

How fast does a seal swim? Variations in swimming behaviour under differing foraging conditions

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Summary

The duration of breath-hold dives and the available time for foraging in submerged prey patches is ultimately constrained by oxygen balance. There is a close relationship between swim speed and oxygen utilisation, so it is likely that breath-holding divers optimise their speeds to and from the feeding patch to maximise time spent feeding at depth. Optimal foraging models suggest that transit swim speed should decrease to minimum cost of transport (MCT) speed in deeper and longer duration dives. Observations also suggest that descent and ascent swimming mode and speed may vary in response to changes in buoyancy. We measured the swimming behaviour during simulated foraging of seven captive female grey seals (two adults and five pups). Seals had to swim horizontally underwater from a breathing box to a submerged automatic feeder. The distance to the feeder and the rate of prey food delivery could be varied to simulate different feeding conditions.

Diving durations and distances travelled in dives

recorded during these experiments were similar to those recorded in the wild. Mean swim speed decreased significantly with increasing distance to the patch, indicating that seals adjusted their speed in response to travel distance, consistent with optimality model predictions. There was, however, no significant relationship between the transit swim speeds and prey density at the patch. Interestingly, all seals swam 10–20% faster on their way to the prey patch compared to the return to the breathing box, despite the fact that any effect of buoyancy on swimming speed should be the same in both directions. These results suggest that the swimming behaviour exhibited by foraging grey seals might be a combination of having to overcome the forces of buoyancy during vertical swimming and also of behavioural choices made by the seals.

Key words: swimming speed, foraging behaviour, minimum cost of transport, grey seals.

Introduction

Breath-holding divers must meet several challenges if they are to forage effectively in the marine environment. Firstly, they must balance the time spent exploiting underwater food resources with time spent unloading CO₂ and loading oxygen at the surface. Secondly, they have to operate in a three-dimensional environment where food resources may be scattered in aggregated patches, sometimes at great depths. This means that at the end of a surface period, they have to either relocate the previously visited patch or search for another more profitable patch (Ydenberg and Clark, 1989). Most optimal foraging models assume that the number of prey encountered during a feeding event is a linear function of the time spent foraging, i.e. foragers should maximise time spent feeding in the prey patch. To do this, they should reduce both their transit time to the feeding area and their recovery time between two successive feeding events (e.g. Ydenberg and Clark, 1989). When marine divers feed at greater depths, the time spent

travelling to depth and hence the energy cost increase. Consequently, the expected net foraging gain of a dive decreases with increasing depth, and the time–energy trade-off becomes more constrained, thereby limiting the behavioural options available to the diver (Charnov, 1976; Kramer, 1988; Houston and Carbone, 1992; Beauchamp et al., 1992).

The rate of oxygen consumption during a dive is directly proportional to the rate of energy expenditure, which is in turn a function of the swimming speed (Davis et al., 1985; Feldkamp, 1987; Fedak et al., 1988; Thompson et al., 1993; Stelle et al., 2000; Rosen and Trites, 2002). The swimming speeds employed during a dive will have a major impact on the rate of depletion of limited oxygen reserves (Davis et al., 1985; Williams et al., 1991; Thompson et al., 1993; Wilson et al., 2002). Effectively, in order to maximise prey ingestion while minimising the cost of transport, breath-holding divers are expected to modulate their swim speed, body angle and swimming pattern (Dunstone and O'Connor, 1979; Sato et al.,

2003). Thompson et al. modelled how the optimal foraging tactics of seals may change as a function of the interactions between physiological constraints (cost of swimming) and constraints of prey availability (Thompson et al., 1993). Their optimality model suggested that seals should swim at the minimum cost of transport (MCT) speed in deep dives, but in shallower dives they could increase the proportion of time spent at the foraging area by swimming faster between the surface and the prey patch.

Animals swimming in the water column are affected by buoyancy, which has been reported to significantly affect the diving behaviour of seabirds and marine mammals (Lovvorn and Jones, 1991; Webb et al., 1998; Skrovan et al., 1999; Beck et al., 2000; Williams et al., 2000; Biuw et al., 2003; Watanuki et al., 2003; Sato et al., 2003; Miller et al., 2004; Sato et al., 2007). In diving air-breathing animals that do not trap air in thick fur or feathers, or that regularly dive below the depth at which lung collapse occurs, the net buoyancy is largely determined by the relative amounts of low-density lipid and high-density lean tissues in the body. Individuals that are positively or negatively buoyant expend more energy to maintain a position in the water column than individuals of the same species that are neutrally buoyant (Lovvorn and Jones, 1991), and net buoyancy might be expected to directly influence the speeds and swimming modes during descent and ascent swimming (e.g. Webb et al., 1998; Beck et al., 2000). However, in studies on free-diving animals, it is often difficult to distinguish between the effect of buoyancy and effects of drag and motivational state, and results from these studies are therefore often inconclusive on this point.

This paper describes the swimming behaviour of grey seals in relation to food resource availability (prey density and patch distance) in an experimental set-up that provided us with a unique opportunity to remove the effect of buoyancy on dive behaviour. We describe the swimming patterns employed during foraging dives. We use observed behaviours to examine whether divers decrease their swim speed as patch distance increases, as predicted by the swimming behaviour model of Thompson et al. (Thompson et al., 1993). As all dives are horizontal rather than vertical and therefore not affected by buoyancy, we hypothesise that the descent and ascent swimming mode and speed will be similar in any particular dive.

Materials and methods

Study animals

Seven female grey seals *Halichoerus grypus* Fabricius 1791 (five juveniles <1 year of age and two adults) were used in this study. All seals were caught in the wild at Abertay Sands (Fife, Scotland, UK) and kept in outdoor seawater pools in the captive facility at the Sea Mammal Research Unit (SMRU, St Andrews, UK). Seals were fed daily on herring *Clupea harrengus* and sandeels *Ammodytes marinus*. They were regularly weighed (to ± 0.1 kg) and body composition was determined periodically using isotopically labelled water (Speakman, 2001; Sparling et al., 2006). Seals were released back into the wild after a maximum of 10 months in captivity. All captures and handling procedures occurred between 2002 and 2004 and conformed to the Animals (Scientific Procedures) Act 1986 under project licence number 60/2589.

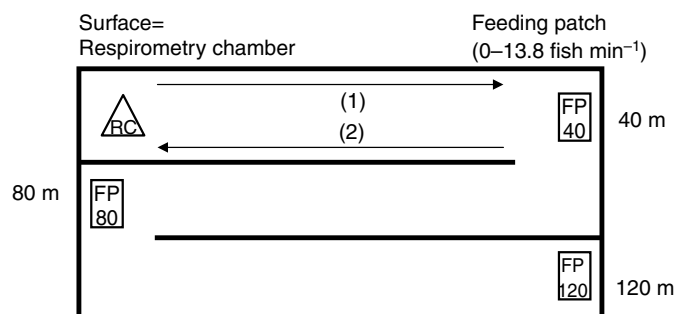


Fig. 1. Plan of the experimental pool (40 m \times 6 m \times 2.5 m). Animals could only surface to breathe at the respirometry chamber (RC). The feeding patch (FP) could be placed at 40, 80 or 120 m away from the surface. This set-up allowed us to measure dive duration, 'descent' speed (1), bottom time, 'ascent' speed (2), oxygen consumption and quantity of prey eaten, for every dive.

Experimental set up

The SMRU experimental facility comprises a large seawater pool (40 m \times 6 m \times 2.5 m) that can be covered by aluminium meshed panels to restrict animals to surface only in a breathing box linked to an open circuit respirometry system. The pool could also be longitudinally partitioned with nets into lanes so that the distance between the breathing box and a simulated foraging patch (i.e. travel distance) could be varied between 40 and 120 m (Fig. 1). As phocid seals have no air in their fur and routinely exhale before diving, they have few compressible spaces, so that change in depth has only a small effect on buoyancy and no discernible effect on shape or drag. Net buoyancy effects due to high or low body density will approximately cancel out during the descent and ascent phases in vertical dives, so horizontal, underwater swimming to and from the feeder will be energetically similar to vertical diving to an equivalent depth. Hereafter, travel distance from the breathing box (equivalent to the surface) to the feeding patch (equivalent to the bottom) will be referred as 'descent' and 'ascent'.

The foraging patch consisted of a purpose built device that delivered food on a conveyor belt to a feeding window 2 m below the surface (see Sparling et al., 2007). An important aspect of the design was that seals were free to dive at will and select their own foraging behaviour.

The experimenter controlled the prey encounter rate (PER) by varying the spacing of prey items on the conveyor belt. PER was held constant within a given dive, but changed randomly between dives. PER varied between 0 and 13.8 fish min^{-1} . The upper limit of PER corresponds to the highest PER recorded in the wild with video cameras attached to freely diving harbour seals *Phoca vitulina* feeding on sandeel (Bowen et al., 2002).

Measurement of foraging behaviour

Foraging behaviour was investigated in relation to both prey density and the distance between the prey patch and the breathing box. Trials were conducted with the feeding station positioned 40 m, 80 m and 120 m from the breathing box. Five of the seven seals were tested at all three distances while two

of the juvenile seals were only tested at 80 m. Animals were fasted for >15 h before each feeding trial.

The start and the end time of each dive and times of arrival at and departure from the feeder were recorded from direct observation at the breathing box and an underwater video system at the feeder. These recorded observations represent the visual data. Swim speed was estimated as distance between breathing box and feeder divided by time between observed departure and arrival. Time–depth recorders (TDR; MK 8, Wildlife Computers, Redmond, WA, USA), attached to the seals' heads, provided an independent measure of swimming speeds and of durations of travelling and surface periods. The MCT speed was estimated from the metabolic rate–swim speed relationship for grey seals swimming in a flume tank (Fedak et al., 1988; Thompson et al., 1993). The measured MCT speed was approximately 1.3 m s^{-1} and unrelated to body mass.

Linear mixed effect model for swim speeds

Swimming speed in relation to patch distance and prey density was assessed using linear mixed effect models in R (v2.01). Models were constructed to predict the 'descent' and 'ascent' speed during the dives. We could expect a seal to alter its 'ascent' speed in response to the prey encountered during a dive, but its 'descent' speed could also be a response to the prey encountered on the preceding dive. Therefore we calculated an index of transit swim speeds from visual data for each dive for each animal. To make the indices easily comparable between seals we calculated an index as the sum:

$$\text{Index} = (\text{AS}_n - \text{M}_{\text{AS}}) + (\text{DS}_{n+1} - \text{M}_{\text{DS}}),$$

where AS_n is the 'ascent' swim speed on dive n and DS_{n+1} is the 'descent' swim speed on the next dive. M_{DS} and M_{AS} are the mean 'descent' and 'ascent' speeds for a given seal's overall distances. The index is positive when a seal swims faster to and from the feeder on a particular dive compared to the overall mean 'descent' and 'ascent' speeds for a given seal over all distances and *vice versa*.

PER and mass as continuous variables and patch distance as a factor (40 m, 80 m, 120 m) were included as fixed effects and seal ID and PER were included as random effects. This allows the model to fit separate slopes and intercepts for the relationship between index and PER for each seals. We used swim speed data obtained visually from five seals travelling to 40, 80 and 120 m to carry out this analysis. Deletion tests were used to assess the significance of each parameter in the models.

TDR data analyses

Swimming behaviour was investigated using Mk8 TDRs that incorporated a turbine swim speed sensor. The TDR was set to log velocity every second. Each TDR velocity meter was calibrated for both pups and adults by recording the times taken to swim fixed distances along lanes in the pool. Swim speed profiles were plotted and examined visually for each dive for each animal (Fig. 2).

Swim speed profiles were characterised by a 'descent' phase (active swimming from the breathing box to the feeder), a phase of foraging at the feeder, and an 'ascent' phase (active swimming from the feeder to the breathing box). The start and end of the dive were determined both by the wet/dry sensor of the TDR and by a sudden change in swim speed between 0 and $1.5\text{--}2 \text{ m s}^{-1}$ within 2 s. The foraging phase was characterised by stationary periods or relatively slow swimming in the vicinity of the feeder with occasional bursts of activity. The 'ascent' phase was similar to the 'descent' phase with a rapid increase in swim speed as seals left the feeder and a decrease upon arrival to the breathing box. For each dive, we calculated the mean speeds and the number of acceleration/deceleration phases (resulting from so-called 'burst-and-glide' swimming) during the 'descent' and the 'ascent' phases. Speeds are presented as means ± 1 standard deviation (s.d.).

Buoyancy calculation

Because seals were swimming horizontally, buoyancy cannot directly explain potential differences between 'descent' and 'ascent' speeds in our study. However, it is possible that seals may employ a different level of swimming effort during 'descent' and 'ascent' as a conditioned response to their actual body condition and buoyancy. To test this hypothesis, we estimated the buoyancy for each seal through the year where body composition measures were available.

For five of the experimental seals, body composition was used to calculate the seal density according to:

$$\rho_{\text{seal}} = (\rho_l \times P_l) + (\rho_p \times P_p) + (\rho_b \times P_b) + (\rho_{\text{bw}} \times P_{\text{bw}}),$$

where ρ is the density of the component and P the proportion of the component for lipid (l), protein (p), bone (b) (ash) and body water (bw), respectively. We used published values for the density of body components in humans (Moore et al., 1963) ($\rho_l = 0.9007 \text{ g cm}^{-3}$, $\rho_p = 1.340 \text{ g cm}^{-3}$, $\rho_b = 2.300 \text{ g cm}^{-3}$ and $\rho_{\text{bw}} = 0.994 \text{ g cm}^{-3}$).

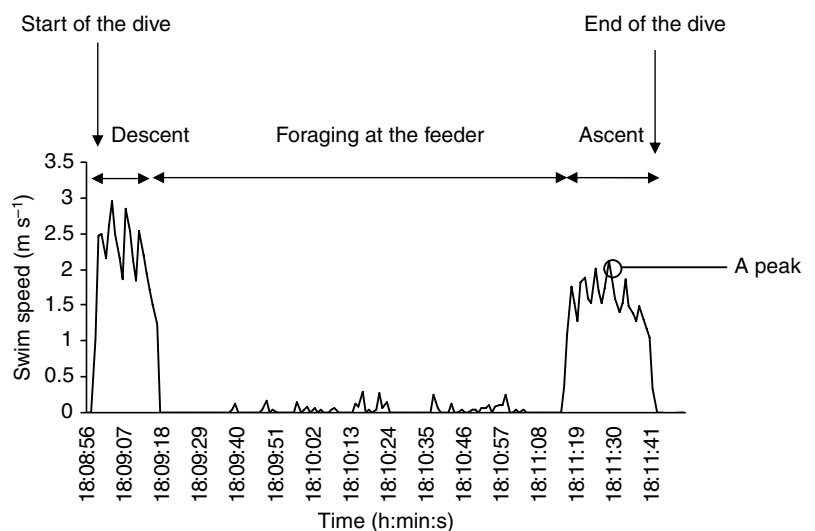


Fig. 2. Time–depth recorder (TDR) data for seal K on the 8th of April 2002 showing changes in velocity over a dive. This was a dive to 40 m with a density of $3.2 \text{ fish min}^{-1}$ at the patch.

The proportions of body water, lipid, protein and bone mineral were estimated using published equations for grey seals (Reilly and Fedak, 1990):

$$P_{bw} = -0.234 + 0.971(^3H_2O_{space}),$$

$$P_l = 105.1 - 1.47(P_{bw}),$$

$$P_p = 0.42(P_{bw}) - 4.75,$$

$$P_b = 100 - (P_{bw} + P_l + P_p).$$

Buoyancy was then calculated using the following equation:

$$B_T = (\rho_{seawater} - \rho_{seal}) \times V \times g,$$

where B_T is total buoyancy (N), $\rho_{seawater} = 1.028 \text{ g cm}^{-3}$, ρ_{seal} is the density of the seal (g cm^{-3}), V is the volume of the seal in cm^3 and g is the gravity constant.

Buoyancy at the surface and at 1 m and 2 m depths was calculated by adding the density of the diving lung volume (DLV) for these different depths to the density of the seal. DLV is about 50–60% of total lung capacity (TLC) in phocid seals. TLC was estimated from the scaling relationship (Kooyman, 1989):

$$TLC = 0.10M_b^{0.96},$$

where TLC is the volume (l) and M_b is body mass (kg).

Results

A total of 3220 dives obtained from visual data were analysed for seven female grey seals (two adults: L and Q, and five pups: K, N, R, W and X). Dive characteristics recorded during these experiments were similar to those recorded in the wild (for details, see Sparling et al., 2007).

A summary of the swim speed characteristics is shown in Table 1. Overall mean 'descent' and 'ascent' speeds were $1.71 \pm 0.41 \text{ m s}^{-1}$ and $1.37 \pm 0.36 \text{ m s}^{-1}$, respectively. Mean 'descent' swim speeds were faster than the estimated MCT speed (1.3 m s^{-1}) (Thompson et al., 1993) for all seals except for the adult Q. Mean 'ascent' swimming speeds were faster than the calculated MCT speed for all pups (range $1.53\text{--}2.00 \text{ m s}^{-1}$), while for adults, ascent swimming speeds were close to or less than MCT speed (Table 1).

Of the 3220 dives for which swim speed was calculated from visual data, independent swim speeds were also obtained from the TDR data for 1289 dives. There was a strong positive

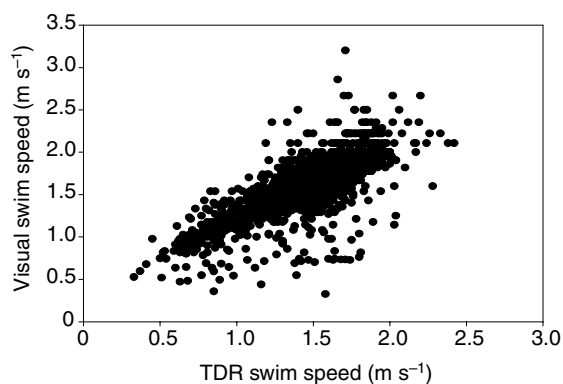


Fig. 3. Swim speeds (in m s^{-1}) obtained from TDR and from visual observations. Each point represents the mean swim speed for the 'descent' or 'ascent' of a particular dive.

correlation between the visual and TDR data (correlation = 0.786, $Z = 53.51$, $P < 0.001$), but the speed estimates obtained from visual data were significantly higher than those from TDR records (paired t -test, $T = 25.17$, $P < 0.001$) (Fig. 3). The variance in the relationship is due to measurement error in recording the start and end of active swimming and seals slowing or stopping when out of view during transit to and from the surface. Visually recorded swim speed therefore provides a noisier index of true swim speed, while TDR-derived data may be less noisy but may slightly underestimate the true swim speed. While this will reduce the statistical power of any comparisons and increase the probability of type II error it does ensure that any observed relationships are likely to be real, i.e. there is little chance of type I error.

Swimming behaviour

A total of 1672 dives obtained from visual data for five female grey seals (L, Q, K, N and R) were used to create linear mixed effects models. X and W only swam to 80 m, therefore their data were not used in this analysis. A summary of the parameters obtained is presented in Table 2.

The full mixed effects model including data from all five seals suggested that body mass had a significant negative effect on swim speed. However, it was clear that this was being driven mainly by the mass change of one large pregnant adult female

Table 1. Summary of swim speed characteristics obtained visually for each seal at each patch distance

Seal ID	Age	Swim speed (m s^{-1})										
		N		40 m		80 m		120 m		All distances		
		Descent	Ascent	Descent	Ascent	Descent	Ascent	Descent	Ascent	Max	Descent	Ascent
L	A	536	530	1.87 ± 0.28	1.49 ± 0.25	1.81 ± 0.20	1.45 ± 0.26	1.79 ± 0.27	1.35 ± 0.20	2.67	1.82 ± 0.26	1.42 ± 0.24
Q	A	432	432	1.25 ± 0.28	0.98 ± 0.24	1.16 ± 0.27	0.90 ± 0.24	1.16 ± 0.1	0.99 ± 0.14	2.00	1.2 ± 0.26	0.95 ± 0.22
K	P	313	296	2.27 ± 0.28	1.78 ± 0.26	1.91 ± 0.25	1.45 ± 0.21	1.90 ± 0.19	1.57 ± 0.16	2.86	2.00 ± 0.30	1.53 ± 0.25
N	P	165	150	2.20 ± 0.33	2.00 ± 0.23	1.85 ± 0.27	1.55 ± 0.1	1.88 ± 0.24	1.66 ± 0.15	2.86	2.01 ± 0.33	1.77 ± 0.5
R	P	193	194	2.06 ± 0.27	1.53 ± 0.23	1.81 ± 0.14	1.61 ± 0.19	1.77 ± 0.25	1.59 ± 0.22	2.86	1.87 ± 0.24	1.58 ± 0.21
W	P	1239	1228			1.77 ± 0.15	1.63 ± 0.18			2.42	1.77 ± 0.15	1.63 ± 0.18
X	P	309	309			1.7 ± 0.27	1.54 ± 0.29			3.2	1.7 ± 0.27	1.54 ± 0.29

A, adult; P, pup.

Swim speeds are means \pm s.d.

Table 2. Summary of the parameters obtained from linear mixed-effect models in R (v2.01) with and without seal Q included

	AIC	L.Ratio	Slope	P
With Q:				
Full model	1037.75			
Term removed:				
PER	1037.3	1.55		0.213
Mass	1080.05	44.30	-0.0058±0.001	<0.0001
Distance 80			-0.2731±0.025	
	1155.64	121.89		<0.0001
Distance 120			-0.2463±0.029	
Individual			0.5820±0.124	<0.0001
Without Q:				
Full model	642.68			
Term removed:				
PER	641.57	0.89		0.344
Mass	641.50	0.82		0.365
Distance 80			-0.3592±0.030	
	808.36	169.69		<0.0001
Distance 120			-0.3830±0.032	
Individual			0.2539±0.033	<0.0001

Seal ID (see text) and prey encounter rate (PER) were included as random effects; distance, mass and PER as fixed effects; the index was the response variable. The significance of a parameter was tested by removing each parameter from the full model and looking at the effect of the deletion on the fit of the model using likelihood ratio tests. The slope values ± s.e.m. are given for significant terms (in bold).

AIC, Akaike information criterium; L.ratio, likelihood ratio test.

TBF, total body fat; DLV, diving lung volume.

‘Q’, whose swim speed index decreased throughout the study (Fig. 4). This was also apparent when comparing swim speeds to different distances. During the early pregnancy of seal Q, swim speed index to 80 m was 0.5 and in late pregnancy the index fell to -0.6 (Fig. 5). Seal Q was therefore considered separately and removed from the overall analysis.

Four seals (three pups, N, R, K, and one adult, L) were therefore included in the final model. Results are summarised in Table 2.

There was significant variation between individual seals, but the model indicated that seals did not adjust their transit swim speeds in response to changes in either PER (Fig. 6) or body mass (Fig. 4). However, they did appear to adjust their swim speed in response to patch distance (Table 2, Fig. 7). Transit swim speeds decreased significantly with increasing patch

distance. This decrease in swim speed was most pronounced between 40 m and 80 m, with little change between 80 m and 120 m.

Swimming pattern

In order to describe the swimming patterns of our animals, swim speed profiles obtained from TDR records of 1289 dives were examined from all seven seals (L, Q, K, N at 40 m and 80 m and R, W, X at 80 m).

The mean ‘ascent’ speed was always significantly slower

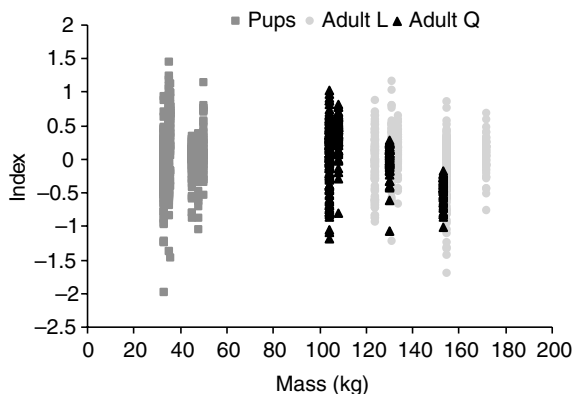


Fig. 4. Index of transit swim speeds in relation to body mass (kg). There is a different symbol for the pups, the adult L and the adult Q.

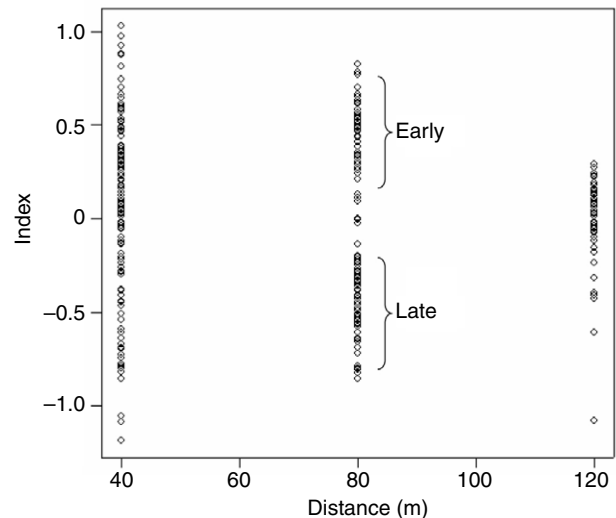


Fig. 5. Transit swim speeds index in relation to distance (40, 80 and 120 m) for the adult female Q. Data for early and late experiments at 80 m are indicated on the graph.

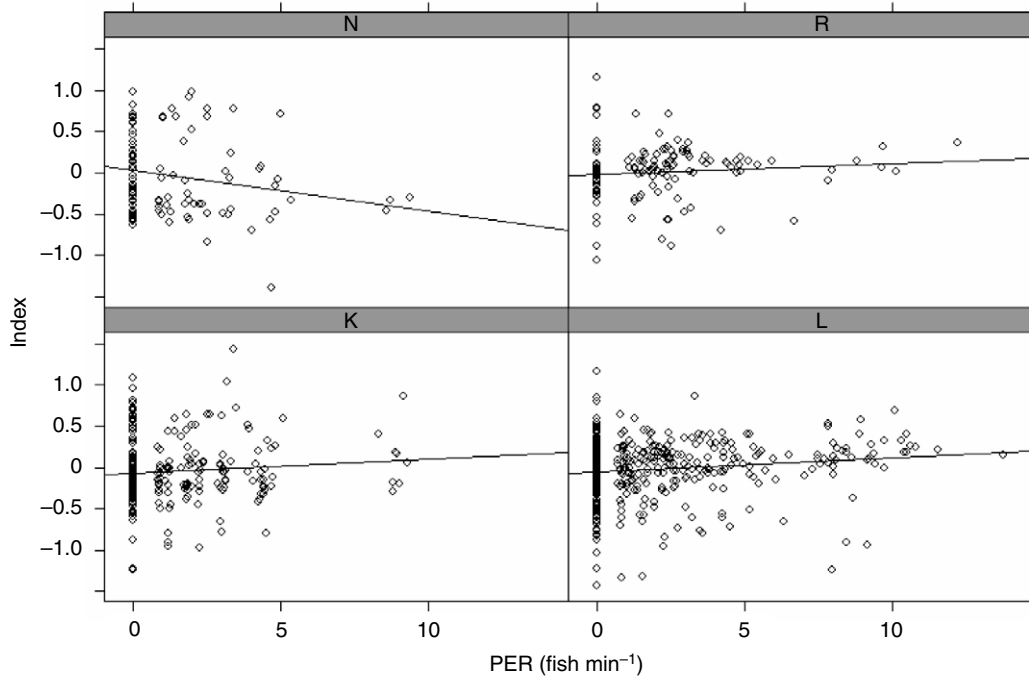


Fig. 6. Index of transit swim speeds in relation to prey encounter rate (PER; fish min⁻¹) for each animal (N,R,K,L). Each point represents the index of transit swim speed during a particular dive. The solid lines give linear least-squares fit.

than the mean ‘descent’ speed for all seals, at all distances (paired *t*-test, *P*<0.01). Interestingly, all seals swam between 10% and 20% slower on their way back to the breathing box despite not having to work against buoyancy in either direction (Fig. 8). We calculated the buoyancy through the year for each seal where body composition was available. The mean body mass of the adult grey seal was 129.7 kg and 34 kg for the pups,

with adipose tissue accounting for between 7.1% and 40.8% of body mass (Table 3). There was no relationship between estimated buoyancy and the relative swim speed during ‘descent’ and ‘ascent’. ‘Ascent’ swimming was always slower than ‘descent’ swimming whereas buoyancy varied widely from +16 N to -20 N.

All seals used burst and glide swimming during both

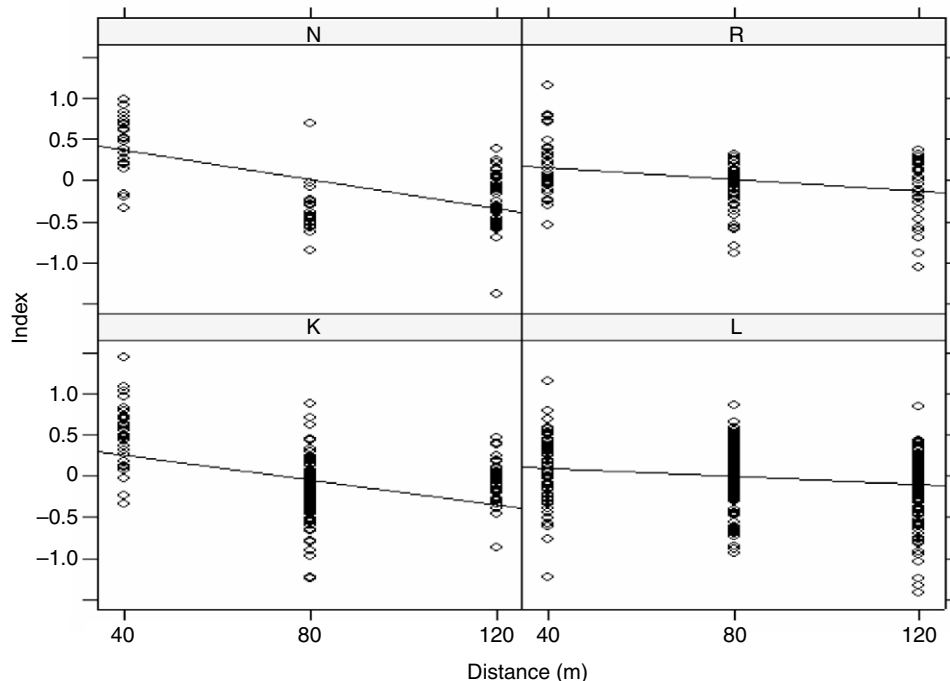


Fig. 7. Index of transit swim speeds in relation to distance (m) for each animal (N,R,K,L). Each point represents the index of transit swim speed during a particular dive.

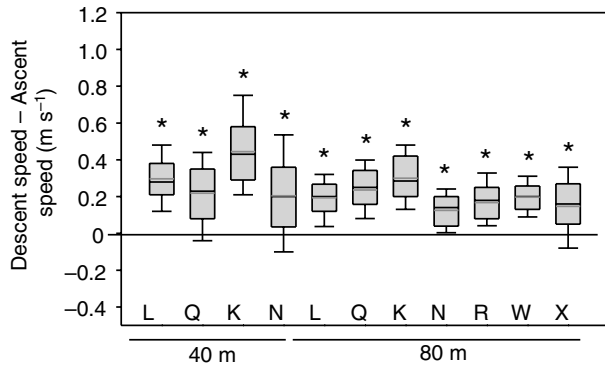


Fig. 8. Boxplot of the differences in mean swim speeds (in m s^{-1}) between the 'descent' and the 'ascent' of dives to 40 m and to 80 m for each seal. *Mean swim speed significantly higher on the 'descent' (paired t -tests, $P < 0.05$). The bottom and top of each box marks the 25th and 75th percentile, respectively. The black and grey lines within the box represent the median and mean, respectively. Whiskers above and below the box indicate the 90th and 10th percentiles.

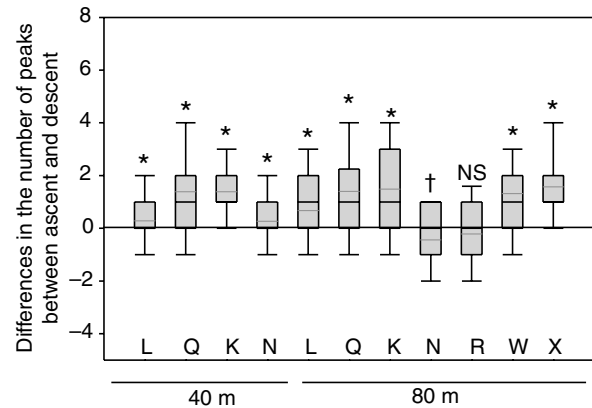


Fig. 9. Boxplot of the differences in the number of peaks between the 'ascent' and the 'descent' for dives to 40 m and to 80 m for each seal. *Number of strokes significantly higher on the 'ascent'; †number of strokes significantly higher on the 'descent'; NS, not significant (paired t -tests, $P < 0.05$). The bottom and top of each box marks the 25th and 75th percentile respectively. The black and grey lines within the box represent the median and mean respectively. Whiskers above and below the box indicate the 90th and 10th percentiles.

'descent' and 'ascent'. Repeated acceleration (stroke) and deceleration (glide) phases were apparent in swim speed records in all dives (Fig. 2). The number of burst and glide phases was generally significantly higher on the 'ascent', except for N and R at 80 m (paired t -test, $P < 0.05$, Fig. 9).

Discussion

This study examines the swimming behaviour of grey seals in relation to resource availability, i.e. prey density and patch distance. The experimental set-up allowed us to test theoretical models of swimming speeds in breath-holding divers. In addition, we investigated 'descent' and 'ascent' swimming in the absence of buoyancy effects. The study was based on a sample of seven female grey seals, a relatively large sample compared to previous captive marine mammal studies.

Although the sample size restricts our ability to investigate size-related effects, the behaviour of the non-pregnant adult was qualitatively similar to that of the pups throughout.

Swimming speed

The observed mean swimming speeds for both adults and pups were similar to those reported for adult grey seals foraging in UK waters (Thompson et al., 1993) but were higher than those of adult grey seals foraging around Sable Island (Beck et al., 2000). However, Beck et al. reported 'descent' and 'ascent' rates that are only analogous to swim speed if the seals were diving vertically to the bottom (Beck

Table 3. Buoyancy values at different depths for seals where body composition was available

Seal ID	Date	Mass (kg)	TBF%	DLV (l)	Buoyancy (N)			
					With no air in lungs	At the surface	At 1 m	At 2 m
L	Mar-02	131	13.38	5.39	-74.13	-19.84	-24.77	-28.89
	May-02	124	17.23	5.11	-61.50	-9.99	-14.68	-18.58
	Jun-02	134	22.88	5.51	-50.96	4.53	-0.51	-4.72
K	Feb-02	42.5	40.77	1.6	0.36	16.48	15.02	13.80
	Mar-02	30.4	21.73	1.4	-12.25	1.85	0.57	-0.50
	Jun-02	32.5	12.79	1.45	-19.02	-4.42	-5.74	-6.85
N	Feb-02	34.6	40.32	1.46	-0.03	14.68	13.34	12.22
	Mar-02	33	32.54	1.44	-5.75	8.76	7.44	6.34
	Jun-02	36.4	31.05	1.57	-7.51	8.31	6.87	5.67
W	Jul-04	23.9	8.07	1.14	-16.22	-4.74	-5.78	-6.65
	Aug-04	28	12.27	1.14	-16.70	-5.21	-6.25	-7.12
	Sep-04	31.4	18.69	1.23	-14.63	-2.23	-3.36	-4.30
	Sep-04	39	21.9	1.23	-15.58	-3.19	-4.32	-5.26
X	Aug-04	26.8	7.1	1.17	-18.70	-6.86	-7.94	-8.84
	Aug-04	31.6	16.26	1.38	-16.30	-2.43	-3.69	-4.74
	Sep-04	41.6	28.99	1.79	-10.40	7.66	6.01	4.65
	Oct-04	44.6	24.76	1.92	-15.18	4.11	2.36	0.90

TBF, total body fat; DLV, diving lung volume.

et al., 2000). At any other angle, such rates would underestimate swim speed.

Marine mammals and penguins should swim at or near the MCT speed when swimming to and from the surface in order to maximise the amount of oxygen available during the foraging phases of dives (Davis et al., 1985; Feldkamp, 1987; Ponganis et al., 1990; Ponganis et al., 1992; Fish, 1993; Thompson et al., 1993; Williams et al., 1993; Ropert-Coudert et al., 2002). The MCT speed for grey seals swimming in a flume tank was approximately 1.3 m s^{-1} (Fedak et al., 1988; Thompson et al., 1993), which was similar to those recorded for harbour seals in similar conditions (between 0.85 and 1.4 m s^{-1}) (Davis et al., 1985). On average, our seals swam approximately 20% faster than the estimated MCT speed when returning to the surface (Table 1), and over 40% faster than the expected MCT speed when going to the feeder. Estimates of MCT speed based on animals swimming in flume tanks may be underestimates. Seals had to swim actively against the flow while breathing at the surface. Drag is greatly enhanced at or close to the surface (Hertel, 1966) so seals in flume tanks would experience higher drag than during submerged swimming at similar speeds in our set-up or in the wild. At higher speeds this effect is exacerbated by seals spending proportionately longer breathing (Fedak et al., 1988). Our seals may therefore have been swimming at or close to MCT speeds during 'ascent'. If so, however, they must have been swimming faster than MCT speed when travelling to the feeder.

There was no clear relationship between body mass and swimming speed in our study. Because drag scales to surface area while available power scales to body mass, larger animals should be capable of higher sustained swim speeds (Feldkamp, 1987; Videler and Nolet, 1990; Stelle et al., 2000). However, animals would be expected to swim at or close to their MCT speed during ascent and descent and the relationship between mass M_b and MCT speed is not obvious. MCT speed scales to $M_b^{0.27}$ over a wide range of body masses (Videler and Nolet, 1990). While this is apparent over the size range investigated by Videler and Nolet (0.027 – 11.5 m), it is not clear that such a relationship holds within the range of sizes and swim speeds observed in marine mammals, and it does not appear to fit the observed patterns of swim speeds in marine mammals (Sato et al., 2007; Hassrick et al., 2007). The broad-scale allometric relationship, which was determined across swimmers from many taxa, is due to the fact that drag coefficient C_D decreases as Reynolds number (Re) increases over a wide range of Re values, and Re scales linearly to body length. However, at the high Re ($>200\,000$) experienced by swimming pinnipeds, the simple relationship breaks down and C_D remains relatively constant (Vogel, 1981). If we can assume that C_D is constant over the observed range of sizes and swim speeds for pinnipeds, we can approximate the metabolic costs of swimming (SMR) in terms of body mass (M_b) and swim speed (U), with an equation of the form,

$$\text{SMR} = aM_b^{0.75} + bM_b^{0.67} \times U^3,$$

where a and b are constants; resting or maintenance metabolic rate scales to $M_b^{0.75}$ and power required to overcome drag is proportional to U^3 and surface area, which scales to $M_b^{0.67}$.

Cost of transport (J m^{-1}) is simply the metabolic rate divided by the speed:

$$\text{COT} = (aM_b^{0.75} + bM_b^{0.67} \times U^3) / U.$$

By differentiating with respect to U and setting the derivative equal to zero we can see that MCT should scale to $M_b^{0.027}$, i.e. MCT is almost independent of mass.

Our largest animal was approximately six times heavier than our smallest so we would expect its MCT to be only around 5% higher. This is consistent with previous studies on animals in the wild showing that swim speed is relatively constant at around 1 – 2 m s^{-1} and not correlated to body mass over a wide range, from 30 tonne sperm whales to 0.5 kg seabirds (Ponganis et al., 1990; Sato et al., 2007).

Foraging behaviour in relation to food resource availability

Although dive duration is ultimately limited by oxygen stores, it has been suggested that seals may alter their diving behaviour in response to their perception of both the quality and depth of a prey patch (Thompson and Fedak, 2001). Grey seals do alter their dive durations in response to changes in patch quality, by ending their dives early at low prey densities (Sparling et al., 2007). The results presented here suggest that transit swim speeds are not simply related to prey density. This is consistent with the assumption that seals will maximise prey acquisition by maximising the rate of delivery of oxygen to the foraging patch irrespective of patch quality.

Swim speeds in deep dives should approach, but never go below, MCT speed, whereas in shallow dives higher swim speeds would allow animals to maximise the proportion of time spent foraging at the bottom (Thompson et al., 1993). All seals tested in this study did alter their swimming behaviour in response to changes in patch distance, swimming faster to 40 m compared to 80 m or 120 m .

Sparling et al. found that dives to 40 m were generally much shorter than the estimated aerobic dive limit (ADL; equivalent to the oxygen stores divided by the metabolic rate) but in dives to 120 m , seals were approaching ADL at the highest prey densities (Sparling et al., 2007). Reducing swim speeds and therefore metabolic rates during transit in deep dives would allow seals to spend longer at the feeding patch without exceeding their estimated ADL. In contrast, studies on Northern fur seals, New Zealand sea lions and Brunnich's guillemots found that swimming speed during descent increased significantly in deeper dives (Ponganis et al., 1992; Crocker et al., 2001; Lovvorn et al., 2004). Unlike phocid seals, these species store air in their lungs, fur or plumage and therefore have to work hard against buoyancy at the start of the dive. In shallow dives a higher proportion of the descent is spent working against buoyancy so that the apparent drag forces experienced by the animal will be greater in shallow compared to deep dives.

Swimming mode in absence of pressure effect

Differences between 'descent' and 'ascent' swim speeds are usually explained in terms of changes in buoyancy forces (Webb et al., 1998; Williams et al., 2000; Beck et al., 2000; Sato et al., 2003). However, despite the fact that all swimming between the surface and the foraging site was horizontal in our study, seals nevertheless swam slower on 'ascent' than on 'descent' despite

not having to work against negative buoyancy (Table 1 and Fig. 7). This difference between 'descent' and 'ascent' speeds was maintained with increasing patch distance and there was no indication that the slower 'ascent' swimming was a conditioned response to perceived buoyancy. Seals were choosing to swim faster to their feeding patch. Buoyancy cannot therefore completely explain why negatively buoyant seals swim more slowly during 'ascent'. Motivational state may have a direct effect on swim speeds; seals may swim faster to the feeding patch in anticipation of finding food while they might save energy for the next dive by swimming slower on their way back.

All our seals used burst and glide swimming during both 'descent' and 'ascent' (Fig. 2). This is possibly an energy-efficient way of travelling for marine mammals (Lovvorn et al., 1999; Williams et al., 2000; Lovvorn et al., 2001). Data from TDRs in this study indicate that there were fewer acceleration and deceleration phases during the faster 'descent' compared to the slower 'ascent' (Fig. 8). Seals might have increased the frequency and/or the amplitude of their strokes to increase their speed on the 'descent', but our TDR records were not sensitive enough to detect individual swimming strokes. Several studies have suggested that speed and acceleration are mediated *via* changes in stroke amplitude rather than stroke frequency (Lovvorn et al., 1999; Wilson and Liebsch, 2003; Lovvorn et al., 2004). In order to determine in detail the swimming tactics used by the seals in our set-up, however, we would need to use more precise accelerometer devices.

In summary, the results of the present study indicate that swim speeds in grey seals are closely related to resource accessibility, i.e. distance, but not to the patch quality. Seals adjusted their swim speeds in relation to dive distance allowing them to increase their time spent foraging underwater. In addition, our unexpected discovery that seals swim slower on their way back to the surface in the absence of buoyancy effects suggests that the swimming behaviour exhibited by foraging grey seals during vertical swimming is primarily dependent on behavioural choices rather than a result of buoyancy effects (Fedak and Thompson, 1993; Thompson and Fedak, 2001; Sparling et al., 2007).

List of abbreviations

ADL	aerobic dive limit
COT	cost of transport
DLV	diving lung volume
ID	identification
MCT	minimum cost of transport
PER	prey encounter rate
TBF	total body fat
TDR	time–depth recorder
TLC	total lung capacity

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