

# The behavioural and physiological ecology of diving

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**A**ir-breathing homeotherms that dive for aquatic prey are presented with behavioural and physiological problems that are largely absent for animals foraging in the terrestrial environment or at the surface. Diving species exploit prey from a few metres below the surface to depths of many hundreds of metres with limited supplies of oxygen (O<sub>2</sub>) and often in water temperatures only a few degrees above freezing. Recent advances in instrumentation have allowed the detailed measurement of diving behaviour in free-ranging divers and these have shown that many species have diving performances exceeding expectation in terms of both the depth and duration. The need for parsimonious O<sub>2</sub> use during breath-hold diving has been at the centre of most

physiological and some recent behavioural research on diving. In particular, behavioural observations are reinforcing the need for a better understanding of the metabolic physiology involved in diving<sup>2</sup>. They also add to the mystery of how these natural divers avoid the problems of nitrogen narcosis, shallow-water blackout and high-pressure nervous syndrome, all of which are problems for the human diver<sup>1</sup>.

Recent interest in diving behaviour has also emerged from a purely theoretical direction<sup>3,4</sup>. Expressed at its simplest level, a dive is a convenient and well-defined unit of behaviour in which an animal makes an excursion from a central point (the surface) to achieve a specific goal (e.g. capture food) in a specific period of time (dive duration). Diving may be viewed as a special example of central-place foraging in which the surface is the central place from which the individual forages<sup>5</sup>.

Divers must organize their behaviour and foraging around the necessity to return to the surface to breathe. If an animal makes an aerobic dive then the principal metabolic pathways used during the dive will involve aerobic metabolism and the animal must return to the surface before its O<sub>2</sub> reserves are exhausted. Aerobic diving behaviour has particular attractions on theoretical grounds because there is a fixed upper limit to the costs of a dive, determined by the amount of O<sub>2</sub> the diver is able to carry in its tissues. If assumptions are made about the type of metabolic substrate being used during diving<sup>6</sup> and the metabolic rate<sup>7</sup>, then the time available to forage during aerobic dives is determined by the amount of O<sub>2</sub> the diver is able to deliver to the region of the water column where the food is located. Such theory is beginning to provide a framework for testing specific hypotheses about whether diving performances of many species are indeed so extraordinary and, if so, what

**Recent measurements of remarkable dive performances in oceanic seabirds and marine mammals suggest the use of a range of physiological and behavioural adaptations for the parsimonious use of oxygen. Access to food at different depths may be directly related to the duration of the breath-hold, and several physiological strategies may be used to extend dive duration. But there is also a growing appreciation of the importance of behavioural strategies adopted by divers to minimize the effects of physiological limitations on diving performance and to maximize access to food.**

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type of physiological adaptations might be required in order to explain the observed patterns of behaviour (e.g. Ref. 8).

Although aquatic birds and mammals of inland waters provide tractable subjects for studying diving<sup>9,10</sup>, new technology has allowed expansion of knowledge to marine mammals and birds. These species are the most revealing when it comes to unexpected diving performances. For example, female elephant seals (*Mirounga leonina* and *Mirounga angustirostris*) spend about 10% of their time at the surface and the remaining 90% is spent at depths between 250 and 500 m, or moving back and forth to the surface to breathe<sup>11</sup>. The mean dive duration is usually 30–40 min with an interval at the surface of about 2–3 min<sup>12</sup>, but dive depths can exceed 1500 m and the

maximum recorded dive duration is 2 h. It is probably more appropriate to describe elephant seals as *surfacers* rather than *divers*, and many species of whales probably also fit into this category.

## Aerobic dive limits

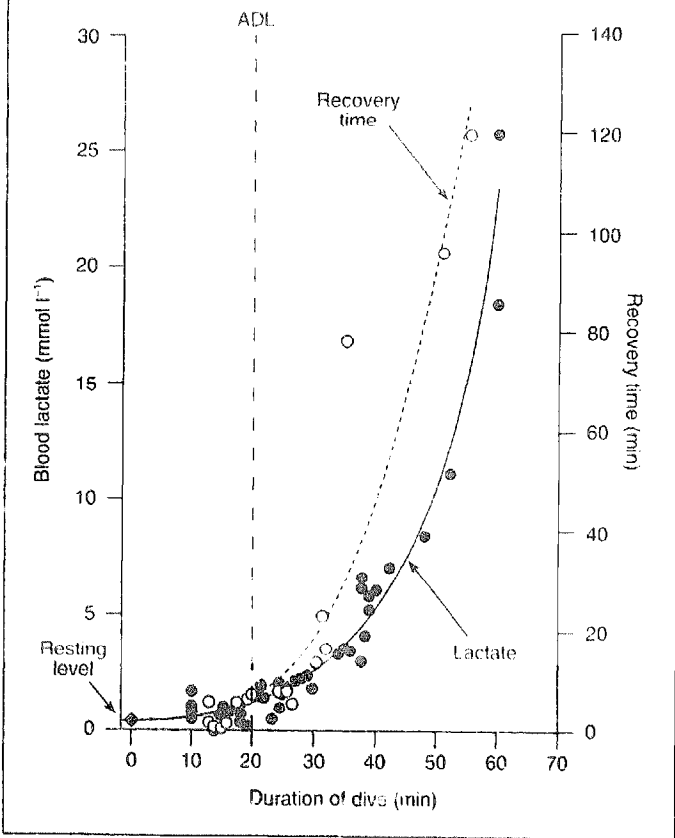
In relation to most other marine mammals, the elephant seal is indeed extraordinary. Much of our knowledge of diving physiology in marine mammals comes from studies conducted by Kooyman and others on Weddell seals (*Leptonychotes weddellii*) (Box 1). In dives lasting >20 min, post-dive blood lactic acid concentrations increased in direct relation to dive duration, whereas in dives lasting <20 min lactic acid concentrations remained low<sup>13</sup>. This result has been at the centre of much of the behavioural and physiological ecology of diving for the past 15 years because the increase in lactic acid concentrations after 20 min indicates that, after this time, Weddell seals were relying to a large degree on anaerobic metabolism. Consequently, Kooyman defined an aerobic dive limit (ADL) for Weddell seals as 'the maximum breath-hold that is possible without an increase in the blood lactic acid concentration during or after the dive'. Although, based on Kooyman's definition, the ADL has not been measured in any other diving species, nevertheless the ADL has been adopted as a useful benchmark against which to measure and compare diving performances across species of different body sizes<sup>14,15</sup>. The problem is that calculation of ADLs requires assumptions to be made about both the O<sub>2</sub> storage capacity of tissues and the metabolic rate of divers.

Only in a few species has the O<sub>2</sub> storage capacity of tissues been measured<sup>1</sup>, and metabolic rate during dives has never been measured directly in free-ranging species. In the laboratory, it has been possible to measure diving

**Box 1. Measurement of aerobic dive limits**

In the 1970s, an experimental paradigm was developed to examine diving physiology in semi-captive Weddell seals (*Leptonychotes weddellii*)<sup>13</sup>. Since Weddell seals often survive in the Antarctic sea ice by keeping breathing holes open through the winter, this provided Kooyman and his colleagues with an opportunity to study diving physiology in detail.

Weddell seals were captured and transported to an area nearby on the sea ice over McMurdo Sound, Antarctica, where there were no breathing holes. A hole was drilled in the ice and the seal was allowed to forage from that hole. When first placed in the experimental ice hole, the seals would search for other ice holes in the vicinity or spend time exploring their new environment. This led to some individuals making extremely long dives and in some of these the post-dive concentrations of lactic acid in the blood were measured (see Figure below). They show that for dives lasting up to c. 20 min there was no significant increase in blood lactic acid concentrations suggesting that these dives made use of aerobic metabolism. For dives >20 min the post-dive lactic acid concentration increased in proportion to dive duration, as did the time taken to recover after the dive. This led Kooyman<sup>13</sup> to define an aerobic dive limit (ADL) for Weddell seals. Figure modified from Ref. 13.



metabolic rate in ducks using heart rate as an indicator of metabolic rate<sup>16</sup>. Although measurements of mean metabolic rate are available for many species, these tend to average out potential fluctuations in metabolic rate ranging from high metabolic rate (hypermetabolism) at the surface to low metabolic rate (hypometabolism) while diving. Even with these limitations, comparisons of these theoretical aerobic dive limits (TADLs) for species may prove to be instructive even though TADLs may be quite different from actual ADLs. For example, based on measurements of the average metabolic rate, gentoo penguins (*Pygoscelis papua*) exceed their TADL in 62% of their dives<sup>15,17</sup> (Fig. 1), and female southern elephant seals exceed their TADL in >90% of their dives<sup>18</sup>. Seabirds often exceed their TADLs<sup>19</sup> and, after taking body size into consideration, seabirds have longer dive durations than pinnipeds (Fig. 2). In general, pinnipeds tend not to exceed their TADLs<sup>15</sup>. For example, female fur seals (e.g. *Arctocephalus gazella*) exceed their TADL during ~6% of dives<sup>15</sup>.

**Aerobism versus anaerobism**

Two principal hypotheses attempt to explain the observed diving behaviour (Box 2). The hypothesis that diving can be extended by the use of anaerobic metabolism, thus releasing individuals from the constraint of the ADL, has attracted the attention of theoreticians<sup>8,20</sup>. Although there may be qualitative support in some data for the predictions from such models<sup>21</sup>, other forms of metabolic adjustment not involving anaerobic metabolism could be equally plausible explanations. The alternative, that divers make use of some form of metabolic depression and generally remain aerobic during most dives, appears to find greater support in the available data.

Based on Kooyman's work on Weddell seals, divers occasionally exceed their ADLs<sup>13</sup>, but this may be the exception rather than the rule. First anaerobic metabolism is not an efficient use of energy. One-eighteenth of the total amount of ATP is derived from anaerobic compared with aerobic metabolism. Even if some of the ATP can then be recovered by the oxidative metabolism of lactate after the animal has returned to the surface, the overall effect will be to reduce metabolic efficiency<sup>22</sup>. Therefore, purely on grounds of efficiency, it seems unlikely that divers will make use of anaerobic metabolism (i.e. exceed their actual ADLs) except in order to exploit an extremely rich and ephemeral prey resource (i.e. a resource that is rich enough to make up for the additional energetic costs of anaerobism). Perhaps the reason that Kooyman observed increases in lactate in Weddell seals was because his animals were extending their dive while attempting to find alternative ice holes.

In addition, observations of time spent at the surface between dives, also known as the dive recovery time, do not suggest that animals that regularly exceed the TADLs are making use of anaerobic metabolism<sup>15</sup>. Weddell seals took up to 60 min to recover from dives involving anaerobic metabolism<sup>13,23</sup> (Box 1), whereas observations of free-ranging divers show little or no increasing relationship between time spent at the surface between dives and dive durations. In fact, for gentoo penguins, surface interval even declines in relation to dive duration<sup>15</sup>. Even in cases where a relationship exists between dive duration and recovery time at the surface

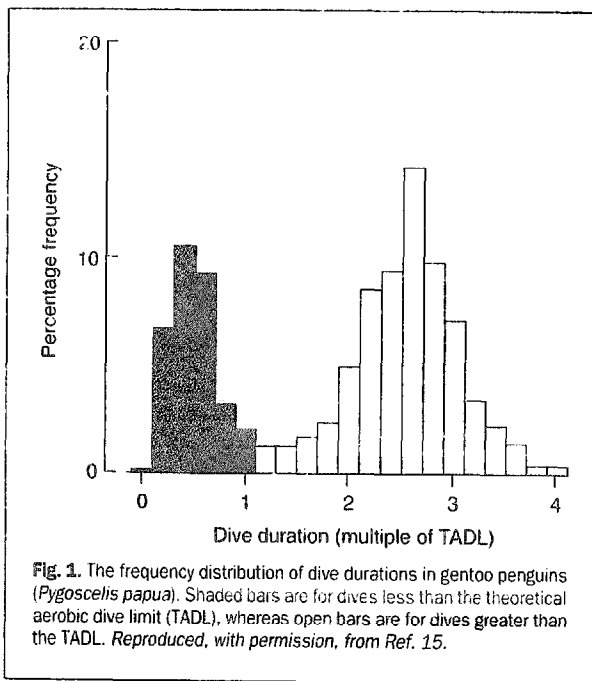


Fig. 1. The frequency distribution of dive durations in gentoo penguins (*Pygoscelis papua*). Shaded bars are for dives less than the theoretical aerobic dive limit (TADL), whereas open bars are for dives greater than the TADL. Reproduced, with permission, from Ref. 15.

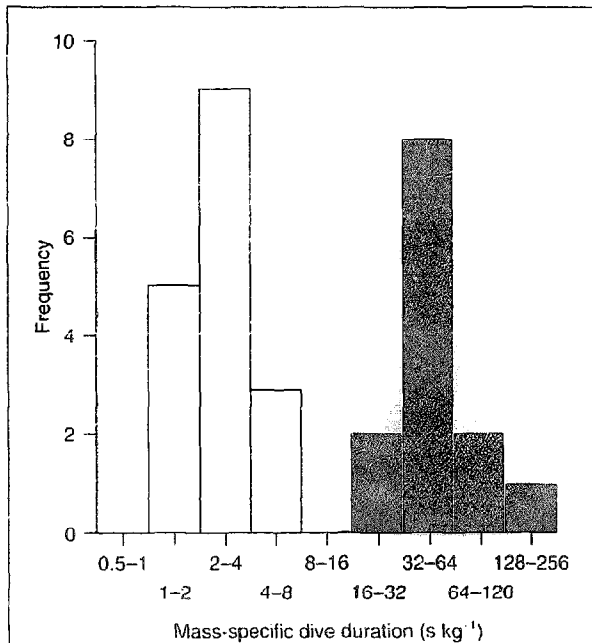


Fig. 2. Comparison of dive durations for pinnipeds (unshaded bars) and seabirds (shaded bars). Data from Ref. 15. Dive duration is expressed in proportion to metabolic body mass using allometric equations for field metabolic rate in mammals and non-passerine birds (see Ref. 15).

after the dive, the recovery time is not normally long enough to provide evidence that animals are recovering from anaerobic metabolism during dives.

### Mixed metabolic strategies

Most evidence points to TADLs being particularly poor indicators of the actual ADL in many species of divers and, therefore, one or both of the assumptions about O<sub>2</sub> storage capacity or metabolic rate made when calculating a TADL must be wrong. Although it is possible that the O<sub>2</sub> storage capacity of the tissues of divers has been underestimated for some species<sup>24</sup>, such errors are unlikely to account for the very large discrepancies between observed diving performances and those expected from theoretical aerobic dive limits.

There is circumstantial evidence to suggest that hypometabolism and not anaerobic metabolism is the most common metabolic strategy used by divers<sup>25</sup>. For example, anaerobic metabolism cannot easily explain the diving behaviour of elephant seals<sup>18</sup>. However, it remains possible that anaerobic metabolism is relied upon in specific, albeit infrequent, circumstances. Divers are, therefore, likely to use a mixed metabolic strategy. Some evidence

for a mixed strategy comes from the bimodality of dive durations in some seabirds (e.g. Fig. 1). One mode suggests that some dives conform to the limits of the TADL, whereas the other suggests that there may be another type of dive, possibly involving a different metabolic strategy that allows divers to exceed the TADL.

An explanation for the mechanisms underlying hypometabolism in divers could come from consideration of body size and of how divers manage heat and O<sub>2</sub>. Many divers are found in the thermally-challenging environments of polar and sub-polar waters. It is now almost axiomatic that the thermal insulation of these species (blubber and hair in marine mammals, feathers and subcutaneous fat in birds) is an adaptation to reducing heat loss<sup>26</sup>. However, it may be more accurate to describe this insulation as an adaptation to managing heat loss. There may be advantages to losing heat under specific circumstances.

Several recent studies have shown body temperature reductions as a result of diving activity (e.g. Refs 9,27-29). Some of the temperature changes are likely to be caused by the intake of large food items into the gut at ambient temperature<sup>30</sup>. However, abdominal temperature measurements remote from the stomach also show these declines in temperature<sup>27,28</sup>. Moreover, in Weddell seals, there are declines in blood temperature during diving<sup>31</sup>.

Even the classical dive responses involving the slowing of heart rate (bradycardia)<sup>32</sup> to as low as four beats per minute in free-diving seals<sup>33</sup> and the restriction of blood flow to peripheral tissues during dives, suggest that these animals are likely to find it difficult to thermoregulate without significant blood flow to help disperse heat during prolonged dives. This problem of retaining heat will be exacerbated by small body size. Metabolic rate is sensitive to temperature<sup>34</sup> and heterothermy is a well-established strategy for reducing metabolic rates in homeothermic vertebrates. Therefore, declines in body temperature may reduce metabolic rate sufficiently to allow animals to use O<sub>2</sub> at a lower rate than we would expect for normal metabolism. Consequently, they can extend their dive durations. It is perhaps no coincidence that the longest mass-specific

### Box 2. Competing hypotheses for mechanisms used by divers to extend dive duration beyond the ADL

#### Anaerobism

This hypothesis proposes that divers are able to make use of anaerobic metabolism to extend their dive durations beyond the limitation of the ADL. Thus a diver would switch from using aerobic to anaerobic metabolic pathways as it approaches the limit of its oxygen (O<sub>2</sub>) reserves.

#### Disadvantages

- Anaerobic metabolism yields one eighteenth of the total energy of aerobic metabolism and causes the accumulation of lactic acid (see Box 1). Divers using anaerobic metabolism will, therefore, have to spend additional time at the surface metabolizing lactate. This has an additional cost both in terms of time lost at the surface that could be spent foraging and reduced metabolic efficiency.

#### Advantages

- Anaerobic metabolism could be favoured if divers are exploiting a rich prey resource that would not be otherwise accessible and which is sufficiently rich to repay the additional energetic costs of anaerobism.
- Anaerobic metabolism may also be possible, and difficult to detect, if an O<sub>2</sub> debt is built up progressively in a series of dives that is terminated with an extended period spent at the surface during which lactate is metabolized<sup>35</sup>.

#### Aerobism and hypometabolism

This hypothesis proposes that divers normally only use an aerobic metabolic pathway. They extend their dive durations by reducing their metabolic rate (hypometabolism) thereby reducing their rate of O<sub>2</sub> consumption.

#### Disadvantages

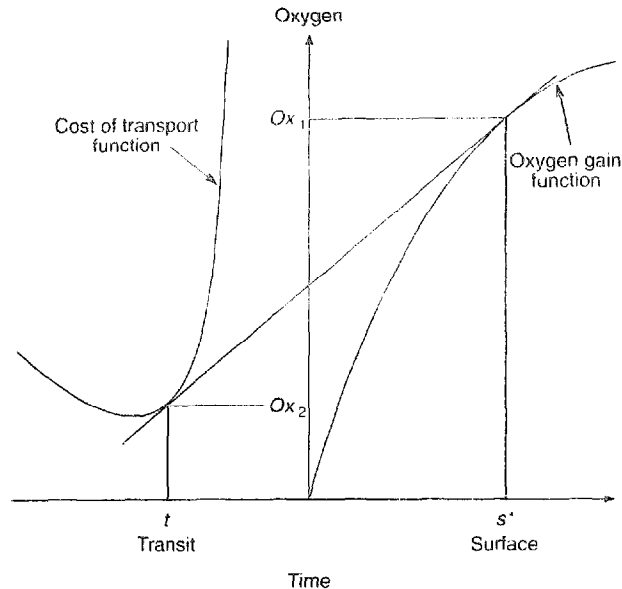
- Hypometabolism would also incur costs such as reduced efficiency of processes like digestion.
- There are additional costs of hypermetabolism at the surface to re-heat tissues.

#### Advantages

- High metabolic efficiency.
- Short recovery times at the surface (which are supported by observations of behaviour that generally do not suggest extended recovery times after long dives in free-ranging divers).
- There is some evidence of low metabolic rates in some species of divers<sup>24</sup>.

**Box 3. An oxygen balance model of diving that describes the optimal behaviour of divers**

The graphical illustration<sup>36</sup> (below) of an oxygen ( $O_2$ ) balance model for diving showing time spent at the surface and time spent in transit during the dive, to the right and left of the origin, respectively. The curve rising to the right of the origin is the  $O_2$  gain function while at the surface, and the curve to the left of the origin is the cost of transport function, that is, the  $O_2$  used to travel to a specific depth in different transit times. The common tangent between these curves defines both the optimal swimming speed to reach a specific depth in the time ( $t$ ) taken to travel to and from that depth, and the optimal time spent at the surface ( $s^*$ ) replenishing  $O_2$  reserves. The difference between the total  $O_2$  carried down ( $Ox_1$ ) and the  $O_2$  used in transit ( $Ox_2$ ) is the  $O_2$  available for foraging. Depending on the metabolic rate, this defines how long a diver can spend foraging. As dive depth increases the cost of transport function will shift up and to the left.



dive durations have been observed in the smallest seabirds<sup>15</sup>. Small body size with low thermal inertia and a large surface area to volume ratio may be important for induction of hypometabolism by heterothermy because these conditions will increase the potential rate of body cooling. Therefore, body size could be one reason for the apparent difference between diving capacities in seabirds and pinnipeds (Fig. 2). Regeneration of heat at the surface, where  $O_2$  is not limiting, would require an increase in thermogenesis that could be achieved more effectively by small individuals because of their generally greater aerobic scope<sup>35</sup>. The relative costs of such heterothermy compared with anaerobic respiration need to be quantified.

**Optimal diving behaviour**

In addition to having the potential to adopt a mixture of metabolic strategies, divers also have the option of adopting behaviour that could minimize the effects of physiological limitations by optimizing the diving time budget. If dive durations were a simple function of the amount of  $O_2$  that individuals can carry in their bodies, then we might expect a diver to stay submerged until its  $O_2$  stores were nearly exhausted. Empirical observations of natural divers show that they often stay submerged for a much shorter time than we would expect from knowledge of their potential dive durations.

Kramer<sup>3</sup> offered an explanation for this behaviour and this has been expanded in subsequent studies<sup>4,36</sup>. These showed that, in theory at least, it is optimal for divers to return to the surface before all their  $O_2$  reserves are used,

providing the time taken to replenish  $O_2$  at the surface increases as an asymptotic function (e.g. a power function) of time spent at the surface (Box 3). The evidence for such an increasing but decelerating function comes from studies of haemoglobin and myoglobin  $O_2$  dissociation curves<sup>1</sup>, forced diving<sup>37</sup> and from Weddell seals<sup>38</sup> in which rate of re-oxygenation of blood following the end of a dive was examined. The function (which requires more-rigorous testing) suggests that the rate of re-oxygenation is rapid when animals initially return to the surface, and slows gradually with time. Consequently, the greatest average rate of re-oxygenation can be achieved if animals spend short times at the surface. This will also maximize the proportion of time spent submerged, but the only possible form of behaviour would be a succession of short dives. Therefore, animals exploiting shallow prey would be able to spend more time actually foraging if they made short dives that were less than the maximum potential dive duration. In general, this prediction appears to be upheld by observations of seals and seabirds foraging on shallow prey in that shallow dives are also the shortest dives<sup>22,39,40</sup>.

As prey is located deeper in the water column, travel time to and from the prey begins to become a significant component of the diving time budget, and times spent diving are expected to increase with the depth of the prey. However, there is likely to be a trade-off between prey depth and profitability so that some prey items that might be exploited when close to the surface are less likely to be exploited as the depth of that prey increases. Based on experiments done with captive pochard ducks (*Aythya ferina*) diving in a tank, Carbone and Houston<sup>10</sup> suggested that this trade-off can exist.

The approach to simulating diving behaviour with  $O_2$  balance models also has the potential to investigate competing hypotheses explaining why animals exceed their TADLs. For example, given the current knowledge of lactate production and metabolism, is it possible for animals to accumulate lactate over a series of dives in which some anaerobic metabolism is used? Lactate could then be metabolized during an extended period spent at the surface after the dive bout. This may be an efficient way to exploit transient or fast-moving patches of prey such as fish shoals or krill swarms. There are substantial practical difficulties involved with addressing these questions by experimentation. Current approaches to modelling could indicate whether such a strategy is possible<sup>20</sup>.

The foraging ecology of divers is one research field where there is a close linkage between studies of behaviour and physiology. The wide range of environments and food types exploited by divers, in addition to the range of body sizes, mean that there is no single solution to the problem of exploiting aquatic prey. Individuals have the option to vary their strategy dive-by-dive. However, species that are keyed to particular prey resources may tend to adopt a narrower range of behavioural and physiological strategies. The current evidence suggests that these may involve the use of anaerobic metabolism and heterothermy or homeothermy in association with metabolism using normal aerobic pathways and behavioural adjustments that optimize the time budget during individual dives or bouts of dives.

The research challenge for the future is to link the physiological and behavioural models of diving to help explore the options open to divers under different food densities and distributions and to test these in the field. The results of such research will have direct relevance to understanding how variation in prey densities in the marine system, including those caused by commercial fisheries, is likely to affect the foraging performance of seals, whales and seabirds.

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