

Drift diving in female northern elephant seals: implications for food processing

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Abstract: We tested predictions from the hypothesis that northern elephant seals, *Mirounga angustirostris*, drift during the bottom segment of some dives (called C dives) using oxygen saved from reduced locomotion to process food. Sixteen free-ranging dive records were obtained with microcomputer dive recorders attached to 13 adult females from Año Nuevo, California, during biannual foraging trips when they were in early or late stages of gestation; swim speed was recorded throughout one dive record. Body composition was measured before and after trips to sea. C dives with a bout length of 2–10 dives and a mean duration similar to those of other dive types made up $6.3 \pm 1.9\%$ of the dives recorded. Swim speed was near or below the recorder stall speed (0.22 m/s) during the second, drift segment of these dives. The rate of vertical depth change while drifting varied little within bouts, was initially significantly correlated with the ratio of fat to lean body mass at departure, and changed systematically as the seals fed while at sea. Females in early gestation, with initial mean body fat of 24%, drifted down at a mean rate of 0.31 ± 0.04 m/s; females in late gestation, with mean body fat approaching 36%, drifted up at an average rate of 0.17 ± 0.05 m/s. The frequency, duration, and temporal pattern of drift dives were correlated with foraging behavior, supporting the hypothesis that drifting while diving is associated with the metabolic cost of processing food. This study provides indirect support for the hypothesis that elephant seals suspend active swimming on certain dives, during which a greater proportion of oxygen stores is allocated to the processing of food, without interrupting the seals' normal pattern of continuous diving and allowing them to remain within their aerobic dive limit.

Résumé : Nous avons vérifié les prédictions de l'hypothèse selon laquelle l'Éléphant de mer boréal, *Mirounga angustirostris*, se laisse aller à la dérive au cours certaines plongées (appelées plongées C) pendant qu'il est au fond de l'eau, utilisant l'oxygène ainsi épargné pour manipuler sa nourriture. Seize données sur des plongées d'animaux en liberté ont été obtenues au moyen de microordinateurs enregistreurs de plongées attachés à 13 femelles adultes d'Año Nuevo en Californie, au cours de leurs excursions bisannuelles de recherche de nourriture, alors qu'elles étaient au début ou à la fin de leur gestation; la vitesse de nage a été enregistrée au cours de toute une plongée. La composition du corps a été mesurée avant et après les excursions en mer. Les plongées C, qui sont des épisodes de 2–10 plongées et qui ont une durée moyenne semblable à celle d'autres types de plongées, constituent $6,3 \pm 1,9\%$ des plongées enregistrées. La vitesse de nage au cours de la deuxième partie, la dérive, de ces plongées, était près du seuil ou sous le seuil d'enregistrement (0,22 m/s) de l'appareil. Le taux des changements verticaux de profondeur pendant la dérive variait peu au cours des épisodes de plongées, était au départ significativement relié au rapport masse des graisses/masse du corps sans les graisses et changeait systématiquement à mesure que les otaries se nourrissaient au cours de leurs excursions en mer. Les femelles en début de gestation, dont le taux initial moyen des graisses était de 24%, se laissaient dériver vers le fond à une vitesse moyenne de $0,31 \pm 0,04$ m/s; les femelles en fin de gestation, dont le taux moyen des graisses atteignait 36%, se laissaient dériver vers le haut à une vitesse moyenne de $0,17 \pm 0,05$ m/s. La fréquence, la durée et la séquence temporelle des plongées avec dérive étaient en corrélation avec le comportement de recherche de nourriture, ce qui appuie l'hypothèse selon laquelle la dérive au cours des plongées est associée au coûts métaboliques de la manipulation de la nourriture. Cette recherche confirme indirectement l'hypothèse qui veut que les Otaries à fourrure suspendent leur nage active au cours de certaines plongées pendant lesquelles une plus grande proportion des réserves d'oxygène sert à la manipulation de la nourriture, sans qu'elles aient à interrompre leurs activités de plongée continue et sans outrepasser les limites de leurs plongées aérobiques.

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Introduction

Diving mammals and birds have finite oxygen stores that cannot be exceeded if aerobic metabolism is to be main-

tained while they are submerged. Dives fueled by anaerobic metabolism require rest at the surface and are rare (Kooyman et al. 1980, 1981; Gentry and Kooyman 1986). Total foraging time relative to time spent at sea is maximized with aerobic dives (Kooyman et al. 1980).

While foraging, diving mammals and birds must expend oxygen for locomotion, food processing, and body maintenance. How they resolve and balance these competing demands on their oxygen stores is a key life-history trait that helps to characterize the species and its mode of life. The aerobic metabolism of an organism diving on fixed oxygen stores can be partitioned as follows:

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$$[1] S = R_m t + R_f t + R_a t$$

where S is the total oxygen stores available for consumption ($\text{mL oxygen} \cdot \text{kg}^{-1}$), R_m represents the rate of maintenance oxygen requirements while diving, R_f is the rate of expenditure due to the heat increment of feeding (HIF), R_a is the rate of metabolic expenditure associated with locomotion, and t is the duration of the dive.

Equation 1 shows that several strategies are available to a diving mammal for balancing the oxygen demands of maintenance, active swimming, and food processing: (i) A diver can process food while actively swimming and foraging. If the diver uses only aerobic metabolism, the metabolic cost associated with processing food will result in a reduction in dive duration relative to the nonprocessing state. Alternatively, the diver can maintain dive duration by utilizing anaerobic metabolism. This strategy, however, produces little energy and necessitates an interruption in diving while the animal rests at the surface clearing lactic acid before it can dive again (Kooyman 1989). (ii) A diver can forage and then process food while resting at the water surface, on land, or on ice. Resting at the water surface makes the animal vulnerable to surface predators such as white sharks, *Carcharodon carcharias*, and killer whales, *Orca orcinus* (Ainley et al. 1981; Le Boeuf et al. 1982). Resting on land or ice requires time and incurs transportation costs between the foraging and resting sites (Costa 1991). (iii) A diver can forage and then process food while reducing locomotion costs. By ceasing to swim, i.e., by drifting during the course of a dive, oxygen saved from not locomoting, R_a , can be spent on food processing, R_f , while the animal continues to dive aerobically. This strategy allows the animal to maximize the duration of foraging dives, process food while diving, and continue to dive.

Weddell seals, *Leptonychotes weddelli*, may utilize the first and second strategies. Their dive bouts are separated by several hours of rest on sea ice, and elevated metabolic rates during this period appear to reflect HIF (Kooyman 1989). Davis et al. (1983) suggested, however, that the lack of change in glomerular filtration rate from resting values and the appearance of increased levels liposomes in the plasma indicated that some digestion was taking place during diving. In some otariids, the intervals between peaks of diving activity match gut clearance time, suggesting that satiation is followed by a period of inactivity, i.e., use of the second strategy (Gentry et al. 1986).

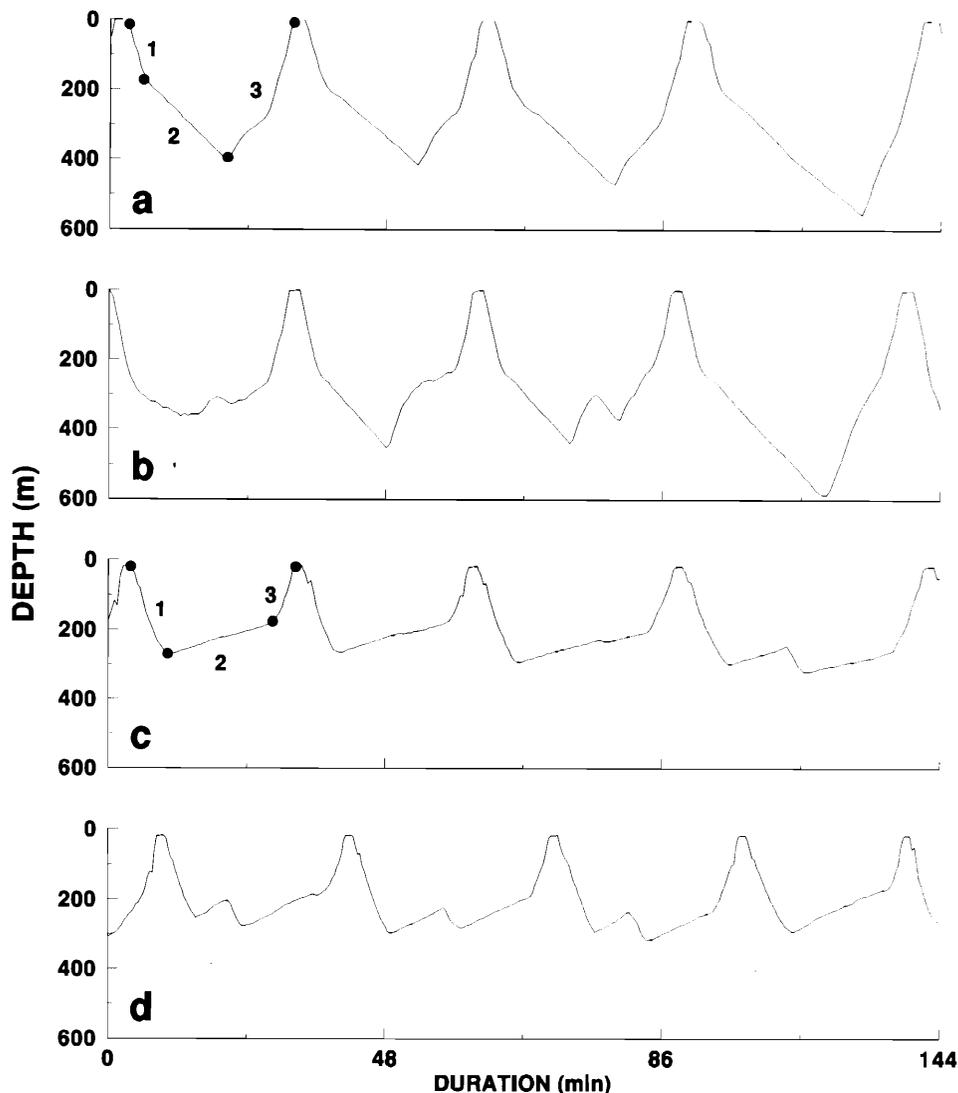
Frequent haulouts on land or ice, characteristic of otariids and some phocids during lactation (Costa 1991), are not possible in species, such as elephant seals, *Mirounga angustirostris* and *M. leonina*, that lead a predominantly pelagic existence utilizing highly dispersed and distant food resources (Le Boeuf et al. 1988, 1993; Hindell et al. 1991a; McConnell et al. 1992). Adult female northern elephant seals make two foraging trips per year into the northeastern Pacific Ocean from their rookeries in California and Baja California, Mexico (Le Boeuf et al. 1993). After giving birth to a single pup between mid-December and mid-February and nursing it for 28 days, a female copulates and then weans her pup by going to sea (Le Boeuf et al. 1972). She has lost a mean of $36.8 \pm 2.8\%$ of her parturition mass during the lactation fast (Deutsh et al. 1994) and her body fat has decreased to 24% (Worthy et al. 1992). Trip 1 lasts a mean of 72.6 ± 5 days, beginning

in late February and ending in early May (Le Boeuf et al. 1988). Although females increase their body mass by a mean of $24.1 \pm 4.6\%$ over the period at sea (Le Boeuf et al. 1988), their body fat remains at 24% (Worthy et al. 1992). Gestation is arrested during this period and the blastocyst remains free in the uterus (Laws 1956). After a 1-month stay on the rookery, molting the outer skin and pelage, females embark on trip 2, an 8-month foraging period at sea extending from about April to December. During this period, implantation occurs (Laws 1956), the fetus grows to maturity, and body composition increases from 24 to 36% fat (Crocker 1995).

Elephant seals appear to remain within their aerobic dive limits throughout their time at sea because surface intervals are brief, even following the longest dives lasting over an hour. Alternatively, if anaerobic metabolism occurs, lactate is cleared while the animal continues to dive. Despite continuous diving while at sea, the at-sea metabolic rate of elephant seals is estimated to be near resting or terrestrial values (Le Boeuf et al. 1988; D.P. Costa, unpublished data). Since swimming muscle must remain perfused at rates proportional to swimming velocity (Hochachka 1986) and oxygen consumption increases exponentially with swim speed (Davis et al. 1985; Williams and Kooyman 1985; Fedak 1986; Feldkamp 1987; Williams et al. 1991), a significant compromise must be reached between the oxygen demands of active swimming and the apparent HIF to obtain low at-sea metabolic rates. Moreover, feeding experiments with elephant seals in the laboratory show that postprandial metabolic rates may increase up to 1.65 times resting levels (Barbour 1993). Thus, the oxygen requirements of HIF in the free-ranging seal may require a reduction in locomotion costs, thereby saving oxygen, in order to maintain the duration of foraging dives and maintain continuous diving. Strategies for separating the metabolic costs of digestion and locomotion have been proposed for fish (Furnell 1987; Vahl and Davenport 1979; Preide 1985), birds (Diamond et al. 1986), and mammals (Saarikko and Hanski 1990).

In a previous investigation of swim speed and its metabolic implications in adult female elephant seals, we suggested that during a major segment of C type dives, oxygen reserves are allocated to internal physiological processes at the expense of locomotion (Le Boeuf et al. 1992). C dives are one of the four principal dive types that are distinguishable in two-dimensional dive records of northern elephant seals (Fig. 1). C dives occur in short series of 2–10 dives between putative transit (A dives) and putative foraging dives (D dives for pelagic feeding and E dives for benthic feeding) (Le Boeuf et al. 1993). They account for approximately 5–13% of the dive types observed in dive records of adults and juveniles of both sexes. The mean duration of C dives is similar to that of other dive types, but about 50% less horizontal distance is covered. C dives are distinguished by three consecutive segments. Le Boeuf et al. (1992) characterized these segments from swim velocity and dive data in one adult female as (1) a vertical descending speed of about 1 m/s, at an angle of about 40° , to a depth of 411 ± 94 m; (2) slow descent at the rate of 0.36 m/s or less, i.e., near the stall speed of the recorder; and (3) vertical ascent to the surface at a rate of 0.85 m/s and at an angle of 52° . They concluded that the slow vertical movement during segment 2, which accounted for up to 47% of the dive duration, reflected passive drifting and, hence, reduced diving effort. In a more

Fig. 1. Examples of bouts of C dives observed in the dive records of early-gestation females during trip 1 and late-gestation females during trip 2, showing the three segments into which each dive is divided (*a*, *c*), the direction of vertical movement during the second segment, including descent (*a*, *b*) and ascent (*c*, *d*) and stair-stepped variants (*b*, *d*).



recent study, juveniles drifted down or up during the second segment of C dives, depending on their body composition (Le Boeuf et al. 1996). Similar dives have been described in southern elephant seals (Hindell et al. 1991*b*; Jonker and Bester 1994).

In this study, we show that adult female elephant seals emphasize the third strategy for balancing the oxygen demands of maintenance, active swimming, and food processing. We advance the general hypothesis that northern elephant seals suspend active swimming while diving, directing the oxygen saved to metabolism associated with feeding. We describe the frequency, attributes, and temporal patterning of dives involving cessation of swimming, and the context in which they occur, and test predictions derived from the general hypothesis. We obtained and analyzed data bearing on predictions from four specific hypotheses.

Hypothesis 1: C dives are associated with foraging and digestion of prey

This hypothesis predicts that C dives are temporally associ-

ated with foraging dives, and are less frequent when females are in transit early in the migration than later, when they are involved in concentrated feeding. C dives might be concentrated in the early morning because elephant seals exhibit a strong diurnal pattern in both the depth and duration of dives, which are shallower and of shorter duration at night than during the day (Le Boeuf et al. 1988). This suggests that elephant seals are feeding on prey in the deep scattering layer which approach the surface at night and migrate down during the day. If foraging is more productive at night, the subsequent period would be optimal for food processing, allowing maximum dive durations for daytime foraging.

Hypothesis 2: Seals do not swim during segment 2 of C dives; they drift passively

If this is true, the measured swim speed during segment 2 of C dives should be equal to or lower than the stall speed of the recorder. An earlier study indicated that this was true (Le Boeuf et al. 1992). If passive drifting occurs during this dive segment, the percentage of fat in the total body mass

will determine the specific gravity, and the vertical direction of drift and the descent rate. During trip 1, females will drift down because they are 24% fat and have a specific gravity slightly greater than 1.0 g/cm³. During trip 2, females in the third trimester of gestation will drift up because they are approaching 36% fat and are neutrally or positively buoyant, with a specific gravity slightly lower than 1.0 g/cm³ (Crocker 1995). Moreover, if drifting is passive, there should be little variation in the rate of depth change between dives within a bout lasting a few hours, but as feeding progresses over time, a seal's body composition and specific gravity will change and be reflected by correlated changes in drift rate, e.g., the descending drift rate of female with a low percentage of body fat will get increasingly slower with time at sea.

Hypothesis 3: Oxygen saved from reduced locomotion during C dives is spent on food processing

Oxygen saved from reduced locomotion should allow longer dives. If the mean duration of C dives is no longer than that of other dive types, oxygen saved from reduced locomotion will be available for food processing. We also predict that females in late gestation should exhibit shorter drift durations relative to total dive duration than females in early gestation. The logic derives from the fact that pregnant females have a higher metabolic rate than nonpregnant females (Brody 1945). Pregnancy increases the maternal metabolic rate by an amount that is approximately proportional to the mass of the fetus and placenta (Barcroft et al. 1939). Since perfusion of the fetus is most likely never compromised during diving (Zapol et al. 1979), elephant seals should consume more oxygen and exhibit shorter relative durations in late pregnancy than in early gestation, before the fertilized egg is implanted in the uterine wall. If necessary, females in late gestation could compensate for shorter drift durations by having longer bouts of drifting. Lastly, drift duration might be expected to increase systematically across a bout of C dives as oxygen utilization for processing food decreases over the course of food processing. This prediction is suggested by laboratory studies of HIF showing that metabolic rates elevated in association with feeding gradually return to base-line levels (Barbour 1993). A decrease in oxygen consumption required for food processing might be associated with an increase in the amount of time the animal is able to spend drifting per dive over a bout.

Hypothesis 4: On rare occasions, food processing will be completed at the surface

If oxygen consumption for HIF is greater than oxygen stores, food processing might occur at the surface. This predicts that extended surface intervals (ESIs), which are rare (Le Boeuf et al. 1988; Le Boeuf 1994), will be associated temporally with C dives.

Methods

Subjects

This analysis is based on dive records obtained from 16 time–depth recorders and one swim speed recorder attached to 13 different known-age, individually tagged female northern elephant seals at Año Nuevo, California, in 1989, 1990, and 1994. Eleven adult females, 4–10 years old, were instrumented in mid-February in order to record their diving behavior during the first of two foraging trips in the year (trip 1). Five females 4–9 years old, were instru-

mented in May for recording diving behavior during the last third of trip 2. Three of these females had also carried instruments in trip 1. All seals went to sea within 3 days after instrument attachment.

In this paper, we refer to the 11 females in trip 1 as early-gestation (EG) females. Females in trip 2 are defined as late-gestation (LG) females. Reproductive status of all females were assumed from observations of mating behavior and confirmed from observations made in the subsequent breeding season.

Dive recording instruments

For 15 of the deployments, a time–depth recorder (Mk.3, Wildlife Computers, Redmond, Wash.) with 256 kilobytes (kb) of random access memory and a radio transmitter (Advanced Telemetry Systems, Asanti, Minn.) was glued to the pelage of the seal on the dorsal midline behind the shoulders with marine epoxy following chemical immobilization (see Le Boeuf et al. 1988, 1989). Depth and temperature data were sampled at 30-s intervals and stored in memory with reference to an internal electronic clock. The recorder was encased in a tubular titanium housing measuring 15.4 × 2.9 cm and weighing 196 g.

One female carried a custom-made velocity–time–depth recorder (B-H Mk1, Santa Cruz, Calif.) during trip 1 that recorded both depth and swim speed. It measured 6.5 × 3 × 15 cm, weighed 0.45 kg, and incorporated a Tattletale Fast Lite datalogger, Model L-512PSF (Onset Computer Corp., Pocasset, Mass.). The instrument has 512 kb of memory and was programmed to sample dive depth and relative velocity every 10 s. Dive depth was measured with a Keller pressure transducer (KPSI, Oceanside, Calif.) calibrated between 0 and 1000 m before deployment; error was estimated at ±2.5 m. Relative velocity was sampled using a Logtron paddle wheel (Flash Electronic GmbH, Dachau, Germany) whose revolutions were counted and stored in memory until sampled.

The instruments deployed on all females during trip 1 began collecting data as soon as the animals entered the water, sampling depth, temperature, and light until the memory was full. Mean record duration was 44.7 ± 17.2 days (range 18–71 days).

The instruments deployed on LG females during trip 2, having insufficient memory to record the entire trip at sea, were programmed to begin recording approximately 5 months into the foraging migration or 3 months prior to the seal returning to the rookery to breed. The record period coincided with the last trimester of pregnancy. Mean record duration for LG females was 72.6 ± 3.3 days (range 67–76 days).

Body composition

Body composition was calculated for all subjects when the instruments were attached, less than 2 days before they departed on the foraging migration, and within 2 days of their return to the Año Nuevo rookery. Dorsal, lateral, and ventral blubber depth were measured at each of six points along the seal's body using an ultrasound scanner accurate to ±1 mm (Scanoprobe, Ithaca, N.Y.). In addition, length and girth measurements were made at each of these points. The seal was modeled as a series of truncated cones to calculate total blubber mass as a proportion of body mass (Gales and Burton 1987; Crocker 1995).

Dive classification

Dives were classified individually for all animals into four major types and their variants: A, C, D, and E dives (Le Boeuf et al. 1992, 1993). We assume that A dives are primarily transit dives, D dives reflect pelagic foraging, and E dives reflect benthic foraging. Unpublished data that we have collected from elephant seals whose daily locations are monitored with Argos satellite tags give credence to these assumptions.

We determined the duration and number of dives in C dive bouts as well as the frequency, duration, and type of dives that preceded

and following them. A bout of C dives was defined as two or more C dives in sequence. C dives were characterized and measured according to their three segments (Fig. 1), hereafter called C1 for the initial dive descent, C2 for the middle segment, and C3 for the ascent. The mean depth and duration of C dives, as well as the depth at which segment C2 began and the duration of C2, were calculated for each female. When possible, we determined the swim speed of each segment. We distinguished C dives according to the vertical direction of movement during C2, i.e., descending or ascending.

Variants included in this analysis were dives in which C2 was stair-stepped (Fig. 1). In the stair-step variant, all portions of C2 in the direction of diving (i.e., ascending or descending) are parallel. Rates of descent or ascent and duration were calculated for all segments of C dives for all records. For comparison, rates of descent or ascent were calculated for all segments of transit and pelagic foraging dives for six EG females during trip 1.

Swim-speed calibration

The swim-speed recorder was calibrated using depth and velocity data collected by the animal (Fletcher et al. 1996). The rate of change in depth, or vertical speed, was calculated every 30 s and plotted against the total number of paddle-wheel rotations over the same 30 s, expressed in revolutions per minute (rpm). Assuming that the lowest rpm values for a given swim speed represents vertical diving, then the lowest swim speed for each vertical speed equals the change in depth. A regression line through the lowest rpm value for each vertical speed is the calibration line ($\text{rpm} = -0.53 + 505.1 \times \text{swim speed}$ ($r^2 = 0.98$, $P < 0.05$)). The stall speed of the recorder was determined experimentally to be 0.22 m/s. Speeds below this value were considered indistinguishable from zero.

Statistics

Values are presented as ± 1 standard deviation from the mean. Correlation was determined using Pearson's product correlation coefficients, r . Significance of between-group comparisons was tested using Student's t test or the Mann-Whitney rank sum test. The α level for statistical significance was set at 0.05.

Results

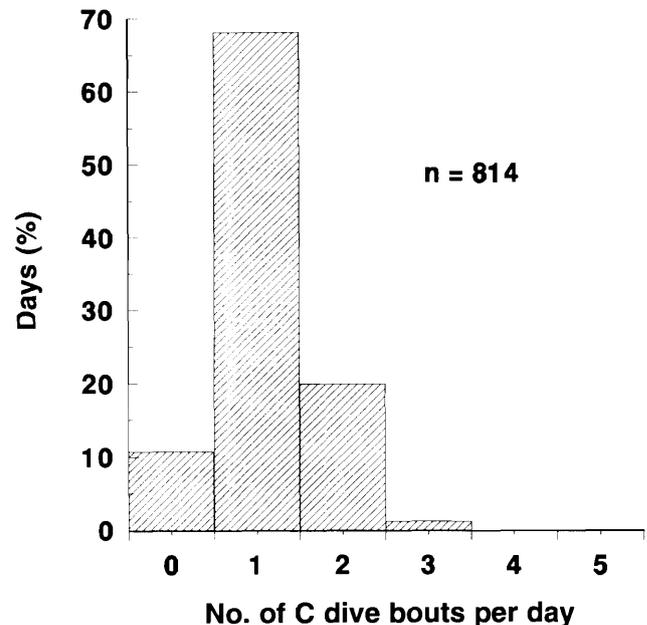
Characteristics and context of C dives

C dives made up $6.3 \pm 1.9\%$ of the total dives of all females, $5.6 \pm 1.3\%$ of the dives in the records of EG females during trip 1, and $7.1 \pm 1.5\%$ of the dives of LG females in trip 2. Four percent of the C dives of EG females and 22.2% of those of LG females were stair-stepped (Fig. 1). In comparison, pelagic foraging (D) dives were the most frequent type in all records (mean $60.4 \pm 8.2\%$). Transit or A dives accounted for a mean of $24.0 \pm 8.2\%$ of the dives and flat-bottomed E dives accounted for a mean of $4.5 \pm 2.4\%$ of the dives.

C dives occurred in bouts containing a mean of 3.81 ± 2.06 dives (range 2–10 dives per bout). The incidence of C dive bouts was 1.12 ± 0.58 per day (Fig 2). LG females during trip 2 had significantly more bouts per day (1.26 ± 0.57) than EG females during trip 1 (1.00 ± 0.58) (t test = 3.58, $df = 13$, $P < 0.05$).

The mean duration of C dives was 22.9 ± 2.2 min for EG females, 52.3% of which was spent in segment C2. Correspondingly, the C dives of LG females lasted a mean of 33.8 ± 1.18 min, 39.1 % of this duration being taken up by C2. This difference is due not to reproductive condition but to the length of time at sea; mean dive duration per

Fig. 2. Frequency distribution of C dive bouts per day in the records of all females.



day increases with time at sea (Le Boeuf 1994; Le Boeuf et al. 1996).

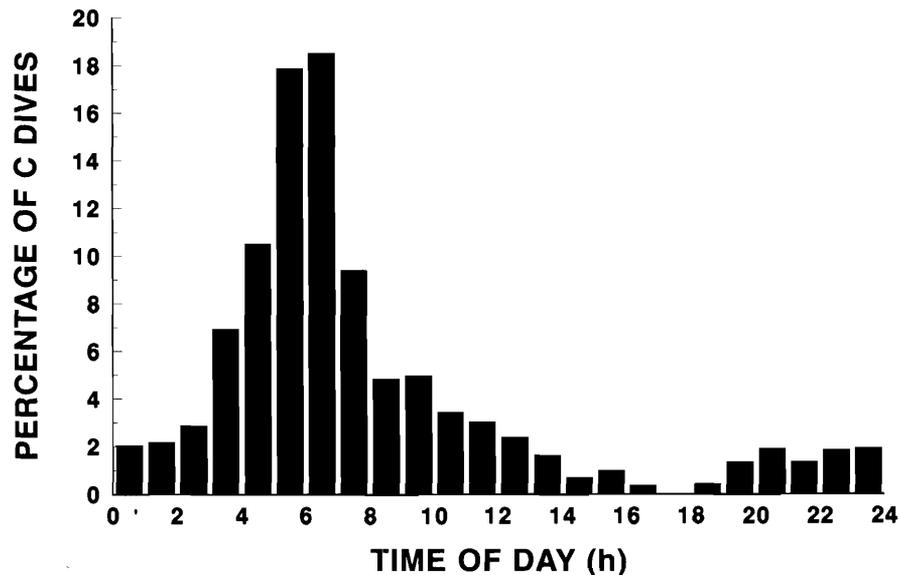
EG and LG females differed in the direction of vertical movement of segment 2 of C dives (Fig. 1). Segment C2 of all EG females and one LG female descended; in four other LG females it ascended. The mean descent rate of EG females decreased abruptly from 1.18 ± 0.25 m/s for C1 to 0.31 ± 0.04 m/s for C2, and the dive concluded with an ascent rate of 0.76 ± 0.25 m/s for C3. The mean descent rate of LG females during C1 was 0.58 ± 0.18 m/s, followed by an ascent rate of 0.17 ± 0.05 m/s for C2 (in four females), ending with an ascent rate of 0.84 ± 0.29 m/s for C3. One LG female differed from others by descending during C2. Her mean descent rate during C2 was 0.19 ± 0.02 m/s. Despite a different overall shape, in this female, C2 was virtually identical in duration with that of the other LG females (13.3 ± 3.0 min). This female's C dives had a mean depth and duration of 349 ± 64 m and 33.2 ± 5.6 min, respectively, 62.6% of them being the standard type and 37.4% being the stair-stepped variant.

Segment C2 began at a mean depth of 171 ± 52 m and ended at a mean depth of 400 ± 79 m in EG females; parallel values for the four similar LG females were 312 ± 77 m and 219 ± 84 m. The depth at which C2 began was often highly consistent within a bout of C dives, but varied significantly between bouts.

Hypothesis 1: C dives are associated with foraging and digestion of prey consumed

C dives are associated with D dives

The frequency of C dives and foraging-type (D) dives, computed on a weekly basis, were positively correlated in the records of all females. The mean correlation coefficient was 0.74 ± 0.16 for 10 EG females and 0.59 ± 0.18 for 5 LG females ($P < 0.05$). Frequency of C dives was not positively correlated with that of any other dive type.

Fig. 3. Percentage of total dives that were C dives in the records of all females as a function of time of day.**Table 1.** Mean swim speed (m/s) \pm 1 standard deviation for segments of three dive types recorded directly from an early-gestation female during trip 1.

Dive type	No. of dives	Dive segment		
		1 (descent)	2	3 (ascent)
A	1049	1.58 \pm 0.31	na	1.28 \pm 0.18
C	99	1.45 \pm 0.11	0.26 \pm 0.08	0.83 \pm 0.08
D	754	1.74 \pm 0.27	1.43 \pm 0.23	1.64 \pm 0.24

C dives follow nighttime foraging

C dives peaked in the early morning between 05:00 and 07:00 (Fig. 3). They followed long bouts of shallow foraging dives that occurred during the night. The frequency of occurrence of C dives was lowest in late afternoon between 14:00 and 19:00.

C dive frequency varies with stage of migration

In 9 EG females and 3 LG females, C dives were negatively correlated with A dives (mean Pearson's product r for all females = -0.73 ± 0.22 , $P < 0.05$). The only days on which no C dives occurred were at the beginning of all trip 1 records, when the EG females were crossing the continental shelf en route to deep water and, for some of them, the first few days of pelagic diving. During the first 5 days at sea, C dives comprised 1.1% of all the dives of EG females. After the first 5 days at sea, C dives accounted for 7.1% of the dives in the records.

Hypothesis 2: Seals do not swim during segment C2

Swim speed during segment C2 is very low or nil

For the female whose swim speed was measured directly during trip 1 (Table 1), swim speed during C2 was 0.26 ± 0.08 m/s, a significant reduction in swim speed from C1 and C3 (t test, $t = 91.5$ and 50.1 , $df = 196$, $P < 0.05$) and from

Table 2. Mean variance and coefficient of variance (in boldface type) in rate of depth change of dive segments of early-gestation females during trip 1 within a bout of dives of the same type.

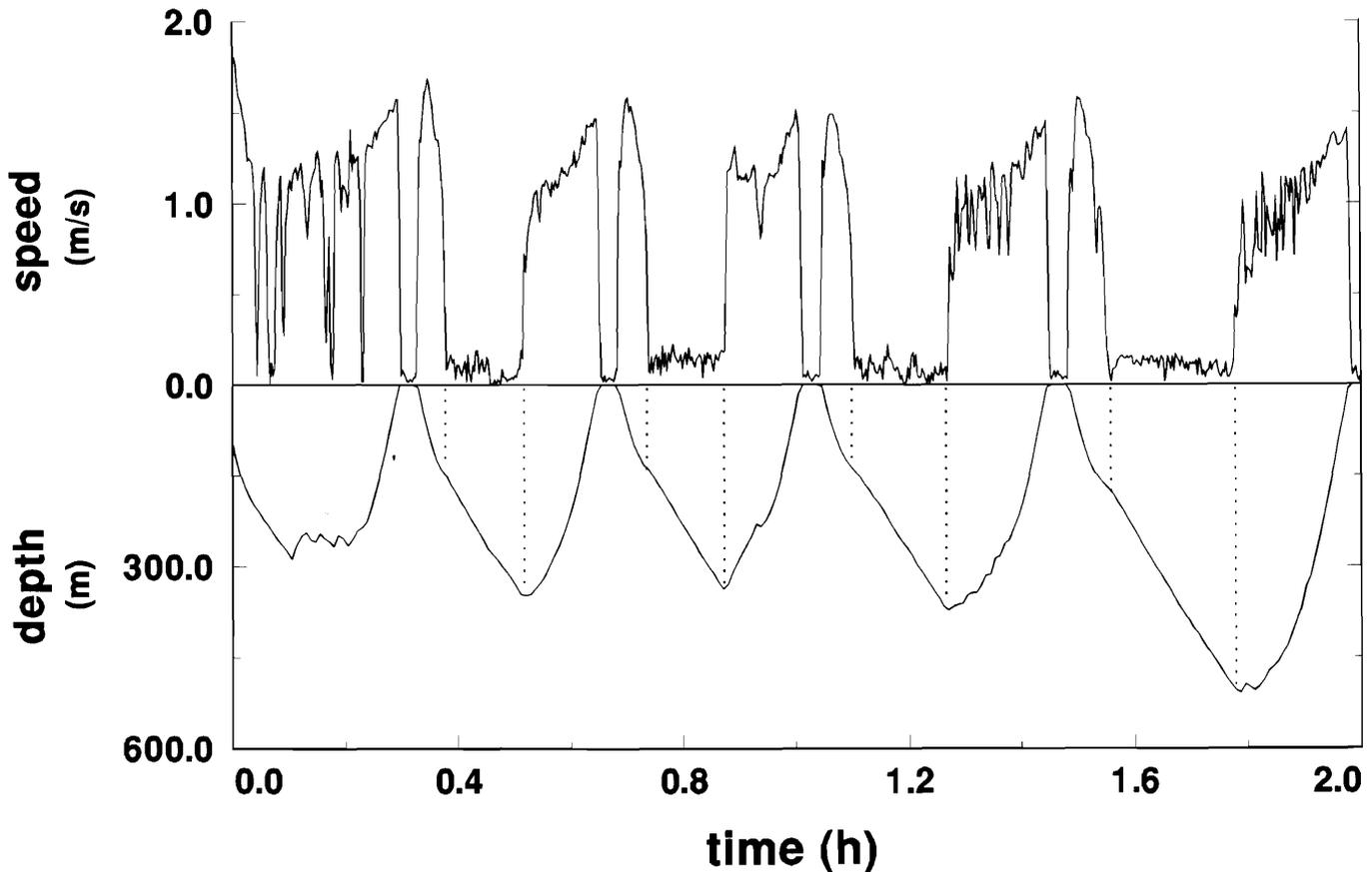
Dive type	No. of bouts	Dive segment		
		1 (descent)	2	3 (ascent)
A	238	0.018		0.036
		9.75		13.13
C	357	0.046	0.0001	0.032
		24.71	3.09	12.96
D	525	0.023		0.022
		18.47		15.26

all segments of other dive types. Since 0.2 ± 0.25 m/s was the stall speed of the recorder, the seal was either swimming very slowly during C2, an average reduction of 82% in swim speed from C1, or not at all. Swim speeds during a typical bout of C dives are shown in Fig. 4. Swim speeds were never so low in other segments of C dives or in dives of any other type, save for momentary decreases correlated with changes in vertical direction such as that illustrated in the D dive in Fig. 4.

Seals drift passively during segment C2

Variance in the rate of depth change was significantly lower for C2 in EG females than for all other dive segments analyzed (Table 2). Within-bout variance for C2 was significantly lower than that of segments C1 and C3 ($F_s = 383$, 267 ; $v_1, v_2 = 356$; $P < 0.05$), A dives ($F_s = 150$, 300 ; $v_1 = 237$, $v_2 = 356$; $P < 0.05$), and D dives ($F_s = 192$, 183 ; $v_1 = 524$, $v_2 = 356$; $P < 0.05$). The coefficient of variance for C2, 3.1%, was significantly lower than that for C1 ($F = 26.29$, $df = 356, 356$, $P < 0.05$) and C3 ($F = 9.59$, $df = 356, 356$, $P < 0.05$) and for all segments of all other dive types ($F = 4.96$ or above, $P < 0.05$) (Table 2). A similar pattern was observed in LG females.

Fig. 4. Swim speed and depth for a segment of the dive record of an early-gestation female during trip 1. The figure shows one D dive followed by four C dives with associated swim speeds. Swim speed decreases to the stall speed of the recorder during the second segment of C dives (the area bounded by vertical dotted lines). The period of low swim speed increases with each succeeding C dive.



Body composition determines the direction and rate of depth change

The descent rate of EG females during C2 decreased with increasing proportion of adipose tissue in the body composition. Their descent during C2 in the first bout of C dives after going to sea (10 departures) and the last bout of C dives before returning to the rookery (2 arrivals) was negatively correlated with the percentage of adipose tissue in the body composition (Fig. 5; $r = -0.91$, $P < 0.05$).

For all EG females the descent rate during C2 decreased with time at sea until it reached approximately 0.22–0.28 m/s (Fig. 6). For all of these females, the descent rate during C2 was more rapid at the beginning, or in the first half of the record, than at the end of the period at sea. In contrast, 4 of the 5 LG females ascended during C2. Figure 7 shows that the ascent rate increased over time to 0.13–0.24 m/s then decreased, possibly owing to the growth of the fetus, which is mostly lean tissue. In one female, Sydney, ascent during C2 changed to descent on Julian day 365.

Hypothesis 3: Oxygen saved from reduced locomotion during C dives is spent on food processing

Oxygen, activity, and dive duration

The mean duration of C dives of EG females, 22.9 ± 2.2 min, was not significantly greater than the mean duration of transit dives (21.9 ± 1.1 min; paired t test, $t = 1.46$,

$df = 9$, $P > 0.05$), pelagic foraging dives (21.6 ± 1.2 min; paired t test, $t = 1.81$, $df = 9$, $P > 0.05$), or benthic foraging dives (21.1 ± 2.9 min; paired t test, $t = 1.52$, $df = 9$, $P > 0.05$). Similarly, the mean duration of C dives of LG females, 33.8 ± 7.1 min, was not significantly greater than that of other dive types for this category of females. This suggests that oxygen saved from reduced exercise during C dives was available for other needs, such as food processing, and that this oxygen was expended.

LG females exhibit shorter C2 segments relative to total dive duration than EG females

EG females exhibited a mean ratio of C2 duration to total dive duration of 0.52 ± 0.08 ($n = 1557$ dives), whereas LG females had a significantly lower mean ratio, 0.39 ± 0.10 ($n = 1025$) ($t = 35.1$, $df = 2580$, $P < 0.05$, or for three matched females, $t = 16.4$, $df = 2$, $P < 0.05$). This is a 25% reduction in the proportion of time LG females spent drifting during each C dive relative to EG females.

LG females compensated for this reduction by increasing the number of dives in a bout of C dives. Whereas EG females exhibited a C dive bout length of 3.42 ± 1.74 dives, LG females had a significantly longer bout length, 4.24 ± 1.90 dives ($t = 7.2$, $df = 1237$, $P < 0.05$, or for three matched females, $t = 5.93$, $df = 2$, $P < 0.05$). This represents, on average, a 24% increase in bout length for LG females compared with EG females.

Fig. 5. Descent rate during segment C2 in the first or last bout of C dives of all early-gestation females during trip 1 as a function of percentage of adipose tissue in body composition, measured just prior to departure from the rookery and immediately after return to the rookery after about 72 days.

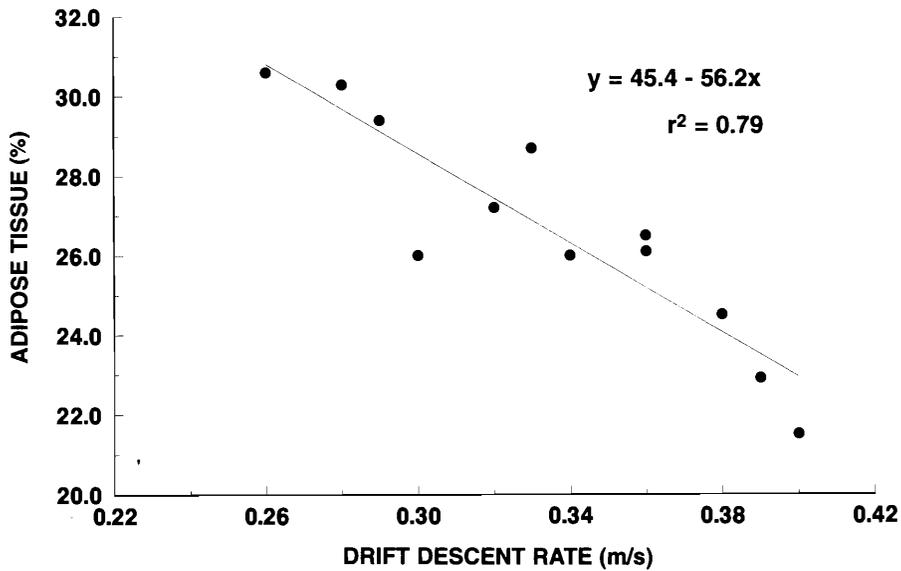


Fig. 6. Changes in mean descent rate during segment C2 per bout of C dives for the entire dive records of 4 early-gestation females during trip 1.

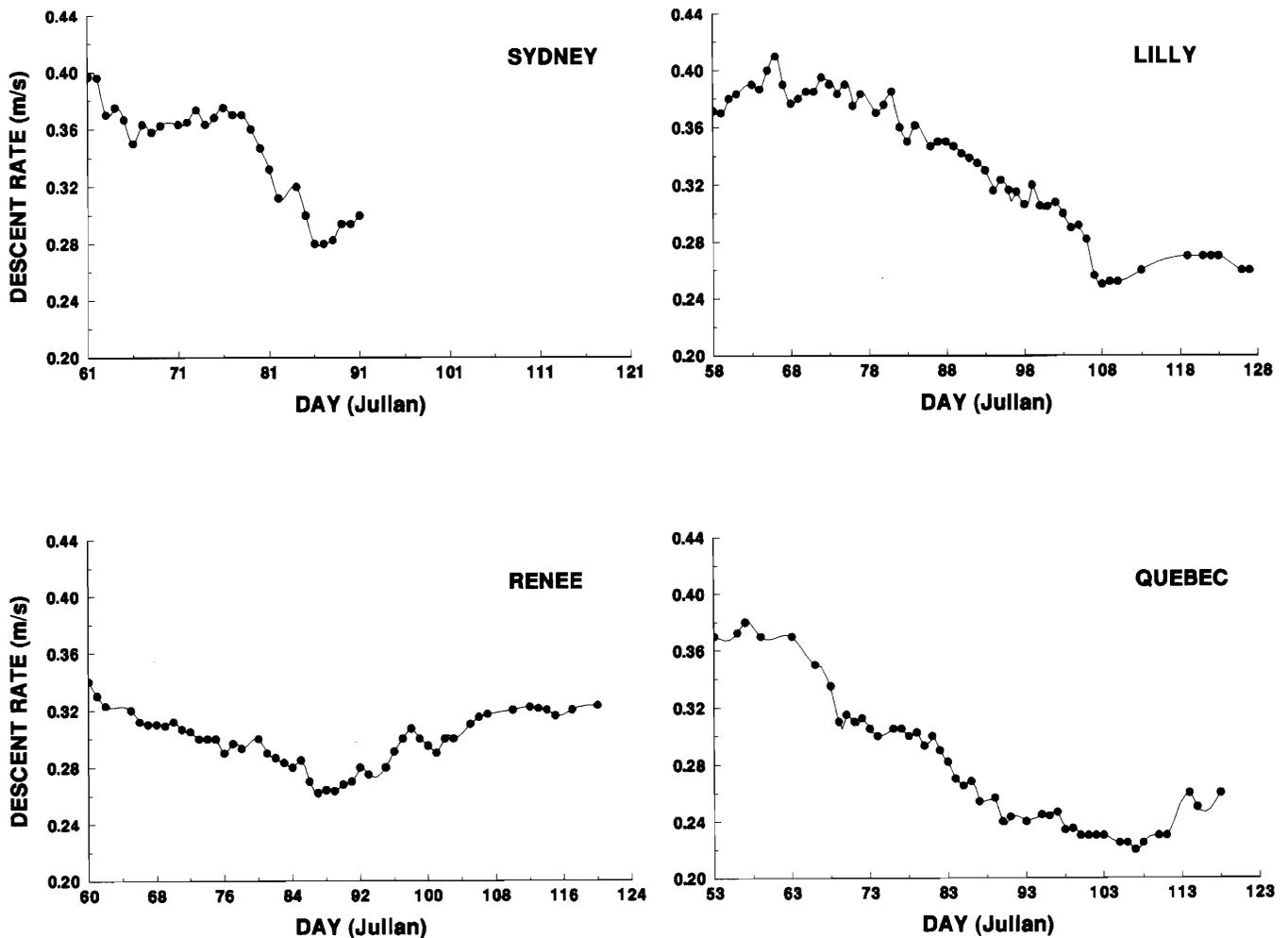


Fig. 7. Changes in mean ascent rate during segment C2 per bout of C dives for the entire dive records of 4 females in the third trimester of pregnancy during trip 2. Note that the female Sydney goes from being positively buoyant to negatively buoyant on Julian day 5 (January 5, 1992).

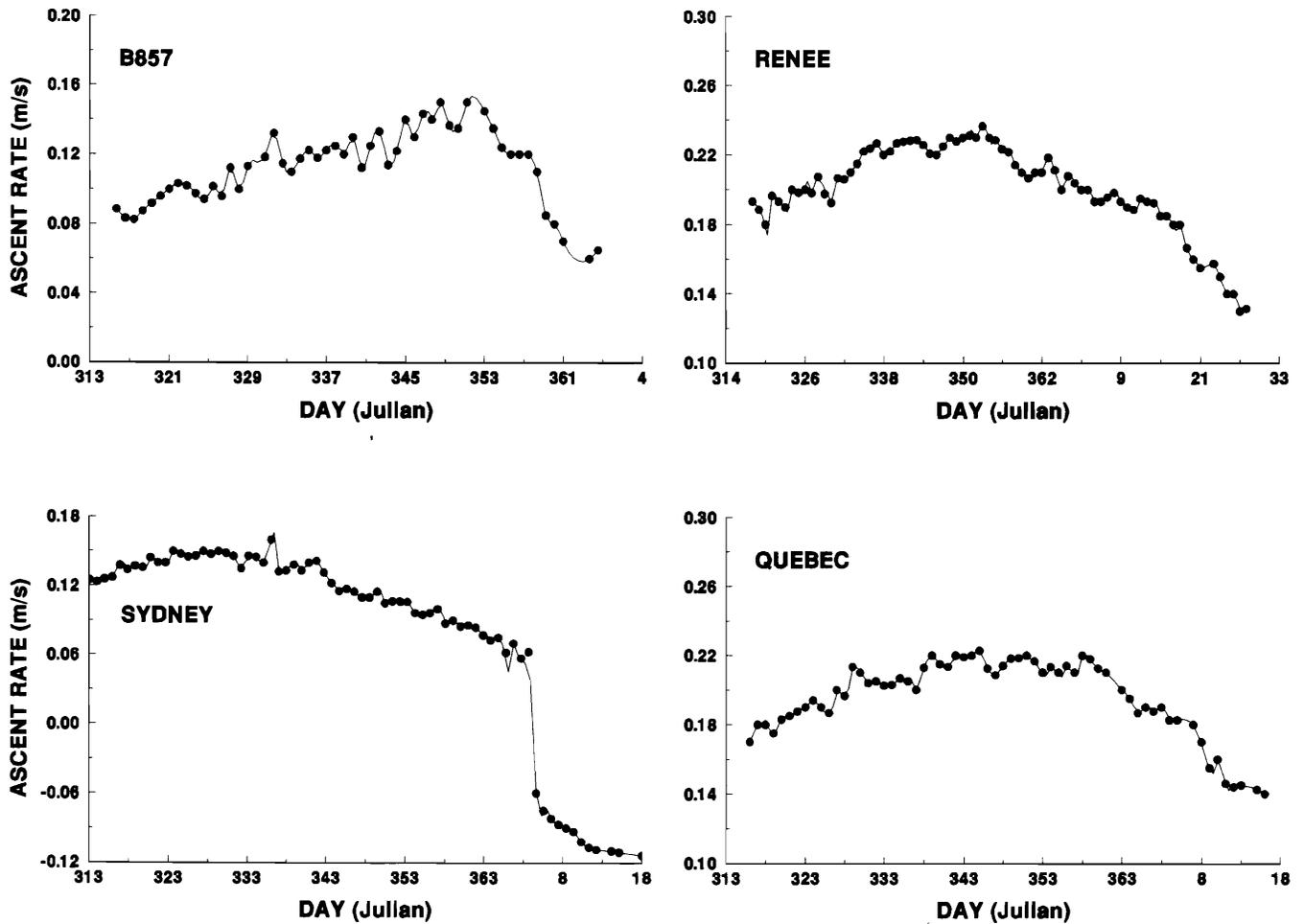


Fig. 8. Mean change in duration of segment C2 of all early-gestation females during trip 1 as a function of dive number in a bout of C dives. The duration of each succeeding drift period in a bout was expressed as a percentage of the initial drift segment in the bout.

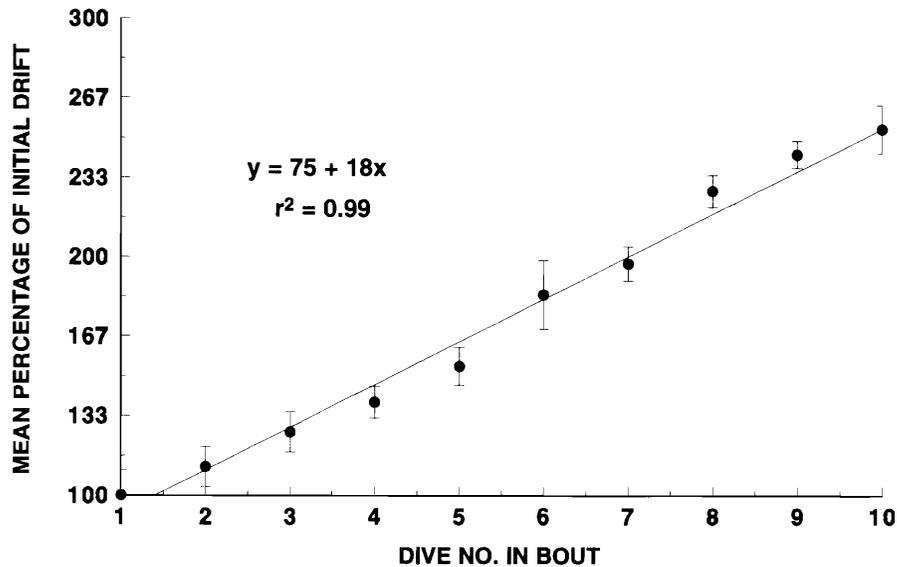


Table 3. Incidence of C dive bouts and extended surface intervals (ESIs) (greater than 10 min) and percentage of ESIs preceding, following, and between bouts of C dives of 10 early-gestation (EG) females during trip 1 and 5 late-gestation (LG) females during trip 2.

	Percentage of C dives in record	Percentage of C dives in record	Percentage of ESIs		
			Preceding C dives	Following C dives	Between C dives
EG females, trip 1	5.5±1.6	0.11±.001	74	67	75
LG females, trip 2	7.8±1.4	0.28±.001	86	80	92
All females	6.3±1.9	0.16±.001	86	79	84

The duration of drifting increases with bout length

The time spent drifting per dive increased significantly with each dive within a bout of C dives (Fig. 8; see also Fig. 4). For EG females, the mean drift duration of the first C dive in a bout was 9.8 ± 1.7 min, increasing by 40.8% to 13.8 ± 2.5 min for the fourth dive in a bout and by 150% to as long as 24.5 ± 2.1 min for the last dive in a bout of 10 dives. On average, EG females spent a total of 43.5 ± 22.1 min and LG females 56.0 ± 25.1 min drifting per bout of C dives.

Hypothesis 4: On rare occasions, food processing occurs while the animal rests at the surface

C dives are associated with extended surface intervals

C dives comprised 6.3% of the total dives in records during both trips to sea. If C dives were not associated with ESIs we would expect 12.2% of ESIs to be preceded or followed by a C dive and 0.4% of ESIs to be between two C dives. ESIs preceded or followed C dives 84% of the time and ESIs were bordered by C dives 68% of the time (Table 3).

Discussion

Our analysis provides indirect support for the general hypothesis that elephant seals direct oxygen saved from reduced locomotion to metabolism associated with food processing. That is, they partition the metabolic costs of locomotion and food processing while maintaining continuous and long-duration diving throughout extended foraging trips at sea. Support for this hypothesis is provided by data showing that (i) female elephant seals do not swim, but drift instead, during parts of certain dives, (ii) dives with reduced swim speeds are associated with putative foraging, and (iii) predictions are upheld regarding allocation of oxygen saved from reduced activity to food processing. We will discuss the relevance of this evidence to the general hypothesis and its general significance and implications.

Drifting during dives

Measurement of swim speed in one female showed that during the second segment of C dives swim speed was greatly reduced relative to descent, ascent, and bottom speeds during this and other dives. Speeds recorded during this stage of diving were indistinguishable from the stall speed of the recorder and showed little variability; the seal was swimming either very slowly or not at all. These results

are similar to those reported previously for another female (Le Boeuf et al. 1992).

In all females in this study, the close link between body composition and descent rate provides strong support for passive, buoyancy-dependent drifting during segment 2 of C dives. The general pattern of females drifting down during trip 1 and females in late pregnancy drifting up during trip 2 is consistent with our data and previous data on changes in body composition. Despite increasing their departure mass by 24% at the rate of 1.1 ± 0.2 kg/day (Le Boeuf et al. 1988), female elephant seals return from trip 1 with about the same proportion of adipose tissue, 24%, with which they departed (Worthy et al. 1992; Crocker 1995). This makes females negatively buoyant and causes them to drift down when not swimming. The data suggest that as females forage, they increase the proportion of lean tissue during the first 1/2 to 2/3 of the foraging trip and drift down progressively faster until buoyancy is stabilized.

In contrast, most females in late pregnancy ascend while drifting. We assume that when they first go to sea, a period during which we have not made recordings, their body composition is similar to that of females during trip 1, and they drift down during C2. But after 5 months of foraging, they ascend while drifting, which suggests that they are depositing more energy as fat than as lean tissue. As they approach term, however, the ascent rate begins to decline, coinciding with the rapid growth of the predominantly lean-tissue fetus. One pregnant female (Sydney; see Fig. 3) switched from being positively buoyant to negatively buoyant at the end of her record. The shift in descent rate is symmetric around zero and is consistent with the fact that as an object approaches neutral buoyancy, slight changes in buoyancy produce great changes in the rate of movement (Aleyev 1977). This delicate balance may explain the performance of the aberrant LG female who drifted down during C dives like EG females during trip 1. This suggests that she did not acquire sufficient resources to reach positive buoyancy. Indeed, this female had the lowest proportion of adipose tissue (28%) of 20 females returning to give birth (Crocker 1995), and she weaned an unusually small pup, 93 kg, compared with the mean weaning mass, 135 kg.

Data from weanling elephant seals going to sea for the first time at 3 1/2 months of age support the statement that drifting occurs during C dives. Like females in late pregnancy, weanlings are positively buoyant, owing to an extremely high

fat content, measured at 48% (Kretzmann 1990; Kretzmann et al. 1993; Crocker 1995). Le Boeuf et al (1996) report that two weanlings studied drifted up during the second segment of C dives. One seal ascended during all C2 segments during its first 12 days at sea, the duration of the record. The second seal did the same, but on the 24th day at sea, it shifted from drifting up to drifting down and continued this way until the end of the record 2 days later. Descent rates during all dive types were slower before the reversal in drift direction than after the reversal, which suggests that diving effort was greater before the shift than afterwards. Moreover, all ascent rates during the drift segment of C dives got progressively slower, leading to the reversal in drift direction. Older juveniles up to 2 years of age, whose body composition is less than 33% fat, descended while drifting, like EG females during trip 1.

Dive records of adult males suggest that they drift down during C dives, at least during the early stages of migration (Le Boeuf et al. 1993). But because males appear to spend some time diving and foraging on the ocean bottom, during which they may stop swimming, reduced locomotion is not limited to C dives and this complicates analysis. If adult males are positively buoyant at any time during the year, we predict that it will be just prior to the breeding season, when their mass is greatest and their blubber layer thickest (Deutsch et al. 1990).

The observed relationship between body composition and passive drifting may provide an important tool with which to examine changes in body composition while foraging and resource accrual at sea. Fluctuations in specific gravity suggest that diving effort may vary with reproductive condition and age, and could affect foraging economics.

Association of drifting dives with foraging

The correlation between C dive bouts and putative foraging dives is high and positive. A negative relationship was found between C dive bouts and transit dives: C dives are infrequent or absent during the period of rapid transit from the rookery (Le Boeuf et al. 1993), and C dives increase in frequency when the animals appear to begin foraging, i.e., remain on station for several days. This suggests that the primary function of C dives is related to feeding rather than alternatives such as sleep or rest, although multiple simultaneous functions are possible. Furthermore, the daily occurrence of C dives in the early morning coincides with a decrease in the frequency of foraging dives just prior to the downward trend in the diurnal variation in foraging depth. C dives precede the period of the day when dives are made to greater depths, and dive durations increase accordingly (Le Boeuf et al. 1993). This is the period when the metabolic cost of processing food might most significantly decrease the ability of the animal to forage effectively.

Linking drifting behavior to food processing and HIF is more difficult, and is limited by the strictly behavioral nature of the data. The distinct early-morning pattern of C dives is consistent with a food-processing role. This does not preclude alternative explanations such as sleep or rest. The relatively small amount of time spent drifting (29–156 min per bout), however, seems overly brief to account for sleep or rest.

Drifting, oxygen saved, and food processing

Although changes in the dive patterns of females in late pregnancy do not specifically relate drift behavior to food processing, they strongly suggest a reapportioning of oxygen reserves to an internal physiological process. LG females reduced the average proportion of each dive spent drifting, possibly devoting a lesser proportion of their oxygen reserves to food processing. They appeared to compensate for this by increasing the number of C dives in a bout by the same proportion. This represents a change in the form and frequency of C dives predicted by the hypothesis.

The increase in drift duration across a bout of C dives was also consistent with the hypothesis. Although differences in diet could alter the rate of oxygen consumption due to HIF, all animals exhibited a regular and similar increase in drift time across a bout. While it does not link oxygen savings directly to HIF, this strongly suggests that the rate of oxygen consumption during the drift segment is decreasing across a bout of C dives. An alternative explanation is that anaerobic metabolites acquired during active swimming are being cleared. The overall pattern of evidence, however, supports a relationship with at least some metabolic costs of food processing.

The association of C dives and HIF with rare, unusually long periods at the surface is necessarily speculative. The temporal association between C dives and ESIs suggests that elephant seals may rest at the surface following a long bout of feeding, when reductions in locomotion are not sufficient to allow continued diving. Thus, the distinctive patterning of ESIs suggests that HIF might be an important constraint on the oxygen budget of the seal.

Foraging implications

The partitioning of locomotor and feeding metabolism has a number of implications for foraging behavior in elephant seals. The hypothesis implies that elephant seals are gorge feeders, storing up food for later processing. This is plausible, given what we know about digestive physiology in general and the morphology of the elephant seal digestive tract in particular. Gastric motility and emptying are highly sensitive to low oxygen tension (Van Lier 1941). This could provide a physiological switch by which gut perfusion controls the movement of food into the small intestine. The pyloric sphincter muscle is highly resistant to the effects of anoxia (Van Lier et al. 1935). In general, gastrointestinal secretions are relatively resistant to hypoxia (Hellebrand et al. 1935). The gastric part of digestion can begin under conditions of reduced perfusion. Important metabolic costs associated with HIF, like warming the food to body temperature, can be amortized across many dives. In contrast, the absorptive processes of the small intestine involve energy exchange and can be reduced or abolished by degrees of anoxia *in vitro* (Johnston 1958).

The gut morphology of the elephant seal is particularly well suited to the function implied by the hypothesis. The gastrointestinal tract of carnivores is usually characterized by a relatively simple stomach and short intestinal tract (Davenport 1966). In contrast, phocids, particularly elephant seals, have an unusually long small intestine that appears well adapted to processing large amounts of food in a concentrated time period (Laws 1953; Scheffer 1958; Helm 1983). *In vivo* laboratory measurements of rates of intestinal

nutrient uptake could yield estimates of the processing capacity of the elephant seal gut and allow comparison with the behavioral data.

We conclude that northern elephant seals drift while processing food and, in this way, balance the oxygen demands of foraging and locomotion while diving continuously and remaining within their aerobic limits. This behavior might be an important element in the life history of an animal that spends a significant part of its life in a pelagic environment utilizing highly dispersed food resources.

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References

- Ainley, D.G., Strong, C.S., Huber, H.R., Lewis, T.J., and Morrell, S.H. 1981. Predation by sharks on pinnipeds at the Farallon Islands. *Fish. Bull.* **78**: 941–945.
- Aleyev, Yu. G. 1977. Nekton. Dr. W. Junk b.v., The Hague.
- Barbour, A. 1993. Heat increment of feeding in juvenile northern elephant seals. M.Sc. thesis, University of California, Santa Cruz.
- Barcroft, J., Kennedy, J.A., and Mason, M.F. 1939. Direct determination of oxygen consumption of foetal sheep. *J. Physiol. (Lond.)*, **95**: 269–275.
- Brody, S. 1945. Bioenergetics and growth. Hafner, New York.
- Costa, D.P. 1991. Reproductive and foraging energetics of pinnipeds: implications for life history patterns. *In Behaviour of pinnipeds. Edited by D. Renouf. Chapman and Hall, London.* pp. 300–338.
- Crocker, D.E. 1995. Reproductive effort and fasting physiology of female northern elephant seals. Ph.D. thesis, University of California, Santa Cruz.
- Davenport, H.W. 1966. Physiology of the digestive tract. Year Book Medical Publishers, Chicago.
- Davis, R.W., Castellini, M.A., Kooyman, G.L., and Maue, R. 1983. GFR and hepatic blood flow during voluntary diving in Weddell seals. *Am. J. Physiol.* **245**: 743–748.
- Davis, R.W., Williams, T.M., and Kooyman, G.L. 1985. Swimming metabolism of yearling and adult harbor seals, *Phoca vitulina*. *Physiol. Zool.* **58**: 590–596.
- Deutsch, C.J., Haley, M.P., and Le Boeuf, B.J. 1990. Reproductive effort of male northern elephant seals: estimates from mass loss. *Can. J. Zool.* **68**: 2580–2593.
- Deutsch, C.J., Crocker, D.E., Costa, D.P., and Le Boeuf, B.J. 1994. Sex- and age-related variation in reproductive effort of northern elephant seals. *In Elephant seals: population ecology, behavior and physiology. Edited by B.J. Le Boeuf and R.M. Laws. University of California Press, Los Angeles.* pp. 169–210.
- Diamond, J.M., Karasov, W.H., Phan, D., and Carpenter, F.H. 1986. Digestive physiology is a determinant of foraging bout frequency in hummingbirds. *Nature (Lond.)*, **320**: 62–63.
- Fedak, M.A. 1986. Diving and exercise in seals: a benthic perspective. *In Diving animals and man. Kongsvald Symposium, Royal Norwegian Society of Sciences and Letters, June 3–7, 1985. Edited by A.D. Brubakk, J.W. Kanwisher, and G. Sundnes. Tapir, Trondheim.* pp. 11–32.
- Feldkamp, S.D. 1987. Swimming in the California sea lion: morphometrics, drag, and energetics. *J. Exp. Biol.* **131**: 117–136.
- Fletcher, S., Le Boeuf, B.J., Costa, D.P., Tyack, P.L., and Blackwell, S.B. 1996. Onboard acoustic recording from diving northern elephant seals. *J. Acoust. Soc. Am.* In press.
- Furnell, D.J. 1987. Partitioning of locomotor and feeding metabolism in sablefish, *Anoplopoma fimbria*. *Can. J. Zool.* **65**: 486–489.
- Gales N.J., and Burton, H.R. 1987. Ultrasonic measurement of blubber thickness of the southern elephant seal, *Mirounga leonina* (Linn.). *Aust. J. Zool.* **35**: 207–217.
- Gentry, R.L., and Kooyman, G.L. (Editors). 1986. Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, N.J.
- Gentry, R.L., Kooyman G.L., and Goebel, M.E. 1986. Feeding and diving behavior of northern fur seals. *In Fur seals: maternal strategies on land and at sea. Edited by R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J.* pp. 61–78.
- Hellebrand, F.A., Brogdon, E., and Hoopes S.L. 1935. The effect of acute anoxemia on hunger, digestive contractions, and the secretion of hydrochloric acid in man. *Am. J. Physiol.* **112**: 451–460.
- Helm, R.C. 1983. Intestinal length of three California pinniped species. *J. Zool. (1965–1984)*, **199**: 297–304.
- Hindell, M.A., Burton, H.R., and Slip, D.J. 1991a. Foraging areas of southern elephant seals, *Mirounga leonina*, as inferred from water temperature data. *Aust. J. Mar. Freshwater Res.* **42**: 115–128.
- Hindell, M.A., Slip, D.J., and Burton, H.R. 1991b. The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia: Phocidae) *Aust. J. Zool.* **39**: 595–619.
- Hochachka, P.W. 1986. Balancing conflicting metabolic demands of exercise and diving. *Fed. Proc.* **45**: 2948–2952.
- Johnston, J.M. 1958. An *in vitro* study of fatty acid absorption. *Proc. Soc. Exp. Biol. Med.* **98**: 836–838.
- Jonker, F.C., and Bester, M.A. 1994. The diving behaviour of adult southern elephant seals, *Mirounga leonina*, cows from Marion Island. *S. Afr. J. Antarct. Res.* **24**: 75–93.
- Kooyman, G.L. 1989. Diverse divers. Springer-Verlag, Berlin.
- Kooyman, G.L., Castellini, M.A., and Davis, R.W. 1981. Physiology of diving in marine mammals. *Annu. Rev. Physiol.* **43**: 343–356.
- Kooyman, G.L., Wahrenbrock, E.A., Castellini, M.A., Davis, R.W., and Sinnett, E.E. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior. *J. Comp. Physiol.* **138**: 335–346.
- Kretzmann, M. 1990. Maternal investment and the post-weaning fast in northern elephant seals: evidence for sexual equality. M.Sc. dissertation, University of California, Santa Cruz.
- Kretzmann, M., Costa, D.P., and Le Boeuf, B.J. 1993. Maternal energy investment in elephant seal pups: evidence for sexual equality. *Am. Nat.* **141**: 466–480.
- Laws, R.M. 1953. The elephant seal (*Mirounga leonina*). I. Growth and age. *Falkl. Isl. Depend. Surv. Sci. Rep.* **8**: 1–62.
- Laws, R.M. 1956. The elephant seal (*Mirounga leonina* Linn.). III. The physiology of reproduction. *Falkl. Isl. Depend. Surv. Sci. Rep.* **15**: 1–66.
- Le Boeuf, B.J. 1994. Variation in the diving pattern of northern elephant seals with age, mass, sex, and reproductive condition. *In Elephant seals: population ecology, behavior and physiology. Edited by B.J. Le Boeuf and R.M. Laws. University of California Press, Los Angeles.* pp. 237–252.

- Le Boeuf, B.J., Riedman, M., and Keyes, R.S. 1982. White shark predation on pinnipeds in California coastal waters. *Fish. Bull.* **80**: 891–895.
- Le Boeuf, B.J., Whiting, R.J., and Gantt, R.F. 1972. Perinatal behaviour of northern elephant seal females and their young. *Behaviour*, **43**: 121–156.
- Le Boeuf, B.J., Costa, D.P., Huntley, A.C., and Feldkamp, S.D. 1988. Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Can. J. Zool.* **66**: 446–458.
- Le Boeuf, B.J., Naito, Y., Huntley, A.C., and Asaga, T. 1989. Prolonged, continuous, deep diving by northern elephant seals. *Can. J. Zool.* **67**: 2514–2519.
- Le Boeuf, B.J., Naito, Y., Asaga, T., Crocker, D.E., and Costa, D.P. 1992. Swim speed in a female northern elephant seal: metabolic and foraging implications. *Can. J. Zool.* **70**: 768–795.
- Le Boeuf, B.J., Crocker, D.E., Blackwell, S.B., Morris, P.A. and Thorson, P.H. 1993. Sex differences in foraging in northern elephant seals. *In Marine mammals: advances in behavioral and population biology. Edited by I.L. Boyd.* Oxford University Press, London. pp. 149–178.
- Le Boeuf, B.J., Morris, P.A., Blackwell, S.B., Crocker, D.E., and Costa, D.P. 1996. Diving behavior of juvenile northern elephant seals. *Can. J. Zool.* **74**: 1634–1644.
- McConnell, B.J., Chambers, C., and Fedak, M.A. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarc. Sci.* **4**: 393–398.
- Preide I.G. 1985. Metabolic scope in fishes. *In Fish energetics: new perspectives. Edited by P. Calow and P. Tyler.* Croom Helm, Sydney, Australia. pp. 33–64.
- Saariko, J., and Hanski, I. 1990. Timing of rest and sleep in foraging shrews. *Anim. Behav.* **40**: 861–869.
- Scheffer, V.B. 1958. Seals, sea lions and walruses: a review of the pinnipedia. Stanford University Press, Stanford, Calif.
- Vahl, O., and Davenport, J. 1979. Apparent specific dynamic action of food in the fish, *Blennius pholis*. *Mar. Ecol. Prog. Ser.* **1**: 101–107.
- Van Liere, E.J. 1941. The effects of anoxia on the alimentary tract. *Physiol. Rev.* **21**: 307–323.
- Van Liere, E.J., Chrisler, G., and Wiles, I.A. 1935. The effect of anoxia on the pyloric sphincter. *Am. J. Physiol.* **117**: 330–334.
- Williams, T.M., and Kooyman, G.M. 1985. Swimming performance and hydrodynamic characteristics of the harbor seal, *Phoca vitulina*. *Physiol. Zool.* **58**: 576–589.
- Williams, T.M., Kooyman, G.L., and Croll, D.A. 1991. The effect of submergence on heart rate and oxygen consumption of swimming seals and sea lions. *J. Comp. Physiol. B*, **160**: 637–644.
- Worthy, G.A.J., Morris, P.A., Costa, D.P., and Le Boeuf, B.J. 1992. Molt energetics of the northern elephant seal (*Mirounga angustirostris*). *J. Zool. (Lond.)*, **227**: 257–265.
- Zapol, W.M., Liggins, G.C., Schneider, R.C., Qvist, J.V.M., Snider, T., Creasy, R.K., and Hochachka, P.W. 1979. Regional blood flow during simulated diving in the conscious Weddell seal. *J. Appl. Physiol.* **47**: 968–973.