

## CARDIAC RESPONSES OF GREY SEALS DURING DIVING AT SEA

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### Summary

Heart rate, swimming speed and diving depth data were collected from free-ranging grey seals, *Halichoerus grypus*, as they foraged and travelled in the sea around the Hebrides Islands off western Scotland. Information was collected on a tracking yacht using a combination of sonic and radio telemetry. Diving heart rate declined as a function of dive duration. In long dives, grey seals employed extreme bradycardia, with heart rates falling to  $4\text{beatsmin}^{-1}$  for extended periods, despite the animal being free to breathe at will. This extreme dive response is part of the normal foraging behaviour. Seals spent 89% of the time submerged during bouts of long dives; swimming was restricted to ascent and descent. Dive durations exceeded estimated aerobic dive limit, even assuming resting metabolic rates. These results indicate that behavioural, and possibly cellular, energy-sparing mechanisms play an important role in diving behaviour of grey seals. This has implications not only for studies of mammalian energetics but also for our understanding of the foraging tactics and prey selection of marine mammals. If some seals are using energy-sparing mechanisms to reduce metabolic costs while at depth, they may be forced to wait for and ambush prey rather than to search for and chase it.

### Introduction

Forcing a seal under water elicits a set of dramatic defensive responses including extreme bradycardia and extensive vasoconstriction (Scholander, 1940; Irving, 1934, 1964; Butler and Jones, 1982; Elsner and Gooden, 1983; Blix and Folkow, 1983). Selective vasoconstriction increases peripheral resistance to blood flow, maintaining blood pressure and blood flow to the brain and cardiac muscle, even when heart rates fall as low as  $10\text{beatsmin}^{-1}$ . In forced submersions, extreme bradycardia is generally associated with high post-surfacing blood lactate levels and an extended recovery period at the surface (Scholander *et al.* 1942; Murphy *et al.* 1980). This suggests that unperfused skeletal muscle and organs deplete their *in situ*  $\text{O}_2$  stores and use anaerobic metabolism (Scholander, 1940). These extreme responses, often referred to as the classical dive response, have until now been seen only in laboratory studies of forced submersion or when access to the surface is restricted. In the wild, it has only been observed in freely

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swimming seals diving under ice (Kooyman and Campbell, 1973; Elsner *et al.* 1989) or when seals were subjected to conditions of stress, such as underwater fights, or when frightened (Fedak *et al.* 1988).

In laboratory studies where seals have been allowed to dive voluntarily with access to a free water surface, a less dramatic version of the forced dive response has been observed (Pasche and Krog, 1980; Fedak, 1986). In this situation, dives are generally short and well within estimates of the animals' aerobic dive capabilities. These observations led to the suggestion that the extreme dive response is primarily an emergency measure, enabling seals to withstand extended and/or unplanned submergence (Kanwisher *et al.* 1981). In the wild, such extreme responses have most often been observed in Weddell seals (*Leptonychotes weddelli*) during occasional long exploratory dives under ice (Kooyman *et al.* 1980; Kooyman and Campbell, 1973). These long dives are often followed by an extended period at the surface and are always followed by a post-surfacing surge in blood lactate levels.

The post-dive surge in blood lactate level is taken as indicating that the animal has exceeded its aerobic dive limit (ADL). ADL can be defined as the maximum dive duration for which there is no net production of lactate (Kooyman *et al.* 1983; Kooyman, 1989). This implies that, for dives shorter than the ADL, a seal has sufficient oxygen reserves to accommodate the total ATP demand through aerobic pathways. If any tissues become anoxic, their anaerobic byproducts must have been taken up by aerobic pathways or reconverted through gluconeogenesis.

Long times spent in recovery at the surface may not be desirable in marine predators, which presumably try to maximize the time spent at depth catching prey. Indeed, records from several species show that the great majority of dives in the wild are short and aerobic (Kooyman *et al.* 1980; Fedak *et al.* 1988). Recent dramatic records from elephant seals (*Mirounga leonina*, *M. angustirostris*) (Hindell *et al.* 1991, 1992; Le Boeuf *et al.* 1988, 1989) seem to conflict with this picture. These seals sometimes seem to dive beyond their estimated ADL continuously for long periods, whilst maintaining very short inter-dive breathing intervals and high percentage dive times (Hindell *et al.* 1991). Clearly, either the estimates of their oxygen stores or of their metabolic rates must be wrong.

Two questions arise from these observations. (1) What, if any, is the role of the extreme dive response in nature (Blix, 1987); is it simply a protection against life-threatening anoxia or restricted breathing or is it a regular component of diving activity under a free water surface? (2) How can seals apparently regularly exceed their ADL and yet spend over 90% of their time submerged over periods of weeks?

Data are presented on heart rates, swimming speed and diving behaviour collected from free-ranging grey seals (*Halichoerus grypus*, Fabricus) exhibiting a wide range of behaviour while at sea. These data have allowed us to examine the cardiac response to diving in relation to the behavioural variables of swimming speed and dive depth.

### Materials and methods

We monitored heart rate ( $f_H$ ), diving depth and swimming speed in free-ranging grey seals as they rested, travelled and foraged in the sea around western Scotland during the

summer of 1989. Seals were caught in tangle nets and immobilised with Zoletil ( $1.0\text{mgkg}^{-1}$  i.v.) (Baker *et al.* 1990). VHF radio (173MHz) and ultrasonic acoustic transmitters (65–90kHz) were glued to the fur of three seals (estimated mass 210, 150 and 110kg) using a fast-setting epoxy glue (Fedak *et al.* 1983). After 0.5–1h the seals were allowed to return to the water and swim away. The radio transmitter (Mariner Radar Ltd, Lowestoft, UK) was used to locate the seals at a distance and to verify surfacing. Acoustic transmitters sent heart rate (ECG) (SINTEF, Trondheim, Norway), depth and speed data (VEMCO Ltd, Halifax, Nova Scotia). Depth and swim speed transmitters incorporated a pressure transducer and paddle-wheel flow meter. Data were encoded in a train of acoustic pulses which provided updates of these variables every 4s. ECG information was obtained from skin surface-mounted electrodes (2cm copper discs) glued over small shaved patches of skin dorsal and ventral to the heart (Fedak *et al.* 1988). The ECG signal was sent as a frequency-modulated tone. The analogue nature of the heart-beat signal precluded misinterpretation of electromyogram (EMG) or motion artefacts and continuous reception of the carrier signal ensured inclusion of all heart beats.

Pressure transducers were calibrated in a purpose-built pressure vessel during manufacture of the depth and velocity tags. Pressure readings were accurate to within 5% of full-scale depth. Velocity sensors were calibrated in the field as follows: transmitters were fixed to a  $10\text{cm}\times 20\text{cm}$  metal plate, mounted 50cm below a 1m long floating plastic sled, and were towed through the water at speeds between 0.3 and  $3.0\text{ms}^{-1}$ . Speed was calculated by timing the arrival of 5m distance markers on the non-stretch towing line. The paddle-wheels stalled at speeds below  $0.3\text{--}0.5\text{ms}^{-1}$ . The relationship between speed and pulse interval was fitted by least-squares regressions.

Seals were tracked at sea from a 45 foot ocean-going yacht. Signals from VHF transmitters (173MHz) were processed by a purpose-built automatic direction finder which gave both direction to the animals and signal strength information. Times of VHF receptions were automatically recorded on computer disk. Three directional hydrophones, mounted at  $30^\circ$  to each other on the keel (giving an overall  $150^\circ$  'view') collected acoustic signals and were used for close-range tracking. Data could be recorded up to 1km away from the seal. Depth/velocity data were decoded and stored on computer disk. ECG signals were stored on tape and were later manually decoded and logged using a portable personal computer as an event recorder.

## Results

### *Dive behaviour*

Three seals were successfully followed as they moved in the seas around the western isles of Scotland. Swimming speed, dive depth and heart rate data were obtained from all three animals as they moved between distant haulout areas and during foraging trips. Fig. 1A shows data from a representative 5h period of travelling by the 150kg adult female S1. Seals always remained motionless while breathing at the surface even when travelling from place to place. No swimming speeds above the stall speed of the tag were

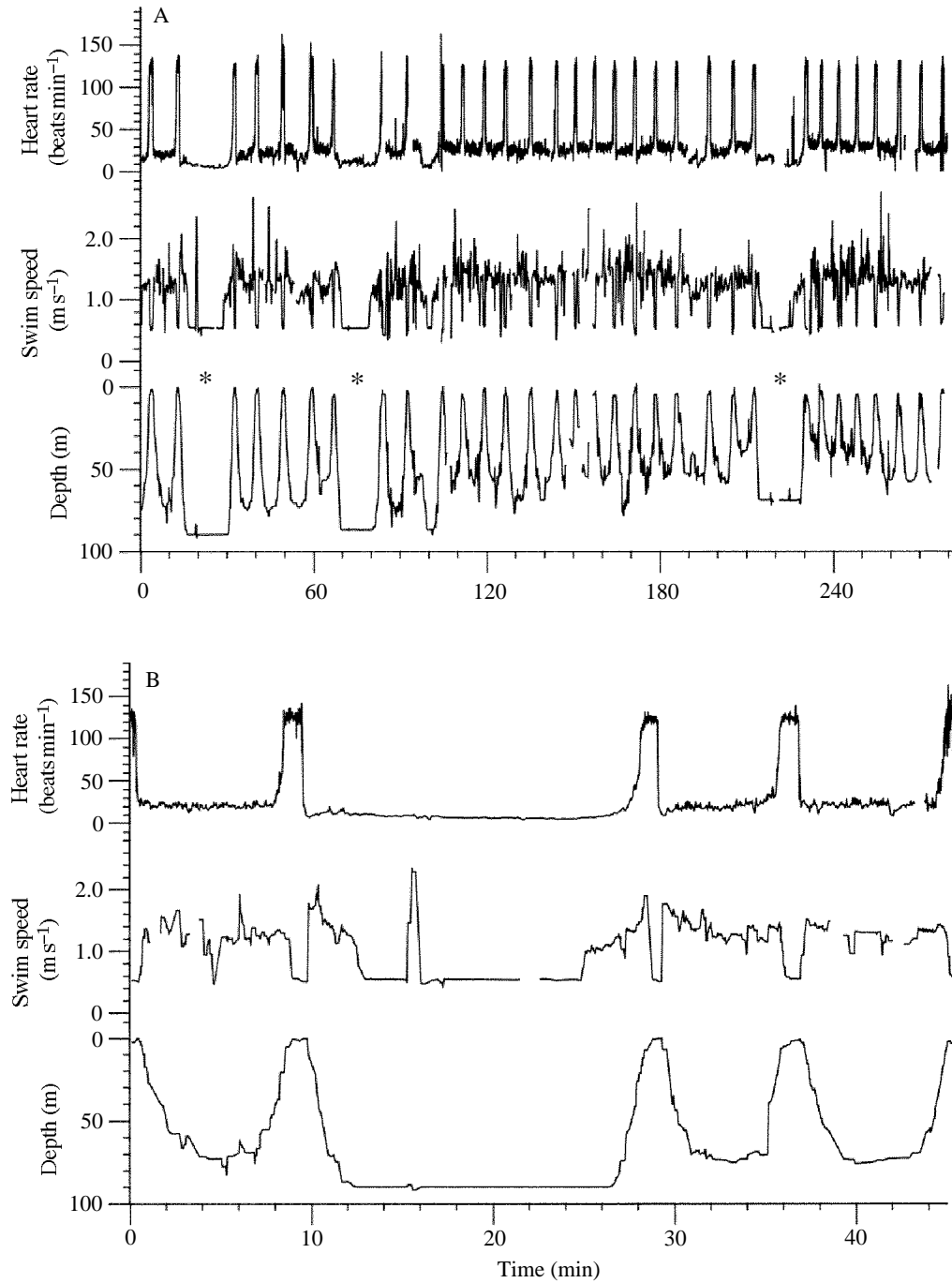


Fig. 1. Typical traces of heart rate (top), swimming speed (centre) and dive depth (bottom) obtained from grey seals. Data from a 150kg female as she swam between haulout sites in the Inner Hebrides, off western Scotland. The seal swam to depths near the bottom at the midpoint of each dive. At points marked with an asterisk the animal paused in her travels. (B) Detail of the first four dives in A.

recorded from surfaced seals (Fig. 1B). Seals were observed on several hundred surfacings at sea, but were never seen actively swimming at the surface. However, seals sometimes swam slowly at the surface when inspecting haulout sites.

While submerged, seals usually swam over a narrow range of speeds ( $1\text{--}2\text{ ms}^{-1}$ ). Patterns of diving were very similar to those observed in grey seals in previous studies, allowing behaviour to be classified on the basis of dive profiles as travelling, foraging or resting (Thompson *et al.* 1991). When travelling, the seals displayed a V- or U-shaped dive profile, swimming continuously throughout the submergence. When apparently foraging, the animals dived directly to near the bottom and then usually remained motionless or possibly swam only very slowly at speeds below the stall speed of the transmitter,  $0.5\text{ ms}^{-1}$ .

Surface periods were generally short ( $0.77\pm 0.41\text{ min}$ , mean  $\pm$  s.d.,  $N=314$ ). Surface duration increased with duration of the previous dive for short dives, but not for dives of over 7 min (Fig. 2).

#### Heart rates

While the animals were stationary at the surface, heart rates were high ( $119\pm 8.9\text{ beats min}^{-1}$ ,  $N=314$ ) and rhythmic. The surface heart rate was related to the size of the animal. The largest (S3, an adult male) had a surface heart rate 17% lower than the smallest (a female, S2). Surface  $f_H$  did not vary with duration at the surface, i.e. the number of heart beats was a linear function of time spent at the surface (Fig. 3).

Heart rate fell by a factor of three or more immediately as the seals dived and started to swim. Bradycardia was maintained throughout the dive, irrespective of the velocity profile. A pre-surfacing 'anticipatory' tachycardia was present in all dives;  $f_H$  began to

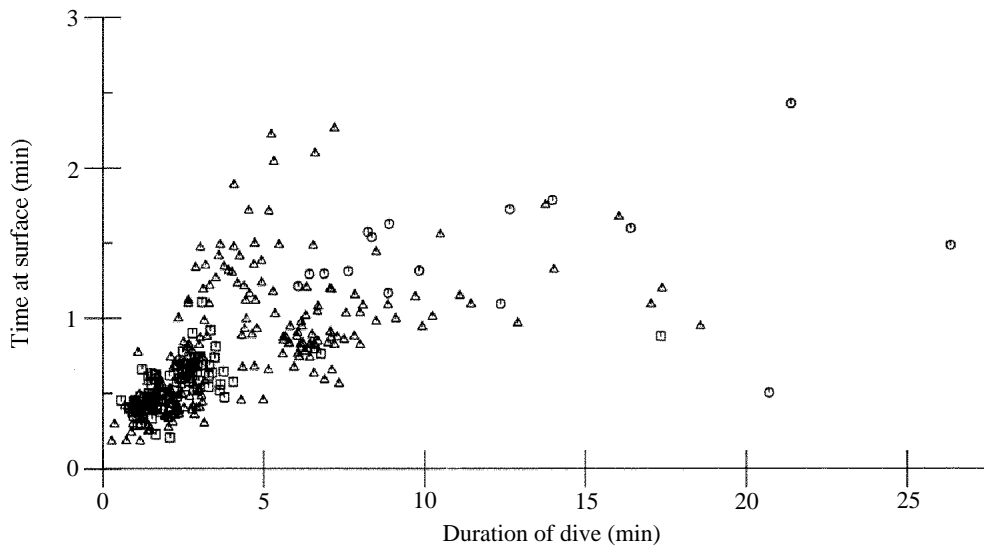


Fig. 2. Duration of surface breathing periods plotted against duration of the preceding dive. Data from three grey seals during foraging and travelling dives. Surface duration increases with dive duration for dives of up to about 7 min, but levels out for longer dive durations.

increase up to 1min prior to surfacing. During foraging dives where the seals were stationary at depth, the increase in  $f_H$  began after the animal started to swim for the surface.

The intensity of bradycardia increased as a function of dive duration (Fig. 4). This is due, in part, to the inclusion of a pre-surfacing tachycardia of fixed length in dives of varying duration. However, this has only a minor effect and does not fully account for the shape of the curve. A corollary of this heart rate curve is that the number of heart beats in a dive increases as a function of dive duration only for short dives. The number of beats reaches a maximum in dives of 7min and then remains constant irrespective of duration (Fig. 5). In all three seals the number of beats in a dive levels out at about 220.

The lowest heart rates were observed in long dives. Fig. 6 shows two foraging dives made by the 210kg adult male (S3) diving to the bottom at depths of 70–80m. In most long dives (as in Fig. 6A),  $f_H$  was arrhythmic, with long pauses between beats, followed by two or more beats in quick succession. Even here, the average rate is typical of that encountered in forced dives in the laboratory. During one dive (Fig. 6B),  $f_H$  fell to  $2\text{beatsmin}^{-1}$ , and remained below  $4\text{beatsmin}^{-1}$  for most of the dive, until the pre-surfacing tachycardia. Pauses between beats of up to 32s were recorded in some dives.

As in previous field studies of phocid diving behaviour, most dives were short and probably aerobic (Fig. 7), but a significant number of dives (6%) lasted longer than

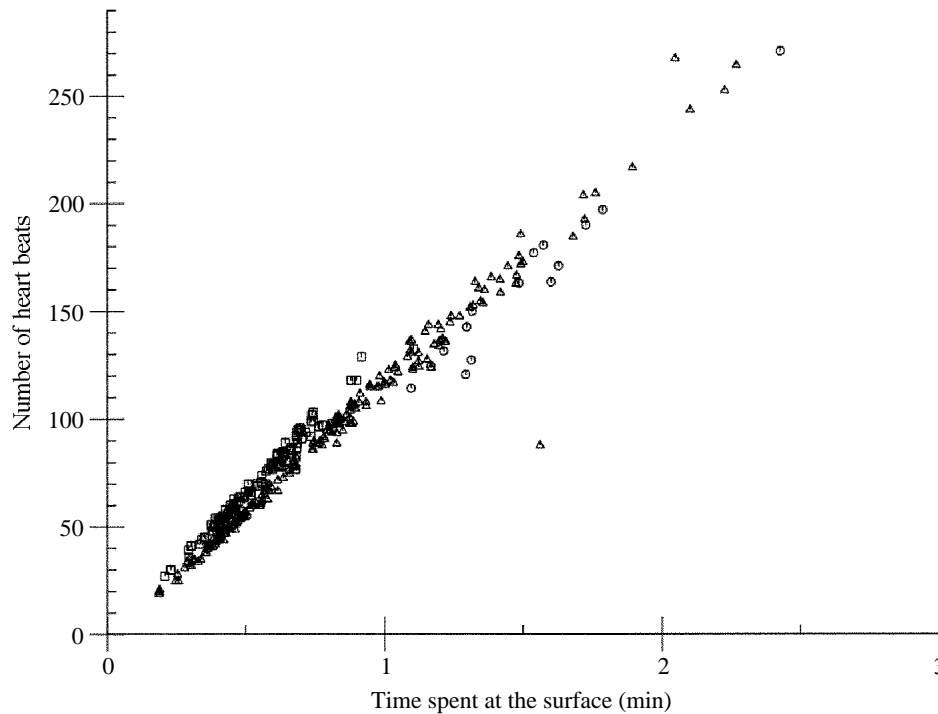


Fig. 3. Number of heart beats during surface breathing periods plotted against the time spent at the surface. Data from three grey seals,  $N=314$  dives. The surface heart rate is constant with respect to time spent at the surface.

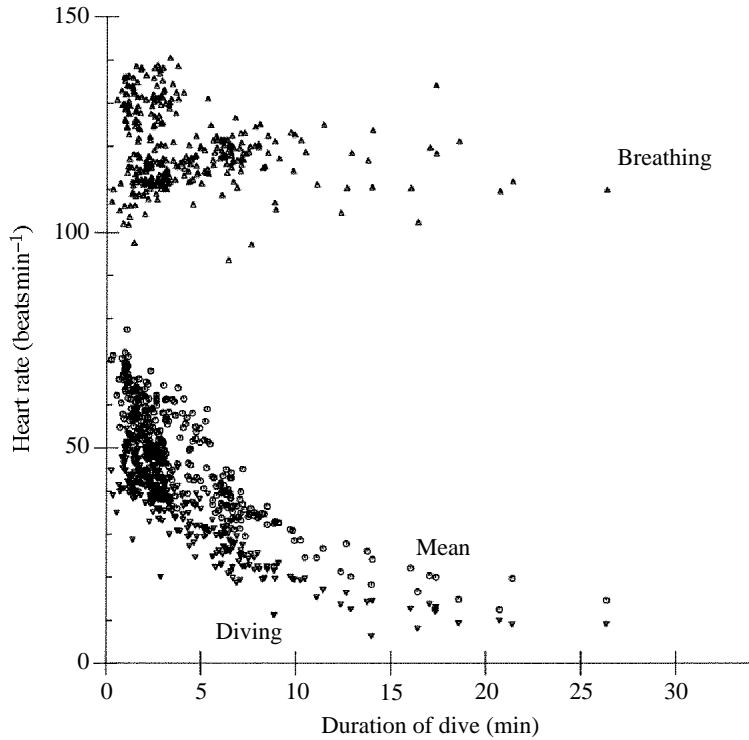


Fig. 4. Heart rate while diving ( $\nabla$ ), during surface breathing periods ( $\Delta$ ) and mean for complete dive/surface cycles ( $\circ$ ) plotted against duration of dive. Dive heart rate declines as a function of dive duration. Heart rate for complete dive cycles also declines as a function of dive duration, despite the heart rate at the surface remaining fairly constant.

10min. These long dives were not isolated events with extended recovery periods. They occurred in bouts during the normal foraging activity of seals. Fig. 8 shows a sequence of surface and dive times from a grey seal foraging at or near the bottom in 70–90m of water. The long dives were neither preceded nor followed by extended times at the surface. This was true even of the longest dive for which we recorded complete  $f_H$  data (26.3min) and the longest dive we observed (32min) for which we had only an incomplete  $f_H$  record.

## Discussion

### *Dive behaviour*

Thompson *et al.* (1991) suggested that dive behaviour could be classed as transit or foraging simply on the basis of time/depth profiles. The patterns of dive profiles seen in the present study were very similar to those previously described for grey seals and the velocity data obtained here support their classification. In V-shaped (transit) dives, swimming is continuous during submergence, and seals tend to proceed in straight lines, conducive to rapid and efficient travelling between foraging areas. In square-profile

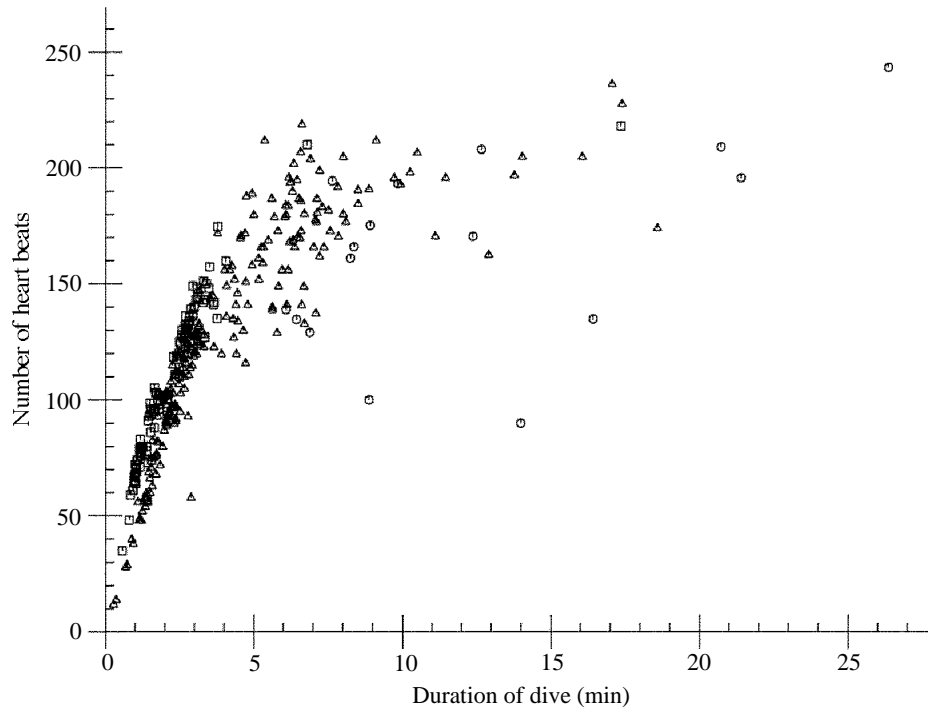


Fig. 5. Number of heart beats during a dive plotted against dive duration. Data from three grey seals, a 150kg female ( $\Delta$ ), a 110kg female ( $\square$ ) and a 210kg male ( $\circ$ ). The number of beats increases with dive duration in short dives but levels out at around 220 beats in dives exceeding about 7min.

(foraging) dives, seals invariably dived to the sea bed. Swimming was restricted mainly to the descent and ascent, with only occasional bursts of activity or continuous slow swimming while near the sea bed. This suggests that the seals were either slowly searching along the sea bed or were adopting a wait-and-ambush foraging pattern.

While at sea, even when travelling, seals did not swim at the surface. This pattern has also been noted in common seals (*Phoca vitulina*; D. Thompson, M. A. Fedak and A. Bjorge, in preparation) and in Northern elephant seals (B. J. Le Beouf, personal communication). The absence of active swimming at the surface suggests that seals surface primarily to carry out gas exchange and possibly other physiological processes. Avoiding swimming at the surface will help to minimise energy expenditure as drag on an animal swimming at the surface is up to three times that experienced only a few metres down (Blake, 1983). This has implications for estimates of swimming metabolism based on swimming flume studies. In such studies, seals are usually forced to swim against the stream while breathing at the surface. Thus, the apparent cost of swimming at a particular speed may be an overestimate of the cost of submerged swimming at that speed.

#### *Heart rate*

These results show that grey seals can and do make use of extreme bradycardia while



swimming and foraging, even when diving in relatively shallow water and free to breathe at any time. These diving heart rates observed in long dives in the wild were at least as low as the most intense forced dive responses seen in the laboratory, despite the presence of the extended pre-surfacing tachycardia. Extreme bradycardia is therefore a physiological response that is used in normal behaviour by grey seals and represents one extreme of a graduated response to differing dive durations. The relationship between dive duration and dive heart rate in short dives (up to 7min) is very similar to the pattern seen in common

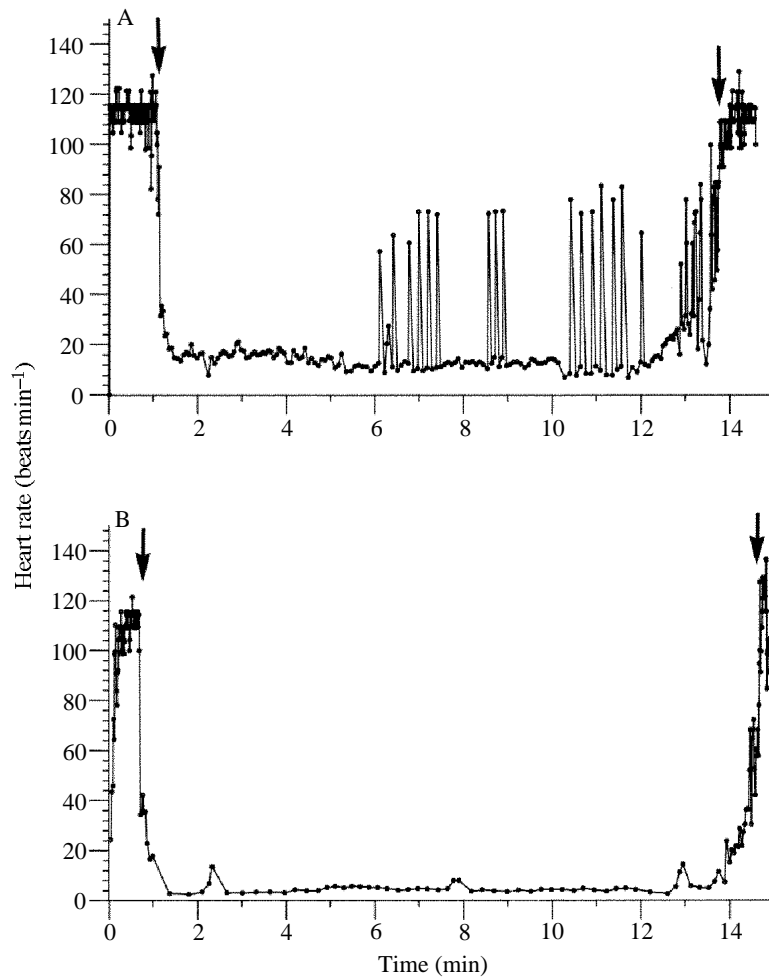


Fig. 6. Heart rate during two different dives by the same seal on one feeding trip. Each dot represents a single beat.  $\downarrow$  marks the start of a dive and  $\uparrow$  represents surfacing. (A) A typical foraging dive. Note that heart rate was extremely arrhythmic, with occasional pairs of beats close together. Heart rate averaged  $16 \text{ beats min}^{-1}$  for the entire submergence including the anticipatory tachycardia. (B) A dive from the same foraging trip showing the most extreme bradycardia recorded in this study. For the entire voluntary dive, heart rate averaged  $6.5 \text{ beats min}^{-1}$  and was below  $4 \text{ beats min}^{-1}$  for 90% of the time.

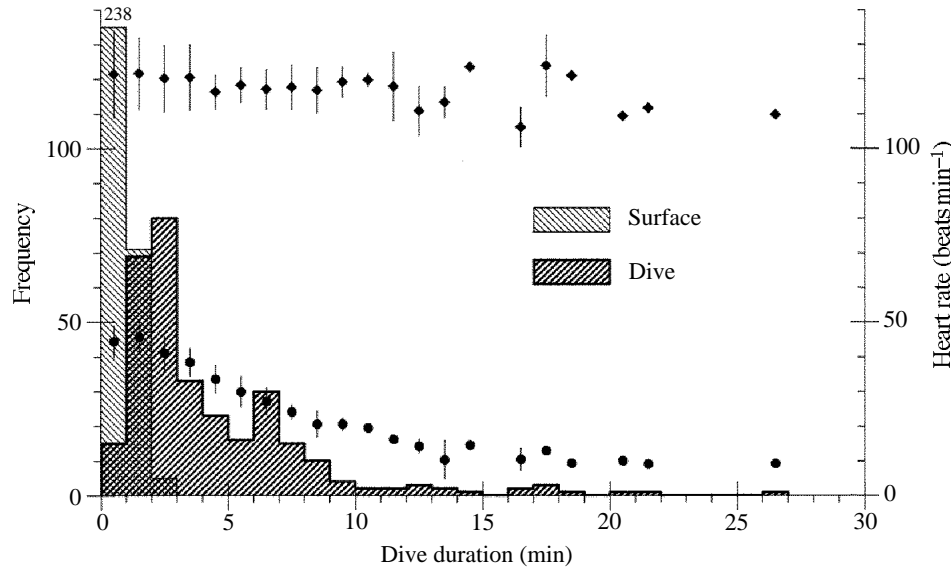


Fig. 7. Histograms of the durations of breathing periods and dives. Mean heart rates during dives (●) and in the surface periods after those dives (◆) (in 1min categories) are plotted in each column with bars indicating one standard deviation. This distribution is not a random sample of the dive durations displayed by these seals. Rather, we made every effort to concentrate our recording on times away from haulout areas while seals travelled or foraged.

seals (Fedak *et al.* 1988), with heart rate declining as a function of dive duration. However, the grey seal data show that heart rates continue to decline, dropping to spectacularly low levels during the longest dives. Such intense bradycardia has not been observed in free-swimming common seals (Fedak *et al.* 1988), probably because of the absence of dives over 8min long. Recent time/depth studies of common seals off California suggest that they may dive for as long as grey seals (Stewart and Yochem, 1989). Weddell seals diving under ice also show a decline in heart rate with dive duration and perform very long dives but, in this species, heart rates do not seem to approach the very low levels seen in grey seals. In 50min dives, heart rate only dropped to  $15 \text{ beats min}^{-1}$  (Kooyman and Campbell, 1973; Hill *et al.* 1987), three times the rate observed in our slowest records, despite the fact that grey seals are smaller than Weddell seals.

Diving heart rate does not appear to be immediately coupled to swimming speed. In all dives the onset of bradycardia was commensurate with the start of active swimming for the bottom; there were no obvious direct heart rate responses to changes of swimming velocity during dives, and the onset of the pre-surfacing tachycardia was gradual and did not correspond to the onset of active swimming.

It is interesting to note that the form of the relationship between diving heart rate and dive duration appears to be caused by the seal rationing out a fixed maximum number of heart beats. An obvious implication of this rationing is that the seal is either consciously pre-setting its diving heart rate to fit to an expected dive duration or, more likely, the seal's activity pattern while submerged is directly influencing the heart rate and the seal surfaces after a set amount of heart activity. For example, if more muscular activity

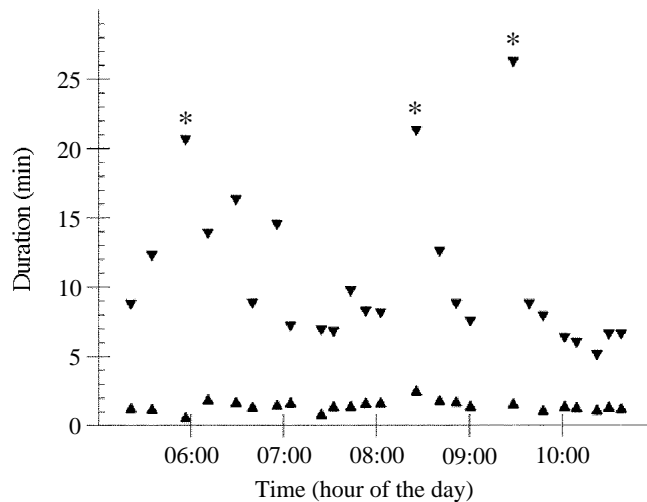


Fig. 8. A 6h sequence of surface (▲) and dive (▼) times from a grey seal foraging trip with the animal repeatedly diving to near the bottom in 70–90m of water. Note that long dives (marked with an asterisk) are not preceded or followed by extended times at the surface.

occurred diving a particular dive, the circulation to the active muscles might open more frequently, the heart would have to beat faster,  $P_{O_2}$  would fall more rapidly in circulating blood and the animal would choose to surface sooner (see Kooyman, 1985). As stated above, diving heart rate is not directly coupled to swimming activity but it may respond to a longer-term activity index.

It is not clear why seals should surface after a set amount of heart activity. Blood glucose levels are sufficient to maintain heart, lung and brain metabolism for very long periods (Hochachka and Somero, 1984). If we assume that the limit is in some way linked to oxygen transport, the simplest hypothesis would be that the blood is optimally deoxygenated after a set amount of pumping. How such a mechanism would operate is not clear. Reducing  $f_H$  would not alter the rate of  $O_2$  uptake by the brain and other perfused tissue, unless blood flow was slow enough to allow local deoxygenation. It is more likely that reduced heart rates indicate a reduction in tissue perfusion, and that this effect is greater in longer dives. Duration at the surface and number of heart beats per dive reach their maxima at about the same dive duration (7min), which is consistent with the idea that some optimal level of depletion is reached after a set amount of pumping.

The presence of an extended, anticipatory tachycardia in all dives (as in Fig. 1) has also been reported in common seal dives in the wild (Fedak *et al.* 1988). It has been known since the earliest studies of forced diving that seals can raise their heart rate from 6–8beats $min^{-1}$  to 120–140beats $min^{-1}$  in the space of only a couple of beats (Scholander, 1940). Why then should they increase the rate gradually as they approach the surface when diving in the wild? Opening up the blood circulation and increasing blood flow will have several effects, but we suggest that one important consequence of increasing heart rate is that the centrally circulating blood will be pushed around the skeletal musculature and the under-perfused organs. Oxygen-depleted tissues and

myoglobin in the muscles could then remove residual oxygen from the blood, thereby reducing the blood  $P_{O_2}$ . This would help to maximise oxygen uptake at the start of a breathing bout and reduce the time needed at the surface.

If surfacing is primarily for gas exchange, the relationship between surface and dive durations in grey seals (Fig. 2) could result from the seal replenishing its body oxygen stores to some set level after each dive. If this is the case, the increase in surface period with dive duration for short dives would suggest that the level of depletion increased with time submerged. For dives over 7min, however, the duration at the surface is relatively constant. This suggests that the level of oxygen depletion during longer dives is also relatively constant. It is no longer related to dive duration but may be reduced to some 'optimal' level determined by the need to maximise time spent under water. This would also imply that a grey seal takes approximately 2min to reload 'optimally'-depleted  $O_2$  stores.

#### *Aerobic or anaerobic diving*

The relationship between surface duration and dive duration seen here should be compared with the same data for Weddell seals (Fig. 6 in Kooyman *et al.* 1980). In Weddell seals, recovery periods increase very rapidly for dives of over 20min; this is thought to be correlated with a switch to dependence on anaerobic metabolism in long dives and closely follows the patterns of blood lactate levels from the same animals. However, we have shown that, in grey seals, surface duration reaches a maximum of approximately 2min and is reasonably constant for dives over 7min long. The absence of an increase in surface duration in grey seals may indicate that, even in the longest dives we observed, there was no net production of lactate or that grey seals frequently continue to dive with high blood lactate levels.

In adult Weddell seals, long dives produce high blood lactate levels and are generally followed by long recovery periods at the surface (Kooyman *et al.* 1980). These recovery periods allow them to clear lactate from the blood either by oxidation or by resynthesis to glucose or glycogen. Davis *et al.* (1991) show that only 27% of blood lactate turnover in resting seals is oxidised; the rest is presumably reconverted to glucose and glycogen. On rare occasions, long dives by Weddell seals have been followed by sequences of short aerobic dives during which lactate clearance has continued (Castellini *et al.* 1988). This shows that long anaerobic dives need not necessarily be followed by long surface recoveries. However, in the Weddell seal, sequences of continued short dives during recovery are rare (four occasions in over 23000 dive records; Castellini *et al.* 1988); the far more usual response to long dives is an extended period at the surface.

In the dive sequence shown in Fig. 8, two long dives marked by asterisks are followed by a series of short dives. If this represents continued diving with high blood lactate levels, this grey seal seems to be using this strategy after all long dives rather than resorting to extended recovery periods (Fig. 2). If so, the behaviour of grey seals in response to long dives is different from that of Weddell seals. Of course, these dives occur in very different circumstances.

The length of the recovery period (the time taken for blood lactate concentration to return to resting levels) will depend on the fate of the lactate produced (i.e. the absolute

and relative amounts burned and recycled) and on the rates of each of these processes during recovery. To simplify the following arguments, we make the assumption that metabolic rate during diving and recovery is constant (i.e. the rate of ATP utilisation does not change between the surface and dive or in subsequent dives). This is very probably not the case, but the basic argument and relationships will still apply.

When oxidised as a metabolic substrate 1mol of lactate releases about 17mol of ATP, compared with only 1mol of ATP released during its production (Hochachka and Somero, 1984). If there were no recycling and all the lactate was oxidised, we would expect the recovery period to be around 17 times as long as the period of reliance on anaerobic metabolism. Also, because oxidising lactate produces 6% less ATP per mol of O<sub>2</sub> than is produced by oxidation of glucose, dives made during recovery would need to be about 6% shorter than the normal ADL to remain aerobic. If lactate is reconverted to glucose or glycogen, however, extra ATP will be required. For each glucose molecule converted to lactate, 2 ATP molecules are generated, but to resynthesise 1 glucose molecule from lactate requires 6 ATPs. An important consequence of this is that a given period of anaerobic diving will produce a requirement for ATP, for resynthesis, equivalent to three times the amount of ATP used during a period of aerobic diving of the same duration. If this ATP is produced aerobically, the seal must either increase the length of time spent at the surface or shorten subsequent dives. Therefore, oxidation of lactate while diving during recovery from an anaerobic episode should require an extended sequence of shorter aerobic dives; alternatively, reconvertng lactate would require excess oxygen, shortening dives and reducing the percentage dive time. Seals will probably employ some combination of oxidation and resynthesis, and the result will be some combination of reduced dive duration, longer surface durations and reduced percentage dive time.

Kooyman *et al.* (1983) estimated the ADL of 185–205kg Weddell seals to be 13min. Our largest study animal, weighing 210kg, occasionally dived for 20–26min. Correcting for size by scaling mass to the power 0.75, this duration is equivalent to dives of 32–46min by a 400kg animal. Such dives in 350–450kg Weddell seals generally required 30–70min of recovery (Kooyman *et al.* 1980). The grey seals used about 2min. In one instance (Fig. 8), a 21min dive by the grey seal was followed by only 21s at the surface. If we assume that about 2min is needed to return O<sub>2</sub> stores to typical pre-dive levels (see above), the seal may have replenished only 20% of its O<sub>2</sub> stores before diving again for 14min. This sequence suggests that an extended anaerobic period should have occurred even if metabolism stayed at around resting rates (see below). However, during the following hour, percentage dive time remained high (at 89%) and the three following dives were at or beyond measured ADL for Weddell seals of similar size to the grey seal (Kooyman *et al.* 1983). When Weddell seals have continued to dive during recovery periods, the percentage dive time was reduced to around 75% and dives were shorter than the estimated ADL (Castellini *et al.* 1988). Clearly the grey seal's response to extended diving is different from the Weddell seal's response. In grey seals, the very high percentage dive time and the ability to continue to perform dives around the estimated ADL, subsequent to long dives, suggests to us that these animals may have maintained aerobic respiration.

*Energy saving*

The most obvious means by which grey seals could extend the length of dives without resorting to anaerobic metabolism is to reduce their activity levels while submerged. During all long dives, swimming activity was restricted to the descent and ascent phases, with the seals remaining motionless or swimming very slowly (below stall speed of the flow meter) while on the bottom. However, most long dives of Weddell seals for which blood metabolites have been measured were apparently active exploratory dives during which it is presumed that the seals swam for a high proportion of the submergence (Kooyman, 1981). Most of the differences between these two species' responses to long dives could be explained by the different activity levels. To avoid lactate build up during long foraging dives, grey seals seem to minimise activity. That is, they apparently choose to wait for and ambush prey rather than to chase it; alternatively, they may be restricted to feeding on sessile organisms. Such behavioural reductions in metabolic demand will allow the animal to remain on the bottom for as long as possible. However, in the grey seals, some additional reduction in metabolic demand seems to be needed to explain the ability to remain submerged for long periods.

Resting metabolic rates in diving vertebrates are notoriously difficult to define: in seals, estimates vary from one to five times that estimated from Kleiber's allometric equation (Kleiber, 1961; Lavigne *et al.* 1986). Assuming standard mammalian values for seal basal metabolic rate (BMR), using estimates of phocid body oxygen stores (Kooyman, 1989; Kleiber, 1961; Lavigne *et al.* 1986) and further assuming all body stores are fully available, the longest dives by S3 (the 210kg male) would have been 20% longer than the total body oxygen store would allow. These are conservative assumptions. Calculation of total O<sub>2</sub> stores from blood, muscle and lung content may overestimate available stores by 5% (Kooyman, 1989); other methods suggest even greater overestimates (up to 40%; Packer *et al.* 1969). These estimates of maximum ADL are made even more conservative because, during these dives, the seal swam actively to and from the bottom at depths of 80–100m. During this 2.5min of swimming, metabolic rate would be expected to have been elevated to between two and three times resting levels (Davis *et al.* 1985; M. A. Fedak, unpublished data). Thus, using these estimates, this seal exceeded its estimated ADL by at least 30%. Even if there was no activity during these dives, in order to maintain net aerobic respiration seals would have had to reduce their metabolic rates to below normal mammalian resting levels and to less than the measured resting levels in phocids (Davis *et al.* 1985; M. A. Fedak, unpublished data). Dive patterns, however, as we argue above, do not suggest anaerobic metabolism.

Elephant seals appear to be able to exceed their estimated ADL on consecutive dives over long periods (Hindell *et al.* 1992). Kooyman (1989) suggested that in bouts of long dives lactic acid concentration could build up in a stepwise manner over long periods and then be reduced slowly by a long period of short dives. He postulated that in elephant seals this would require the animals to withstand blood lactate levels of up to 26mmol l<sup>-1</sup> after 3h of long diving. Such levels have been observed in an adult Weddell seal after a 61min dive, but this dive was followed by a 2h surface recovery period. If the metabolic rate during long dives can be depressed to less than the apparent resting rate, the dive

patterns in elephant seals need not involve a massive lactate accumulation. This could go some way towards explaining the startling dive duration of 2h in a southern elephant seal female (Hindell *et al.* 1991).

These data certainly demonstrate that extreme dive responses should be considered to be part of the normal physiological repertoire of diving seals and that their occurrence need not involve situations where restrictions on breathing might be imposed. This extreme response is associated in grey seals with reduced activity levels, and its utilization may influence their choice of foraging tactics. The occurrence of extended bouts of long dives with no detectable decrease in percentage dive time or increase in the duration of intervening surface periods suggests that we should consider hypometabolism as well as anaerobiosis as a possible strategy to increase dive times in foraging marine mammals.

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