The Journal of Experimental Biology 203, 2323–2330 (2000)
Printed in Great Britain © The Company of Biologists Limited 2000
JEB2558

SEASONAL CHANGES IN BUOYANCY AND DIVING BEHAVIOUR OF ADULT GREY SEALS

CARRIE A. BECK[1,*], W. DON BOWEN[2] AND SARA J. IVERSON[1]

[1]*Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1* and [2]*Marine Fish Division, Bedford Institute of Oceanography, Department of Fisheries and Oceans, Dartmouth, Nova Scotia, Canada B2Y 4A2*

*e-mail: cbeck@is2.dal.ca

Accepted 11 April; published on WWW 10 July 2000

Summary

Phocid seals go through dramatic seasonal changes in body mass and composition as a result of the spatial and temporal separation of foraging, reproduction and moulting. These changes in body fat content and body mass result in seasonal changes in buoyancy, which in turn may influence diving behaviour. We examined the longitudinal changes in buoyancy and diving behaviour of 14 adult grey seals (*Halichoerus grypus*) during two periods that represent maximal contrast in body mass and composition. During both the post-moulting (PM) and pre-breeding (PB) periods, grey seals were negatively buoyant. However, buoyancy increased by 47.9 % between the PM and PB periods. Descent rate was significantly faster during the PM period (1.0±0.07 m s^{-1}) than during the PB period (0.7±0.06 m s^{-1}), suggesting that seals were aided by negative buoyancy during the downward portion of dives. Ascent rate was also significantly faster during the PM period (0.8±0.06 m s^{-1}) than during the PB period (0.6±0.05 m s^{-1}), contradicting the prediction that more buoyant animals should ascend faster. The effects of drag could not account for this discrepancy. Dive depth and surface interval between dives did not differ significantly between the two periods. Similarly, the distribution of dive shapes used by individuals did not differ between the two periods. However, dive duration was significantly longer during the PB period than during the PM period (5.5±0.25 min compared with 4.4±0.24 min, respectively) as was time spent at the bottom of the dive (3.1±0.22 min compared with 2.5±0.15 min, respectively).

Key words: buoyancy, diving, season, grey seal, *Halichoerus grypus*, drag, body mass, body composition.

Introduction

Two vertical forces affect objects that are immersed in fluid: the force of gravity and the buoyant force. The force of gravity is directed downwards and has a magnitude determined by the mass of the object. The buoyant force is directed upwards and is equal to the weight of the fluid displaced by the object (Cromer, 1977). When the gravitational force is greater than the buoyant force, the object is negatively buoyant and will sink. Conversely, when the buoyant force is greater than the gravitational force, the object is positively buoyant and will float upwards. Aquatic organisms must deal with these forces during the course of their daily activities. Individuals that are negatively or positively buoyant must expend energy to maintain their place in the water column or to move in the direction opposite to the total force acting upon them. Organisms that are neutrally buoyant must exert effort to move vertically within the water column, regardless of direction.

In pinnipeds (true seals, fur seals, sea lions and walruses), as in other marine mammals, buoyancy is determined by the ratio of adipose to lean body tissue and by the mass of the individual. Adipose tissue is positively buoyant while lean tissue is negatively buoyant; hence, an animal with a high ratio of adipose to lean tissue is more buoyant than an animal of similar mass but with a lower ratio. Mass affects buoyancy since the force of gravity is related to the mass of an object. Thus, a large animal, with the same ratio of adipose to lean tissue as a small animal, would be less buoyant (see Table 1 in Webb et al., 1998). In phocids (true seals), terrestrial reproduction and moulting result in periods of fasting on land alternating with periods of foraging at sea. This pattern results in dramatic seasonal changes in body mass and composition (Sergeant, 1976; Ryg et al., 1990; Lager et al., 1994; Chabot et al., 1996; Worthy et al., 1992; Costa et al., 1986). For example, following the moulting period, female grey seals (*Halichoerus grypus*; *N*=16) have a mean body mass of 126.2 kg and a fat concentration of 13.2 %. In contrast, females average 210.2 kg, with fat accounting for 32.8 % of body mass at the start of the breeding season 7 months later (C. A. Beck, W. D. Bowen and S. J. Iverson, unpublished data). These large seasonal changes in body mass and composition will affect the buoyancy of individuals.

In many aquatic species, physiological mechanisms or

anatomical structures have evolved that allow individuals to regulate their buoyancy (e.g. the swimbladder of fish, increased lung volume in sea otters, the ability of deep-sea shrimps to replace heavy ions in their tissues with lighter ions). In general, phocids cannot adjust body mass or composition over the short term to regulate their buoyancy. Webb et al. (1998) therefore argued that phocids may modify their diving behaviour in response to changes in buoyancy.

Webb et al. (1998) experimentally examined the effects of buoyancy on the diving behaviour of 13 juvenile northern elephant seals (*Mirounga angustirostris*). They found that descent rate differed significantly between buoyancy groups, with less buoyant animals having a faster rate of descent than more buoyant animals. Surprisingly, the ascent rate of individual seals did not vary with buoyancy in the elephant seal study. Webb et al. (1998) concluded that the effect of buoyancy on ascent rate would be minimal relative to the lift generated by active swimming of individuals towards the surface. They also concluded that differences in descent rate between buoyancy groups, and the strong correlation between descent rate and buoyancy among animals, confirmed the influence of buoyancy on diving behaviour. While this relationship appears fairly strong, the adjusted buoyancy of animals in the study of Webb et al. (1998) ranged from +1.07 to −65.05 N or 43.7 to 24.2 % adipose tissue, respectively. With the exception of newly weaned pups and some tentative evidence regarding pregnant elephant seals (Crocker et al., 1997), phocid seals do not achieve a body composition that would result in positive buoyancy (e.g. grey seals, this study; *Phoca vitulina*, Bowen et al., 1992; *Phoca hispida*, Ryg et al., 1990; elephant seals, Williams, 1995; Worthy et al., 1992). Thus, by including individuals that had been manipulated to be positively buoyant, Webb et al. (1998) may have extended the relationship between descent rate and buoyancy over a range of buoyancy that is not entirely representative of that found in nature.

In the present study, we tested the hypotheses of Webb et al. (1998) that phocids modify their diving behaviour in response to seasonal changes in buoyancy. Specifically, we address the hypothesis that less buoyant individuals descend more rapidly than more buoyant individuals but have similar rates of ascent. To test this hypothesis, we measured longitudinal changes in buoyancy and diving behaviour of free-ranging adult grey seals during two periods that represent the maximum contrast in buoyancy of this species.

The grey seal is a relatively large phocid species found on both sides of the North Atlantic Ocean. Sable Island, Nova Scotia, Canada, in the northwest Atlantic supports the largest breeding colony of grey seals in the world. Grey seals in this population congregate on Sable Island in May and June to moult and again in late December and January for the breeding period. As indicated above, adult grey seals are particularly lean (and consequently least buoyant) following the terrestrial moulting period in May. During the 7-month period following the moult, grey seals equipped with time/depth data loggers spend much of their time at sea diving and presumably foraging (C. A. Beck, W. D. Bowen, J. I. McMillan and S. J. Iverson, unpublished observations). Animals return to the island in late December and January for the breeding season having increased their body mass by approximately 45 % and their adipose tissue mass by approximately 68 % (C. A. Beck, W. D. Bowen and S. J. Iverson, unpublished observations). Thus, adult grey seals are most buoyant at the start of the breeding season.

Materials and methods

Body composition and buoyancy measurements

Our study was conducted between May 1997 and January 1999 on Sable Island, a 45 km long, crescent-shaped, vegetated sandbar located 277 km southeast of Halifax, Nova Scotia, Canada (43°90′N, 60°00′W). Fourteen adult grey seals (six males and eight females) were captured using hand-held nets (see Bowen et al., 1992) shortly after the spring moulting period in May 1997 or May 1998 and again in January of the following year when these individuals returned to Sable Island at the beginning of the breeding season. All procedures used on grey seals in this study were in accordance with the principles and guidelines of the Canadian Council on Animal Care.

The body composition of each seal was measured using tritium (as tritiated water, HTO) dilution at initial capture and again when recaptured in January. Individuals were weighed to the nearest 0.5 kg, using Salter spring balances, and then administered a precisely weighed dose of HTO ($18.5\ MBq\ ml^{-1}$; at $0.02\ g\ kg^{-1}$ body mass). HTO was injected intramuscularly, and the needle and syringe were rinsed with unlabelled water (also injected) to ensure complete delivery of the weighed isotope. A blood sample was taken from the extradural vein at 90 min post-administration and again 15–20 min later to confirm that isotope equilibration had occurred. Previous studies on grey seals have shown that HTO injected intramuscularly equilibrates with body water in 90 min or less and that 15–20 min intervals are sufficient to detect any continued changes (Mellish, 1999; C. A. Beck, W. D. Bowen and S. J. Iverson, unpublished data).

Blood samples were collected into Vacutainers without additives and later centrifuged for 20–30 min. Serum samples (5 ml) were stored frozen (−20 °C) in cryovials until analysis. Total water was recovered from each sample by distilling 50 µl samples of serum directly into pre-weighed scintillation vials, using the evaporated freeze-capture method described by Ortiz et al. (1978). The vials were then reweighed to obtain the mass of distillate to the nearest 0.1 mg, and 10 ml of Scintiverse II was added to each vial. The radioactivity in each sample was counted for 5 min in a Beckman scintillation counter. Samples were analyzed in triplicate, and the average specific activity was expressed as counts per minute per gram distillate ($cts\ min^{-1}\ g^{-1}$). In cases where the triplicate samples had a coefficient of variation greater than 2 %, the two closest values were used. The

specific activity of the injectate was determined at the same time as that of the serum samples.

HTO dilution space (D_{HTO}) was calculated using published equations (Bowen et al., 1999), and total body water (TBW) was estimated from a regression of isotope dilution space on TBW (Bowen and Iverson, 1998). The percentage of total body fat (TBF) was then calculated using the equation:

$$\%TBF = 105.1 - 1.47(\%TBW) \quad (1)$$

developed for grey seals by Reilly and Fedak (1990).

In January, females were not recaptured until 1–3 days *postpartum* to allow mothers time to bond with newborns. Since mean female mass loss during the first 5 days of lactation is 4.3 kg per day, with fat comprising 58 % of the loss (Mellish et al., 1999), these rates of mass and fat loss were used to correct female body mass and percentage fat to initial *postpartum* levels. Pup birth mass (5 % of which is fat; Iverson et al., 1993; Mellish et al., 1999) was added to female mass to estimate body composition during late-term pregnancy. Mass lost in the placenta and amniotic fluid was not considered in this back-calculation of female mass and composition because of a lack of data. Male grey seals were usually captured within 2 days of appearing on the breeding grounds, as indicated by the dry time (i.e. time on land) recorded by their time/depth recorders. During the breeding season, male grey seals on Sable Island lose mass at an approximate rate of 2.5 kg per day, with fat constituting 62 % of mass loss (Godsell, 1991; D. C. Lidgard, D. J. Boness and W. D. Bowen, unpublished results; Coltman et al., 1998). These rates of loss and our best estimate of when the male returned to the island (from the first sighting of the male on the island or from diving data) were used to correct body mass and composition of males to pre-breeding conditions.

Adipose mass was calculated assuming that fat accounts for 76.9 % of adipose tissue following the moulting period and 92.3 % at the beginning of the breeding season. In the absence of data on grey seals, these estimates of the lipid content of adipose tissue were based on the equation developed by Bowen et al. (1992) for female harbour seals (*Phoca vitulina*) during lactation. We used this equation to determine the lipid content of adipose tissue for an animal in a high-fat condition (i.e. at the start of the lactation/pre-breeding season) and in a relatively low-fat condition (i.e. post-moulting season/at the end of lactation).

Buoyancy was calculated for each animal at initial post-moult (PM) capture and again at pre-breeding (PB) recapture using the equation from Webb et al. (1998):

$$B_T = (0.8871 M_a) + (-0.6689 M_{lb}), \quad (2)$$

where B_T is total buoyancy (N), $0.8871\ N\ kg^{-1}$ is the mass-specific buoyancy of adipose tissue, M_a is adipose tissue mass (kg), $-0.6689\ N\ kg^{-1}$ is the mass-specific buoyancy of lean tissue and M_{lb} is lean body mass (kg). Mass-specific buoyancy coefficients from Webb et al. (1998) were determined by calculating the buoyancy of 1 kg of tissue based on published estimates of tissue density (P. M. Webb, personal communication; Webb et al., 1998; Worthy et al., 1992; Nordøy and Blix, 1985).

Diving behaviour

At the initial PM capture, animals were anaesthetized using Telazol (equal parts of tiletamine and zolazepam) immediately after the first equilibration blood sample had been taken. Males and females were given an average dose of 0.45 and 0.85 mg kg^{-1} body mass, respectively (Bowen et al., 1999). Once immobilized, time/depth recorders (TDRs) or satellite-linked, time/depth recorders (SLTDRs) were glued to the pelage of the animal using 5 min epoxy resin. TDRs, weighing 65–300 g or less than 0.3 % of initial body mass, were placed on the lower back of the animals. SLTDRs, weighing approximately 600 g or less than 0.6 % of initial body mass, were placed on the head of the seals. TDRs and SLTDRs were programmed to record depth every 20 s. Because the memory capacity of instruments differed, they were duty-cycled (25–60 % of days sampled) such that data were collected every few days over the entire 7-month deployment period.

In January, at the PB recapture, the instruments were removed and TDR dive data were processed using software from Wildlife Computers (Woodinville, WA, USA). Zero-offset correction software was used to correct for shifts in the calibration of the pressure transducer of the instruments over the data collection period. Data files could only be corrected for transducer drift in blocks of dives. Therefore, only dives of 4 m or deeper were analyzed because instrument noise causes drift that is slightly greater than the depth resolution of the instrument (2 m). Dive analysis (DA) software was used to analyze the corrected dive records and to provide estimates of the individual dive variables: depth, duration, time spent at the bottom of the dive (bottom time), surface interval between dives, descent rate and ascent rate. Webb et al. (1998) found that the rates of ascent and descent of elephant seal dives calculated automatically by the DA program were often unacceptable and therefore manually set markers within DA to determine these rates. However, we did not experience this problem. Dives during the first 2 weeks after PM deployment were selected to represent diving behaviour when the animals were thin and, consequently, least buoyant. Dives during the 2 weeks prior to haul-out on Sable Island in January were considered to represent diving behaviour when the animals were at their fattest and most buoyant.

Statistical analyses

Statistical analyses were performed using SPSS 8.0. The standard error (S.E.) is given as a measure of variability about the mean. Dive variables were examined for normality and transformed where necessary. Depth was strongly correlated with rates of descent (Spearman's ρ=0.553, P=0.002) and ascent (Spearman's ρ=–0.555, P=0.002). Repeated-measures analyses of variance (ANOVAs) with depth as a covariate was therefore used to examine differences in rates of travel between the PM and PB periods. Paired *t*-tests were used to

Table 1. *Body composition and buoyancy of individuals during the post-moult (PM) and pre-breeding (PB) periods*

		Mass (kg)		Fat (kg)		Adipose tissue (%)		Buoyancy (N)	
Seal	Sex	PM	PB	PM	PB	PM	PB	PM	PB
B541	F	150.0	287.5	18.5	99.6	16.0	37.5	−63.0	−24.4
E358	F	127.0	220.5	14.6	64.3	15.0	31.6	−55.4	−39.0
E463	F	126.5	195.0	19.2	63.2	19.8	35.1	−45.7	−23.9
M538	M	195.0	288.0	23.4	95.6	15.6	36.0	−83.1	−31.5
1C1	F	131.0	266.2	14.3	86.6	14.2	35.2	−58.7	−32.1
M523	M	155.0	227.0	6.2	67.7	5.2	32.3	−91.1	−37.7
M190	M	192.0	301.0	21.3	83.7	14.4	30.1	−85.3	−60.2
K448	F	116.0	148.0	12.5	47.5	14.0	34.8	−52.2	−18.9
8C9	F	111.0	222.7	10.1	76.9	11.8	37.4	−53.8	−19.3
K171	F	117.5	210.1	24.7	65.6	27.3	33.8	−28.7	−29.9
M18	M	170.0	269.0	26.2	93.3	20.0	37.6	−60.7	−22.6
F757	F	138.0	230.7	17.0	66.0	16.0	31.0	−58.0	−43.1
S-4272	M	201.5	305.0	7.3	92.1	4.7	32.7	−120.1	−48.7
S-4274	M	242.0	316.0	14.5	97.3	7.8	33.4	−132.5	−47.3
Mean		155.2	249.1	16.4	78.5	14.4	34.2	−70.6	−34.2
S.E.		10.55	13.05	1.66	4.34	1.60	0.66	7.69	3.31

Table 2. *Summary diving statistics for study animals during post-moult (PM) and pre-breeding (PB) periods*

		Number of dives		Mean depth (m)		Mean duration (min)		Mean bottom time (min)		Mean surface interval (min)		Mean descent rate ($m\,s^{-1}$)		Mean ascent rate ($m\,s^{-1}$)	
Seal	Sex	PM	PB	PM	PB	PM	PB	PM	PB	PM	PB	PM	PB	PM	PB
B541	F	601	712	39.6	49.3	3.9	6.2	2.4	3.7	5.1	1.8	1.0	0.7	0.9	0.6
E358	F	1324	812	48.7	41.3	6.0	5.6	3.5	3.7	2.6	1.2	0.7	0.9	0.6	0.8
E463	F	1155	911	27.4	10.9	4.1	4.6	1.9	3.0	1.8	1.8	0.4	0.3	0.4	0.3
M538	M	597	609	80.1	85.6	4.5	6.0	2.4	2.7	1.7	4.3	1.5	0.9	1.1	0.7
1C1	F	1631	796	55.0	68.9	3.9	5.2	1.8	2.4	1.2	2.4	0.9	0.9	0.8	0.8
M523	M	987	276	45.3	46.2	4.1	6.0	2.4	3.6	1.2	2.9	1.1	0.8	0.9	0.7
M190	M	1178	988	34.9	53.8	3.2	4.6	1.8	1.8	1.4	1.2	1.0	0.6	0.8	0.5
K448	F	743	859	38.0	51.2	3.7	6.8	2.2	4.2	2.6	1.0	1.0	0.9	0.8	0.7
8C9	F	1182	1059	59.2	66.7	3.6	4.2	1.9	1.9	2.2	1.5	1.2	0.9	1.2	0.9
K171	F	903	966	33.8	34.6	4.1	4.9	3.0	2.9	2.0	1.2	1.1	0.6	1.1	0.6
M18	M	1074	811	26.6	56.1	3.6	6.0	2.4	3.5	0.9	3.0	0.9	0.9	0.8	0.7
F757	F	836	725	76.8	75.3	5.8	7.0	3.4	4.4	3.5	1.7	1.2	1.0	1.1	0.9
S-4272	M	778	381	45.9	12.8	5.1	4.0	2.7	2.2	2.5	8.1	0.8	0.3	0.5	0.3
S-4274	M	318	213	58.4	55.4	5.6	5.9	2.9	3.1	10.8	5.0	0.9	0.7	0.5	0.5
Overall															
Mean		950.5	722.7	47.8	50.6	4.4	5.5	2.5	3.1	2.8	2.7	1.0	0.7	0.8	0.6
S.E.		90.84	70.59	4.44	5.68	0.24	0.25	0.15	0.22	0.68	0.53	0.07	0.06	0.06	0.05
P-value[a]				0.810		0.003		0.008		0.850		*		*	

[a]Paired-sample *t*-test.
*See Table 3.

compare all other dive variables between the PM and PB periods.

The shape of individual dives can be represented in two dimensions as a function of time and depth. Dive shapes were classified using discriminant function analysis (DFA) as described in Scheer and Testa (1995). Briefly, a subset of 2000 dives was visually inspected, with individual dives being classified as one of five shapes: square, wiggle, V-shaped, left-skewed square and right-skewed square. Discriminant functions were derived from this subset such that DFA correctly classified 96.2 % of the dives. The resulting discriminant functions were used to classify the remaining dives. A repeated-measures, two-way ANOVA was used to determine whether dive shape frequency differed between the PM and PB periods.

Results

Buoyancy

The mean body mass of the recently moulted grey seals was 155.2 kg, with adipose tissue accounting for approximately 14 % of body mass (Table 1). At the beginning of the breeding season, the mean body mass of the same individuals had increased to 249.1 kg (i.e. by 60.5 %), with adipose tissue mass more than doubling to 34 % of body mass. At both times, animals were negatively buoyant (Table 1); however, buoyancy was 47.9±5.51 % greater at the beginning of the breeding season than in recently moulted seals (paired *t*-test: $P<0.001$, $N=14$).

Diving behaviour

In total, 13 307 dives were sampled in the 2 weeks following the moult. During this PM period, the number of dives per seal ranged between 318 and 1631, representing 3–9 days of sampling. In the 2 weeks prior to the breeding season on Sable Island, 10 118 dives were recorded from these same individuals. The number of dives per seal ranged between 213 and 1059, representing 4–6 days of data during the PB period.

There were no significant differences in mean dive depth (paired *t*-test: $P=0.520$, $N=14$) or surface interval between dives (paired *t*-test: $P=0.850$, $N=14$) between the two periods (Table 2). Mean dive duration and mean bottom time were significantly longer during the PB period (paired *t*-test: $P=0.003$, $N=14$) than during the PM period (paired *t*-test: $P=0.008$, $N=14$) (Table 2). Rates of descent and ascent increased with dive depth (Fig. 1) and were significantly faster (Table 3) during the PM period, when animals were less buoyant, than during the PB period, when they were more buoyant.

We also examined the effects of changes in buoyancy on diving behaviour by calculating the difference between descent and ascent rates for each dive. The mean difference between descent and ascent rates was significantly correlated with buoyancy within the PM period ($r=-0.829$, $P<0.001$), but not during the PB period ($r=-0.055$, $P=0.853$). In almost all cases, descent rate was faster than ascent rate (Fig. 2) and, as individual animals became more buoyant (from PM to PB), the magnitude of the difference between the two rates decreased (paired *t*-test: $P=0.010$, $N=14$).

Changes in buoyancy might also be reflected by the frequency distribution of dive shapes used by grey seals during the PM and PB periods. However, the distribution of dive shapes did not differ between the two periods (Fig. 3). A repeat-measures, two-way ANOVA also showed no significant interaction between dive shape and condition of the individual ($F=2.13$, d.f.=4,65, $P=0.087$). Square-shaped dives were by far the most frequently used, accounting for more than 70 % of

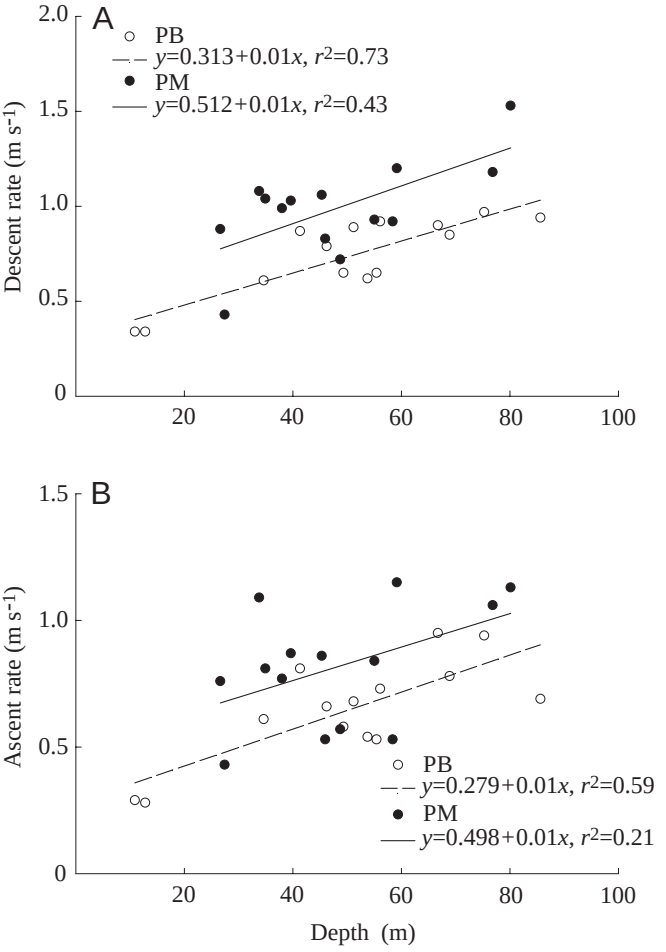

Fig. 1. Relationships between mean dive depth and (A) mean descent rate and (B) mean ascent rate during the post-moulting (PM; filled circles) and pre-breeding (PB; open circles) periods for 14 adult grey seals. See Table 3 for statistical analysis.

Table 3. *Results of repeated-measures ANOVA comparing post-moult (PM) and pre-breeding (PB) grey seals with depth as covariate*

	Descent rate, $N=14$			Ascent rate, $N=14$		
	Parameters	*t*	*P*	Parameters	*t*	*P*
Condition (PB) on depth						
Constant	0.5071	4.058	0.002	0.4508	2.748	0.017
Slope	0.0103	6.030	<0.001	0.0084	3.749	0.003
Within-subject difference (PM *versus* PB)						
Constant	0.1809	4.370	<0.001	0.1186	3.197	0.008
Slope	0.003	0.658	0.523	–0.0001	–0.018	0.986

dives during both periods. Right-skewed square dives were the second most common shape, representing 12.1 and 13.9 % of dives during the low- and high-buoyancy periods, respectively. None of the remaining dive shapes accounted for more than 6.6 % of dives used during either period.

Discussion

Buoyancy estimation

Our calculations of buoyancy are affected by two potential sources of error. The equation developed by Webb et al. (1998) for determining buoyancy uses mass-specific values of buoyancy for adipose and lean tissue and requires accurate measurements of the mass of both tissues. Thus, the first source of error involves the estimation of the mass of these tissues. In estimating body composition from total body water, lipid mass, not adipose tissue mass, is estimated. Adipose tissue mass must subsequently be calculated from fat mass on the basis of the percentage of lipid in adipose tissue. Although adipose tissue is composed primarily of lipid, water and protein are also significant components. It is reasonably well established that, when animals fatten, the fat cells (adipocytes) fill with lipid. Conversely, when animals lose fat, the adipocytes empty, resulting in a lower lipid and greater water and protein content of adipose tissue (Emery, 1969). This change in adipose tissue composition will have substantial effects on the estimation of adipose tissue mass from lipid mass and, therefore, on the calculation of buoyancy.

Data on the lipid content of adipose tissue in grey seals are not available during the PM or PB periods. However, Bowen et al. (1992) found that the adipose tissue of fattened female harbour seals at parturition contained 92.3 % fat, 2.2 % protein and 5.5 % water. In contrast, 20 days later, after substantial mass and fat loss during lactation, adipose tissue contained 76.9 % fat, 5.9 % protein and 17.2 % water. Individual grey seals at the end of the moulting period and harbour seal females near the end of lactation appear to be similarly depleted, so the lipid content of adipose tissue at these times is likely to be similar. Body fat content is similar in both species at the start of the breeding season. Hence, the values for the proximate composition of harbour seal blubber should provide reasonable estimates of grey seal adipose tissue and, therefore, buoyancy during the PM and PB periods. The assumption of a constant value of lipid content in adipose tissue would clearly lead to erroneous estimates of buoyancy, particularly in studies examining temporal changes in buoyancy.

The second source of error involves the relationship between mass-specific buoyancy and tissue density (Webb et al., 1998; P. W. Webb, personal communication). Given the expected large seasonal changes in the lipid content (see above), the density of adipose tissue will not be constant. As individuals become depleted of fat, adipose tissue should become denser as the relative lipid content decreases and protein content increases. This being the case, the density and, hence, mass-specific buoyancy of adipose tissue will differ between the PM and PB periods. However, seasonal changes in the density of adipose tissue are not known for grey seals or other phocid species. By assuming a constant mass-specific buoyancy of adipose tissue, we have probably underestimated the seasonal change in buoyancy of individuals.

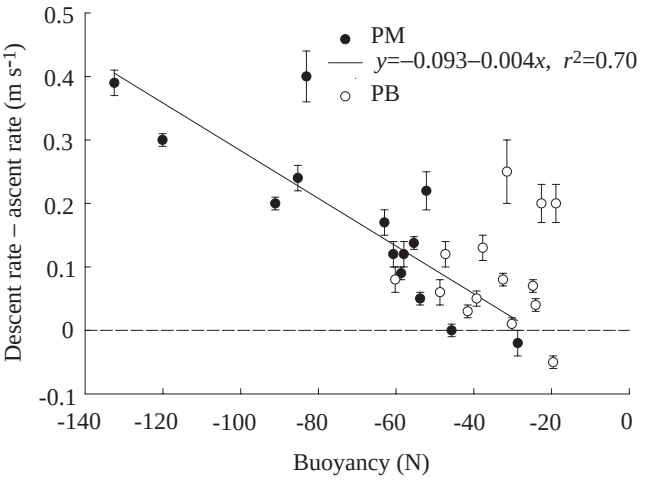

Fig. 2. Relationship between buoyancy and the difference between descent and ascent rates of individual dives for 14 adult grey seals during both the post-moulting (PM; filled circles) and pre-breeding (PB; open circles) periods. Values are means ±1 S.E. *r* and *P* values refer to Pearson's correlation statistics.

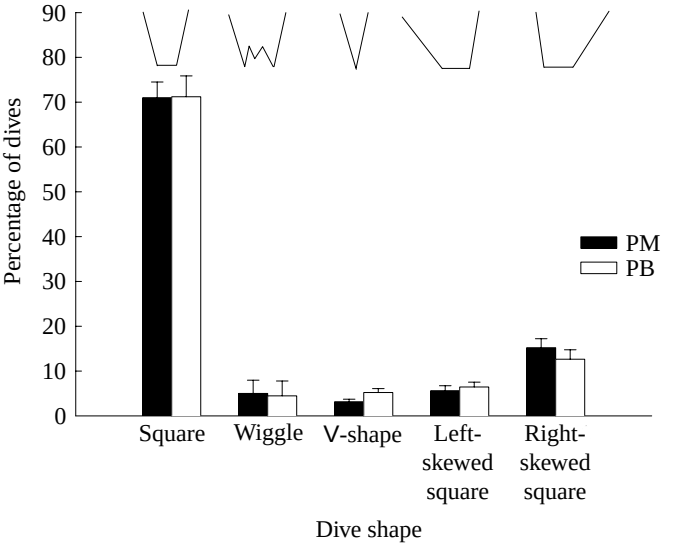

Fig. 3. Dive shape distribution of 14 adult grey seals during both the post-moulting (PM; filled columns) and pre-breeding (PB; open columns) periods. Values are means + S.E.

Buoyancy and drag effects on diving

Adult phocid seals undergo dramatic seasonal changes in body composition and body mass. These changes in turn affect the force of buoyancy acting on individuals. Despite these dramatic seasonal changes, we found that adult grey seals were always negatively buoyant. However, the magnitude of this downward force decreased significantly as individuals

increased their lipid stores for reproduction. Changes in buoyancy should be most evident in the rates of ascent and descent. Consistent with this expectation, grey seals descended at a significantly faster rate when less buoyant (during the PM period), suggesting that individuals were aided by negative buoyancy during descent. This finding confirms the results of Webb et al. (1998) that the descent rate of elephant seals is affected by changes in buoyancy. Given the relationship between descent rate and buoyancy, we expected grey seals to ascend faster during the PB period (i.e. when they are relatively more buoyant) than during the PM period. Although fatter individuals would not be aided by lift from buoyancy (they are not positively buoyant), they would have less downward force to work against while actively swimming to the surface. Webb et al. (1998) found no difference in the ascent rate of elephant seals relative to changes in buoyancy. In contrast, less buoyant grey seals ascended faster than more buoyant seals (Table 2), contradicting the predicted effect of buoyancy. Our results indicate that grey seals travel to and from the surface faster when they are thin and consequently less buoyant.

Mobile aquatic organisms are also affected by drag. The force of drag impedes movement through a fluid and is a function of velocity, fluid density, body cross-sectional area and hydrodynamic shape (i.e. the coefficient of drag). In the present study, drag would be greater on an animal during the PB period than during the PM period, given the increase in cross-sectional area associated with fattening (assuming the same travel speed). To decrease drag, grey seals could travel more slowly during the PB period. This is consistent with the observed slower rates of travel when animals were more buoyant. To compare the relative magnitude of drag and buoyancy during vertical travel, we calculated drag (D) for PM and PB individuals based on girth measurements for grey seals in eastern Canada (M. Hammill, unpublished data).

Drag was calculated using the equation:

$$D = 0.5\rho a U^2 C_D, \quad (3)$$

where ρ is the density of sea water (1024 kg m^{-3}), a is the frontal area of the seal calculated from girth measurements (thin, girth=1.12 m, a=0.10 m^2; fat, girth=1.84 m, a=0.27 m^2), U is the swimming velocity, and C_D is the drag coefficient (0.09; Williams and Kooyman, 1985; Webb et al., 1998). The calculated drag for a thin grey seal travelling at a mean swimming speed of 0.9 m s^{-1} is 3.73 N and that of a fat individual is 10.08 N. While the force of drag is almost three times larger for a fat seal, the magnitude of drag is small relative to the buoyant force affecting the animals in their respective conditions (Table 1). Hence, buoyancy increases by a larger amount than drag as the animal fattens. As a result, the effect of drag cannot explain the association of increased buoyancy and decreased rate of ascent.

Descent rate was almost always faster than ascent rate for individual dives (Fig. 2). When considering the combined role of buoyancy and drag on the rate of vertical movement, this result seems logical (Webb et al., 1998). During descent, the force of buoyancy and drag work in opposite directions. However, since the negative buoyancy exceeds the magnitude of drag, the animal is aided in descent by a downward force. On ascent, individuals are faced with the cumulative force of negative buoyancy and drag and, as a result, will have to work harder to ascend (Webb et al., 1998). Thus, regardless of buoyancy, descent is energetically less costly than ascent, resulting in faster rates of descent. As an animal fattens and becomes less negatively buoyant, the differential cost of descent and ascent lessens (Fig. 2), providing evidence for the effect of buoyancy.

Webb et al. (1998) suggested that animals with greater fat stores might have to exert a greater effort to maintain position at the bottom while feeding benthically because of lift from buoyancy. If this were the case, given a finite oxygen capacity, more buoyant animals would be expected to have dives of shorter duration and to spend less time at the bottom during the PB period. In our study, grey seals had significantly longer dive durations and bottom times when they were most buoyant, contradicting the prediction of Webb et al. (1998). However, the grey seals in the present study were always negatively buoyant and, as a result, they would not have to expend energy to maintain position on the bottom for benthic feeding. Given that dive depth did not differ with respect to changes in buoyancy, the increased dive duration may be the result of slower rates of descent and ascent in more buoyant individuals. However, this does not explain why time spent at the bottom during dives should increase with buoyancy. Alternatively, increased dive duration and bottom time might be associated with increased foraging effort just prior to the breeding season. Seasonal changes in dive effort, and presumably foraging, occur in both male and female grey seals equipped with TDRs (C. A. Beck, W. D. Bowen and S. J. Iverson, unpublished results) and show that both sexes increase their dive effort as the breeding season approaches.

The interpretation of longitudinal measurements of diving behaviour in free-ranging grey seals is potentially confounded by several factors. In addition to changes in body mass and buoyancy, differences in foraging location and diet may also have affected the characteristics of diving. For example, as discussed above, the observed differences in dive duration and bottom time between the PM and PB periods may be the result of increased foraging effort. However, these confounding factors are unlikely to be the cause of the observed differences in vertical rates of travel for several reasons. First, grey seals exhibited a similar distribution of dive shapes (Fig. 3) and mean dive depth (Table 2) between the two periods, suggesting that individuals were foraging in similar habitats and using similar foraging tactics. Second, animal-borne video data show that rates of vertical travel during diving did not differ significantly among prey types in adult harbour seals (Tully, 1999). Nevertheless, including these potentially confounding factors in future analyses would provide a stronger test of the influence of buoyancy on diving behaviour.

In conclusion, our study confirms the hypothesis of Webb et al. (1998) and demonstrates that seasonal changes in buoyancy in individual adult grey seals affect rates of descent during

diving. Seasonal differences in descent rate are convincingly associated with changes in buoyancy. However, seasonal changes in ascent rates require a different explanation. Seasonal changes in the cost of transport with changes in body mass may better explain the observed seasonal changes in ascent rate. To test this hypothesis, it will be necessary to measure the cost of transport during ascent in thin (less buoyant) and fat (more buoyant) individuals.

We would like to thank Jim McMillan, Debbie Austin, Amy Bowen, Shelley Lang and Dan Tully for their assistance in the field and Paul Fanning for his statistical assistance. Tisha White, Debbie Austin, Paul Webb and an anonymous reviewer commented on earlier drafts of the manuscript. Mike Hammill kindly provided unpublished data on seasonal changes in the girth of adult grey seals. This study was supported by a Natural Sciences and Engineering Research Council (NSERC), Canada, scholarship to C.A.B., by NSERC research grants to W.D.B. and S.J.I. and by the Department of Fisheries and Oceans, Canada.

References

Bowen, W. D., Beck, C. A. and Iverson, S. J. (1999). Bioelectrical impedance analysis as a means of estimating total body water in grey seals. *Can. J. Zool.* **77**, 1–5.

Bowen, W. D. and Iverson, S. J. (1998). Estimation of total body water in pinnipeds using hydrogen-isotope dilution. *Physiol. Zool.* **71**, 329–332.

Bowen, W. D., Oftedal, O. T. and Boness, D. J. (1992). Mass and energy transfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). *Physiol. Zool.* **65**, 844–866.

Chabot, D., Stenson, G. B. and Cadigan, N. B. (1996). Short- and long-term fluctuations in the size and condition of harp seals (*Phoca groenlandica*) in the Northwest Atlantic. *NAFO SCR Doc. 95/42., Serial No. N2551.*

Coltman, D. W., Bowen, W. D., Iverson, S. J. and Boness, D. J. (1998). The energetics of male reproduction in an aquatically mating pinniped, the harbour seal. *Physiol. Zool.* **71**, 387–399.

Costa, D. P., Le Boeuf, B. J., Ortiz, C. L. and Huntley, A. C. (1986). Energetics of lactation in the Northern elephant seal, *Mirounga angustirostris*. *J. Zool., Lond.* **209**, 21–33.

Crocker, D. E., Le Boeuf, B. J. and Costa, D. P. (1997). Drift diving in female northern elephant seals: implications for food processing. *Can. J. Zool.* **75**, 27–39.

Cromer, A. H. (1977). *Physics for the Life Sciences*. New York: McGraw-Hill Companies, Inc. Primsis Custom Publishing. 530pp.

Emery, R. S. (1969). Lipids and adipose tissue. In *Animal Growth and Nutrition* (ed. E. S. E. Hafez and I. A. Dyer), pp. 236–255. Philadelphia: Lea & Febiger Press.

Godsell, J. (1991). The relative influence of age and weight on the reproductive behaviour of male grey seals, *Halichoerus grypus*. *J. Zool., Lond.* **224**, 537–551.

Iverson, S. J., Bowen, W. D., Boness, D. J. and Oftedal, O. T. (1993). The effect of maternal size and milk output on pup growth in grey seals (*Halichoerus grypus*). *Physiol. Zool.* **66**, 61–88.

Lager, A. R., Nordy, E. S. and Blix, A. S. (1994). Seasonal changes in food intake of harp seals (*Phoca greonlandica*) at 69°N. *Mar. Mammal. Sci.* **10**, 332–341.

Mellish, J-A. E. (1999). Physiology of milk fat secretion and neonatal fat deposition during lactation in phocid seals. PhD dissertation, Dalhousie University, Halifax, Nova Scotia. 250pp.

Mellish, J.-A. E., Iverson, S. J. and Bowen, W. D. (1999). Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. *Physiol. Biochem. Zool.* **67**, 677–690.

Nordøy, E. S. and Blix, A. S. (1985). Energy sources in fasting grey seal pups evaluated with computed tomography. *Am. J. Physiol.* **249**, R471–R476.

Ortiz, C. L., Costa, D. P. and Le boeuf, B. J. (1978). Water and energy flux in elephant seal pups fasting under natural conditions. *Physiol. Zool.* **51**, 166–178.

Reilly, J. J. and Fedak, M. A. (1990). Measurement of the body composition of living gray seals by hydrogen isotope dilution. *J. Appl. Physiol.* **69**, 885–891.

Ryg, M., Smith, T. G. and Oritsland, N. A. (1990). Seasonal changes in body mass and body composition of ringed seals, *Phoca hispida*, on Svalbard. *Can. J. Zool.* **68**, 470–475.

Scheer, J. F. and Testa, J. W. (1995). Statistical classification of diving behavior. *Mar. Mammal. Sci.* **11**, 85–93.

Sergeant, D. E. (1976). History and present status of harp and hooded seals. *Biol. Conserv.* **10**, 95–118.

Tully, D. K. (1999). Analysis of foraging behaviour of adult male harbour seals using animal-born video data: effects of prey type on tactics and profitability. MSc dissertation, Dalhousie University, Halifax, Nova Scotia. 52pp.

Webb, P. M., Crocker, D. E., Blackwell, S. B., Costa, D. P. and Le Boeuf, B. J. (1998). Effects of buoyancy on the diving behavior of northern elephant seals. *J. Exp. Biol.* **201**, 2349–2358.

Williams, J. D. (1995). Fasting and lactation in female Northern elephant seals (*Mirounga angustirostris*): Reconciling conflicting energetic and nutritional demands. PhD dissertation, University of California, Santa Cruz, California. 108pp.

Williams, T. M. and Kooyman, G. L. (1985). Swimming performance and hydrodynamic characteristics of harbour seals, *Phoca vitulina*. *Physiol. Zool.* **58**, 576–589.

Worthy, G. A. J., Morris, P. A., Costa, D. P. and Le Boeuf, B. J. (1992). Moult energetics of the northern elephant seal (*Mirounga angustirostris*). *J. Zool., Lond.* **227**, 257–265.