



## How long does a dive last? Foraging decisions by breath-hold divers in a patchy environment: a test of a simple model

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Many theoretical models have been proposed to explain and predict the behaviour of air-breathing divers exploiting a food resource underwater. Many field observations of the behaviour of divers do not fit with the prediction that to maximize energetic gain divers should dive close to their aerobic diving limits. In an attempt to explain this paradox, Thompson & Fedak (2001, *Animal Behaviour*, **61**, 286–297) proposed a model of diving behaviour that takes into account patchily distributed prey patches of varying quality. We tested this model experimentally in a simulated foraging set-up. We measured the diving behaviour of grey seals, *Halichoerus grypus*, diving to patches of varying prey density and distance from the surface. Our results were equivocal with respect to the model predictions. Seals responded to prey density, leaving low-quality patches earlier. However, this pattern was still evident at long dive distances, contrary to the prediction that during deep dives seals should stay at a patch regardless of prey density. While seals maximized dive durations at high prey densities and long distances, they did not do so at short distances. The apparent quitting strategy of the seals always produced higher net rates of energy gain than would have been achieved if they had remained at the foraging site up to their aerobic dive limit on every dive. These results indicate that seals' diving behaviour, particularly bottom duration, may indicate the relative prey availability in their environment.

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Air-breathing divers are faced with the conflict of exploiting food resources underwater, yet needing to surface to breathe. Various models have been proposed to explain how divers should behave, based around the principles of optimality: namely that divers seek to maximize some currency of gain while diving and foraging. 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; Carbone & Houston 1994, 1996;

Carbone et al. 1996). It is always implicitly assumed that the number of prey encountered is a linear function of time spent searching. Maximizing prey acquisition would then be achieved by maximizing time spent in the foraging patch. Divers should therefore maximize the proportion of time spent at the foraging site by minimizing the proportion of time spent travelling and/or replenishing their oxygen stores at the surface. The decision to terminate each dive is 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 aerobic dive limit (ADL: Kooyman 1989) regardless of the depth of the prey patch. Throughout this paper we use the term ADL to represent how long an animal's estimated oxygen stores would last at a particular rate of utilization (directly measured in this study). It is a reasonable and simple metric that allows comparison of dive durations across species and across diving behaviours in a range of contexts.

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Many species of diving birds (e.g. Chappell et al. 1993; Croxall et al. 1993; Jodice & Collopy 1999) and mammals (e.g. Kooyman et al. 1980; Fedak et al. 1988; Thompson et al. 1991; Nolet et al. 1993) apparently choose to terminate the majority of their dives before their oxygen reserves are exhausted. The decision to leave the foraging site and swim to the surface must be determined by some factor other than level of oxygen stores.

This apparent lack of fit between behavioural observations and the predictions of these early optimal diving behaviour models has begun to shift the emphasis away from the constraints imposed by physiology towards other factors, such as predation risk (Heithaus & Frid 2003), the likelihood of relocating prey (Ydenberg & Clark 1989) and prey availability (Thompson & Fedak 2001). Mori et al. (2002) proposed an optimal diving model in which patch quality affects patch residence time (through a nonlinear, rather than linear effect on energy intake rate while in the patch) and also predicted a wide range of optimal dive times over a range of likely patch qualities.

Thompson & Fedak (2001) suggested that diving predators may modify their behaviour in response to perceived changes in prey density. They investigated the effects of changing dive durations in response to real-time assessments of patch quality. Their results suggested that divers exploiting patchy environments could increase the overall rate of energy gain by giving up early (i.e. terminating dives before depleting oxygen stores) in low-quality patches. Significant improvements in average rate of gain could be achieved by using simple rules of thumb to assess patch quality. For example, because the probability of encountering prey early in a dive is a function of prey density, lack of encounters before some threshold time indicates a high probability that the forager is in a low-quality patch. A simple giving-up rule based on encounter rate early in the dive was shown to be highly effective at increasing average prey encounter rate. The model also predicted that, because of increased travel costs, the benefit of giving up would be reduced when seals are diving to deeper depths. Deeper-diving seals would therefore be expected to perform long dives close to aerobic limits.

At present it is hard to measure patch quality at appropriate temporal or spatial scales, so testing such models relies on realistic experimental set-ups with captive studies. Cornick & Horning (2003) examined the effect of prey availability on the diving behaviour of captive Steller sealions, *Eumetopias jubatus*, trained to inspect feeding stations in response to visual signals. Their animals increased dive duration, foraging time and foraging efficiency with increasing number of prey per dive, but the study did not report results from sealions searching when no food was presented.

We experimentally investigated foraging and diving decisions of captive grey seals, *Halichoerus grypus*, in response to changes in prey density and patch depth in quasynatural dives. We examined the relations between fine-scale foraging behaviour at the level of the dive and the availability of prey, in terms of density and distance from the surface, and simultaneously measured both the energetic gain rate and the metabolic cost.

## METHODS

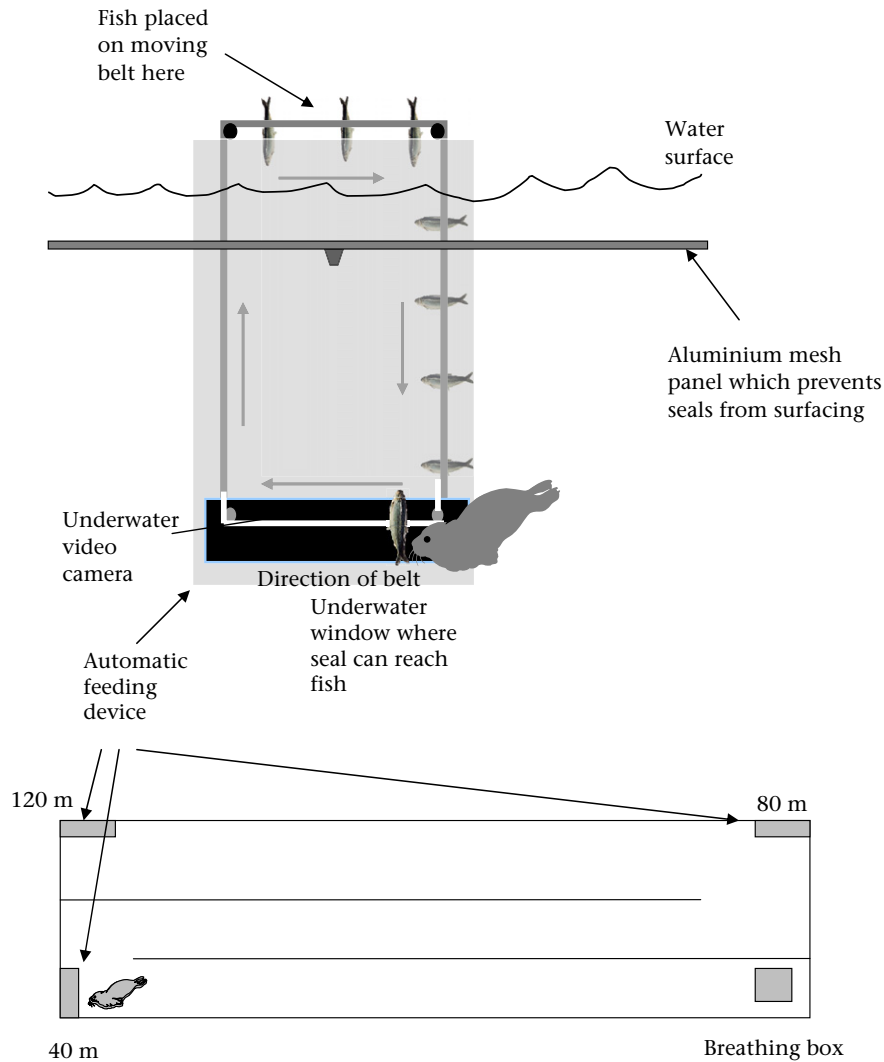
### Study Animals

Five female grey seals (three juveniles and two adults) were captured at Abertay sands (56°25.59'N, 2°45.59'W), an intertidal haul-out site 10 km north of St Andrews, U.K. They were captured by hand, in hoop-nets, while they rested on exposed sand banks at low tide. They were restrained in pole-nets and taken by boat to a purpose-built captive facility of the Sea Mammal Research Unit in St Andrews, a journey of approximately 20 min. Throughout the study, the seals were housed in outdoor sea water pools at ambient temperature and fed a diet of herring, *Clupea harrengus*, and sandeels, *Ammodytes marinus*, supplemented with vitamins (Aquavits, International Zoo Veterinary Group (U.K.), Keighley, U.K.). Training using basic operant-conditioning techniques was used wherever possible to facilitate movement between areas of the facility and for health assessment without having to restrain seals manually. Environmental enrichment was provided in the form of buoys, balls, floating tubes and fish encased in ice blocks. All experiments and animal handling were approved by the Animal Ethical Review Committee of the University of St Andrews and carried out in accordance with a Home Office licence. The seals were inspected by a veterinary surgeon on a monthly basis to ensure their continuing health in captivity. All seals were returned to the wild at point of capture after a maximum period of 10 months in captivity.

### Simulation of Foraging

We trained the seals to swim in a large experimental pool (42 × 6 m and 2.5 m deep) from a clear acrylic breathing chamber (the surface) to a 'prey patch'. For the prey patch we used an aluminium-framed conveyor belt delivering fish underwater semiautomatically at a controlled rate (Fig. 1). The frame was 3 m tall and 1.5 m wide, placed on the bottom of the pool. Within the frame was a conveyor belt holding 80 consecutive slots in which fish could be fitted by hand from an open access at the top of the feeder. This top part of the feeder was housed in a small hut in which the experimenter sat. The conveyor belt was driven by a motor powered by a 12-V DC battery. As the belt turned, fish became available to seals within an opening (1 × 0.3 m) situated at the bottom of the frame. A video camera was mounted above this opening so that the seals' presence at the feeder could be recorded and monitored on a screen inside the hut.

Fish delivery rate was controlled by the belt speed and by the distance between fish on the belt. This enabled us to vary the prey encounter rate (PER) between 0 and 14 fish/min. During any one dive, the prey items were equally spaced on the belt and the time between encounters was therefore constant. Encounter rate was varied randomly between dives. The upper limit of PER used in the experiments corresponded to the highest PER recorded in the wild with remote video cameras deployed on freely diving harbour seals, *Phoca vitulina*, feeding on sandeels (Bowen et al. 2002).



**Figure 1.** Diagram of the automatic feeder and plan of the experimental pool showing the feeder's three positions for the three dive distances, and the breathing box, which is the only place that the seal could surface.

Aluminium mesh panels prevented the seals from surfacing anywhere other than the breathing box. We simulated different patch depths by moving the feeding device to various positions around the pool and using net panels to manipulate the distances the seals had to swim to reach it. Trials were carried out with the feeder at patch distances of 40, 80 and 120 m from the breathing box. Foraging trials took place between 0900 and 1600 hours each day and seals were fasted overnight before an individual trial for 15–20 h. Each trial lasted between 30 and 120 min; the duration was determined by how long it took the seal to consume a set ration. The amount fed to each seal depended on its age and size but was constant between days for all animals. To ensure that the seals did not reach satiation during the trials, the amount fed was always less than the full daily ration. Some food was left over for training and moving the seals after each trial. The automatic feeding device could not be easily moved between dives or even between days, so dive distances were held constant for periods of 1–2 weeks.

We attached time depth recorders (Mk 8 TDR, Wildlife Computers, Richmond, U.S.A., mass 62 g) to the seals' heads to record swim velocity and dive and surface durations. These were attached with Velcro and secured with a cable tie to a patch of nylon webbing (measuring  $4 \times 8$  cm) which was glued to the fur of the seal with a fast-setting epoxy glue. The seals were sedated during this procedure by either intravenous or intramuscular injection of a tiletamine–zolazepam mixture (Zoletil 100, Virbac, France; Baker et al. 1990). These patches fall off during the seals' annual moult. We recorded the start and end time of each dive, the durations of the descent, bottom (time spent at patch) and ascent phases of the dive, and the number of fish eaten. Oxygen consumption was measured with the open-flow respirometry system described in Sparling & Fedak (2004). To convert oxygen consumed to energy expended we used a conversion factor of 20.1 kJ/litre of oxygen (but see Walsberg & Hoffman 2005 and Discussion). To see how close to physiological limits the seals were diving in each case, we calculated

the ADL and expressed each dive duration as a proportion of estimated ADL. We calculated ADL for each individual dive by dividing the calculated whole body store of oxygen (using a figure of 60 ml O<sub>2</sub>/kg, Kooyman 1989) by the rate of diving oxygen consumption or diving metabolic rate (DMR). The DMR varies considerably with the duration of the dive (Castellini et al. 1992; Sparling & Fedak 2004), so we calculated an ADL for each dive using a fixed oxygen store and the lowest measured DMR for each animal at each dive distance.

### Behaviour and Energy Gain Rate

We carried out a set of simulations to test whether the observed responses to variations in prey availability led to an improvement in rate of net gain over what the seals would have achieved by diving to the limit imposed by oxygen stores on every dive. We estimated the number of prey items that would have been encountered if the seals had remained at the feeding device for their maximum aerobic bottom duration (ABL: calculated as ADL minus average travel time) on all dives. As with the actual trials, prey density was held constant within a dive but varied between dives. We used the same sequences of randomly generated PERs that were presented during the actual foraging trials. Each simulated trial ended when the number of food items 'eaten' was equal to the seals' set daily ration. To estimate the energy cost of each simulated dive, we used the lowest measured DMR at that distance for each animal. Then for each day, we compared the simulated rate of net energy gain (energy gained minus energy used) over all the dives with that observed in the feeding trials.

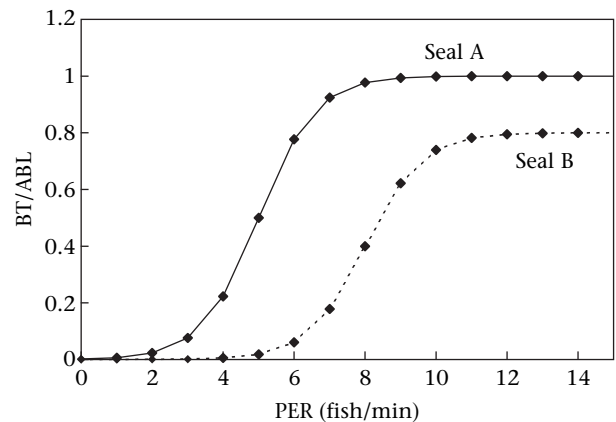
### Statistical Analysis

The effect of dive distance on dive duration and bottom duration was initially assessed with linear mixed-effects models in R (version 2.01) (R Development Core Team 2006) with seal identity included as a random effect. Models were constructed for each response variable for PER = 0 and PER > 0 separately. We used deletion tests to assess the significance of each term in the models, whereby in a likelihood ratio test the full model (containing all terms) was compared to a model with the term of interest omitted. A significant result indicated that the model including the term was a better fit to the data than the model with that term omitted.

To examine in more detail each seal's behavioural response to changing prey densities and how this changed with depth we chose a three-parameter sigmoidal model of the form:

$$y = (a / (1 + \exp(-(x - x_0) / b)))$$

This model describes the relation between prey encounter rate and bottom duration for each animal at each dive distance. Because a seal's mass often differed between dive distances, rather than using actual bottom duration in the model, which can be affected by mass through the



**Figure 2.** Illustration of the derived parameters of the relation between bottom duration/aerobic bottom duration (BT/ABL) and prey encounter rate (PER). In this example for seal A parameter  $a$  (the maximum bottom duration at each depth) is equal to 1, indicating that the seal stays at the feeding patch at the highest prey densities up to its aerobic limits, whereas for seal B this value is 0.8 indicating that the seal is not reaching its aerobic limits. For seal A the parameter  $x_0$  (the PER at half the maximum bottom duration) is equal to 5 and for seal B it is 8 indicating that the likelihood of seal A 'giving up' occurs on dives where PER is less than 3 fish/min, whereas seal B is giving up at a higher PER threshold of 8 fish/min. The Thompson & Fedak (2001) model predicts that  $a$  should increase with patch distance and that  $x_0$  should decrease with increasing patch distance.

effect of mass on ADL, we used bottom duration (BT) as a proportion of ABL (BT/ABL). This model provided easily interpretable parameters where  $y$  is BT/ABL,  $x$  is PER,  $a$  describes the maximum bottom duration (BT/ABL<sub>max</sub>) at each depth,  $x_0$  is the PER at half the maximum bottom duration and is therefore an indication of the prey density threshold below which seals are ending dives early, and  $b$  is the slope parameter that gives an indication of the rate of change around this threshold. The parameters  $a$ ,  $x_0$  and  $b$  (and associated standard errors) were estimated for each animal at each depth, with SigmaPlot version 8.0 (Systat Software Inc., San Jose, CA, U.S.A.; Fig. 2). We used  $t$  tests with Bonferroni correction for multiple comparisons to test for significant differences in these parameters between depths.

The difference between the rate of net energy gain observed and that predicted on the basis of no giving-up rule was assessed with a paired  $t$  test. Statistical significance for all tests described was assumed at  $P < 0.05$  unless otherwise stated.

## RESULTS

We recorded 1735 dives from five female grey seals (two adults and three pups <1 year old). Table 1 summarizes the general diving characteristics. Overall mean  $\pm$  SD dive duration was  $4.30 \pm 2.87$  min. In general, adults dived for longer than pups; however, the proportion of the dive cycle spent submerged was similar across all animals (0.78–0.87). Mean  $\pm$  SD swim speed during travelling

**Table 1.** Summary of dive characteristics for each seal at each dive distance

Dive distance	N	Dive duration (min)		Surface duration (min)	Proportion submerged*
		$\bar{X} \pm SD$	Maximum		
<b>Seal L</b>					
40 m	170	3.49±2.52	13.82	0.65±0.42	0.79
80 m	174	4.80±2.77	11.75	0.97±0.37	0.81
120 m	196	6.92±3.90	17.33	1.39±0.52	0.81
<b>Seal Q</b>					
40 m	155	4.59±2.02	10.93	1.02±0.27	0.80
80 m	172	6.17±2.38	17.03	1.52±0.47	0.79
120 m	78	7.15±2.44	13.40	1.47±0.37	0.82
<b>Seal K</b>					
40 m	136	1.90±1.09	5.18	0.41±0.59	0.82
80 m	195	3.16±1.34	7.60	0.50±0.26	0.86
120 m	46	4.00±1.51	7.47	0.56±0.17	0.87
<b>Seal N</b>					
40 m	134	2.11±1.39	5.85	0.43±0.38	0.83
80 m	28	3.44±1.43	6.90	0.46±0.14	0.87
120 m	58	4.35±1.79	8.47	0.83±0.64	0.83
<b>Seal R</b>					
40 m	58	2.61±0.79	5.97	0.39±0.18	0.87
80 m	93	3.16±0.71	4.90	0.50±0.08	0.86
120 m	48	4.15±1.05	6.25	0.75±0.23	0.85

Seals L and Q were adult, the others were pups (<1 year old).  
\*Proportion of time spent submerged.

phases of dives was  $1.72 \pm 0.42$  m/s for pups and  $1.36 \pm 0.42$  m/s for adults.

### Dive and Surface Duration

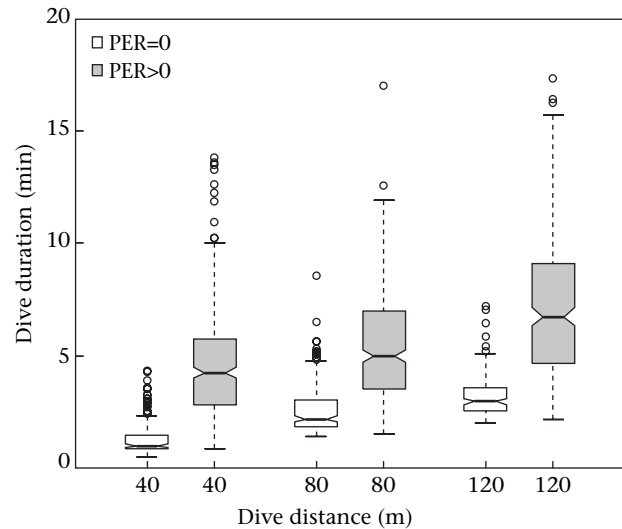
Dive duration varied depending on dive distance and PER (Fig. 3). It increased with dive distance for dives where PER = 0 and PER > 0 (Table 2). For all dive distances, dive duration was always longer for PER > 0 dives than for PER = 0 dives (Fig. 3). Mass had a significant positive effect on dive duration at PER = 0 but not at PER > 0. Where PER > 0, dive duration increased significantly with increasing PER (Table 2).

The proportion of dives above the seals' estimated ADL also increased as dive distance increased (Fig. 4). For adults, 0.6% of dives exceeded ADL at 40 m, increasing to 6% at 80 m and 9% at 120 m. For pups, between 1 and 3% of dives at 40 and 80 m exceeded ADL, with this figure increasing to 18% at 120 m.

Surface duration increased with the duration of the preceding dive (linear least-squares regression: slope = 0.167,  $F_{1,1564} = 709.7$ ,  $R^2 = 0.54$ ,  $P < 0.0001$ ; Fig. 5) with no effect of depth on this relation (ANCOVA:  $F_{2,1564} = 0.20$ ,  $P = 0.659$ ).

### Bottom Duration

For dives where PER = 0, bottom duration did not change with increasing dive distance (Table 2). However, over all dives with PER > 0 there was a slight but



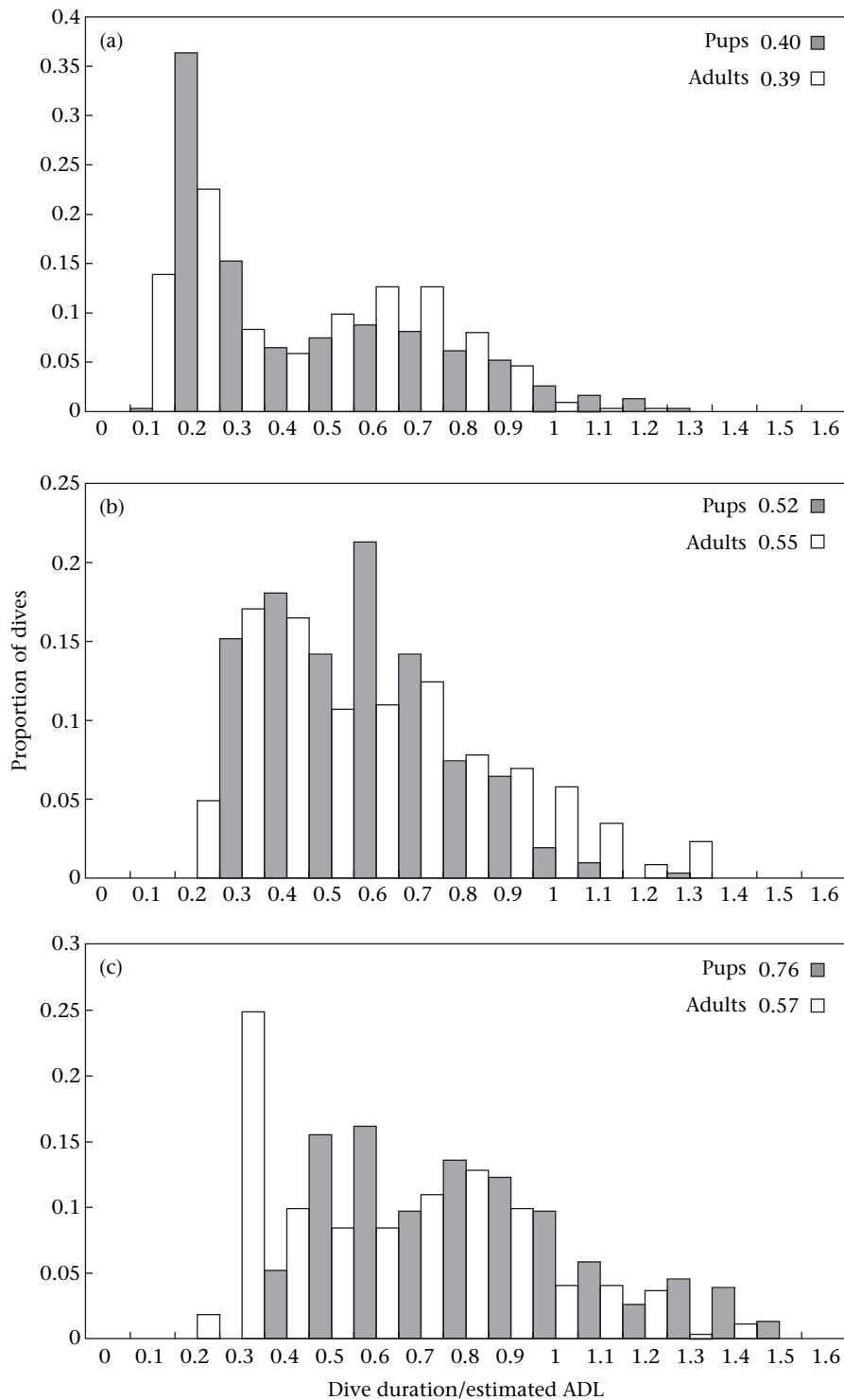
**Figure 3.** Box plots of dive duration in relation to dive distance and presence/absence of prey on a dive. PER: Prey encounter rate. Data from all five seals are included. Each box stretches from the first to the third quartile. The median is shown as a line across the box. The notches either side of the median extend to the 95% confidence limits (calculated as  $\pm 1.58$  interquartile range,  $IQR/\sqrt{(n)}$  according to Chambers et al. 1983). The whiskers extend to the most extreme data point which is no more than  $1.5 \times IQR$ . Points beyond this limit are shown as outliers.

**Table 2.** Results of linear mixed-effects models describing dive duration and bottom duration

	AIC*	LRT	Slope value±SE	P
<b>Dive duration PER=0</b>				
Full model	1329.6			
Term removed:				
<b>Dive distance</b>	1728.9	<b>401.3</b>	<b>0.024±0.001</b>	<b>&lt;0.0001</b>
<b>Mass</b>	1331.7	<b>4.2</b>	<b>0.005±0.002</b>	<b>0.042</b>
<b>Dive duration PER&gt;0</b>				
Full model	4215.4			
Term removed:				
<b>Dive distance</b>	<b>4225.5</b>	<b>307.5</b>	<b>0.031±0.001</b>	<b>&lt;0.0001</b>
<b>PER</b>	<b>4825.5</b>	<b>612.1</b>	<b>0.554±0.019</b>	<b>&lt;0.0001</b>
Mass	4215.4	2.9		0.087
<b>Bottom duration PER=0</b>				
Full model	1204.2			
Term removed:				
Dive distance	1206.0	3.8		0.053
<b>Mass</b>	<b>1212.2</b>	<b>9.9</b>	<b>-0.007±0.002</b>	<b>0.002</b>
<b>Bottom duration PER&gt;0</b>				
Full model	4200.3			
Term removed:				
<b>Dive distance</b>	<b>4213.6</b>	<b>15.3</b>	<b>0.007±0.002</b>	<b>&lt;0.0001</b>
<b>PER</b>	<b>4777.1</b>	<b>578.8</b>	<b>0.561±0.022</b>	<b>&lt;0.0001</b>
Mass	4199.2	1.0		0.318

PER: Prey encounter rate. The statistical significance of each term was assessed with likelihood ratio tests (LRT) by removing each term and comparing the full model including all terms with the model minus that term. For significant terms, the slope value and standard errors are given. Significant terms are in bold type.

\*Akaike's information criterion.

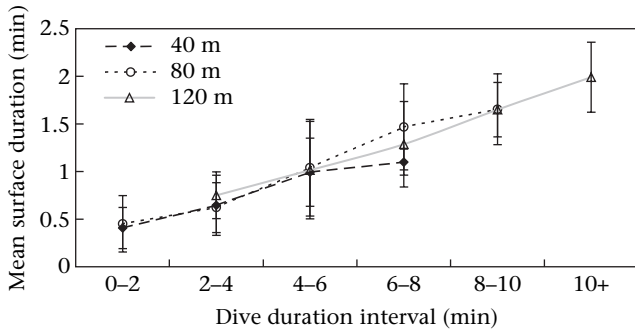


**Figure 4.** Dive duration in relation to estimated aerobic dive limits, ADL, at (a) 40 m, (b) 80 m and (c) 120 m for pups and adults. Means for each distance are given.

significant increase in bottom duration with increasing dive distance. This difference in bottom duration occurred exclusively between 80 and 120 m (Fig. 6). At  $PER > 0$ , bottom duration also increased significantly with increasing PER. Similar to its effect on dive duration, mass had an effect on bottom duration at  $PER = 0$ , but not at  $PER > 0$ .

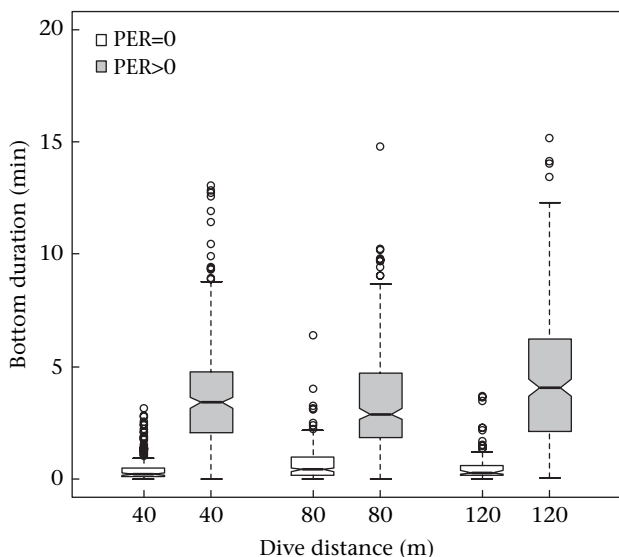
This effect was negative in direction suggesting that larger animals spent less time than smaller animals at the patch when no prey was present.

At all dive distances, bottom duration (as a proportion of ABL) increased curvilinearly with increasing PER (Fig. 7). At low PER values, bottom duration was low but



**Figure 5.** Duration of the postdive surface period in relation to dive duration. Mean  $\pm$  SD surface durations were calculated for all dives in each duration bin, for each depth.

started to increase with increasing PER at an encounter rate of around 2–4 fish/min. This rate of increase levelled off at higher PER values apparently reaching an asymptote in each case. In only one case (seal Q, 120 m) do the residuals of the fit suggest that a plateau might not have been reached, but in that case there were few data at high prey densities. Fitting nonlinear regression models to these data allowed us to parameterize and fit standard errors to various descriptors of these responses (Table 3). Across all animals and depths, the nonlinear model provided a good fit to the data, with adjusted  $R^2$  values of between 0.53 and 0.90 (Table 3). The parameter  $a$  ( $BT/ABL_{max}$ ) increased significantly with distance for four of five seals. Consistent with the positive relation between dive distance and bottom duration in the combined data for all nonzero patch densities, this increase in asymptotic bottom duration indicates that seals were staying longer at deeper depths for the highest prey densities. There was a significant increase in  $x_0$  (i.e. PER at half  $Bt_{max}$ ) with dive distance for only one of the five seals, with no



**Figure 6.** Bottom duration in relation to dive distance and presence/absence of prey on a dive. PER: Prey encounter rate. Data from all five seals are included. For an explanation of the box plots see legend to Fig 3.

significant trend for the remaining seals, indicating that the tendency for seals to give up at low prey densities did not change with dive distance.

### Energetic Consequences of Foraging Behaviour

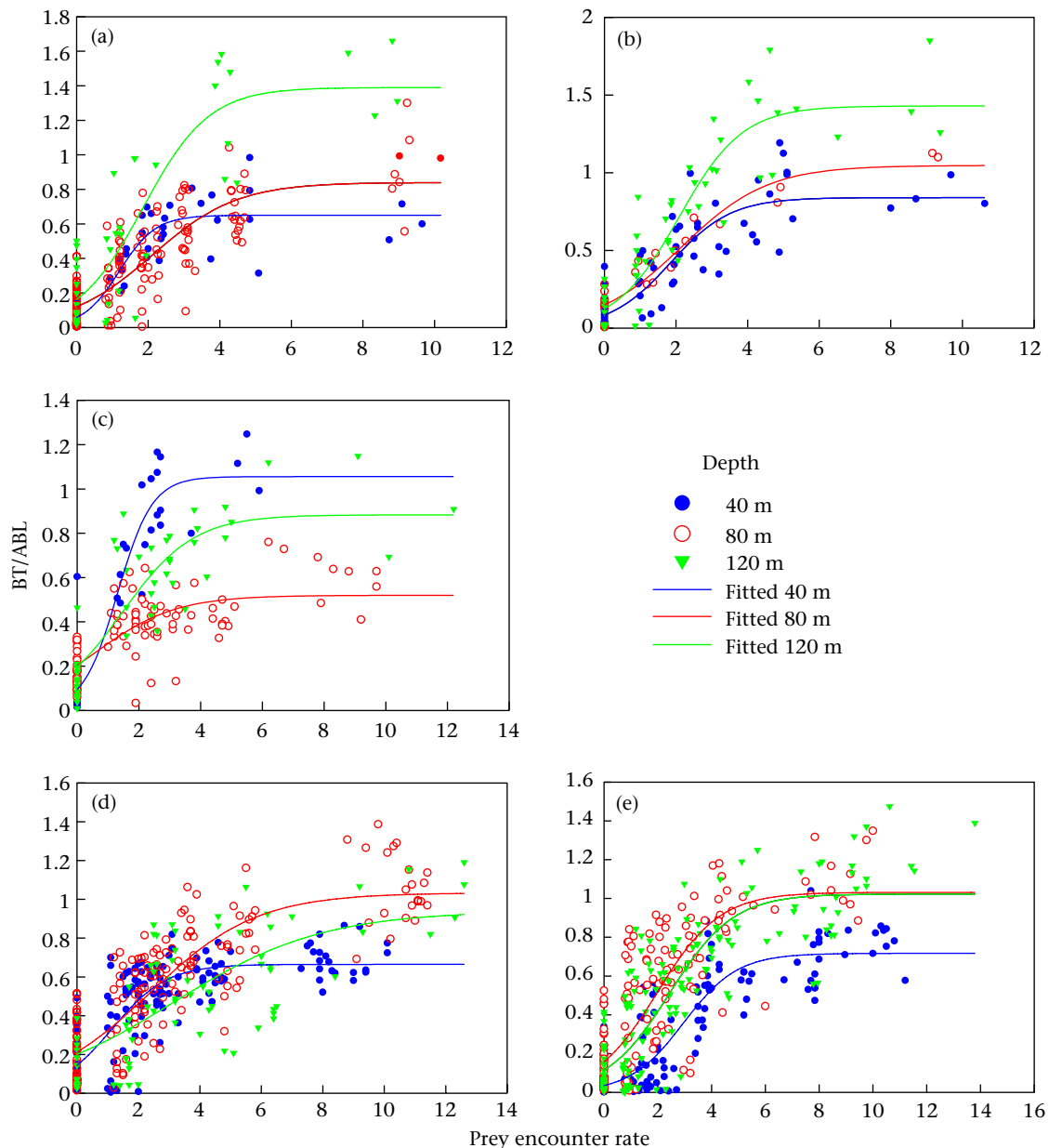
The observed rates of net energy gain in all of the feeding trials were consistently higher than those predicted for seals with no giving-up strategy (i.e. remaining at the feeder for the full ABL on each dive regardless of prey density; paired  $t$  test:  $t_{121} = 9.15$ ,  $P < 0.001$ ; Fig. 7). Analysis of variance on the difference between predicted and observed rates of net energy gain revealed significant differences between depths, with the difference being significantly greater at a dive distance of 40 m than at the other two distances ( $F_{2,122} = 4.49$ ,  $P = 0.013$ ). The relative gain, i.e. the proportional increase in net energy gain resulting from the observed dive strategy, decreased with dive distance in the pups but not in the adults (Fig. 8).

### DISCUSSION

In the past 20 years there has been an explosion in the number of studies of the behaviour of diving mammals at sea. Interpreting this behaviour in relation to fine-scale prey availability has been more problematic. Various techniques such as the use of stomach temperature loggers (Bekkby & Bjørge 1998) to estimate prey ingestion, animal-borne cameras to record the rate and timing of prey encounters (Davis et al. 1999; Bowen et al. 2002; Hooker et al. 2002) and innovative use of dive profiles to assess buoyancy and hence body composition changes (Biuw et al. 2003) have allowed us to assess foraging success in a number of wild situations. However, in general we have no reliable means of assessing local prey distributions and have therefore been restricted to using either broad-scale estimates of prey availability or information on other measurable covariates to infer fine-scale prey distributions and densities. As a result we have been unable to interpret the effectiveness of the observed dive behaviours in relation to prey availability.

In the present study, we were able to record simultaneously the costs and benefits of seals' chosen foraging strategies under a range of realistic conditions. By combining experimental manipulation of prey distributions and densities in an appropriately sized diving tank and allowing our captive animals freedom to determine their own foraging patterns, we successfully tested the predictions of foraging and diving models under controlled quasynatural conditions.

Our results clearly show that our captive seals did alter their behaviour in relation to prey density, leaving low-quality patches earlier. However, our results were equivocal with respect to the model's predictions. The effect of patch quality on foraging time was still evident at long dive distances, contrary to the prediction that during deep dives seals should stay at a patch regardless of prey density. While seals did maximize dive durations at high prey densities at long dive distances, they did not do so at



**Figure 7.** Bottom duration, BT, as a proportion of aerobic bottom duration, ABL, in relation to prey encounter rates and depth. Each point is an individual dive. (a) Seal K, (b) seal N, (c) seal R, (d) seal Q and (e) seal L. The solid lines are the fitted model in each case (sigmoid three-parameter model). See Table 2 for details of the model fits.

short dive distances. The apparent giving-up strategy of our seals always produced higher net rates of energy gain than they would have achieved if they had remained at the foraging site up to their ADL on every dive. These comparisons assume a simple, fixed relation between oxygen consumption and energy expenditure. Although there is some debate over the accuracy of this relation (Walsberg & Hoffman 2005) any error would affect all estimated profitabilities and would therefore not alter the relative profitabilities of different strategies.

The patch distances used in this study were similar to the range of dive depths commonly seen in wild grey seals foraging at sea around the U.K. (Thompson et al. 1991; Thompson & Fedak 1993; McConnell et al. 1999). The

range of prey encounter rates was chosen to be similar to those experienced by wild seals foraging on sandeels (Bowen et al. 2002). However, there were clear differences between our experimental foraging set-up and reality.

(1) Our seals did not have to pursue or capture prey, so foraging costs were lower than for wild seals. The costs associated with travelling to the prey patch were similar, but at the patch seals were effectively at rest. However, studies of wild grey seals indicate low levels of activity during the bottom phase of their benthic foraging dives (Thompson & Fedak 1993).

(2) Diving to a patch could be recreated only in the horizontal plane, so any consequence of changes in pressure associated with depth could not be simulated.

**Table 3.** Summary of derived parameters from nonlinear regression on the relation between prey encounter rate and bottom duration

Dive distance	<i>a</i>	SE	$x_0$	SE	<i>b</i>	$R^2_{adj}$	<i>P</i>
Seal N							
40 m	0.84 <sup>a</sup>	0.047	1.84 <sup>a</sup>	0.182	0.84	0.79	<0.0001
80 m	1.04 <sup>a</sup>	0.066	2.15 <sup>a</sup>	0.260	1.20	0.90	<0.0001
120 m	1.42 <sup>b</sup>	0.078	2.08 <sup>a</sup>	0.178	0.89	0.85	<0.0001
Seal K							
40 m	0.65 <sup>a</sup>	0.027	1.19 <sup>a</sup>	0.111	0.51	0.87	<0.0001
80 m	0.84 <sup>b</sup>	0.046	2.12 <sup>b</sup>	0.197	1.18	0.72	<0.0001
120 m	1.39 <sup>c</sup>	0.107	1.86 <sup>a,b</sup>	0.320	0.92	0.78	<0.0001
Seal R							
40 m	1.06 <sup>a</sup>	0.060	1.31 <sup>a</sup>	0.145	0.56	0.89	<0.0001
80 m	0.52 <sup>b</sup>	0.030	0.57 <sup>b</sup>	0.250	1.31	0.51	<0.0001
120 m	0.88 <sup>a</sup>	0.069	1.45 <sup>a</sup>	0.305	1.16	0.72	<0.0001
Seal L							
40 m	0.72 <sup>a</sup>	0.025	2.96 <sup>a</sup>	0.154	1.00	0.82	<0.0001
80 m	1.03 <sup>b</sup>	0.055	1.99 <sup>b</sup>	0.202	1.16	0.68	<0.0001
120 m	1.02 <sup>b</sup>	0.036	2.44 <sup>a,b</sup>	0.155	1.18	0.78	<0.0001
Seal Q							
40 m	0.66 <sup>a</sup>	0.024	1.15 <sup>a</sup>	0.130	0.89	0.67	<0.0001
80 m	1.03 <sup>b</sup>	0.039	2.37 <sup>b</sup>	0.207	1.74	0.72	<0.0001
120 m	0.94 <sup>b</sup>	0.111	3.15 <sup>b</sup>	0.770	2.42	0.53	<0.0001

Parameters: *a* is the maximum bottom duration as a proportion of the aerobic dive limit;  $x_0$  is the prey encounter rate at half the maximum bottom duration; *b* is the slope indicating the rate of change around this threshold. Different superscript letters indicate significant differences between depths (within animals) in *t* tests with Bonferroni-corrected alpha ( $P < 0.016$ ).

However, as phocid seals generally exhale before diving, they descend with little air in their lungs, so the relative contribution of lung compression to changes in buoyancy is likely to be less than in other marine mammals. Gliding during ascent or descent has been postulated as a possible energy-saving mechanism (Williams 2001; Williams et al. 2004). This is a result of net positive or negative buoyancy, but during vertical dives any energetic savings made on either the ascent or the descent would be balanced by increased costs on the opposite portion of the dive. The total energetic cost of travelling to a patch is therefore likely to be similar regardless of whether it comprises horizontal swimming or two opposite vertical components. In this way we maintain that dive distance is equivalent to dive depth for free-ranging grey seals.

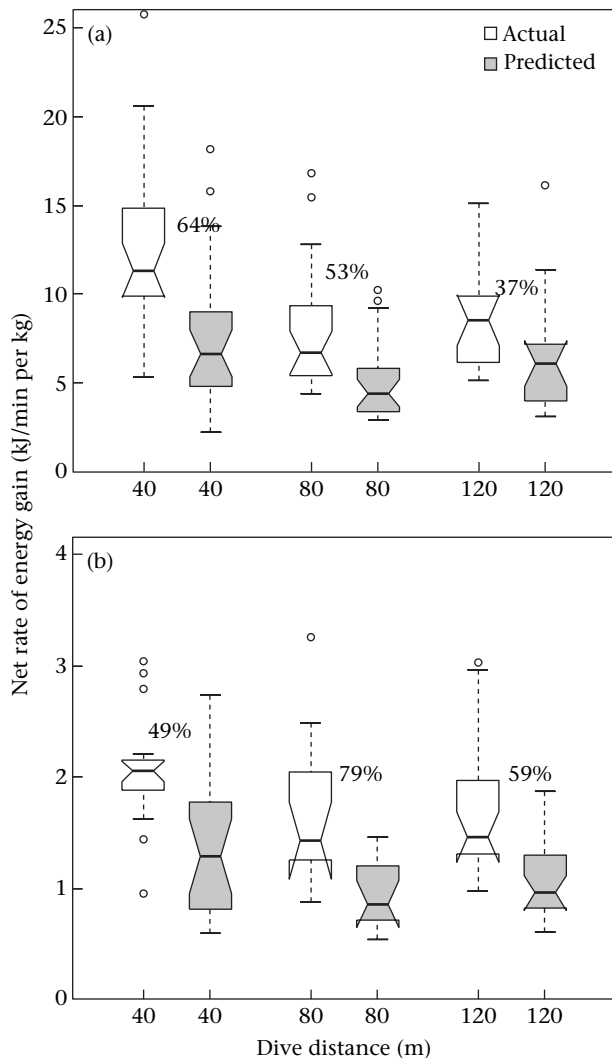
(3) Because we could not easily move the automatic feeding device between dives or even between days, dive distances were set for consecutive days. It is possible that the predictability of dive distance affected the seals' behaviour. However, grey seals are benthic divers and are likely to be able to predict distance to patches, i.e. water depth, at least on the level of a foraging bout in nature.

(4) Because the quantity of food delivered to the seals over each trial was constant and possibly predictable, it is possible that seals' motivation varied with the time in the trial. However, the amounts fed during trials were not the full maintenance ration and the seals' responses to additional food given for training purposes after each foraging trial indicated that they did not reach satiation during the trials.

(5) During any one dive, the prey items were equally spaced on the belt and the time between encounters was therefore constant. In the wild, the encounter rate would be approximately randomly distributed with something between a uniform and a Poisson distribution.

Notwithstanding these approximations to reality, the dive behaviour recorded in this study was similar to that recorded from wild grey seals. Mean and maximum dive durations were consistent with those of dives recorded in studies of wild grey seals in the U.K. (Thompson et al. 1991; Thompson & Fedak 1993; McConnell et al. 1999) and elsewhere (Björge et al. 1995).

Thompson & Fedak (2001) predicted that seals hunting prey distributed in patches would increase their net rate of gain if they altered their dive durations in response to some perceived correlate of prey density. They postulated that the observed preponderance of short dives in wild seals might result from such behaviour. In general our results support this, with all seals showing a clear nonlinear increase in patch residence time in response to increasing prey encounter rates. The good fit of sigmoidal models to the data suggests that there is a gradual transition between giving up and staying at intermediate prey densities. We could not detect any clear, simple giving-up rule based on time to first encounter. Because the seals could see the fish belt across the full width of the window and approximately 1.5 m into the feeding device, they could instantly assess whether any fish would arrive in the next 30–40 s or whether any had arrived in the previous 20–30 s. Thus a seal apparently giving up immediately was equivalent to a seal giving up because PER was less than about 1 fish/min. The ability to see more of the approaching fish belt would be analogous to the seals having a greater effective detection distance, i.e. equivalent to being able to detect the prey and therefore perhaps estimate density over a larger area of their foraging patch. Conversely, because the seals' arrival was independent of the fish's position on the belt, there was a finite probability that a prey item would be encountered on or soon after



**Figure 8.** Actual net rate of energy gain measured compared to that predicted on the basis of seals diving to their aerobic dive limit on every dive. (a) Pups, and (b) adults. The numbers on the plot refer to the mean percentage difference between actual and predicted rates of net gain at each depth. For an explanation of the box plots see legend to Fig. 3.

arrival even at low prey densities. Our protocols might therefore not have been sensitive enough to detect or identify an exact giving-up threshold.

It is clear, however, that the seals were terminating dives with lower PERs earlier than those with higher PERs, leading to an improvement in overall prey encounter rate. The seals were evidently making some assessment of patch quality and they were adjusting their foraging time accordingly, continuing to forage for longer when encounter rates were high, and were not simply maximizing time spent at the foraging site.

Dive duration increased with increasing dive distance, regardless of the presence or absence of prey. This is consistent with the increased time required for travel. However, on dives where prey were present, asymptotic bottom duration (parameter  $a$ ) also increased with dive distance indicating that seals were foraging for longer

when travel costs were higher. This result is consistent with predictions of the marginal value theorem as applied to central place foragers (Charnov 1976; Parker & Stuart 1976).

There was no consistent relation between estimates of the  $x_0$  parameter and dive distance. These results are not consistent with the predictions of the giving-up strategy model, which suggest that seals should be less likely to use this strategy in deeper dives so that  $x_0$  would be expected to decrease with increasing dive distance. The giving-up strategy of our study animals was always advantageous, in terms of net energy gain, even at the highest dive distances. It is possible that even at the highest dive distance in this study, travel time was not high enough to warrant abandoning the giving-up strategy; travel time reached on average only 35% of ADL at 120 m.

The net benefit from using a giving-up rule was predicted to decrease with dive depth (Thompson & Fedak 2001). This was apparent in the pups but not in adults. The prediction arises from the fact that when travel time increases as a proportion of dive duration, the reduction in foraging time resulting from giving up in low-density patches declines as a proportion of the total time budget. When seals dive to the maximum depth that they can attain aerobically, there will be no benefit from giving up. In shallow dives with relatively short travel times, the proportional increase in travel costs in abandoned dives is easily offset by the increased time spent in good patches. Over the range of dive distances we used, the adult seals were able to increase their dive durations to maintain a constant proportion of time spent travelling but pups might not have had that capacity. This hypothesis is supported by the observation that pups' dives approached and exceeded their ADL more frequently than adults'.

While diving to 40 m, seals rarely exceeded their estimated ADLs, even at the highest prey densities. The ratio of dive duration to ADL increased with dive distance so that at 120 m all seals were approaching ADL at the highest prey densities. This raises an intriguing question: why do seals leave high-density patches well before their ADL while diving to 40 m? One would expect seals to maximize time spent in the highest-quality shallow patches, but our seals did not. Clearly, neither oxygen balance nor variation in prey availability can fully explain the preponderance of short, shallow dives. Seals may be attempting to minimize other costs associated with longer dives, such as possible damage caused by elevated levels of reactive oxygen species following reperfusion of ischaemic muscle after long dives (Elsner et al. 1998) or increasing requirements for postdive physiological processing as a result of reduced organ function during dives.

Dive duration was positively related to mass during zero prey dives. This is probably due to the larger seals swimming more slowly (and travel taking up proportionately more of the total dive duration when no prey were present). Conversely, mass had a significant negative effect on bottom duration when no prey were present, indicating that larger seals gave up earlier when prey were scarce, which may be an effect of experience.

These experimental results may help us interpret observations of foraging behaviour of wild seals. During

long-range, transit swimming, grey seals generally dive to the sea bed. They perform sequences of V-shaped dives, with little time spent at the bottom, interspersed with flat-bottomed dives, where a significant but variable proportion of the dive is spent at the bottom (Thompson et al. 1991; Thompson & Fedak 1993). The variable-length, flat-bottomed dives are assumed to represent foraging in suitable habitats whereas the V-shaped dives may indicate that the seals assess prey density as low. This pattern is entirely consistent with the dive patterns seen in our captive studies.

This study adds to a growing body of empirical evidence of the links between observed dive behaviour and prey availability. Boyd (1996) used variation in the distributions of travel durations between foraging bouts to infer differences in prey distribution. Mori & Boyd (2004) showed that the behaviour of foraging Antarctic fur seals, *Arctocephalus gazella*, is an effective indicator of prey availability that correlated well with independent measures of prey abundance. Hooker et al. (2002) showed increased bout duration with increased prey encounter rate of Antarctic fur seals feeding on krill. Mori et al. (2005) have directly shown that dive profiles can be used to calculate a relative index of the richness of prey patches for Weddell seals, *Leptonychotes weddellii*. Cornick & Horning (2003) found that dive duration and foraging time of captive sealions increased significantly with prey encounter rate. Our results suggest that variability in the length of the bottom portions of dives may indicate relative conditions in different foraging habitats. Houston et al. (2003) have shown that for single-prey loaders faced with a choice of prey types, the probability of foraging success on a given dive is not a good indicator of conditions in the foraging area. However, the behaviour of divers that feed on multiple prey items during each dive, like the seals in our experiments, is likely to be an indicator of relative habitat richness in terms of the prey available.

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