ARTICLES

How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment

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Although diving birds and mammals can withstand extended periods under water, field studies show that most perform mainly short, aerobic dives. Theoretical studies of diving have implicitly assumed that prey acquisition increases linearly with time spent searching and have examined strategies that maximize time spent foraging. We present a simple model of diving in seals, where dive durations are influenced by the seal's assessment of patch quality, but are ultimately constrained by oxygen balance. Prey encounters within a dive are assumed to be Poisson distributed and the scale of the patches is such that a predator will encounter a constant prey density during a dive. We investigated the effects of a simple giving-up rule, using recent prey encounter rate to assess patch quality. The model predicts that, for shallow dives, there should always be a net benefit from terminating dives early if no prey are encountered early in the dive. The magnitude of the benefit was highest at low patch densities. The relative gain depended on the magnitude of the travel time and the time taken to assess patch quality and the effect was reduced in deeper dives. As the time taken to decide decreased, the relative benefit increased, up to a maximum, but fell as decision time was reduced further. Frequency distributions of different aspects of dive durations from three deep-diving and two shallow-diving seal species are presented and compared with the model's predictions.

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Perhaps the most striking aspect of the behaviour of diving birds and mammals is their ability to withstand extended periods under water (e.g. Kooyman & Campbell 1973; Butler & Jones 1982; Blix & Folkow 1983; Elsner & Gooden 1983; Le Boeuf et al. 1988, 1989; Elsner et al. 1989; Hindell et al. 1991, 1992; Croll et al. 1992; and see Kooyman 1989 for an extensive review). This emphasis on extended breath-hold dives initially led physiologists to concentrate on the mechanisms that facilitate extended apneas (Irving 1934, 1964; Scholander 1940). However, when diving behaviour is considered in an ecological context it is apparent that increasing the proportion of time at depth may be more important than increasing the duration of individual dives (Fedak 1986). Recent field studies have shown that most freely diving mammals and birds perform short, aerobic dives. The majority of species perform some dives that exceed their estimated aerobic diving limit (ADL; Kooyman 1989), but these usually represent less than 10% of foraging dives

(Kooyman et al. 1980; Gentry & Kooyman 1986; Fedak et al. 1988; Thompson et al. 1991; Chappell et al. 1993; Croxall et al. 1993; Nolet et al. 1993; Thompson & Fedak 1993; but see Croll et al. 1992; Hindell et al. 1992).

To date, all theoretical studies of foraging behaviour by diving animals have examined strategies that maximize either total time, or proportion of time spent submerged (Kramer 1988; Houston & Carbone 1992; Thompson et al. 1993; Carbone & Houston 1994, 1996; Carbone et al. 1996). It is implicitly assumed in all of these models that the number of prey encountered is a linear function of time spent searching. Maximizing time spent in the foraging patch is therefore synonymous with maximizing prey acquisition. Divers should maximize the proportion of time spent at the foraging site by minimizing the proportion of time spent travelling and/or recovering. The decision to terminate each dive has been assumed to be based entirely on the level of oxygen reserves. In all such models, the optimal dive durations are predicted to be close to, and in some cases beyond, the ADL. Ydenberg & Clark (1989) incorporated the effect of prey distribution on foraging decisions in a study of western grebes,

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Aechmophorus occidentalis, diving in patchy environments. The likelihood of relocating a food patch was included in their state variable modelling approach. However, patch quality became important only at the end of the aerobic phase of a dive. Mori (1998) used a marginal value approach to examine optimal dive schedules in patchy environments. Both patch quality and patch depth affected the time budget of the dive cycle. However, these effects became important only in dives close to or beyond the ADL. Where aerobic diving was described as 'favourable', the time budget was affected little by patch quality.

If these oxygen balance models realistically portray the optimal behaviour for breath-hold divers, we are left with a paradox: why do many marine mammals apparently choose to terminate the majority of their dives before their oxygen reserves are exhausted (e.g. Gentry & Kooyman 1986; Fedak et al. 1988; Thompson et al. 1991; Chappell et al. 1993; Croxall et al. 1993; Nolet et al. 1993)? In most dives, the decision to leave the foraging site and swim to the surface may be influenced by some factor other than level of oxygen stores.

Dives would be terminated before oxygen reserves were exhausted, if prey capture and handling prevented further searching. For example, both harbour seals, *Phoca vitulina*, and grey seals, *Halichoerus grypus*, bring large prey items, such as salmonids, to the surface before eating them (Roffe & Mate 1984). However, if the diet comprised mostly large prey items, the predators would require only a few successful captures. It is unlikely that the high percentage of short dives observed in the wild would result from catching large prey. In fact even those species known to eat large prey at the surface often include a high proportion of small prey items in their diet (Roffe & Mate 1984; Hammond & Prime 1990; Hammond et al. 1994a, b; Thompson et al. 1998). These small prey are generally eaten underwater.

No matter how prey are distributed, a randomly searching predator will maximize its encounters by maximizing the total time spent searching. This holds for any situation where the predator has no prior knowledge of the distribution of prey and where prey items are uniformly distributed or occur in discrete, widely scattered units (either as large prey items or small prey in concentrated schools). However, uniformly distributed prey or discrete large prey items may not be the general case. Many pinnipeds rely on small prey, for example crabeater, *Lobodon carcinophagus*, and leopard seals, *Hydrurga leptonyx*, prey extensively on krill (Siniff 1991), various otariid species prey on krill and small fish (Sinclair et al. 1994; Reid 1995; Reid & Arnould 1996; Thompson et al. 1998), harp seals feed extensively on capelin, *Mallotus villosus*, and small crustaceans (Nilssen et al. 1995; Lawson & Stenson 1997), elephant seals (*Mirounga leonina* and *M. angustirostris*) prey on relatively small squid (Rodhouse et al. 1992; Antonelis et al. 1994; Slip 1995) and grey and harbour seals prey on small benthic or epibenthic fish (Hammond et al. 1994a, b; Tollit et al. 1997).

If the diet comprises mainly small fish, seals will need to catch large numbers of individuals. For example, a 150-kg grey seal, eating sandeels (*Ammodytes* spp.) weighing 10 g on average (Hammond et al. 1994a, b), would require approximately 400 fish per day or four to five fish per dive (Thompson et al. 1991; Thompson & Fedak 1993; McConnell et al. 1994; Boily & Lavigne 1997). As sandeels occur in patches of variable size and density, separated by regions with zero or low density (Wright & Bailey 1993) it is unlikely that a seal will hit a food patch on each dive. When hunting such prey it may benefit the predator to alter its behaviour in response to the perceived local prey density.

Deciding when to give up or when to move from a patch is an important aspect of foraging theory. The marginal value theorem (Charnov 1976; Parker & Stuart 1976) is perhaps the most familiar model of foraging incorporating a giving-up rule, that is, that a forager should remain in a patch until the density of prey or other resources falls to the average density for the environment. Thus, foragers may be expected to give up when they perceive that patch quality has reached a particular threshold (see Bell 1991 for a review). A criticism of early optimality models was their often implicit assumption that foragers have complete knowledge of the environment (Stephens & Krebs 1986; Bouskila & Blumstein 1992). This is unlikely to occur in nature, and it is generally accepted that animals probably use rules of thumb to assess such factors as prey density, patch quality, predation hazard, etc. (Bouskila & Blumstein 1992).

Simple alterations in search behaviour can lead to animals leaving low-quality patches, for example if turning rate declines with time since the last prey encounter, searchers will 'drift' away from low-quality areas (Carter & Dixon 1982; Fromm & Bell 1987). At a higher level, patch quality assessment may be based on a range of factors, such as recent prey capture rate (Werner & Hall 1974; Krebs et al. 1977; Roche & Glanz 1998), time since last capture (Simons & Alcock 1971), number of food items taken (Gibb 1962, but see also Krebs et al. 1974) or any of a range of sensory perceptions (Rice 1983; Persons & Uetz 1996).

In the majority of studies, patch departure decisions are assumed to be based on some aspect of prey acquisition such as net rate of energy intake or net rate of energy delivery to some central place (Charnov 1976; Parker & Stuart 1976; Orians & Pearson 1979). Where constraints on patch residence have been investigated, they have usually taken the form of increased predation risk or some medium- to long-term temporal limit, for example seasonal, diurnal or tidal effects (e.g. Erwin 1985).

There are more rigid and immediate constraints for divers such as seals. Patch residence times are constrained to be relatively short by the requirement to return to the surface to replenish oxygen stores. Thus, to interpret the observed patterns of diving we must combine studies that address dive behaviour in terms of oxygen management, with studies of patch foraging that address behaviour in terms of prey acquisition.

We present a simple model of the diving behaviour of foraging seals. Decisions on when to return to the surface are influenced by assessments of the patch quality, but
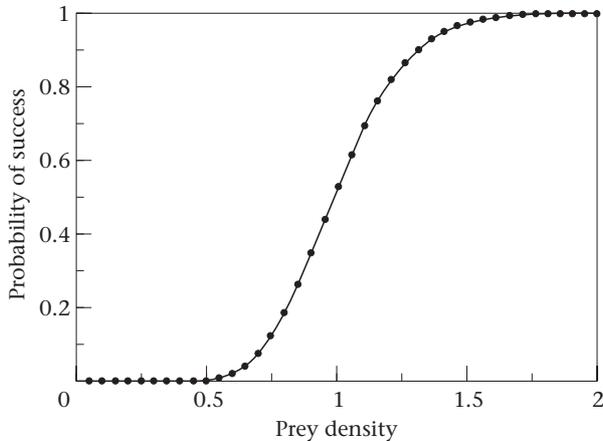
Figure 1. The probability of encountering an arbitrarily chosen number of prey items in a fixed length dive as a function of the density of prey within a patch.

Figure 2. A family of curves showing the probability of encountering zero prey items as a function of time during the dive. Each curve represents a different prey density from 0.01 to 2.0.

are ultimately constrained by oxygen balance. We show that using a giving-up rule in low-density patches increases the overall rate of encounters with prey, and we investigate the effect of varying both the depth and density of foraging sites. We suggest that patch quality may be assessed on the basis of encounter rate alone using a simple rule of thumb. We use data on the foraging behaviour of a range of phocid seal species to illustrate the model.

MODEL

We make the following simplifying assumptions about the foraging behaviour of seals.

(1) Foraging is restricted to near the sea bed or to some predetermined depth, for example some stratum of the deep scattering layer.

(2) Since prey cannot be detected from the surface, seals must swim to this fixed depth to commence searching.

(3) On arriving at the foraging depth, seals begin searching in some random fashion swimming at a constant speed v m/s.

(4) Seals begin each dive with a set level of oxygen stores, swim up and down at a constant speed and therefore arrive at the foraging site with a fixed amount of oxygen. This amount is a simple function of the depth of the dive. As foraging speed is assumed to be constant, seals will be able to forage for a fixed time T_f before exhausting their oxygen reserves.

(5) Seals can detect prey at a range of S m in a 180° field ahead. If S is small relative to the distance swum, the area searched will approximate to $2T_f VS$ m^2.

If we assume that prey are randomly distributed within a patch, with mean density D/m^2, the rate of encounters in that patch will be defined by a Poisson process with rate $\lambda = DVS$, assuming that all prey in the searched area are encountered. The scale of the patches and interpatch distances are assumed to be large enough for a seal to encounter a constant prey density during any one dive; this is equivalent to saying that 'a patch' is defined as
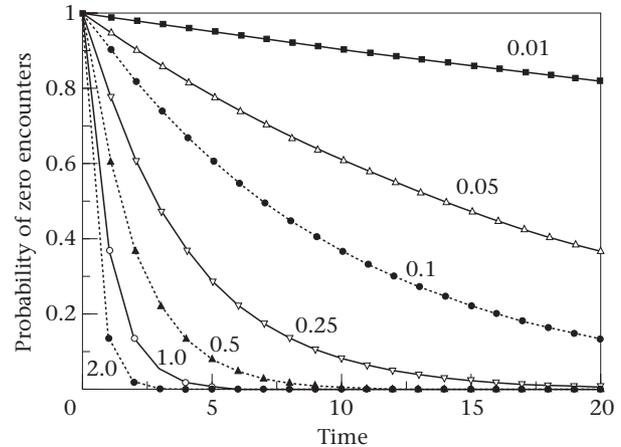
encompassing all points that can be reached during a dive.

Figure 1 shows the probability of encountering an arbitrarily chosen number of prey items in a fixed length dive, as a function of the density of prey within a patch. At low density, the probability of attaining a target is effectively zero. There is a small range of intermediate densities over which the probability of achieving the target increases rapidly as prey density increases. At high prey densities the probability of achieving the target approaches unity. There is a steep transition between success and failure that shows the importance of correctly determining the quality of a patch.

Even in the absence of any a priori estimate of prey density a foraging seal may be able to assess the likely outcome of a dive by keeping track of its encounters in that dive. Figure 2 shows the probability that a foraging seal will have encountered zero prey items as a function of time in foraging sites with a range of prey densities. It is intuitively obvious that at very low prey densities the probability of obtaining no encounters remains high throughout the dive. As prey density increases the probability of zero encounters rapidly falls, so that at moderate densities the probability of failing to encounter any prey in the first quarter of the dive is very low.

Conversely, as the probability of zero encounters early in the dive declines so the probability of achieving some target number of encounters in the remainder of the dive increases. For a range of prey densities (λ values from 0 to 2), we calculated the probability of achieving a target of 20 prey encounters in a dive of 20 time units (success) and the probabilities of having zero encounters before a set time t_q (giving-up time). Figure 3 shows the probability of success for different probabilities of giving-up. Obviously, the longer a seal takes to estimate patch quality, the less likely it is to make a mistake, but more time will be wasted in unsuccessful dives. Thus a seal may be able to increase its prey acquisition rate by using a simple rule of thumb, for example abandon dives where no prey are encountered before some threshold time.
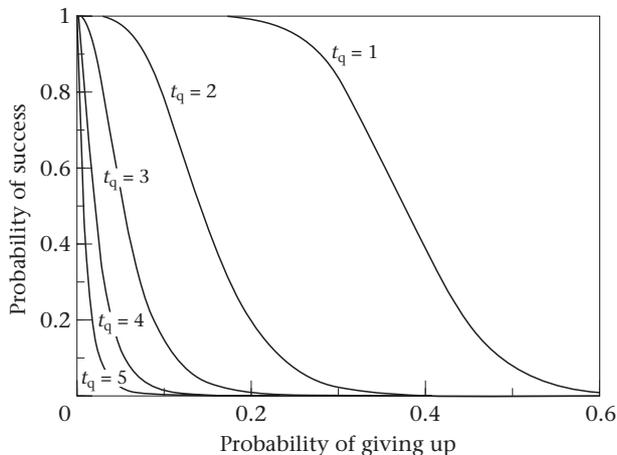
Figure 3. The probability of encountering an arbitrarily chosen target of 20 prey items during a dive versus the probability of giving up where each curve represents a different time to give up (t_q).

SIMULATION METHOD

To examine the probable consequences of different decisions, we ran a series of simulations. In each simulation a seal performed a foraging trip of 1000 dives. In control runs, the seal spent 20% of each dive swimming to and from the bottom, and remained in the foraging patch until its oxygen reserves were just sufficient for aerobic swimming to the surface; this was given an arbitrary value of 20 time units. It therefore remained in the foraging patch for the maximum time on each dive, and arrived at the surface with fully depleted oxygen stores. This strategy maximizes both the duration of individual dives, and the proportion of time spent at the foraging site. Recovery time was a simple linear function of the preceding dive duration, set so that the seal spent 90% of the time submerged. As prey encounters were assumed to result from a Poisson process, the expected prey intake on any dive was $\lambda\,T_f$, a linear function of the total time spent at the foraging depth.

In test runs the seal was given a simple giving-up rule: return to the surface if no prey were encountered before a threshold time t_q, or continue searching if at least one prey item had been encountered by t_q. Successful dives were terminated after 20 time units, as in the controls.

In the absence of any published information on the small scale distribution or density of prey species, we chose the following simple prey distribution model. First, we randomly assigned dives to be within or outside patches. Each dive was allocated a value (X_0) chosen at random from a uniform distribution between 0 and 1. We obtained the desired overall density of patches by setting a threshold value so that all dives with X_0 higher than the threshold were designated as within patches. Next, each patch was allocated a randomly selected prey density value (λ), from a uniform distribution between 0 and 1. All nonpatch densities were set to 0.

For each dive, the probability of zero encounters in the first t_q time units (P_{fail}) was calculated, assuming a Poisson distribution of encounters (Fig. 2). For each dive, a single random Bernoulli trial was performed, with

probability equal to P_{fail}, that is, for each dive, a random number, between 0 and 1, was generated and compared to the value of P_{fail}. If the resulting value was less than P_{fail} the seal was deemed to have failed; if it was greater than P_{fail} the seal was deemed to have caught at least one prey item.

If the seal did not succeed before t_q, it left the patch, went to the surface to replenish its oxygen reserves and then started the next dive. If it did succeed, it remained in the patch feeding at a fixed rate proportional to the density of prey (λ), until its oxygen reserves were used. The total number of prey encountered in a trial of 1000 simulated dives was summed and divided by the total time for those dives. We compared this rate of encounters with the same output from a control run where the seals foraged for as long as possible on each dive irrespective of prey density. The ratio of trial encounter rate to control encounter rate was classed as the proportional benefit.

In the first runs, total transit time to and from the foraging site was set to 20% of the ADL. The simulations were then run with a range of t_q values with a fixed transit swim, and a range of transit swimming times at a fixed value of t_q.

DIVING BEHAVIOUR

Dive behaviour data were collected during telemetry-based studies of movements and foraging behaviour of four phocid seal species: harbour, grey, southern elephant and hooded, *Cystophora cristata*, seals.

Harbour and grey seals were tracked with a combination of vhf radio and ultrasonic acoustic telemetry as they foraged in coastal waters of Scotland and western Norway. The methods of animal capture, handling, tag attachment and tracking have been described elsewhere (Thompson et al. 1991; Thompson & Fedak 1993; Bjorge et al. 1995). Acoustic transmitters attached to seals gave estimates of swimming depth and speed at 4-s intervals. All depth and speed profiles were plotted and inspected and dives were classed as complete if there were no gaps larger than 30 s between readings. Six points were digitized for each complete dive; the start and end of descent, maximum depth, start and end of ascent and end of subsequent surface phase. The end of descent and start of ascent were recorded where a sharp inflection occurred in the dive time profile, or at the maximum depth point if there were no discrete inflection points. Dive duration, bottom time (i.e. time between end of descent and start of ascent), maximum depth and rate of change of depth during ascent and descent were then calculated.

Hooded and southern elephant seals were tracked with satellite relayed depth loggers (SRDLs) which relayed position and profiles of dive depth and swim speed from a pseudorandom sample of dives. The methods of animal capture, handling, tag attachment and tracking for southern elephant seals have been described elsewhere (McConnell et al. 1992; McConnell & Fedak 1996). The same methods were applied to hooded seals, under permits issued by the Canadian Department of Fisheries and Oceans (G. Stenson, unpublished data). SRDL records gave times of surfacing and diving, maximum depth
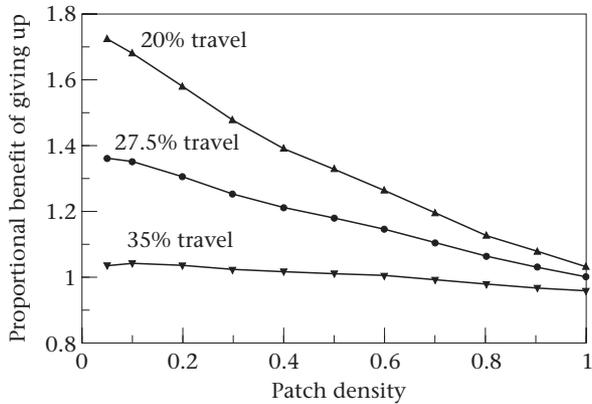
Figure 4. The proportional benefit of giving up when no prey are encountered before t_q as a function of the density of patches where each curve represents dives to a different depth. Dive depth is represented by % travel time, i.e. the percentage of the dive spent travelling vertically between the surface and the foraging site.

Figure 5. The proportional benefit of giving up when no prey are encountered before t_q as a function of the density of patches where each curve represents a different t_q from 5 to 50% of the dive time.

Figure 6. The proportional benefit of giving up as a function of t_q at one prey density.

achieved and four other depth records evenly spaced at intervals of 20% of the dive duration. Dive duration, bottom time and duration of ascent and descent phases were estimated from the SRDL data. On any dive, a seal was assumed to be at the bottom whenever depth readings exceeded 90% of the maximum depth reading. If the first or last depth reading met this criterion, we assumed that the descent ended or ascent started at the time of the reading. Thus for any dive, the maximum possible bottom time was equal to 60% of the dive duration. Otherwise, the end of descent was assumed to occur in the interval preceding the first bottom depth reading. The timing of the end of descent was estimated by extrapolation, assuming that the rate of change of depth in the preceding interval was maintained until the seal reached the bottom, that is, 90% of the maximum depth reading. Start of ascent was calculated in a similar fashion.

Published data on dive durations from northern elephant seals, collected with time depth data loggers (LeBoeuf et al. 1988, 1989), were included for comparison.

RESULTS

In all simulation runs where travel time was set to 20% of the dive duration, the giving-up strategy won. There was always a net benefit from terminating dives early if no prey were encountered in the early part of the dive. The magnitude of the benefit was highest in simulations with the lowest density of patches (Fig. 4). At higher densities, the benefit from giving-up early is reduced simply because a lower proportion of dives are unsuccessful so the relative improvement must be lower. However, even when patch density was set to 1, that is, all dives were in patches, the rate of prey encounters was still increased by giving-up early in low-quality patches.

The relative gain from giving-up depended on both the magnitude of the travel time and the speed with which a seal assessed patch quality. In deeper dives, the benefit
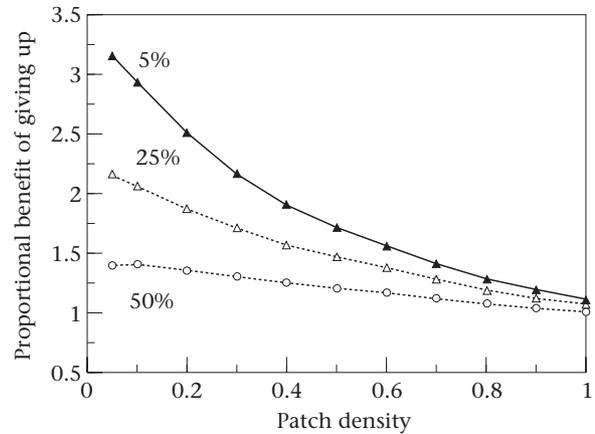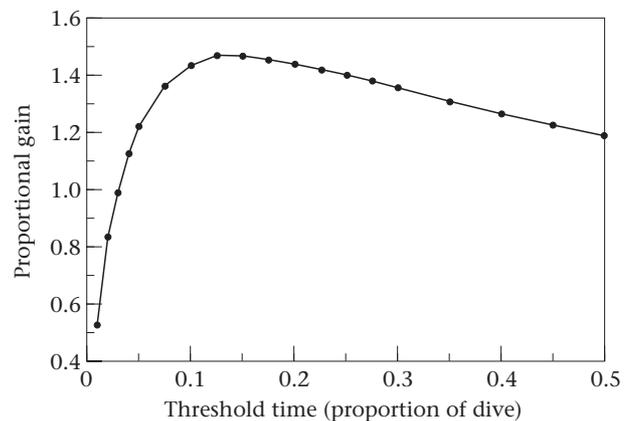
from giving-up after any particular t_q was reduced (Fig. 4). When travel time increased as a proportion of dive duration, the reduction in foraging time from giving-up in low-density patches declined as a proportion of the total time budget. In the limit, when seals dive to the maximum depth they can attain aerobically, there will be no benefit from giving-up. However, in simulations with relatively short travel times, the proportional increase in travel costs in abandoned dives was easily offset by the increased time spent in good patches. The same pattern was apparent in the relationship between relative benefit and length of time taken to decide (Fig. 5). As the time taken to decide decreased, the relative benefit increased, up to a maximum (Fig. 6). If decision time is too short the net benefit falls rapidly, dropping below 1, that is, the seal gains less prey per unit time than if it stayed.

Figure 7 shows frequency distributions of dive durations from two shallow-diving (grey and harbour seals) and three deep-diving phocid seal species (hooded seal and northern and southern elephant seals). In the deep-diving species, short dives were rare and the majority of dive durations were close to estimates of the ADL for active swimming seals. Conversely, for harbour and grey
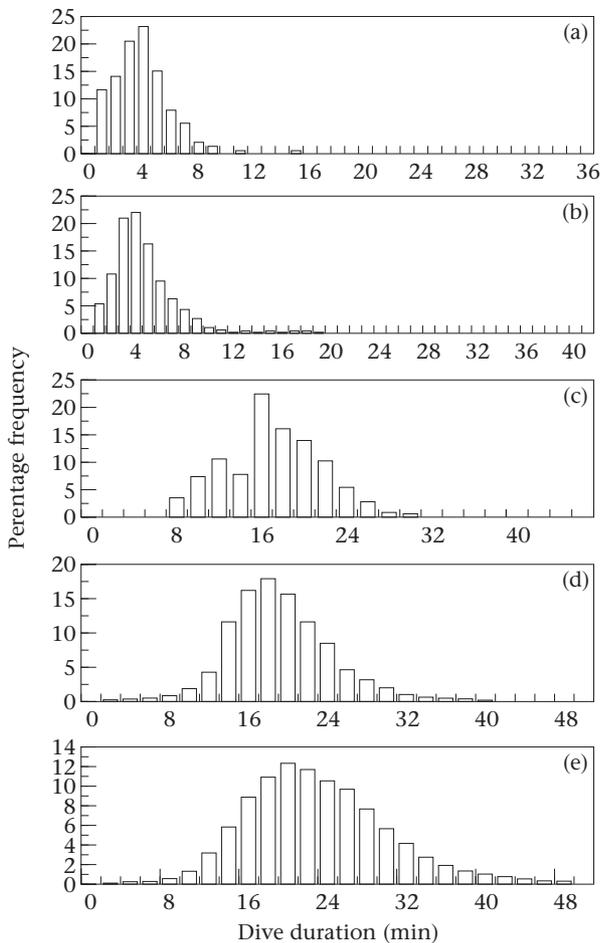
Figure 7. Frequency distributions of dive durations from free-swimming wild (a) harbour, (b) grey, (c) hooded, (d) northern elephant and (e) southern elephant seals. (a) $N=4$ seals, 632 dives; (b) $N=4$ seals, 477 dives; (c) $N=3$ seals, 1474 dives; (d) $N=6$ seals, 3026 dives and (e) $N=6$ seals, 8497 dives (LeBoeuf et al. 1988). The x axes are labelled in real time units, but have been scaled to account for differences in body size (i.e. scaled to body mass$^{0.75}$) so that dives of equivalent durations in biological time are on the same vertical.

seals, which dive to shallow depths, short foraging dives were common and the majority of dives were well below their estimated ADLs. For shallow divers, frequency distributions of dive durations were positively skewed, while for deep divers they were either symmetrical or negatively skewed (Fig. 7).

Figure 8 shows the frequency distributions of times spent at the bottom of dives, for two shallow-diving and two deep-diving seal species. To make the data comparable across a range of dive depths, we first calculated the aerobic bottom time, defined as the estimated ADL minus the time taken to swim to and from the bottom. This was then used to calculate the aerobic bottom proportion (ABP), equal to the time spent at the bottom, expressed as a proportion of the aerobic bottom time. In each case ADL was estimated from allometric relationships between metabolic rate, body oxygen stores and body mass (Kleiber 1975; Schmidt-Nielsen 1983; Kooyman 1989; Lydersen et al. 1992; see Fig. 8 for details). Deep divers

appeared to stay at the bottom for as long as possible, with most dives apparently close to or often in excess of their aerobic capacity. Over 66% of southern elephant seal's and 77% of hooded seal's dives had estimated ABP >0.9. Conversely, shallow divers generally left the bottom well before reaching their aerobic limits. Less than 1% of harbour seal's and 6% of grey seal's dives had estimated ABP >0.9.

DISCUSSION

Previous modelling exercises have concentrated on those aspects of diving concerned with oxygen balance, and have examined the optimal solutions in respect of dive duration and dive depth. Our simulation results suggest that in the wild, a seal may benefit by varying its dive behaviour in relation to the spatial distribution of the target prey.

It is obvious that a seal hunting either for uniformly distributed prey, or widely scattered discrete units of prey (either single fish or dense shoals), should schedule its diving so as to maximize the time spent at the foraging depth. Prey encounters would be described either by a constant rate or something approaching a Poisson distribution. In either case the number encountered would be a linear function of time spent searching. The patterns of diving and surfacing might therefore be expected to fit the marginal value type approaches of Houston & Carbone (1992). In the case of predators taking single large items, the above patterns may be modified by successful dives being terminated earlier to allow the prey items to be processed at the surface.

Our simulations suggest that a seal hunting prey distributed in more diffuse patches could improve its average encounter rate by varying its dive durations in response to some perceived correlate of prey density. In addition, it is apparent that the magnitude of the benefit would be affected by the depth at which the seal was hunting. The simple models presented above clearly indicate that foraging seals can increase their rate of prey intake by abandoning dives that are likely to be unproductive. They also demonstrate that very simple rules of thumb, based on recent history of prey captures, can dramatically improve the effectiveness of foraging by increasing the overall rate of encounters with prey.

The simple rule of thumb approach used here provides a plausible explanation for the lack of fit between observed dive patterns and those predicted from oxygen balance models. However, many pinnipeds are opportunistic predators which take a wide range of prey types, and it is unlikely that the optimal hunting strategy for one prey species will be optimal for all others. In addition, the pattern of distribution of patches in the model was extremely simple. In some situations alternative patch distribution patterns could enhance or nullify the effects reported here. For example, divers preying on randomly distributed large prey items should show long sequences of dives close to their ADL, interspersed with occasional short successful dives. Such patterns have been identified in wild otters, *Lutra lutra* (Nolet et al. 1993), where
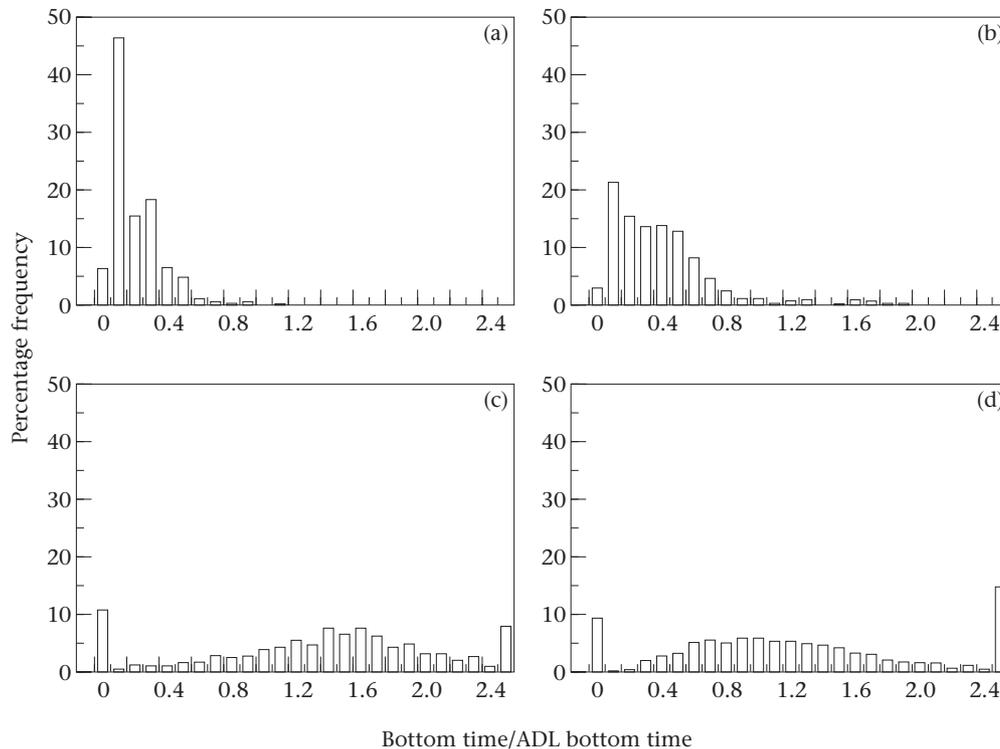
Figure 8. Frequency distributions of bottom times expressed as proportions of the estimated aerobic bottom time, for (a) harbour, (b) grey, (c) hooded and (d) southern elephant seals. (a) $N=4$ seals, 516 dives; (b) $N=4$ seals, 477 dives; (c) $N=3$ seals, 1474 dives and (d) $N=6$ seals, 3026 dives. Aerobic bottom time was estimated from the aerobic dive limit (ADL) minus the travel time to the bottom. Bottom time was defined as time spent below 90% of the maximum depth. ADL was estimated assuming a field metabolic rate of 2×BMR. BMR was estimated from a fitted allometric relationship: BMR= 0.0101 body mass$^{0.75}$. Oxygen stores were estimated as 73 ml O_2/kg for hooded and elephant seals and 59 ml O_2/kg for harbour and grey seals (Kleiber 1975; Schmidt-Nielsen 1983; Kooyman 1989; Lydersen et al. 1992).

successful dives were shorter than unsuccessful dives in the same depth of water. Despite these limitations, the model shows that assessment of and reaction to patch quality could lead to patterns of dive durations similar to those seen in some shallow-diving species, and different from those predicted from oxygen balance models.

In this model we have simply examined rate of prey encounters as a function of time. Clearly, such gross intake measures may not be the appropriate currency. However, if the three behavioural states, exchanging gases at the surface, swimming to and from depth and foraging, all impose similar metabolic demands, the gross rate of energy intake would be linearly related to net rate of energy intake, and will be proportional to the efficiency of energy intake.

We have assumed that descent and ascent swimming speeds are constant and implicitly assumed that swimming efficiency is constant with respect to depth of dive. If swimming efficiency varies with depth, for example as a result of changes in buoyancy, divers may be able to extend the duration of deep dives. This could partly explain the observed increase in dive duration with depth. However, improved efficiency of swimming to deeper depths could, at most, have only a small effect on increasing dive duration in deep dives. The important point here is not that deep dives are longer than expected, but that the majority of shallow dives are very much shorter than possible, often much shorter than ADL.

We assume that surface duration is a simple linear function of dive duration. Data from grey and elephant seals show that, above a certain threshold dive duration, surface durations remain relatively constant (Hindell et al. 1992; Thompson & Fedak 1993). Conversely, in Weddell seals, *Leptonychotes weddelli*, above a threshold dive duration, surface durations increase exponentially (Kooyman 1989). However, for dives shorter than ADL, surface duration is a reasonably linear function of preceding dive duration in all three species. Nonlinear relationships between surface and dive durations above ADL will enhance or reduce the benefits from extending long dives, but will not explain the preponderance of very short dives.

There is little published information on the fine scale distribution of fish prey species. So there are no data on prey distribution patterns with which to test the predictions for seals. In terrestrial systems where prey density can be more easily assessed, there are reports of foragers spending a higher proportion of their time in higher-density patches. Racey & Swift (1985) showed that pipistrelle bats, *Pipistrellus pipistrellus*, make foraging decisions similar to those proposed here, for diving predators. When local prey densities were below a threshold value of 0.3/m^3, bats searched for less than 1 min before moving away. Where prey densities exceeded the threshold, the bats continued to search with an intensity related to prey density until other temporal constraints became important.

Data from an experimental test of an optimality model of diving in the pochard, *Aythya ferina*, appear to contradict our analysis. When Carbone & Houston (1994) altered food concentration and depth in experimental trials, neither foraging times nor dive times were related to prey concentration. However, as each trial consisted of a bout of dives to one patch with a fixed prey concentration, the ducks did not have the option of searching elsewhere. There would therefore be no benefit from giving up early, as the expected prey density on each dive in a bout would be similar.

Our analysis suggests that the benefit of giving-up is reduced in deeper dives. In all but the single prey loading case, we would expect the incidence of abandoning dives to decrease with depth and therefore the average duration of dives to increase. There are now extensive data on dive patterns in several pinniped species. Those species that dive deepest do indeed also dive longest, and perform a high proportion of dives at or above their ADL (Le Boeuf et al. 1988, 1989, 1992; Hindell et al. 1991, 1992; Folkow & Blix 1995). They also often show a positive relationship between dive duration and dive depth even when comparisons are restricted to particular types of foraging dive.

Our data support the suggestion that short dives are rare in deep-diving species. The majority of dive durations were close to estimates of their ADL, suggesting that dive durations are primarily determined by levels of oxygen stores. Conversely, in shallow divers the preponderance of short foraging dives, with the majority well below estimates of their ADLs, suggests that oxygen reserves are not usually the criteria for determining dive durations. However, because of the increased travel times in deep dives it is not surprising that short dives are underrepresented in the deep-diving species (Le Boeuf et al. 1988, 1989, 1992; Hindell et al. 1991, 1992). The observed differences in frequency distributions may simply reflect an increase in travel times in deeper dives.

If our model is realistic, we should also expect that on the majority of dives, the deep divers should maximize the total time spent in the foraging area on each dive. In our data the difference between the deep and shallow divers is striking. The shallow-diving seals generally left the bottom well before reaching their aerobic limits, with only a small proportion of ABPs approaching 1. Conversely, the data suggest that deep divers generally stayed at the bottom for as long as possible. ABP was often much greater than 1, that is, the seals stayed in the foraging patch for several times the aerobic bottom time. To some extent this is an artefact of the way we defined ABP. The amount of oxygen used travelling to and from the bottom was assumed to be a linear function of dive depth, so aerobic bottom time was a decreasing function of depth. In equal duration dives that exceed the ADL, the ABP will be higher in deeper dives. In the limit, if the descent plus ascent time equalled or exceeded the ADL, spending any time at depth would give an infinite ABP.

As our data came from different seal species foraging in different marine environments there may be several plausible explanations for such a relationship, for example the time taken to find, catch and process prey may be longer in the deep divers. It is more difficult to explain the preponderance of short dives in shallow divers. If seals were not assessing patch quality on a dive by dive basis we should expect them to maximize the time spent at those foraging patches. Unless the majority of dives are ended because of some prey-handling constraint, this should lead to ABP distributions similar to those seen in deep divers.

An increase in ABP with dive depth would also be expected with some other patch foraging models. For example, in the marginal value approach, the higher travel costs in deep dives would reduce the average yield of the environment. A forager should therefore spend longer at the bottom of deep dives. Obviously, the constraints imposed by oxygen stores would set some upper threshold on dive duration. Our model is conceptually different to the marginal value theorem in that the likelihood of giving up is a declining function of time spent in the patch with an upper limit set by oxygen stores, and the decision to leave is not driven by patch depletion effects.

The observed patterns of dives by some seals may be explained by this type of simple patch departure model. In previous papers (Thompson et al. 1991; Thompson & Fedak 1993; Bjorge et al. 1995) we noted that when travelling between haul out sites and between patches, both grey and harbour seals performed sequences of V-shaped dives, with occasional long flat-bottomed dives. If during transit the seals inspect the sea bed for suitable foraging habitats, for example a particular sediment type, we should expect dives to unsuitable habitats to be terminated quickly. The small amount of time spent at the bottom would produce a characteristic V-shaped dive profile. If seals encounter a suitable foraging site they will begin foraging, hence the occasional flat-bottomed dives. When in preferred foraging areas, seals perform long sequences of flat-bottomed searching dives. Frequency distributions of bottom times show that a high proportion of these are short; 66% of dives had ABP <0.5 (Fig. 8). Interspersed within these are sequences of longer foraging dives where the seal stays at the patch up to and occasionally beyond the aerobic limit. Such a pattern could result from a seal searching through a patchy habitat, where most dives are terminated early because of poor patch quality, and periodic long dives represent time spent in high-quality patches.

In such a scenario there would be little agreement between observed dive durations and those predicted for optimal delivery of oxygen to the foraging patch (Kramer 1988; Houston & Carbone 1992; Thompson et al. 1993; Carbone & Houston 1994, 1996; Carbone et al. 1996). A lack of fit between the predictions of models of oxygen balance with observed dive patterns does not invalidate the models. It may simply indicate that, in the wild, the apparently simple act of diving to the sea bed is in fact a finely tuned response to a wide range of physiological and environmental demands.

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