The Journal of Experimental Biology 201, 2349–2358 (1998)
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JEB1603

EFFECTS OF BUOYANCY ON THE DIVING BEHAVIOR OF NORTHERN ELEPHANT SEALS

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Accepted 29 May; published on WWW 27 July 1998

Summary

Marine mammals experience radical seasonal changes in body composition, which would be expected to affect their buoyancy in the water. The aim of this study was to examine the relationship between such changes in buoyancy and diving behavior in northern elephant seals *Mirounga angustirostris*. This was achieved by modifying the buoyancy of 13 juvenile elephant seals translocated from Año Nuevo State Reserve, CA, USA, and released at various sites in Monterey Bay, CA, USA. The buoyancy of each seal was calculated and was increased or decreased using syntactic foam or lead weights, and their diving behavior was recorded as they returned to Año Nuevo. The seals were divided into three groups: increased buoyancy (B+), reduced buoyancy (B–) and control seals (Bc). Mean descent rates were 0.77±0.3 m s^{-1} for the B+ seals, 0.82±0.2 m s^{-1} for the control seals and 0.87±0.3 m s^{-1} for the B- seals, and were significantly different. Mean ascent rates for the three treatments were 0.82±0.3 m s^{-1} for the B+ seals, 0.86±0.3 m s^{-1} for the control seals and 0.82±0.3 m s^{-1} for the B– seals. All the B+ seals ascended faster than they descended, while four of the five B– seals descended faster than they ascended. There was a significant negative correlation between buoyancy and descent rate, with less buoyant seals descending faster than more buoyant seals. There was, however, no correlation between ascent rate and buoyancy. This suggests that seals may use negative buoyancy to drift passively during descent, but that all seals may swim continuously during ascent. There was a significant correlation between buoyancy and the drift descent rate of C-type drift dives, including upwards drift in the most buoyant seal. Buoyancy was not correlated with diving depth, trip duration, dive duration or surface-interval duration. This study demonstrates that buoyancy plays a significant role in shaping diving behavior in northern elephant seals and that elephant seals may adjust their behavior to suit their buoyancy, rather than adjusting their buoyancy to suit a dive. This study also validated the truncated cones method of calculating body composition in this species by comparing it with body composition determined using tritium dilution.

Key words: buoyancy, diving, body composition, northern elephant seal, *Mirounga angustirostris*.

Introduction

Buoyancy plays a significant role in the energy budgets of pelagic organisms. Individuals that are positively or negatively buoyant expend more energy to maintain their position in the water column than individuals of the same species that are neutrally buoyant (Lovvorn and Jones, 1991*b*; Hustler, 1992). In diving canvasbacks *Aythya valisineria* and lesser scaup *Aythya affinis*, buoyancy accounts for more of the locomotor costs of shallow diving than does hydrodynamic drag, contributing 36–38 % of the total work during descent, as opposed to 10–12 % due to drag (Lovvorn *et al.* 1991). Compression of air spaces and reductions in buoyancy in lesser scaup also lower the cost of bottom foraging by 36 % at 2 m depth (Lovvorn and Jones, 1991*a*). Reduction in foraging costs may allow for more efficient or longer foraging time, while high energetic expenditure to overcome buoyancy may result in a reduction in overall foraging time.

Several strategies are employed by marine organisms to regulate buoyancy. Deep-sea shrimp *Notostomus gibbosus* (Sanders and Childress, 1988) and squid of the family Cranchidae (Denton, 1971) replace heavy ions with lighter ones, such as NH_4^+, and accumulate large quantities of the lighter ions in their tissues. Many species regulate buoyancy using gas-filled floats that are either rigid-walled, as in the cuttlefish *Sepia officinalis* (Denton and Gilpin-Brown, 1961) and chambered nautilus *Nautilus macromphalus* (Greenwald *et al.* 1980), or soft-walled, as in the swimbladder of fish. In this strategy, buoyancy is modified by varying the amount of gas in the float. Elasmobranch fish control buoyancy by increasing the amount of lighter substances in the body through their large oily livers. For example, the black spiny shark *Etmopterus spinax* has a liver that accounts for 17 % of its body mass (compared with 1–2 % in teleost fish) and is 75 % oil (Schmidt-

Nielsen *et al.* 1934). Most of the oil in the liver is in the form of squalene, an unsaturated hydrocarbon with a specific gravity of 0.86, much less dense than the specific gravity of fats and other oils, which is 0.9–0.92 (Schmidt-Nielsen, 1990). This gives squalene a buoyancy effect in sea water that is 50 % greater than that of fat. In some elasmobranchs, the accumulation of urea and trimethylamine oxide (TMAO) in the tissues may play an important role in buoyancy, in addition to balancing osmolarity (Withers *et al.* 1994*a*,*b*).

Buoyancy in marine mammals has received little attention. Clarke (1978) suggested that the spermaceti organ of the sperm whale *Physeter macrocephalus* might play a role in regulating buoyancy by altering the density of the spermaceti through changes in temperature and pressure. A large lung volume is important to sea otters *Enhydra lutris*, which must be positively buoyant to float on the water, and also to pinnipeds that rest at the surface following inspiration (Kooyman, 1973). The lung probably also plays a role in the buoyancy of diving otariids that inhale before diving (Kooyman, 1973). However, phocid seals exhale before diving, so lung volume should not play a role in buoyancy. Furthermore, the buoyancy effects of air trapped in the lungs would be minimal because the pressure at depth would collapse the lungs and squeeze the air out. For phocids, and to a lesser extent otariids, buoyancy is determined primarily by body composition, particularly the ratio of adipose tissue to total body mass. As adipose tissue is less dense than sea water, seals with thick blubber layers would be more buoyant than those with a greater proportion of lean tissue.

Northern elephant seals experience radical seasonal changes in body composition. A pregnant female departs from the rookery following the molt with a body composition of approximately 25 % adipose tissue (Worthy *et al.* 1992). When she returns 8 months later at the start of the breeding season, her adipose reserves constitute 39 % of her total mass (Costa *et al.* 1986). During the subsequent 26 days of fasting while lactating, her body composition decreases to approximately 24 % adipose tissue before she returns to sea for the post-breeding migration. Similarly, adult males may lose up to 56 % of their blubber thickness during the breeding season (Deutsch, 1990). These large fluctuations in body composition should lead to fluctuations in buoyancy, which may be reflected in diving behavior. The effects of buoyancy should be most evident during the second segment of type C dives, during which the seals cease swimming and passively drift (Le Boeuf *et al.* 1992). Crocker *et al.* (1997) demonstrated that pregnant females departing from the rookery with depleted adipose reserves following the molt are negatively buoyant and descend during the drift segment of C-type dives. As the foraging trip progresses, the females accumulate adipose tissue, making them more buoyant, and the rate of descent during drifting decreases, eventually leading to an upward drift in late-pregnancy females.

The reverse pattern is seen in weanling seals. A weanling seal embarking on its first trip to sea is composed of approximately 48 % adipose tissue (Kretzmann *et al.* 1993). It is therefore positively buoyant, and would be expected to drift upwards during C-type dives in the initial weeks of the migration. This was confirmed for one weanling seal by Le Boeuf *et al.* (1996), who showed that as the trip progressed the rate of upward drift declined steadily before reaching an inflection point at which the seal started to drift down. This change probably corresponded with a decrease in adipose tissue and an increase in denser lean tissue as the seal traveled to its foraging grounds (Le Boeuf *et al.* 1996).

It is possible, therefore, that variations in body composition and consequently in buoyancy lead to changes in the diving behavior of northern elephant seals and that these changes in behavior may affect their energy budgets. While the costs of increased buoyancy during descent may be balanced by a decrease in energy expenditure on ascent, and *vice versa*, there may be significant effects on the effort required to remain at depth while foraging in the water column or to maintain position on the bottom for benthic feeding (Fedak *et al.* 1994). The aim of this study was to determine experimentally the relationship between buoyancy and diving behavior in these animals. This was carried out by modifying the buoyancy of translocated seals and examining the resultant changes in their diving behavior.

Materials and methods

Thirteen juvenile northern elephant seals *Mirounga angustirostris* (Gill) (six males, seven females, aged 1.4–2.4 years) were captured at Año Nuevo State Reserve, CA, USA, and transported to Long Marine Laboratory, Santa Cruz, CA, USA. Seals were captured during the spring and autumn haul-outs in 1995 and the spring haul-out of 1996. Time–depth recorders were deployed, and the buoyancy of the seals was modified before releasing them in Monterey Bay for their return to Año Nuevo.

The seals were divided into three treatment classes: seals made more buoyant (B+), seals made less buoyant (B–) and control seals (Bc) (Table 1). We sought to reproduce a range of buoyancies corresponding to the range of body compositions observed in nature, approximately 20–50 % adipose tissue. For the B+ seals, noncompressible syntactic foam discs were constructed (7.6 cm diameter, 1.1 cm thick; density 545 kg m^{-3}, Flotation Technologies, Biddeford, ME, USA), so that each disc had a positive buoyancy of 0.25 N. After the buoyancy calculations had been made and the extent to which buoyancy was to be modified had been determined, the appropriate number of discs were placed in two 3 inch (7.62 cm) inner diameter polyvinyl chloride tubes (length 44 cm), capped at each end with polyvinyl chloride pipe caps. The total frontal area of each buoyancy tube was 63.6 cm^2. The caps were fastened to the pipes with rubber cement, and the posterior cap had several holes drilled into it so that water could enter and drain from the tubes. The tubes were covered with black electrical tape to make them less visible to predators. For seals whose buoyancy was reduced (B–), the same procedure was followed, with measured amounts of lead weight substituted for the foam discs and fastened to the inside of the tubes (Table 1). To keep the drag effects of the polyvinyl chloride tubes constant in all three treatments, animals that served as controls (Bc) received empty tubes.

Prior to attaching instruments in the laboratory, the seals were

Table 1. *Age, mass, body composition and buoyancy for each seal*

Group	Seal	Age (years)	Mass (kg)	Initial body composition (% adipose tissue)	Initial buoyancy (N)	Buoyancy treatment	Adjusted buoyancy (N)	Adjusted body composition (% adipose tissue)
B+	B+F1	1.4	145.6	36.4	–14.93	64 discs	1.07	43.1
	B+F2	1.8	205.6	37.3	–18.20	73 discs	0.05	43.7
	B+M1	1.8	199.7	34.7	–25.75	73 discs	–7.51	40.1
	B+F3	2.4	203.7	36.0	–22.15	41 discs	–11.90	39.0
Bc	BCF1	1.4	155.7	36.5	–15.72	Control	–15.72	36.5
	BCM1	1.8	172.0	35.8	–19.24	Control	–19.24	35.8
	BCM2	2.4	206.4	35.8	–23.09	Control	–23.09	35.8
	BCF2	1.4	165.1	33.3	–24.89	Control	–24.89	33.3
B–	B–M1	2.4	193.1	34.6	–25.20	1.10 kg	–35.00	31.9
	B–F1	1.8	210.5	36.3	–21.91	2.46 kg	–43.80	34.8
	B–M2	1.4	160.5	35.1	–19.70	3.18 kg	–48.02	28.2
	B–M3	1.4	143.8	32.6	–23.24	3.46 kg	–54.10	24.2
	B–F2	2.4	258.5	35.7	–29.32	4.01 kg	–65.05	31.2

Seal names are mnemonics indicating buoyancy treatment and sex (M or F).

Buoyancy treatment refers to the number of syntactic foam discs or the mass of lead weight added to the seals.

immobilized with a 1 mg kg^{-1} intramuscular injection of tiletamine hydrochloride and zolazepam hydrochloride (Telazol, Fort Dodge Laboratories, Fort Dodge, IA, USA) to the flank. Immobilization was maintained using intravenous injections of 100 mg ketamine hydrochloride (Ketaset, Fort Dodge Laboratories, Fort Dodge, IA, USA) into the extradural vein.

The seals were weighed on a platform scale accurate to ±0.1 kg, and body composition was determined using a combination of ultrasound and morphometric measurements. This method requires 18 measurements of blubber depth using an ultrasound scanner (Ithaco Scanoprobe, Ithaca, NY, USA), together with eight measurements of both length and girth along the seal's body. From these measurements, the seal was modeled as a series of truncated cones, and the volumes of blubber and non-blubber compartments of each cone were calculated and summed to estimate a total body composition (Gales and Burton, 1987; Crocker, 1995). To validate the truncated cones method, body composition was determined on an additional nine seals of similar age and mass to the experimental seals using both the truncated cones and tritium dilution methods. These seals were chemically immobilized and weighed as described above. An initial blood sample was taken *via* the extradural vein, and a bolus injection of 37.0 MBq of tritiated water (HTO) was then administered in 5 ml of sterile injectable water. Post-equilibration blood samples were taken after an equilibration period of at least 3 h, the samples were centrifuged at 3400 revs min^{-1} for 15 min, and the serum was collected. Labeled water was collected into scintillation vials from 150 µl samples of serum using the dry ice distillation method (Ortiz *et al.* 1978). The scintillation vials were weighed before and after distillation to determine the yield of distillate recovered, and 9 ml of scintillation cocktail (Ecolite, ICN, Costa Mesa, CA, USA) was added to each vial. The specific activity of each sample was determined in triplicate on a Beckman LS 6500 multi-purpose liquid scintillation counter, along with a diluted HTO standard to calculate the activity of tracer injected. The absolute amount of tracer injected was determined by gravimetric calibration of the injection syringes.

Total body water (TBW) (kg) was determined as the activity of injected isotope divided by the activity of the post-equilibration samples. Total body water values were then reduced by 4 % to correct for overestimation by the HTO dilution method (Nagy and Costa, 1980). Fat mass was determined from the TBW values using the equation:

$$M_\mathrm{F} = M_\mathrm{T} - 1.37\mathrm{TBW} \tag{1}$$

(Iverson *et al.* 1993), where M_F is the fat mass of the seal (in kg) and M_T is the total body mass (kg). Fat mass was calculated from blubber mass assuming that blubber contains 10 % water (D. Crocker, unpublished data).

For the 13 experimental seals, body composition (from the truncated cones method) was used to calculate buoyancy using the equation:

$$B_\mathrm{T} = (0.8871M_\mathrm{T} \times A) + (-0.6689M_\mathrm{T} \times L)\,, \tag{2}$$

where B_T is total buoyancy (N), A is the percentage of adipose tissue, L is the percentage lean tissue, 0.8871 is the mass-specific buoyancy of adipose tissue (N kg^{-1}), assuming an adipose tissue density of 0.94 g cm^{-3} (Worthy *et al.* 1992), and –0.6689 N kg^{-1} is the mass-specific buoyancy of lean tissue (Nordøy and Blix, 1985).

Following the addition of weights or foam, an adjusted buoyancy was calculated. This value recalculates body composition by including the theoretical amounts of blubber or lean tissue required to give the same change in buoyancy as the foam or weights, respectively. The mass of blubber required to produce the same buoyancy effect as a given number of foam discs was calculated as:

$$M_\mathrm{add,blub} = B_\mathrm{F}/0.8871\,, \tag{3}$$

where $M_\mathrm{add,blub}$ is the added blubber mass (kg), B_F is the total buoyancy of the foam discs (N) and 0.8871 N kg^{-1} is the mass-specific buoyancy of blubber. Similarly, the mass of lean tissue required to produce the buoyancy effects of the lead weights was calculated as:

$$M_{\mathrm{add,lean}} = B_{\mathrm{W}}/-0.6689\,, \qquad (4)$$

where $M_{\mathrm{add,lean}}$ is the added lean mass (kg), B_{W} is the total buoyancy of the weights (N) and −0.6689 N kg^{-1} represents the mass-specific buoyancy of lean tissue. The adjusted buoyancy (B_{A}) was then calculated using the equations:

$$B_{\mathrm{A}} = (M_{\mathrm{blub}} + M_{\mathrm{add,blub}})/(M_{\mathrm{T}} + M_{\mathrm{add,blub}})\,, \qquad (5)$$

for the B+ seals, where M_{blub} is the measured blubber mass, and:

$$B_{\mathrm{A}} = M_{\mathrm{blub}}/(M_{\mathrm{T}} + M_{\mathrm{add,lean}})\,, \qquad (6)$$

for the B− seals. The adjusted buoyancy values were then multiplied by 100 to convert them into percentages of adipose tissue. This value is more biologically relevant than absolute buoyancy in newtons, and since buoyancy increases with increasing adipose stores, the terms will be used interchangeably throughout the remainder of the text.

The seals were then instrumented with a time–depth recorder (TDR) built from a modified data logger (Tattletale Lite model L-512psF, Onset Computer Corp., N. Falmouth, MA, USA) (Fletcher *et al.* 1996) that recorded depth at 10 s intervals and had a depth resolution of 1 m. The TDR and buoyancy tubes were attached to the seals using a neoprene saddle into which 12 plastic D-rings were sewn with nylon webbing. The neoprene saddle was glued across the seal's back using neoprene glue (Seal Cement, McKnett, Bellingham, WA, USA). The TDR was centered above the axilla, with the buoyancy tubes located posteriorly and on either side of the TDR. The TDR and buoyancy tubes were attached to the D-rings using stainless-steel hose clamps.

The day after capture and instrumentation, the seals were released at one of three locations near Monterey Bay, CA, USA: four seals each at both Hopkins Marine Station and Pt Lobos State Reserve, and five seals from ships in Monterey Bay at 36°46′42″N, 122°00′95″W, a 1006 m deep site 18 km offshore and 35 km south of Año Nuevo.

Upon returning to Año Nuevo, the seals were immobilized and the instruments removed. The neoprene patches were left on the seals and fell off during the subsequent annual molt.

General diving variables such as depth, duration and surface interval were analyzed using the Wildlife Computers Dive Analysis software (Woodinville, WA, USA). Visual inspection of the endpoints of descent and starting points of ascent generated automatically by the software revealed many instances where a significant portion of the bottom time was included in the calculations, thereby underestimating actual ascent and descent rates. To avoid this error, ascent and descent rates were determined manually (Boyd and Arnbom, 1991; Le Boeuf *et al.* 1996). Descent began when the seal left the surface and ended at the point at which the first significant inflection, or decline in descent rate, occurred in the dive profile, and the onset of ascent was defined by the point from which the dive profile showed a sustained approach to the surface (Boyd and Arnbom, 1991). All ascent and descent rates reported below reflect the manual method of calculation and, while the absolute values of ascent or descent rates differed between the manual and automatic methods of calculation, the trends and relationships presented below were consistent across both techniques.

Statistical analyses were performed using the software packages Axum 3.0 (TriMetrix, Seattle, WA, USA) and SigmaStat (Jandel Scientific, San Rafael, CA, USA). All values are presented as mean ± S.D. unless noted otherwise, and statistical significance was set at P=0.05.

Results

Buoyancy measurements

Fat masses calculated using the truncated cones method agreed very closely with those from the tritium dilution method (Table 2). Regression of fat mass calculated using HTO dilution ($M_{\mathrm{F,HTO}}$) against that calculated using the truncated

Table 2. *Comparison of calculated fat mass from the two body composition methods*

Seal	Mass (kg)	$M_{\mathrm{F,HTO}}$ (kg)	$M_{\mathrm{F,cone}}$ (kg)	% Error	Body composition (% adipose tissue)
1	164.4	55.77	56.22	0.81	38.0
2	166.4	54.85	51.37	−6.34	34.3
3	174.9	53.51	56.83	6.19	36.1
4	175.3	65.22	61.06	−6.38	38.7
5	198.0	55.66	55.78	0.20	31.3
6	155.2	48.41	48.61	0.40	34.8
7	143.0	51.67	52.51	1.63	40.8
8	143.0	42.96	44.92	4.56	34.9
9	263.6	81.68	80.90	−0.96	34.1
Mean				0.01±4.25	

$M_{\mathrm{F,HTO}}$ is fat mass calculated from the tritium dilution method, and $M_{\mathrm{F,cone}}$ is fat mass calculated from the truncated cones method.
The mean of the absolute values of the % error was 3.05±2.75 %.
Body composition is based on the truncated cones method.

cones method ($M_{\mathrm{F,cone}}$) gave the equation $M_{\mathrm{F,cone}}=5.09+0.91M_{\mathrm{F,HTO}}$ ($r^2=0.96$, $P<0.01$). The mean error between the two methods was 0.01±4.25 % ($N=9$), confirming that the ultrasound method is an accurate way of measuring body composition in this species (Table 2). The mean body composition of the 13 experimental seals, based on the ultrasound calculations, was 35.4±1.3 % adipose tissue (Table 1). The mean initial buoyancy, before the addition of weights or foam, was −21.8±4.1 N (range −14.9 to −29.3 N). The ranges of buoyancies following modification were −11.9 to +1.1 N for the B+ group, −24.9 to −15.7 N for the control group and −65.1 to −35 N for the B− group. These corresponded to ranges of adjusted body compositions of 39.0–43.7 % adipose tissue, 33.3–36.5 % adipose tissue and 24.2–34.8 % adipose tissue, respectively.

Transit rates

Of the 13 seals, 12 returned to Año Nuevo, with a mean transit time of 4.6±2.6 days (range 1.9–9.2 days). The seal that did not return to Año Nuevo was from the B− group and went instead to Gorda, a haul-out site approximately 120 km south of Año Nuevo, arriving 2.6 days after release. For comparisons of transit time, only seals that returned to Año Nuevo were considered. There were no significant differences in return rates between the three buoyancy treatment groups (one-way ANOVA, $F=1.93$, d.f.=11, $P=0.2$). Seals released at Hopkins Marine Station returned the fastest, with a mean of 3.5±1.9 days, followed by seals released by ship (4.9±2.2 days) and at Pt Lobos (6.4±3.6 days). While the differences in transit time from the three locations were not significant (one-way ANOVA, $F=0.53$, d.f.=11, $P=0.61$), the diving profiles suggested that the seals took different routes to return to Año Nuevo, even when released from the same site.

Diving behavior

The general shapes of the dive profiles and dive types were similar to those described by Le Boeuf *et al.* (1992, 1993). For each seal, between 80 and 99 % of all dives were types A and E, putative deep-water transit dives and bathymetrically constrained transit dives, respectively. Mean percentages of types A and E dives per seal ranged from 2.3 to 65.9 %, and from 13.6 to 92.4 %, respectively, and did not differ significantly between the buoyancy treatment groups (one-way ANOVA, $F=2.66$, 1.82; d.f.=12, $P=0.12$ for A dives, $P=0.21$ for E dives) or release locations (one-way ANOVA, $F=1.95$, 1.79; d.f.=12, $P=0.19$ for A dives, $P=0.22$ for E dives).

There were no significant differences in mean dive depth, duration or surface interval between the three buoyancy treatment groups or between the different release locations (one-way ANOVA, all $P>0.11$) (Table 3). Many diving variables were, however, correlated with the proportions of type A and E dives exhibited by the seals, which was a result of the different routes (on *versus* off the shelf) taken by the seals on their return. Seals with a higher proportion of type E dives (and, therefore, a lower proportion of type A dives) had a shorter mean dive duration ($r^2=0.6$, $P<0.01$) and shallower mean dive depth ($r^2=0.9$, $P<0.01$) than seals with fewer type E (and more type A) dives. Conversely, seals with more type E dives had a greater mean bottom time per dive than seals performing fewer type E dives ($r^2=0.87$, $P<0.01$). Overall mean diving depths, while shallower than those reported for migrating seals (Le Boeuf *et al.* 1996), were similar to the mean of 186±183 m for translocated seals released in the same locations by Oliver (1997), which also spent a high proportion of their return diving over the shallow continental shelf.

Effects of buoyancy on ascent and descent rates

Mean descent rates for the three treatments were 0.77±0.3 m s^{-1} for the B+ seals, 0.82±0.2 m s^{-1} for the Bc seals and 0.87±0.3 m s^{-1} for the B− seals, and were significantly different from each other (Dunn's method, $Q>3.16$, $P<0.01$) (Table 3). Mean ascent rates for the three treatments were 0.82±0.3 m s^{-1} for the B+ seals, 0.86±0.3 m s^{-1} for the control seals and 0.82±0.3 m s^{-1} for the B− seals. Comparison among the treatments showed significant differences in ascent rate between both the B+ and B− treatments and the control seals (Dunn's method, $Q=4.89$ for B+, $Q=4.29$ for B−, $P<0.05$), but no significant difference between the B+ and B− animals (Dunn's method, $Q=0.87$, $P>0.05$).

In all four of the B+ seals, mean ascent rates were greater than mean descent rates, with the differences being significant in two seals (Mann–Whitney rank sum test, $T=31{,}049.5$, 534,108; $P<0.01$). For the control animals, three had mean ascent rates that were significantly greater than mean descent rates, with one animal descending significantly faster than it ascended (Mann–Whitney rank sum test, $T=84{,}216$, 446,202;

Table 3. *Summary diving statistics for each buoyancy treatment group*

Group	*N*	Total dives	Mean depth (m)	Mean duration (min)	Mean surface interval (min)	Mean descent rate (m s^{-1})	Mean ascent rate (m s^{-1})
B+	4	736	110.7±50.6	12.4±2.2	2.2±0.4	0.77±0.3	0.82±0.3
Bc	4	736	200.7±81.1	14.0±3.3	2.0±0.1	0.82±0.2	0.86±0.3
B−	5	920	147.4±52.5	11.8±2.0	2.2±0.3	0.87±0.3	0.82±0.3

Values are means ± S.D.

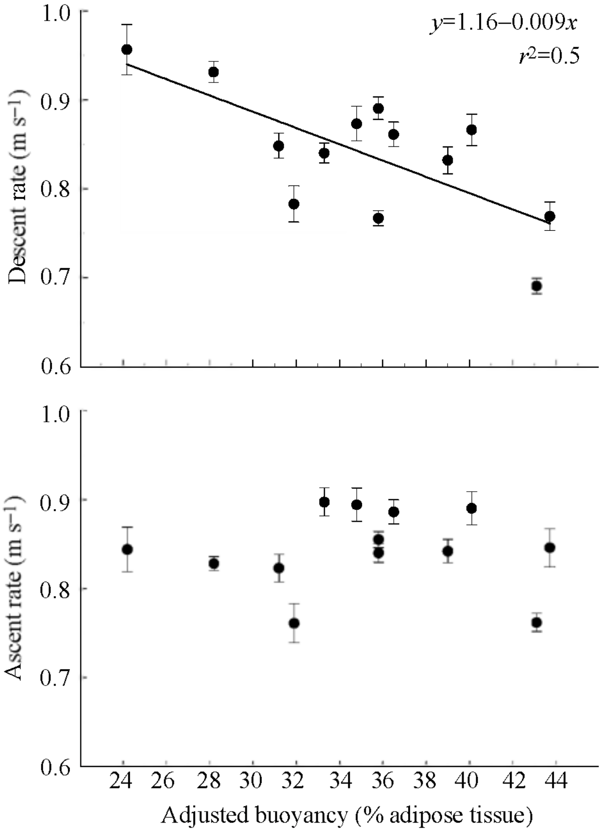

Fig. 1. Relationship between descent or ascent rate and adjusted buoyancy. There is a significant relationship between adjusted buoyancy and descent rate, with fatter, more buoyant seals descending more slowly than less buoyant seals. The regression equation is y=1.16–0.009x, r^2=0.5, P<0.05. There is, however, no significant relationship between ascent rate and buoyancy. Values are means ± S.E.M., N for each seal ranged from 184 to 760.

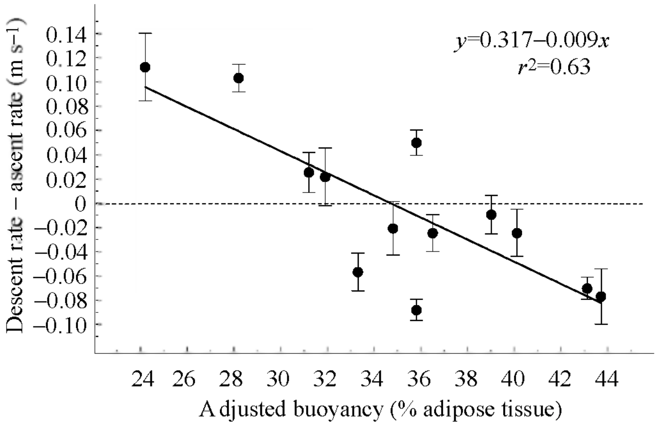

Fig. 2. Relationship between adjusted buoyancy and the mean difference between descent and ascent rates for each seal. The less buoyant the seal, the greater the descent rate relative to the ascent rate, and *vice versa*. The equation is y=0.317–0.009x, r^2=0.63, P<0.05. Values are means ± S.E.M., N for each seal ranged from 184 to 760.

P<0.05). For the B– seals, four of the five animals had mean descent rates greater than ascent rates, with the differences being significant in two seals (Mann–Whitney rank sum test, T=44,568, 391,420; P<0.01).

Buoyancy and descent rate were inversely correlated: the lower (more negative) the buoyancy, the faster the rate of descent (r^2=0.5, P<0.05) (Fig. 1). There was no relationship, however, between buoyancy and ascent rate (r=–0.002) (Fig. 1). To examine the effects of dive depth on the relationships between buoyancy and ascent/descent rates, multiple regressions were also performed with ascent/descent rates as dependent variables and buoyancy and dive depth as independent variables. The inclusion of dive depth strengthened the buoyancy *versus* descent rate relationship somewhat (r^2=0.6, P=0.01), but there was still no significant relationship between buoyancy and ascent rate (r^2=0.04, P=0.82).

The difference between descent rate and ascent rate was calculated for each dive, and the mean difference between descent rate and ascent rate for each seal was negatively correlated with buoyancy (r^2=0.63, P<0.05) (Fig. 2). The less buoyant the seals, the greater the difference between descent and ascent rates in the positive direction, i.e. descent was faster than ascent, while the more buoyant the seals, the greater the difference in the negative direction, i.e. ascent was faster than descent.

Effects of buoyancy on drift dives

While 10 seals exhibited at least one type C dive, all but three seals performed fewer than 10 dives of this type. For comparison of descent rates during C-type dives, only those three seals with more than 10 C-type dives were considered. There was a significant correlation between buoyancy and the rate of descent during the ‘drift’ portion of the dive, with the less buoyant seals descending faster than the more buoyant seals (r^2=0.91, P<0.05) (Fig. 3). One of the B+ seals, which was actually made positively buoyant with the addition of foam, exhibited reverse-C dives, with the seal ascending during the ‘drift’ portion. The mean upward drift rate was 0.17 m s^{-1}. However, only three reverse-C dives were performed, which makes statistical comparison difficult.

Discussion

Body composition measurements

The close agreement between the fat mass values derived from the tritium dilution and truncated cones methods confirms the validity of the truncated cones method for calculating body composition in juvenile northern elephant seals. The mean body composition of the 13 experimental seals, 35.4±1.3 % blubber, is higher than that previously reported in diving studies of juvenile northern elephant seals by Le Boeuf *et al.* (1996), who stated that blubber content for seals of that age does not exceed 33 %. However, in order to reduce the amount of time that the seals spent on land following deployment of diving instruments, all of the animals in the study of Le Boeuf

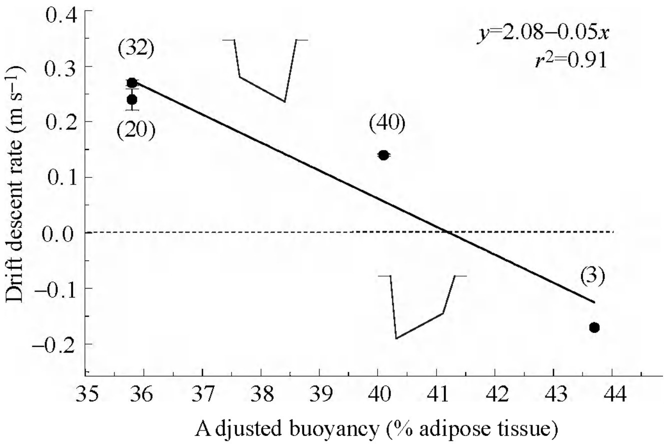

Fig. 3. Relationship between descent rate during the drift portion of type C dives and adjusted buoyancy. These data are from the three seals which performed 10 or more C dives during the recording period and one seal that performed reverse-C dives (upwards drift). A negative value for drift descent rate indicates upwards drift, as shown in the schematic representations of the dive profiles. The higher the proportion of adipose tissue (the higher the buoyancy), the slower the descent rate during the passive drift. The equation for the regression line is y=2.08–0.05x, r^2=0.91, P<0.05. Values are means ± S.E.M., the number of C dives per individual are given in parentheses.

et al. (1996) were measured at the end of the haul-out period after several weeks of fasting, and were selected in part because they appeared thin and were therefore close to departing on their foraging migrations. Conversely, in translocation experiments such as the present study, seals are captured early in the fasting period, and fatter animals are chosen to ensure that they return to the rookery to complete the fast. It is therefore not surprising that the mean body composition of seals departing at the end of the fast (27.5±1.8 % blubber, N=17, D. Crocker, unpublished data) is significantly lower than that of the experimental seals in the present study (t-test, t=13.3, d.f.=28, P<0.01). The mean body composition of the 13 seals in the present study is not, however, significantly different from the mean body composition of juvenile northern elephant seals arriving at the rookery following their foraging migrations (34.6±2.5 % blubber, N=44, D. Crocker, unpublished data) or from that of juvenile elephant seals used in other translocation experiments (34.5±2.6 % blubber, N=29, D. Crocker, unpublished data) (t-tests, t=1.13, 1.10; d.f.=55, 40; P=0.26, 0.28 for returning and translocated seals respectively).

Buoyancy effects

This study demonstrates that buoyancy plays a role in the diving behavior of northern elephant seals. While changes in buoyancy did not affect dive variables such as depth, duration or post-dive surface interval, the significant inverse correlation between buoyancy and descent rate (the more negative the buoyancy, the greater the rate of descent) indicates that buoyancy affects the diving behavior of northern elephant seals. The effect of buoyancy on descent rate might arise from a combination of mechanisms. It is possible that seals swim at similar speeds regardless of buoyancy, exerting the same effort during descent, and that the increased rate of descent comes from the added downwards force of negative buoyancy. Alternatively, less-buoyant seals might use this negative buoyancy to drift passively to depth, either continuously or as part of a burst-and-glide swimming pattern, with the rate of drifting, and therefore the rate of descent, related directly to the buoyancy of the seal. The cessation of swimming in order to drift in negatively buoyant seals would also act to conserve oxygen and thus possibly extend the duration of the dive. Weihs (1973) calculated that negatively buoyant fish swimming in the manner of active ascent and passive drifting descent could experience energetic savings of over 50 % for traveling a given horizontal distance or an increase of over 90 % in the range traveled for a given energetic expenditure.

While it is known that significant portions of C-type dives are spent drifting (Crocker *et al.* 1997), it has been assumed that the other types of dives involve nearly constant swimming, at least during the descent and ascent portions. Recent video recordings of diving elephant seals show that, even in transit dives, seals drift for significant portions of the descent (Williams *et al.* 1996). For juvenile elephant seals, this drifting represents an energetic saving of 23 % of their O_2 stores, which translates to an additional 3 min of gliding or 1.1 min of swimming at 2 m s^{-1} (Williams *et al.* 1996). If it is important for seals to conserve energy during diving, they would be expected to maximize the time spent in the least energetically expensive behavior. For negatively buoyant seals, this might mean maximizing the time spent drifting during descent, while decreasing the duration of the ascent portion of the dive, which requires working against negative buoyancy. However, it is possible that any energy saved by drifting during descent may be negated by extra energy expended during ascent.

With less-buoyant seals descending faster than more-buoyant seals, it follows that, conversely, the more-buoyant seals might be expected to ascend faster, possibly aided by the lift resulting from their buoyancy. With this in mind, it is very interesting that this study found no relationship between ascent rate and buoyancy. This indicates that, regardless of their buoyancy, seals probably power upwards during ascent, swimming continuously until they reach the surface. In this case, the lift generated by propulsive swimming might far outweigh any extra lift due to buoyancy, so that the buoyancy changes matter little. Video data support the hypothesis of powering to the surface, showing that seals swim continuously during the ascent phase of the dive (Williams *et al.* 1996).

Given the passive drift portion of C-type dives, it might be expected that buoyancy would affect that part of the dive most substantially. This was indeed the case, as there was a strong linear relationship between the descent rate during the ‘drift’ phase and the buoyancy of the seal, with less buoyant seals descending faster than more buoyant ones. Considering the small sample size of seals showing significant numbers of C dives, it is not prudent to extrapolate too much from this result, but it is worth noting that the data follow the prediction. Although limited to only three dives, it is also interesting that one of the positively buoyant seals exhibited reverse-C dives and drifted upwards, as predicted. Even more striking is the fact that the mean drift rate during the passive ascent in this seal ($0.17\,\mathrm{m\,s^{-1}}$) is identical to the mean ascending drift rate of four late-gestation adult females reported by Crocker *et al.* (1997).

Another factor to consider for swimming animals is the drag forces that they experience. Boyd *et al.* (1997) experimentally increased the drag on free-ranging Antarctic fur seals *Arctocephalus gazella* and found that, in relation to unencumbered seals, the experimental animals showed an overall reduction in swimming speed, ascent and descent rates and bottom time per dive, and that they dived at a steeper angle than the control animals. In the present study, the ascent and descent rates we report are slower than those reported elsewhere for a weanling elephant seal on its first trip to sea (range 1.15 ± 0.33 to $1.31\pm0.28\,\mathrm{m\,s^{-1}}$; Le Boeuf *et al.* 1996), presumably because of the increased drag of the buoyancy devices. However, it is important to remember that the increase in drag was kept constant among all the experimental seals, so that the changes in diving behavior observed within our experimental animals may be attributed to the experimental changes in buoyancy.

With drag in mind, it is an interesting exercise to consider the drag forces against which an unencumbered seal would normally be working and compare them with the vertical force changes resulting from the buoyancy manipulations. We calculated the drag D on an unencumbered seal using the equation:

$$D=\tfrac{1}{2}\rho aU^2C_\mathrm{d}\,, \qquad (7)$$

where ρ is water density ($1.024\times10^3\,\mathrm{kg\,m^{-3}}$ for sea water), a is the frontal area of the seal ($0.1697\,\mathrm{m^2}$, calculated from the mean axillary girth of the 13 experimental seals), U is swimming velocity and C_d is the drag coefficient (taken as 0.09, calculated for a harbor seal *Phoca vitulina* of similar size by Williams and Kooyman, 1985). For a seal swimming at $1.5\,\mathrm{m\,s^{-1}}$, the calculated drag is 17.6 N, while the forces imposed by the buoyancy modification range from 9.8 to 35.7 N. Of the nine seals whose buoyancy was modified, six of them were subjected to a change in buoyant forces that exceeded the calculated drag force, with the added buoyant force more than double the drag force in one seal. This means that, if the seals were swimming vertically during ascent or descent, drag and buoyant forces could differ by up to a factor of two. This helps explain why the B– seals descend faster than they ascend, while ascent is faster than descent in the B+ seals. In the B– seals, the drag and buoyant forces work in opposite directions during descent, but have a cumulative effect in the same direction on ascent. As the downward buoyant force exceeds the upwards drag force during descent, the net force is directed downwards, and a greater negative buoyancy results in a faster descent rate. During ascent, the seal must overcome both forces directed downwards and, as a result, ascent is slower than descent. Conversely, in the B+ seals, the upwards drag and buoyant forces must both be overcome in the descent phase of the dive, while they may cancel each other out during the ascent phase. This may result in ascent rates that are greater than descent rates, which is supported by the data presented above.

It appears therefore, that the effects of buoyancy may be at least as, if not more, important in shaping diving behavior in elephant seals than the effects of drag. If the drag forces on a diving seal were much larger than the buoyant forces it experiences, we would not expect changes in buoyancy to produce the effects we have reported here. This hypothesis is supported by data from diving canvasbacks and lesser scaup, which show that buoyancy accounts for more of the locomotor costs of shallow diving (contributing 36–38 % of the total work during descent) than does hydrodynamic drag (10–12 %) (Lovvorn *et al.* 1991).

Given that buoyancy is an important factor in the diving behavior of elephant seals, do seals regulate their buoyancy and, if so, how do they do it? A study by Jackson (1969) utilized the same basic technique of adding weights or floats to freshwater turtles *Pseudemys scripta elegans* to see how they regulated buoyancy. Intact turtles compensated for both treatments, while turtles with their cloacas plugged could only compensate for the floats. The turtles regulated buoyancy through the addition or removal of lung air through the mouth, and stored water from their cloacal bursae. This technique is obviously impossible in elephant seals, which do not have a cloaca and dive with collapsed lungs. For elephant seals at depth, buoyancy depends primarily on body composition, which cannot be adjusted in the short term to compensate for buoyancy.

In many marine tetrapods, buoyancy compensation is achieved through hydrodynamic lift as the animals swim through the water (Taylor, 1994). This is not feasible for phocid seals, whose morphology lacks the ‘wings’ of otariids or penguins through which lift is generated. A possible short-term method of buoyancy regulation might be through the ingestion of gastroliths, or stomach stones. Gastroliths have been found in many groups of aquatic tetrapods, such as pinnipeds, crocodiles and penguins (for a review, see Taylor, 1993). Several hypotheses have been formulated for the role of these stones, such as grinding food and reducing hunger, but in many species it is believed that the stones act as ballast to aid in buoyancy regulation (Taylor, 1993). In some pinnipeds, such as the Weddell seal *Leptonychotes weddelli*, small numbers of stones are probably ingested secondarily as a result of bottom feeding (Dearborn, 1965), but other species, such as the Steller sea lion *Eumetopias jubatus*, actively ingest large quantities of stones (Mathisen *et al.* 1962). Gastroliths have been found in elephant seal stomachs – 11 kg of stones was recovered from the stomach of an adult female (D. Costa and B. Le Boeuf, unpublished data) – and it is possible that these stones may be ingested at sea to compensate for buoyancy. However, it is more likely that these stones were ingested close to the rookery before coming ashore, since the majority of dives by adult females occur in water that is deeper than their maximum diving depth (Le Boeuf *et al.* 1993).

It is certainly not possible that short-term buoyancy regulation in elephant seals is carried out by changes in body composition, and it may be that elephant seals are actually unable to regulate buoyancy to suit individual dives. Instead, seals may adjust their diving behavior to conform to their current buoyancy constraints, rather than adjusting buoyancy to suit the dive. As stated previously, these changes in behavior might include extending the descent phase or passively drifting.

The present study has demonstrated the importance of buoyancy on diving behavior in northern elephant seals, yet the energetic costs of overcoming buoyancy remain to be addressed. As buoyancy in elephant seals is due primarily to body composition, the extent of the blubber layer, while reflective of foraging success, may possibly also be seen as a trade-off between the need for a large blubber layer for thermoregulation and energy stores, and the possible extra energy required to overcome the effects of buoyancy during diving. It will be important to quantify the changes in swimming effort and energetics as a result of changing buoyancies, through the acquisition of swim speed, stroke frequency or heart rate data, or an estimation of metabolic rate through heart rate or the doubly labeled water technique. This study also demonstrates that it is important to consider the size of instrument packages when deploying them on marine organisms. The packages our B– seals carried all weighed less than 2.5 % of the seal's body mass, yet they were sufficient to produce an effect on diving behavior. Future studies using large instrument packages must take this into consideration to ensure that the behaviors being measured are not being modified as a result of the package itself.

We thank Dorian Houser, Sean Hayes and several others for field assistance, and the staff at Pt Lobos State Reserve, California, and Hopkins Marine Station for use of their release sites. This manuscript was improved by helpful reviews by Michael Castellini and Michael Fedak. This research was supported by grants from the Dr Earl H. and Ethel M. Myers Marine Biology and Oceanographic Trust, Friends of Long Marine Laboratory Student Research Awards, the Office of Naval Research (ONR N00014-94-1-0455 and N00014-94-1-1013), AASERT grant 443607-23077, ARPA funds for the Acoustic Thermography of Ocean Climate project (ATOC) and a gift from the G. E. MacGowan estate courtesy of George A. Malloch. The research was carried out under NMFS Permit 836 and was approved by the Chancellor's Animal Research Committee at UCSC.

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