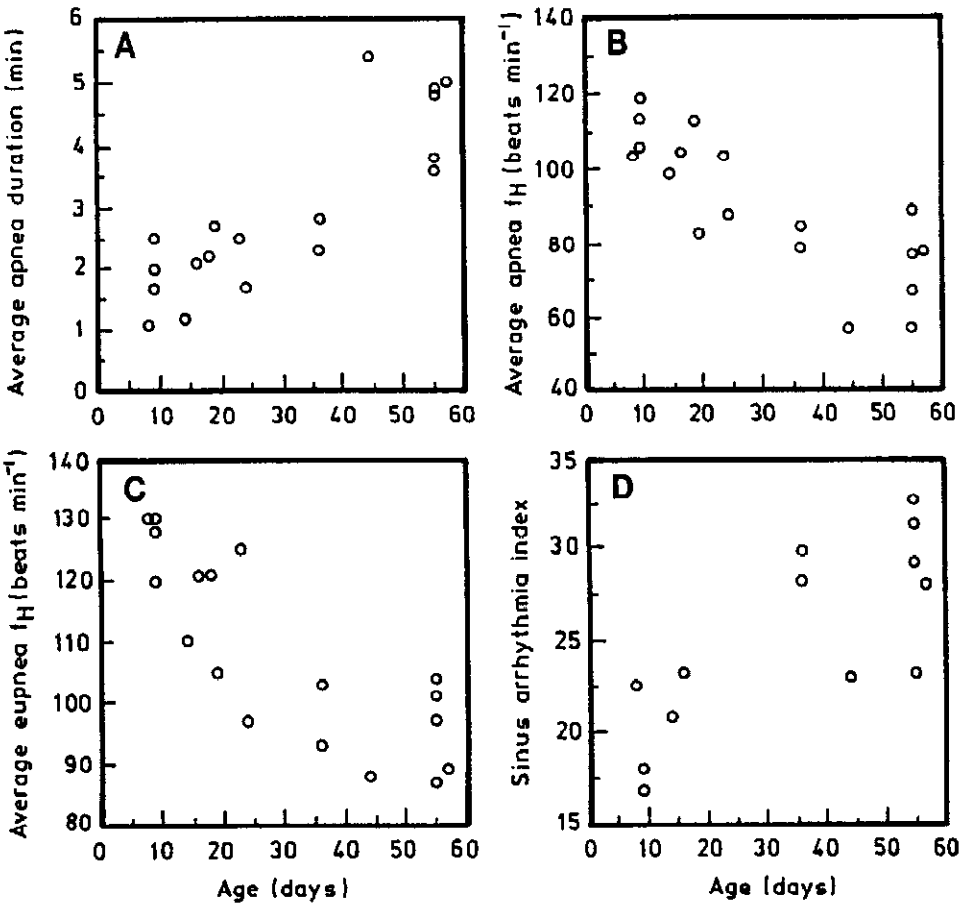


FIG. 36. Changes in apnea duration (*A*), averaged heart rates (f_H) during apnea (*B*), and eupnea (*C*) with age in northern elelphant seal pups. *D*: sinus arrythmia index, which is difference between inspiratory and expiratory heart rates. [From Castellini et al. (78).]

on a perspective plot of heart rates, resulting from vagal and cardiac sympathetic nerve stimulation in domestic ducks (*A. platyrhynchos*), which corresponded to their empirically established predive-dive heart rate relation (Fig. 38). In essence, Furilla and Jones (152) argue that, regardless of the level of cardiac sympathetic excitation, all diving (or trapping) is accompanied by an increase in vagal activity to the heart of some 50% of the maximum possible activation (Fig. 38).

For example, in the first dive of a series, heart rate increases from the resting rate (100–120 beats/min; Fig. 38, *point C*) to 275 beats/min (Fig. 38, *point B*). This increase is rapid, unaffected by β-adrenoceptor blockade, and must be due to withdrawal of parasympathetic nerve activity (152). When a duck dives naturally, heart rate falls to 100 beats/min, representing an increase in vagal activity of some 50%. At the end of a voluntary diving bout, predive heart rate, due to increased sypathetic outflow to the heart, will be 500 beats/min (Fig. 38, *point A*) and during dives, heart rate will fall between 200 and 250 beats/min (Fig. 38, *point F*), representing an increase in vagal activity of 50% of maximum. If this animal is prevented from resurfacing, heart rate will fall from 250 to 100 beats/min (Fig. 38, *point E*), and vagal activity will now be maximal. On the other hand, if the bird is prevented from surfacing after the first dive of a bout, the heart rate will fall from 100 beats/min (Fig. 38, *point C*) to 20 beats/min (Fig. 38, *point D*), and vagal activation will again be maximal. Other predive-dive heart rates can also be recognized on Figure 38. In the laboratory, predive heart rate is low (~100 beats/min) and is unaffected by β-adrenoceptor blockade, so the vagal-sympathetic interplay producing this point must be at *point C* (Fig. 38). Hence, a 50% increase in vagal activity will give a rate of 20 beats/min (Fig. 38, *point D*), which is common during laboratory dives. Finally, predive heart rate in β-adrenoceptor-blocked ducks diving voluntarily never exceeds 300 beats/min and is described by *point B* (Fig. 38). During dives, heart rate in β-adrenoceptor-blocked ducks falls to 100 beats/min (Fig. 38, *point C*) which, again, represents an increase in vagal activation of 50% of maximum.

There is little information about the role of the sympathetic nervous system in regulating circulatory responses to free diving. β-Adrenoceptor blockade in ducks prevents the interdive heart rate from going over 300 beats/min during a diving bout (152). Normally, interdive heart rate will approach 500 beats/min toward the end of a bout (59), and this increase in heart rate, therefore, must be sympathetically driven. However, the increase in heart rate, from rest to 300 beats/min, before the first dive of a

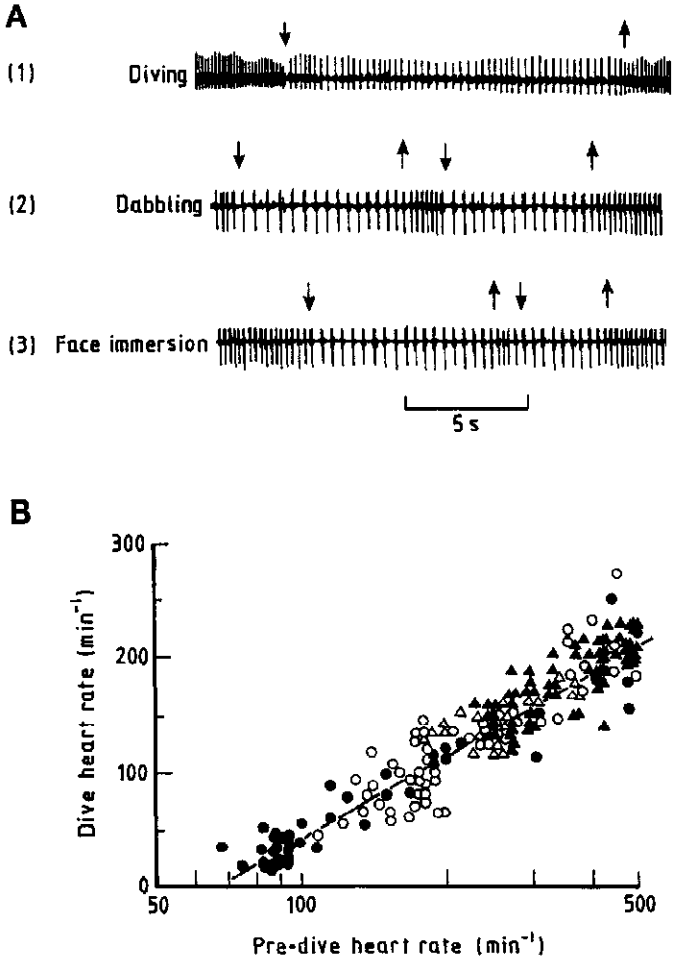


FIG. 37. *A*: electrocardiogram traces from a redhead duck diving voluntarily (*1*), dabbling (*2*), and immersing its head into a beaker of water to retrieve food (*3*). Downward arrows are approximate points of submergence, and upward arrows are points at which duck surfaced. *B*: relationship between dive (or trapped) heart rate and logarithm of predive (or pretrap) heart rate for all dives. ●, Restrained dives including those after exercise; ○, trapped dives; ▲, natural dives including β-adrenoreceptor blocked dives. [From Furilla and Jones (152). Copyright is held by Company of Biologists Ltd.]

bout is probably due entirely to vagal withdrawal. The initial increase in heart rate is associated with a period of hyperventilation, but whether hyperventilation is the causal factor is unknown. The increase in interdive heart rate during a bout (~200 beats/min) is somewhat greater than the increase in diving heart rate (~120–150 beats/min; Fig. 38), suggesting that a 50% of maximal increase in vagal activation on submersion is not effective in overruling the increased sympathetic activation of the heart in a bout of diving.

This interplay between the two branches of the autonomic nervous system in modulating diving bradycardia has been investigated in naturally and forced diving muskrats in some detail. Signore and Jones (351) propose that an accentuated antagonism occurs between the two branches of the autonomic nervous system during diving (255). Intense vagal activity during diving blocks sympathetic inputs to the heart, despite the persistence of sympathetic tone, so complete pharmacological sympathetic blockade will not result in a significant decrease in heart rate. This means that the parasympathetic system takes over cardiac control during diving and that sympathetic input to the heart is ineffective while the animal is underwater. In fact, this would be a very effective way of rapidly suppressing sympathetic influences, because a response to changes in sympathetic activation occurs much more slowly than to changes due to parasympathetic activity (1, 152, 200). A cholinergically mediated reduction of the response of cardiac cells to adrenergic stimulation during diving may also explain why forced-dive harbor seals develop a diving bradycardia, despite a large increase in circulating epinephrine and norepinephrine levels (171). Also, mallard ducks forced to dive for several minutes display the most remarkable increase in circulating catecholamine levels known, yet diving heart rate remains low (237, 238, 239). During forced dives, vagal output is assumed to be maximal and is obviously able completely to overrule β-adrenergic activation.

Interestingly, in the naturally diving muskrat, β-adrenoceptor blockade with nadolol has no effect on diving heart rate, whereas bradycardia is reduced by propranolol

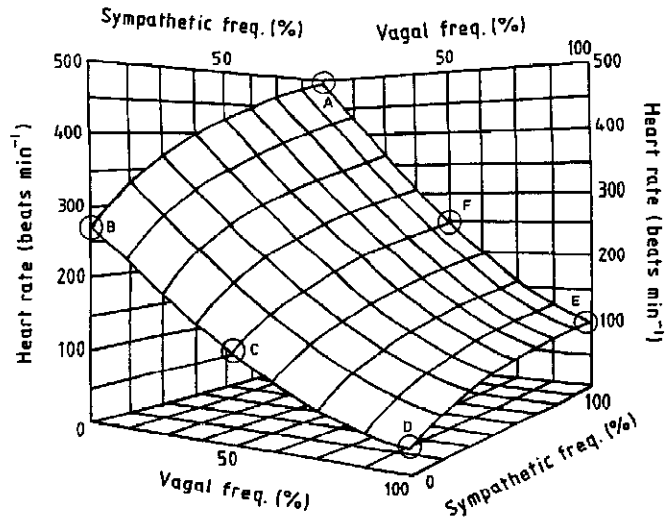


FIG. 38. Relationship of heart rate to bilateral stimulation of distal cut ends of vagus and cardiac sympathetic nerves of Pekin duck (*A. platyrhynchos*); 100% represents frequency of stimulation above which no further changes in heart rate occurred. Heart rate resulting from a given level of vagal and sympathetic stimulation was plotted on "perspective" graph paper and surface was drawn, by eye, to encompass all heart rates obtained in stimulation experiments. *Point B* represents complete cardiac denervation, and *point E* represents maximal vagosympathetic stimulation. Effects of sympathetic stimulation at minimal and maximal vagal activity are represented by *lines A–B* and *D–E*, respectively. Similarly, effect of vagal stimulation at minimal and maximal sympathetic activity are represented by *lines B–D* and *A–E*, respectively. See text for an explanation of *points A–F* relative to diving. [From Furilla and Jones (152). Copyright is held by Company of Biologists Ltd.]

treatment. Propranolol, unlike nadolol, crosses the blood-brain barrier, which suggests that diving bradycardia may be partially regulated by a central catecholaminergic pathway (351). This serendipitous observation gives insight into the pharmacological basis of natural diving bradycardia and complements studies on forced-dived muskrats and rats which have shown the importance of excitatory amino acids as transmitters in early parts of the trigeminal neural circuit (280, 316).

In muskrats, diving bradycardia is also unaffected by α-adrenoceptor blockade with phentolamine (351). This suggests that the cardiac response to submergence is independent of peripheral vasoconstriction. Dissociation of bradycardia and arterial constriction was previously shown in the seal forced to dive (296). Even in the absence of vasoconstriction, muskrats may submerge voluntarily for over a minute in excess of the calculated ADL (270), but underwater survival of forced dived, unrestrained muskrats is reduced to 5 min. Underwater survival time of forcibly submerged animals is not further reduced by treatment with a combination of phentolamine and atropine (351).

Circulatory catecholamines have been measured in Weddell seals on return from natural dives (188). After short dives that are <5 min, there was no increase in epinephrine or norepinephrine during the postdive period. However, after dives longer than this, epinephrine and norepinephrine increased in direct proportion to dive time, reaching levels at least two- or threefold above resting levels after dives longer than 15 min. Interestingly, these increases were in the same range as those from seals forced to dive for up to 15 min (424). The forced-dive measurements were made near the end of the dive and not postdive as with the observations from naturally diving seals. If circulating catecholamines really do increase during diving and not just during the postdive period, then it is possible that they could contribute to circulatory adjustments (including contraction of the spleen; see sect. IV*B*) during submergence. Catecholamines remained elevated for a prolonged period in Weddell seals during recovery (188).

During voluntary diving, heart rate starts to increase in anticipation of surfacing. In larger diving birds and mammals (emperor penguins, Ref. 232; seals, Refs. 4, 378), heart rate may reach predive rates before surfacing, although in smaller species (ducks, Ref. 367; muskrats, Ref. 351) heart rate seldom exceeds resting rates in the immediate period before surfacing and is well below predive rates. Obviously, efferent vagal parasympathetic activity must decline during this period, but how this decline is brought about is speculative. A blindfolded ringed seal showed no increase in heart rate when approaching a hole in the ice cover of a lake, which suggests that suprabulbar influences may be involved (139). If circulating catecholamines increase during the dive, then vagal activity need not be reduced to predive levels, even though heart rate may be approaching predive rates. The accentuated antagonism between the parasympathetic and sympathetic branches of the autonomic nervous system will be reduced by a fall in vagal parasympathetic activity, allowing the cardiac chronotropic response to adrenergic stimulation to be expressed (352).

Breathing rates are high during the postdive period and in elephant seals, for example, appear to approach maximum rates (Andrews et al., unpublished data). Central neural interactions between respiratory and circulatory neurons, as well as afferent neural input from lung receptors, cause heart rate to wax and wane with each breathing cycle. When breathing is slow, these oscillations in heart rate are particularly obvious. Even so, the highest heart rates reached on inhalation are generally below those attained in the interval between dives, when heart rates may approach the maximum rate for the species. In elephant seals, heart rate was almost twice as high at sea, in the interdive periods, than during eupnea on land (5, 70). An increase in sympathetic influence on the heart, either neurally or humorally, accentuates the increase in heart rate in the immediate postdive period initially set in train by a decline or cessation of vagal parasympathetic activity (351, 352). Restoration of normal blood gas values may make a contribution to the elevation in heart rate because in ducks, postdive heart rate was usually higher after carotid body denervation (55). Also, postdive tachycardia was significantly reduced, compared with animals surfacing into air, when ducks breathed a hypercapnic gas mixture after surfacing, whether or not ducks had innervated carotid bodies (55). Because lung receptors in birds are silenced by high levels of carbon dioxide in the airway, their input ensures full expression of postdive tachycardia. Nevertheless, the major contributor to postdive tachycardia remains to be demonstrated, since postdive heart rates were around twice the diving rate even in ducks with intact carotid bodies breathing hypercapnic gases (55).

Control of breathing before and after diving has received scant attention in freely diving animals compared with studies on forced-dived birds and mammals (53, 365, 369). Diving ducks and Weddell seals hyperventilate before submergence. In Weddell seals, Pa_{O_2} increases and Pa_{CO_2} decreases, which has led to the suggestion that Weddell seals have two settings to their respiratory controller (227). The Pa_{O_2} value is lower and the Pa_{CO_2} value higher in resting seals. How the settings are changed just before diving is unknown. In this respect, it could be argued that predive hyperventilation is part of a "feed-forward" or "central command" component of respiratory control (128).

All diving birds and mammals are sensitive to low oxygen and high CO_2 in terms of their respiratory responses (53, 377). The sensitivity ($l \cdot min^{-1} \cdot kPa^{-1}$) of the

ventilatory responses to CO_2 in diving birds and mammals is similar to that in terrestrial species, although the threshold for the response may be raised (32, 56, 94, 159, 289, 317). The response to oxygen lack may be "blunted" in adult seals (317, 318), although newborn gray seals have a brisk hypoxic response, indicating that any blunting of the ventilatory response occurs postnatally (290).

Hence, at the end of a dive, hyperventilation is driven by the low Pa_{O_2} and high Pa_{CO_2} of the blood. However, in Weddell seals, hyperventilation is related to the length of the previous dive and, after an extended dive, may persist for 70 min, yet Pa_{O_2} and Pa_{CO_2} are usually above and below predive levels, respectively, after only 5 min of breathing (235, 331). Consequently, the prolonged phase of hyperventilation is driven not by O_2 or CO_2 but by the change in acid-base status of the blood consequent upon the release of lactate into the blood (227, 235, 331). A similar situation holds during recovery from long forced dives of domestic ducks (M. Shimizu and D. R. Jones, unpublished data).

Single-breath breathers (159) and even Weddell seals on occasion (73) reduce succeeding dive times when recovering from an extended dive. Therefore, control of apnea and control of dive time can be viewed in the same context. Apneas can result from reflexogenic contributions from upper airway receptors (10) or cessation of activity in central respiratory neurons (76), but motivation must also be a powerful factor in determining the length of the breath-hold in diving animals, as it is in voluntarily diving humans (258). In fact, data from animals forced to dive suggest that all three factors make important contributions, because the lungs of diving animals that have died during submergence often do not contain water.

Considerable behavioral evidence suggests that central and peripheral chemoreceptors are important in controlling the length of the breath-hold. Breathing hypoxic or hyperoxic gas mixtures before natural diving shortened and lengthened the normal dive time, respectively, in redhead ducks (151). Breathing hyperoxic gas caused Weddell seals to make unusually long dives, one for 87 min (226). However, hypoxic gas mixtures, down to a Po_2 of 5.3 kPa, did not affect the diving patterns of Weddell seals nor did it significantly reduce dive time, although dive times for these animals, even after breathing air, were unusually short (317). Both male and female harbor seals markedly reduced dive time when inspired Po_2 was <13.3 kPa, refusing to dive when inspired Po_2 fell below 8 kPa (94). Similarly, hypoxic hooded seals also reduced dive time (318).

Even in the manatee, which seems exceptionally insensitive to hypoxia, there is an association between breathing hypoxic gases before diving and dive time (162). The manatee, however, is unusual among mammalian divers in that partial pressures of alveolar CO_2 at end dive are much higher than those in phocids diving for the same length of time (162). In fact, in Gallivan's (159) earlier study, there was no doubt that hypercapnia had more significant effects in reducing dive time than hypoxia. This is similar to the situation in the tufted duck in which hypercapnia reduced dive time much more than hypoxia (55). Interestingly, breathing hyperoxic gas mixtures did not affect dive time at all in manatees (159) or tufted ducks (55) and actually shortened dive time in phocids (318). In phocids, hypercapnia also shortened dive duration, and CO_2 retention could explain the shortened dive time after breathing hyperoxic gases (319).

In tufted ducks, denervation of carotid body chemoreceptors significantly increased natural dive time (61). Furthermore, in intact ducks, virtually the whole of the reduction in dive time caused by breathing hypoxic gas before diving can be attributed to stimulation of carotid body chemoreceptors (55). Looked at in this light, the fact that Weddell seals are claimed to anticipate the duration of a dive and adjust heart rate accordingly (219) may only be a reflection of a lowered rate of blood oxygen utilization when heart rate is low; that is, the seal adjusts dive duration corresponding to heart rate, and rate of fall in Pa_{O_2}, established early in the dive (205). The obvious complex behavioral components associated with surfacing to breathe led Fedak and Thompson (143) to warn that it is unrealistic to expect a single variable alone to terminate breath-holding.

Of course, both behavioral and physiological factors can modify the integration of reflex mechanisms, a most obvious one is sleep. Many diving mammals display both slow-wave sleep (SWS) and rapid-eye-movement (REM) sleep when on land and in water (76, 294, 339). However, the periods of REM sleep are usually reduced when in water (76, 293) and, at the extreme, to the extent that REM sleep has never been observed in gray seals and bottlenosed dolphins in water (293, 339). In terrestrial mammals, change in heart and breathing periodicities are associated with sleep state. In REM sleep, breathing is irregular in harp seal pups (267), is regular in gray seals (339), and does not occur at all in elephant seal pups (76, 287). Elephant seal pups, submerged in shallow water, surface to breathe while sleeping (76). On the other hand, Caspian seals (*P. caspica*) arouse to surface and breathe (292). The northern fur seal sleeps with its nostrils above the water surface but with only one brain hemisphere at a time showing SWS (292). Unihemispheric sleep also occurs in the cape fur seal (*Arctocephalus pusillus*) (266) and, par excellence, in the bottlenosed dolphin (292). Slow-wave sleep can occur in one hemisphere for over 2 h. According to Mukhametov and coworkers (292, 293, 310), unihemispheric SWS and the lack of REM are adaptations that allow the dolphin to swim continuously and to breathe.

VII. CONCLUDING COMMENTS

For thousands of years, the recorded and pictorial histories of widespread civilizations and cultures have at-

tested to the remarkable feats of those animals that extend their territory to environments which appear to be totally hostile. In life, these animals are largely hidden from scrutiny, and early art, myth, and ceremony attempted to portray the invisible aspects of their behavior. Consequently, the large diving vertebrates, being so well adapted to the aquatic environment as to be almost unseen, have frequently been invested with supernatural powers. Early scientific endeavor, in the form of observation and analysis of visible behavior, merely empowered the hunter-gatherers who literally followed the animals' life cycle. Determined, empirically based scientific enquiry over the last 100 years, although narrow and focused, has not abated the fascination and allure of diving vertebrates, whereas overexploitation and greed have added rarity and the need for conservation to our consciousness. The need for continuing innovation and effort, both technically and financially, to reveal the mysteries of diving birds and mammals is obvious. The path forward is ill-defined but veers toward concerted field studies of the type pioneered by Kooyman and Zapol and their many co-workers. The role of all the wonderful reflexes, uncovered in laboratory studies over the past 60 years, in contributing to the success and survival of diving birds and mammals in nature remains obscure.

By incorporating in this review data on the behavior of aquatic birds and mammals when free ranging in their natural environment, it is evident that it is not only the extent of their physiological and biochemical capabilities that determine their diving behavior. The behavior of their prey and the physical characteristics of their environment (e.g., depth of the water column) are also important. Equally, it is clear from the behavior of some animals (e.g., female elephant seals) that we have insufficient knowledge of their physiological and biochemical adjustments to enable us to explain fully how they are able to perform such behavior.

Recent developments in technology have provided much detailed information on the behavior and ecology of these fascinating and important animals. Not surprisingly, the advances in technology have been insufficient to enable physiologists to obtain anything like as much detail on the metabolic rate and physiological adjustments that occur during the time that the animals are submerged underwater. This has led to much speculation and calculations based on many assumptions to explain the observed behavior. As indicated in section I, the total usable body oxygen stores and the rate at which they are used are the basic aspects of any explanation. Together, these have been used by many authors to calculate what Kooyman et al. (220) defined as the ADL based on the measurements of lactate concentration in the blood of Weddell seals upon surfacing at the end of a dive. However, the calculated versions are not the same as the original values obtained by Kooyman and co-workers (235, 220) for Weddell seals. The vagaries of calculating ADL have already been discussed, but one of the fundamental differences between calculated ADLs and experimental ADLs based on the measurement of blood lactate concentration is that, for the former, the assumption is made that all of the usable oxygen is exhausted, whereas this cannot be the case in the latter situation. Weddell seals are able to remain submerged for periods two to three times the duration of their experimental ADL, which would not be possible if they had used all of the oxygen available to them at ADL.

We suggest, therefore, that the dive duration up to which there is no increase in postdive blood lactate concentration is renamed the diving lactate threshold (DLT) and that ADL determined by a calculation of total usable oxygen stores (plus PCr stores?) and rate of oxygen (ATP?) utilization is called calculated ADL (cADL). This may lead to some confusion at first but, because these terms more accurately reflect the differences between the two values, it is hoped that they will add some clarity to what has become a somewhat confusing situation. One important point to note is that, if the estimates of total usable oxygen stores and rate of oxygen utilization during a dive are correct, cADL should be greater than DLT for any particular species.

Despite these criticisms, cADLs have provided useful insights into the degree of adaptations of various species of aquatic birds and mammals to their submerged existence. It would appear that many of these are able to metabolize aerobically when diving at approximately the same (if not greater) rate as when they are at the surface, e.g., ducks, smaller penguins, fur seals, and Weddell seals. In other words, their enhanced oxygen stores are able to support aerobic metabolism at what would not be considered to be unusually low levels for the duration of the dives. There are probably circulatory readjustments to ensure that the oxygen stores are managed judiciously, and it has to be said, we are not too clear what the details of these readjustments might be. On the other hand, some species, such as the larger penguins, South Georgian shag, and female elephant seals, exceed their cADL by such a large extent that the general consensus is they must either be reducing their aerobic metabolic rate when diving (cf. Ref. 36) and/or producing ATP, at least partly, by anaerobiosis and metabolizing the lactic acid when at the surface (although this is hardly likely in the case of the female elephant seals).

An indication that these animals do indeed reduce aerobic metabolism when diving is the recent evidence from data loggers that, in at least some parts of the body, there is a reduction in temperature. Whether this is the cause of or the result of a reduction in metabolism remains to be seen, but it indicates the need for many more physiological data from these animals in their natural environment. We do not begin to understand the subtleties

of the cardiovascular adjustments in these animals associated with feeding, digestion, thermoregulation, locomotion, etc., while underwater, let alone how they are controlled. The unusually low drag coefficients determined in penguins and cetaceans and the discovery that elephant seals and dolphins may glide for a substantial proportion of the descent part of their dives are other explanations for the lower than expected metabolic rates postulated for some aquatic birds and mammals during diving.

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