The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the stroke

Terrie M. Williams[1],*, Lee A. Fuiman[2], Markus Horning[3] and Randall W. Davis[3]

[1]*Department of Ecology and Evolutionary Biology, Center for Ocean Health, Long Marine Laboratory, 100 Shaffer Road, University of California at Santa Cruz, Santa Cruz, CA 95060, USA*, [2]*University of Texas at Austin, Department of Marine Science, Marine Science Institute, 750 Channel View Drive, Port Aransas, Texas 78373, USA* and [3]*Department of Marine Biology, Texas A&M University at Galveston, 5007 Avenue U, Galveston, TX 77553 USA*

*Author for correspondence (e-mail: williams@biology.ucsc.edu)

Summary

Foraging by mammals is a complex suite of behaviors that can entail high energetic costs associated with supporting basal metabolism, locomotion and the digestion of prey. To determine the contribution of these various costs in a free-ranging marine mammal, we measured the post-dive oxygen consumption of adult Weddell seals ($N=9$) performing foraging and non-foraging dives from an isolated ice hole in McMurdo Sound, Antarctica. Dives were classified according to behavior as monitored by an attached video-data logging system (recording activity, time, depth, velocity and stroking). We found that recovery oxygen consumption showed a biphasic relationship with dive duration that corresponded to the onset of plasma lactate accumulation at approximately 23 min. Locomotor costs for diving Weddell seals increased linearly with the number of strokes taken according to the relationship: locomotor cost = $-3.78+0.04 \times$ stroke number ($r^2=0.74$, $N=90$ dives), where locomotor cost is in ml O_2 kg^{-1}. Foraging dives in which seals ingested *Pleuragramma antarcticum* resulted in a 44.7% increase in recovery oxygen consumption compared to non-foraging dives, which we attributed to the digestion and warming of prey. The results show that the energy expended in digestion for a free-ranging marine mammal are additive to locomotor and basal costs. By accounting for each of these costs and monitoring stroking mechanics, it is possible to estimate the aerobic cost of diving in free-ranging seals where cryptic behavior and remote locations prevent direct energetic measurements.

Key words: Weddell seal, *Leptonychotes weddellii*, dive, oxygen consumption, locomotor cost, plasma lactate, stroke frequency, foraging energetics.

Introduction

Foraging by large predators comprises complex, potentially energetically demanding behaviors, depending on the type of prey involved (Stephens and Krebs, 1986). Activities such as locating, pursuing and capturing prey, as well as processing and assimilating food, as occurs in active hunting mammalian predators, can each represent a significant energetic cost to the animal. For example, the maximum aerobic energy used during locomotion can reach 10–30 times resting levels in a wide variety of terrestrial mammals (Taylor et al., 1980, 1987) and 4–11 times resting levels in marine mammals (Elsner, 1986; Williams et al., 1993). Digesting and absorbing prey can also be expensive, with both the quality and the quantity of the food affecting energetic costs. For both terrestrial (Kleiber, 1975) and marine (Costa and Williams, 1999) carnivores, metabolic rate may increase 30–67% over resting levels following the ingestion of prey. Termed the heat increment of feeding (HIF), this metabolic effect may last for hours. For example, in one marine carnivore, the sea otter *Enhydra lutris*, metabolic rate

remained elevated for 4–5 h, peaking at 54% above resting levels following a high protein meal, and provided a thermoregulatory benefit for the animal (Costa and Kooyman, 1984).

Energy intake from prey ingestion must exceed these costs if a predator is to achieve a net positive energy balance. This in turn will dictate the efficiency of the predator, and ultimately its survival (Stephens and Krebs, 1986).

For aquatic birds and mammals, the problem of balancing foraging costs and benefits is complicated by the limited availability of oxygen when diving. Dunstone and O'Connor (1979a,b) investigated the trade-offs associated with underwater predation by air-breathing carnivores, using the American mink (*Mustela vison* Schreber) hunting fish as a model system. These investigators demonstrated an interaction between foraging economics, as predicted by optimality models (Charnov, 1976), and the preferred hunting strategies of the mink, as constrained by oxygen reserves. In this

relatively simple situation, foraging economics explained 51% of the variance in hunting patterns of the mink while oxygen constraints accounted for another 23%.

Kramer (1988) expanded on these studies by predicting optimum foraging patterns of diving birds and mammals based on the physiological and morphological characteristics that dictate oxygen gain during surface intervals. Theoretically, increased distance to feeding sites resulted in longer dive durations and surface times for breathing. Many species of marine mammal fit this pattern (Costa and Gales, 2003), although hunting behavior, type of prey taken and type of dive (e.g. exploratory *versus* hunting) can modify the response.

For actively foraging marine mammals, each energetic demand may simultaneously draw on limited oxygen stores. As a result, the combined energetic costs of locomotion and digestion while submerged can overwhelm the metabolic capacity of some marine mammals, forcing a selection between physiological activities when diving. Indirect evidence is provided from studies on northern elephant seals, which show a temporal separation between the cost of diving and of prey assimilation during submergence (Crocker et al., 1997). Following possible prey ingestion, elephant seals suspend swimming activity, which theoretically allocates a greater proportion of the oxygen reserve to metabolic processes necessary for warming the food, digestion and assimilation. In this way sequential diving may continue and the seal remains within its aerobic diving limits as it forages and processes prey. Similarly, the exceptionally high costs (as estimated from post-dive surface intervals) associated with lunge feeding by blue whales and fin whales confines submergence by these huge marine mammals to comparatively short bouts (Acevedo-Gutierrez et al., 2002).

Except for indirect evidence (Ponganis et al., 1993; Crocker et al., 1997; Acevedo-Gutierrez et al., 2002) and theoretical models (Williams et al., 1996), little is known regarding the energetic cost of foraging dives in marine mammals. This is due in part to the difficulty of simultaneously measuring metabolic rate and foraging behavior in free-ranging diving mammals. To address this problem, we measured the energetic cost of foraging and non-foraging dives in Weddell seals by using open flow respirometry and an isolated ice hole technique coupled with an animal-borne video-data logging system. Energetic costs associated with locomotion and prey warming and assimilation were measured, and the contribution of these costs to the total energetic demands of foraging determined. Using these results, we developed an energetics model to predict the cost of a dive by Weddell seals, based on stroking costs and the post-absorptive or post-prandial state of the animal.

Materials and methods
Experimental design

This study was conducted in McMurdo Sound, Antarctica (77.86°S, 166.22°E) in November and December of 1997, 1998 and 1999. An isolated ice hole paradigm (Kooyman et al., 1973; Castellini et al., 1992) was used in which Weddell seals dived from a man-made hole that had been drilled through the ice. The hole was located where the surrounding sea ice was free of other holes or cracks within a 3–4 km radius, thus ensuring that the animals would return to the isolated hole to breathe. No other restrictions were placed on the seals' behavior and the animals were able to dive freely to the ocean bottom at approximately 585 m in depth. Each seal was instrumented and released into the isolated hole, which was periodically covered with a metabolic dome for collection of expired gases between dives. The dome was removed at 6 h intervals for retrieval of videotapes and data from instrumented seals as they rested on the water surface. Seals routinely dived and rested in the hole for 3–5 days. Afterwards a secondary hole was opened in the ice and used by the seals to haul out.

A climate-controlled research hut was placed over the isolated hole and served as the laboratory for the experiments. Location of the hut and ice hole was approximately 10 km west of Cape Armitage, Ross Island, adjacent to the McMurdo ice shelf.

Animals

Nine adult Weddell seals *Leptonychotes weddellii* Lesson (1 female, 8 males; body mass=387.4±6.6 kg, mean ± S.E.M.) were used in these studies. The seals were captured with a purse-string net on the sea ice near Ross Island and transported approximately 15 km to the isolated ice hole (1.3 m diameter hole in a 2.5 m long × 1.5 m wide shelf) that had been cut into the sea ice. After a 24–48 h holding period the animals were instrumented with a video-data recording system, an indwelling intravertebral extradural vein catheter and swimming stroke monitor, as described in Davis et al. (1999). Following the experiments, the instruments and catheter were removed and the seals returned to their point of capture.

Aerobic and anaerobic costs of diving

Aerobic costs of diving were determined from the rate of oxygen consumption, as measured by open flow respirometry (Williams et al., 2001) following the protocols of Castellini et al. (1992). Breathing by the seals before and after dives was restricted to a Lexan™ dome (2.4 m long × 1.1 m wide × 0.4 m high) mounted at the water level over the isolated ice hole. Air was drawn through the chamber using a vacuum pump (Sears 2.0 hp Wet/Dry Vac; Chicago, IL, USA) at 510–550 l min⁻¹. Flow rates were monitored continuously with a dry gas flow meter (American Meter Co. Inc., DTM-325, San Leandro, CA, USA). At these flow rates the fractional concentration of oxygen in the dome remained above 0.2000 except for the initial seconds following a dive. Samples of air from the exhaust port of the dome were dried (Drierite; Hammond Drierite Co., Xenia, OH, USA) and scrubbed of carbon dioxide (Sodasorb; Chemetron, St Louis, MO, USA) before entering an oxygen analyzer (Sable Systems International, Inc., Henderson, NV, USA; and AEI Technologies S3-A, Pittsburgh, PA, USA). The percentage of oxygen in the expired air was monitored continuously and recorded once per second

on a personal computer using Sable Systems software. Rate of oxygen consumption ($\dot{V}_{O_2}$) was calculated using equations from Fedak et al. (1981) and an assumed respiratory quotient of 0.77. This respiratory quotient was later confirmed in independent tests using simultaneous $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ measurements for a subset of the seals. All values were corrected to STPD.

The entire system was calibrated daily with dry ambient air (20.94% O_2) and every 3–4 days with dry span gases (16.0% O_2) and N_2 gas according to Fedak et al. (1981). The flow of calibration gases into the dome was controlled and monitored by an electronic flow meter (Model #FMA-772V; Omega, Manchester, UK) that was accurate to within 1% of total flow. Calibration of the flow meter was checked before and after the study with nitrogen gas and a rotameter (Cole-Palmer Instruments, Chicago, IL, USA). The theoretical fraction of O_2 leaving the dome was calculated according to Davis et al. (1985) and compared to measured values from the oxygen analyzer.

Oxygen consumption during the dive was calculated from the difference between total recovery oxygen consumption and resting rates in water following the procedures of Hurley and Costa (2001) and Scholander (1940). Prior to the diving experiments, baseline post-absorptive oxygen consumption rates were determined for each Weddell seal resting in the ice hole (Williams et al., 2001). These were later validated with rates determined during prolonged (>20 min) rest periods between dives by foraging and non-foraging seals. Following a dive, oxygen consumption was monitored continuously, and diving metabolism calculated from the recovery oxygen consumed in excess of resting rates for either post-absorptive or post-prandial seals as determined from feeding behavior logged by the animal-borne video-data recorder (see below). Only post-dive recovery periods in which the seals rested quietly and remained on the surface long enough for oxygen consumption to return to within 2% of baseline levels were used in this analysis. In this way, the potential effects of sequential dives on oxygen consumption were avoided.

To assess the contribution of anaerobic metabolism during diving, plasma lactate concentration was measured in post-dive blood samples drawn from an indwelling catheter placed in the extradural vein of the seals. Because the metabolic dome prevented access to the catheter, blood samples were collected in a separate series of dives covering the range of dive durations observed for the respirometry tests. Samples (5–10 ml) were drawn within 1.5–5.0 min of resurfacing from a dive to correspond with peak recovery lactate levels (Qvist et al., 1986). Serial blood samples for seven dives confirmed that peak changes in pH and [lactate] occurred during this period of recovery. Chilled blood samples were immediately centrifuged (approximately 1000 *g* for 10 min) and the plasma stored in cryovials at –30°C until analysis. Total plasma [lactate] was determined using a portable lactate analyzer (YSI 1500 Sport Lactate Analyzer, Yellow Springs, OH, USA) calibrated daily with zero and lactate standard solutions.

Foraging behavior

The underwater foraging behavior of the seals was recorded continuously using a video-data logging system carried by the free-ranging animals. Details of the instrumentation and attachment procedures have been described previously by Davis et al. (1999) and Fuiman et al. (2002). Briefly, seals were sedated with an intramuscular injection of ketamine hydrochloride (2 mg kg^{-1}; Fort Dodge Laboratories, Fort Dodge, IA, USA) and diazepam (0.1 mg kg^{-1}; Steris Corporation, Phoenix, AZ, USA) and weighed. A low light-sensitive camera with an array of near-infrared LEDs was mounted on a small piece of neoprene rubber glued to the fur on the head of the seal, providing a view of the animal's eyes and muzzle, and of the water for approximately 70 cm in front of the nose. Illumination from the LEDs was invisible to the seals and their prey. The camera was attached by a cable to a torpedo-shaped, reinforced housing (35 cm long × 13 cm diameter) that contained an 8 mm videotape recorder and microprocessor (Pisces Designs, San Diego, CA, USA). The video housing rested in a molded, non-compressible foam cradle that was attached to a neoprene rubber pad on the dorsal midline of the seal below the shoulders. The video images were synchronized with measurements of depth from a pressure transducer, swimming speed from a flow meter, compass bearing (Davis et al., 1999) and swimming stroke activity (described below).

The instrument pack and housing were neutrally buoyant in water. The frontal area of the instruments represented less than 5.5% of the frontal area of the seal, and was within the suggested limits and shapes for instrumented free-ranging swimming animals (Wilson et al., 1986; Culik et al., 1994). To assess the potential effects of the instruments on swimming effort, we compared metabolic rates of seals with (N=82 dives) and without (N=63 dives) the video system and camera. Dive durations ranged from 1.4 to 44.0 min and there was no significant difference in recovery oxygen consumption (Mann–Whitney nonparametric test at P=0.917) for the two groups (Fig. 1).

Each 8 mm videotape was duplicated in VHS format immediately after recovery. Videotapes were screened for encounters with prey, almost entirely fishes. The species of fish were identified by size, shape and pigmentation according to Fuiman et al. (2002).

Stroke mechanics and locomotor costs

The mode of swimming (burst-and-coast, continuous stroking, gliding), relative stroke amplitude and stroke frequency were determined for the seals from a single axis accelerometer (±2 g; 6 cm long × 3 cm wide × 2.0 cm high; Ultramarine Instruments, Galveston, TX, USA) mounted on a neoprene pad at the base of the tail of the seals. Lateral sweeps of the posterior half of the body and the hind flippers, characteristic of phocid swimming (Fish et al., 1988), were monitored by the accelerometer. Output from the accelerometer was recorded at 16 Hz with a microprocessor and synchronized with dive depth, time and video images.
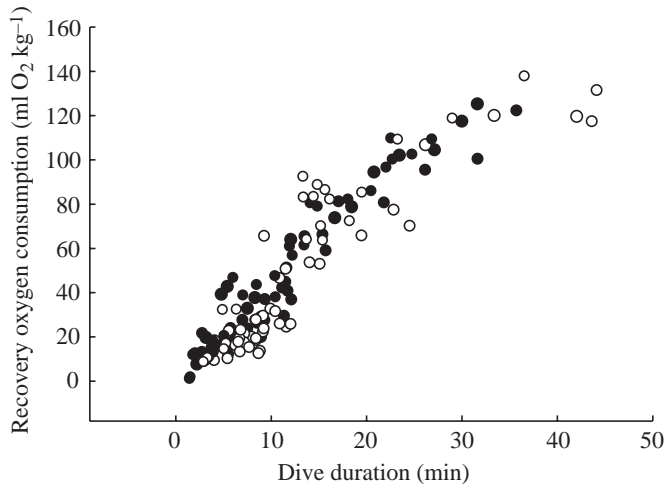
Fig. 1. Post-dive oxygen consumption in relation to dive duration for Weddell seals diving with (closed circles) and without (open circles) the video-data logging system. Each point represents an individual dive. No statistical difference was found in oxygen consumption between the groups (see text), although uninstrumented seals tended to perform the longest dives.

Accuracy of the accelerometer in detecting stroke movements was tested by comparing the output of the microprocessor to video sequences obtained on dives in which the camera was directed backwards on the seal. In this way, the correspondence between peak flipper excursions and peak output from accelerometer microprocessor was confirmed.

To determine the amount of oxygen expended for locomotion, we examined the relationship between total oxygen consumed during the post-dive recovery period and the number of strokes performed during a dive. Prolonged (>12 s) periods of gliding characteristic of the descent (Williams et al., 2000) were accounted for by assuming that metabolism remained at resting levels when the seal was not actively stroking. Therefore, locomotor costs during a dive were determined from the difference between total recovery oxygen and maintenance costs according to the equation:

$$\text{Locomotor cost} = V_{O_2 rec} - (BMRt), \qquad (1)$$

where locomotor cost and $V_{O_2 rec}$ (recovery oxygen consumption) are in ml O_2 kg^{-1}, BMR is the basal metabolic rate in ml O_2 kg^{-1} min^{-1} (according to Kleiber, 1975) and t is dive duration in min. Previous experiments on quiescent, submerged pinnipeds have demonstrated that maintenance costs approach Kleiber's BMR predictions (Hurley and Costa, 2001). Therefore, we assumed that the predicted BMR was a reasonable approximation of the maintenance costs for the diving seals in the present study. To avoid complications associated with anaerobiosis and feeding, only aerobic, post-absorptive dives were used for calculations of locomotor costs.

Statistics

Linear regressions for the relationships between recovery oxygen consumption and dive duration, and plasma lactate concentration and dive duration, were determined by least-squares methods using statistical software (Jandel Scientific Software 1995). Dives were classified as aerobic or anaerobic depending on increases in post-dive plasma lactate concentration above resting levels. To assess the effect of the heat increment of feeding on metabolic rate, we calculated the residuals for total recovery oxygen consumption of post-prandial and post-absorptive seals. Dives were classified as feeding dives if the seals ingested a fish or performed a dive within 5 h of ingesting a large meal (i.e. >5 *Pleuragramma antarcticum*). The latter was used to account for the prolonged metabolic effect associated with heating and assimilating a protein meal, characteristic of marine mammals (Costa and Kooyman, 1984). The recovery oxygen consumption residuals of these dives were then compared to similar residuals for seals performing non-foraging dives (SYSTAT 1998; SPSS, Inc.).

The effects of the instrumentation on diving performance were determined by comparing metabolic rates of seals with and without instrumentation. Because the test for normality failed, a Mann–Whitney nonparametric test was used (Zar, 1974). All mean values are ± 1 S.E.M. unless otherwise noted.

Results
Aerobic and anaerobic cost of diving

The effect of dive duration on aerobic and anaerobic responses by adult Weddell seals is shown in Fig. 2. As reported previously for diving Weddell seals (Kooyman et al., 1980), plasma lactate concentration remained at resting levels (mean=2.10±0.35 mmol l^{-1}, N=38 dives) until the dive duration exceeded 23 min (Fig. 2A). Longer dives resulted in a linear increase in peak post-dive plasma [lactate] that was described by the equation:

$$\text{Plasma [lactate]} = 3.09 + 0.37t, \qquad (2)$$

(r^2=0.47, N=15 dives, P<0.005), where plasma [lactate] is in mmol l^{-1}.

Total oxygen consumption during the post-dive recovery period also showed a biphasic relationship with dive duration (Fig. 2B). Using the breakpoint in plasma lactate concentration at 23 min to define aerobic and anaerobic dives, we found that recovery oxygen consumption of aerobic dives increased linearly as described by the equation:

$$V_{O_2 rec} = -8.20 + 4.74t, \qquad (3)$$

(r^2=0.85, N=137 dives, P<0.001). Dives longer than 23 min resulted in a second linear relationship in which recovery oxygen consumption increased with dive duration according to the equation:

$$V_{O_2 rec} = 74.27 + 1.10t, \qquad (4)$$

(r^2=0.29, N=37 dives, P<0.001).

As reported by Castellini et al. (1992) and Ponganis et al. (1993), the rate of oxygen consumption ($\dot{V}_{O_2}$) measured after
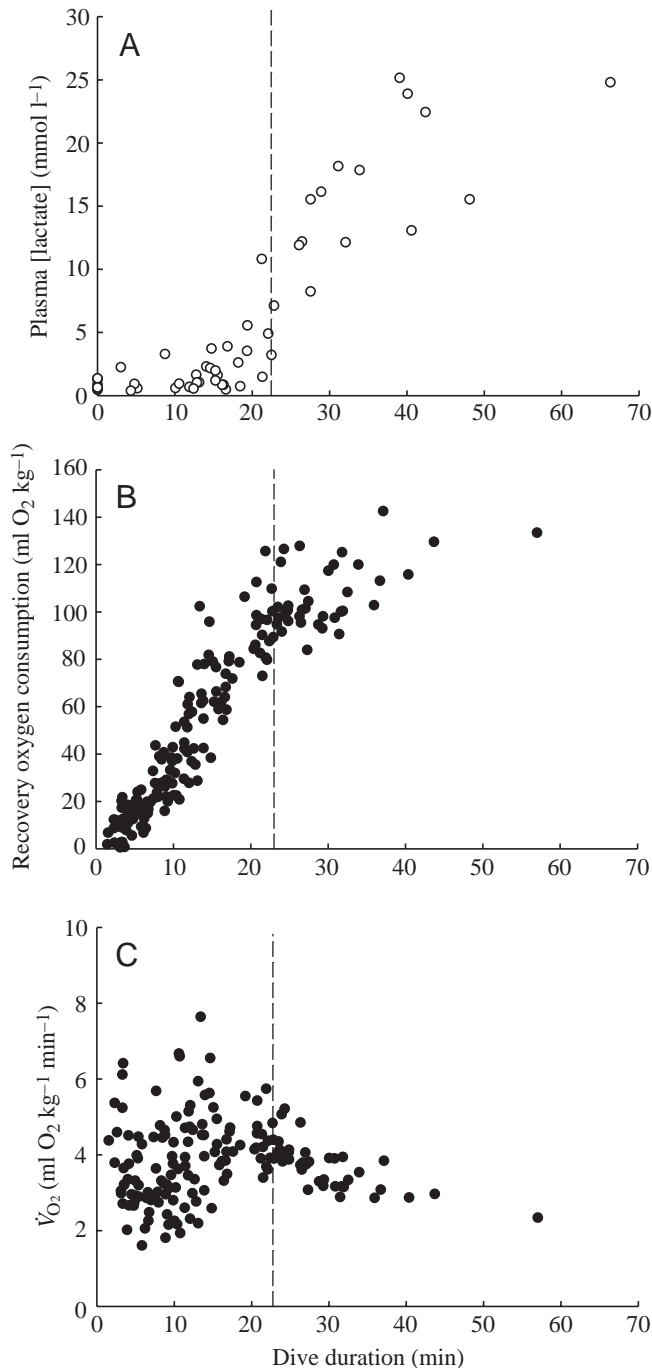
Fig. 2. Changes in plasma lactate concentration (A), recovery oxygen consumed (B) and post-dive oxygen consumption rate (C) in relation to dive duration for nine adult Weddell seals. Measurements were taken during the recovery period immediately following each dive. Points represent individual dives for an animal. The dashed vertical line denotes the change from aerobic to anaerobic dives, as indicated by the increase in plasma [lactate] above resting levels. Equations for statistical relationships are provided in the text.
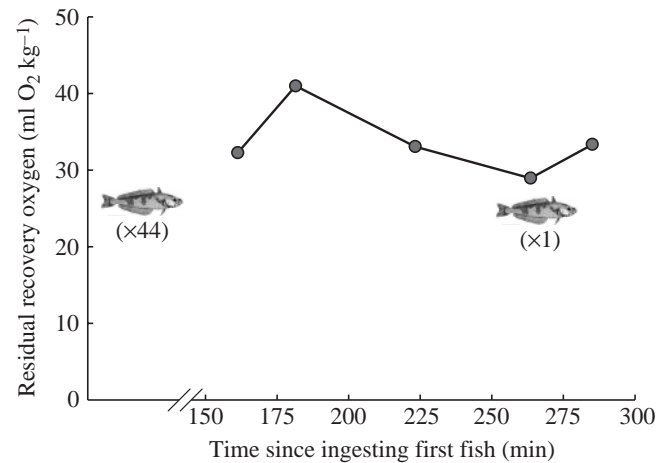

Fig. 3. Residuals for recovery oxygen consumption of a foraging Weddell seal. Data are presented in relation to time following first fish ingestion in a feeding bout. The final five dives of a sequence consisting of 11 foraging dives are shown. Each point represents the residual for the recovery period following a dive. Fish indicate times when we observed the seal eating *Pleuragramma antarcticum*. 44 fish were ingested at the beginning of this bout, with one additional fish caught on the tenth dive of the sequence. Residuals were determined by comparing the observed post-dive recovery oxygen consumption to predicted values based on Fig. 2B and Equation 3.

pattern with dive duration. The mean of this range, 3.84 ± 0.39 ml O_2 kg^{-1} min^{-1} (N=5 seals), was similar to the average metabolic rate measured for animals resting on the water surface. This value is 23.2% lower than reported by Castellini et al. (1992) for short dives by Weddell seals, which may be attributed to differences in the classification of short dives (<23 min in the present study, compared with <14 min in Castellini et al., 1992). For longer dives, $\dot{V}_{O_2}$ decreased with dive duration according to the relationship:

$$\dot{V}_{O_2} = 5.63 - 0.07t , \qquad (5)$$

(r^2=0.50, N=37 dives, P<0.001).

Feeding costs

Antarctic silverfish *Pleuragramma antarcticum* Boulenger were the common prey item of foraging Weddell seals in this study (Fuiman et al., 2002), and ingestion was associated with a higher recovery oxygen consumption than post-absorptive dives of similar duration (Figs 3, 4). The elevation in metabolism lasted for several hours after a foraging dive, suggesting a thermogenic effect associated with the heating and assimilation of the fish. An example of the response is illustrated in Fig. 3 for a Weddell seal performing repetitive dives into an aggregation of silverfish. During a feeding bout of 11 sequential dives the seal ingested 44 fish in the first four dives as well as an additional fish during the tenth dive of this sequence. Residuals for the recovery oxygen consumption showed that metabolic rate remained elevated an average of 33.73 ± 1.98 ml O_2 kg^{-1} for over 5 h, although fish were not necessarily caught on every dive.

diving was highly variable for dives of shorter duration than the aerobic dive limit (Fig. 2C). For dives shorter than 23 min, $\dot{V}_{O_2}$ ranged from 1.61 to 7.64 ml O_2 kg^{-1} min^{-1} and showed no
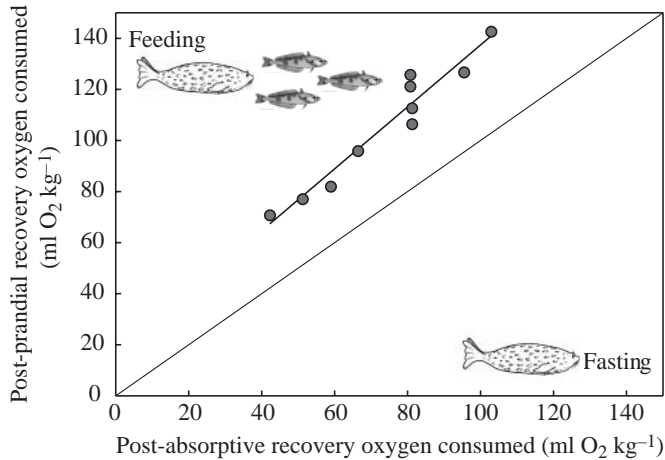
Fig. 4. Recovery oxygen consumption of feeding (post-prandial) and fasting (post-absorptive) dives in free-ranging Weddell seals. Each point represents a feeding dive paired with a fasting dive of equal distance traveled (within 6.8±1.7%) and duration (within 8.3±1.7%) for two male seals of identical body mass (398 kg). The diagonal line through the origin represents the line of equality for the cost of feeding and fasting dives. The short line denotes the least-squares linear regression through the data points, as described in the text.

When comparing the post-dive recovery oxygen consumed for post-absorptive and post-prandial seals, we found that dives associated with feeding were consistently more costly than non-feeding dives of similar duration and distance (Fig. 4). In this subset of dives, the total distance traveled ranged from 1178 m to 5012 m, while duration of the dives ranged from 10.6 min to 37.1 min. Together these resulted in a range of energetic costs for feeding and non-feeding dives as described by the equation:

$$\text{Post-prandial } V_{O_2\text{rec}} = 16.19 + 1.21 \times \text{post-absorptive } V_{O_2\text{rec}} , \quad (6)$$

(r^2=0.94, N=10, P< 0.001).

All paired dives fell above the line of equality with an average post-dive oxygen consumption that was 44.7±3.6% (N=10 paired dives) higher for feeding dives than non-feeding dives. A similar elevation in metabolic rate following the ingestion of prey was observed for one seal at rest. $\dot{V}_{O_2}$ for the quiescent, post-absorptive seal determined prior to diving was 4.42 ml O_2 kg^{-1} min^{-1}. During an extended recovery period following a foraging dive, the same animal showed a resting $\dot{V}_{O_2}$ of 6.78 ml O_2 kg^{-1} min^{-1}, representing a 53% increase in metabolic rate attributed to the assimilation of prey.

Locomotor and stroking costs

Total recovery oxygen consumed during the post-dive period of aerobic dives increased linearly with the number of strokes executed (Fig. 5A) according to the equation:

$$V_{O_2\text{rec}} = 4.74 + 0.08S_n , \quad (7)$$

(r^2=0.87, N=90 dives, P<0.001), where S_n is stroke number.

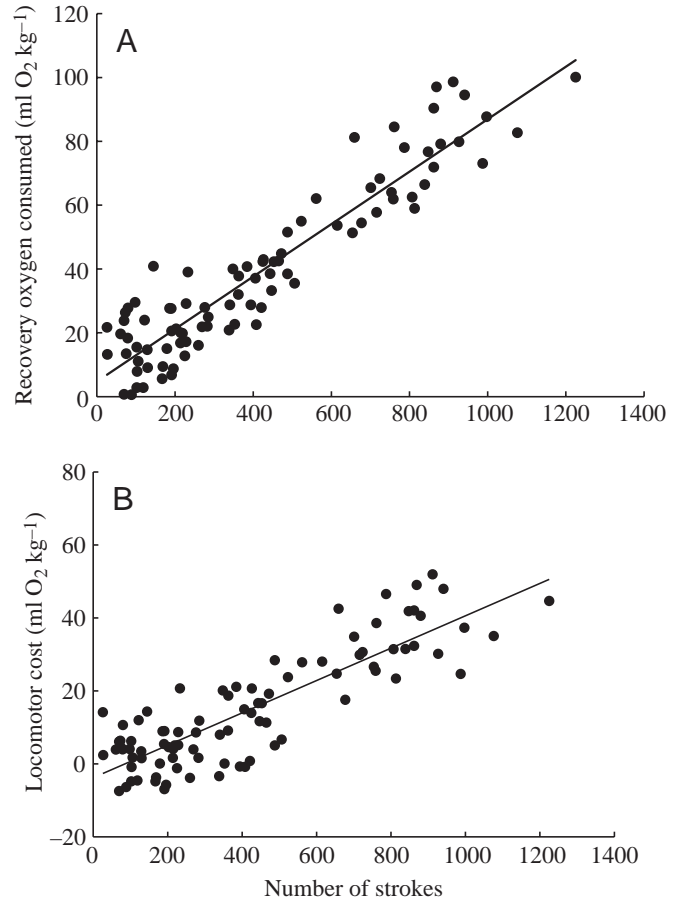As might be expected, there was a linear increase in

Fig. 5. Recovery oxygen consumed (A) and locomotor costs (B) of diving Weddell seals in relation to the total number of strokes taken during a dive. Measurements were taken during the post-dive recovery period. Points represent individual dives. Solid lines are the least squares linear regressions through the data points as described in the text. Note that only aerobic dives, as determined from Fig. 2 were used in these analyses.

locomotor costs as the number of strokes increased (Fig. 5B). The relationship for aerobic dives was described by:

$$\text{Locomotor cost} = -3.78 + 0.04S_n , \quad (8)$$

(r^2=0.74, N=90 dives, P<0.001). Based on the slope of this relationship, the net cost per stroke for an adult Weddell seal is 0.044 ml O_2 kg^{-1} (mean=0.036±0.007 ml O_2 kg^{-1} $stroke^{-1}$, N=90 dives).

Discussion

The foraging energy budget

For Weddell seals the energy expended for foraging includes significant costs associated with swimming as well as with the warming, digestion and assimilation of ingested prey. A generalized model describing the energetic demands of a free-ranging animal in a thermally neutral environment states that total energetic cost=basal metabolic cost + locomotor cost + feeding cost (Costa and Williams, 1999). In this model,

thermoregulatory costs are considered minor relative to the remaining costs or are offset by either skeletal muscle activity or the heat produced by the assimilation of prey. For the following analysis, we will assume that thermoregulatory costs of the diving Weddell seal are likewise included in the remaining energetic costs.

There has been considerable discussion concerning the basal metabolic rate (BMR) of marine mammals, but with little resolution (Lavigne et al., 1986; Andrews, 2002). Current evidence suggests that the BMR of many pinnipeds and cetaceans ranges from 1.4 to 2.1 times that predicted for domestic animals (Kleiber, 1975) and approximates that of other carnivorous mammals (McNab, 2000) when marine mammals are resting on the water surface (Williams et al., 2001). We found similar results for resting Weddell seals. The BMR of Weddell seals was 4.07 ± 0.21 ml O_2 kg^{-1} min^{-1} in air and 3.58 ± 0.24 ml O_2 kg^{-1} min^{-1} in water. The latter value was within 14% of that reported by Castellini et al. (1992) for Weddell seals resting in an isolated ice hole, and $1.6 \times$ the Kleiber (1975) prediction. BMR decreased by approximately 10% if the seals went into prolonged apneas during the rest period. In view of this, it is likely that the metabolic rate of inactive seals is lower when submerged for prolonged periods than when resting and breathing apneustically on the water surface. Evidence for this is provided by sleeping and diving Weddell seals (present study; Castellini et al., 1992) and California sea lions trained to station underwater (Hurley and Costa, 2001). For both species, post-submergence metabolism indicates a flexible resting metabolic rate depending on the duration of breath-hold. In Weddell seals, prolonged breath-holding while sleeping on the water surface or during long (>14 min) dives resulted in the lowest metabolic rates (Castellini et al., 1992). The metabolic rate of sea lions resting on the water surface was 2–3 times predicted values (Kleiber, 1975); this decreased to predicted levels when the animals remained submerged for 7 min (Hurley and Costa, 2001).

We found a similar result for Weddell seals when extrapolating the relationship between recovery oxygen consumption and stroke count (Fig. 5A) to zero strokes performed (i.e. submerged resting). The calculated submerged metabolic rate of Weddell seals was 2.47 ml O_2 kg^{-1} min^{-1}, and was within 10% of the Kleiber (1975) prediction. Therefore, we used this value to represent the minimum basal metabolic costs of the diving Weddell seal in our energetic analyses, recognizing that this minimum value may vary slightly for short duration dives (Fig. 2C).

Of the two remaining costs, the energy expended for locomotion can be considerably higher than both resting and assimilation costs. Overall, locomotor activity resulted in a 1.3- to 3.5-fold increase in metabolism over resting rates, depending on the duration of the dive (Fig. 6). Because oxygen consumption increased linearly with the number of strokes taken during a dive (Fig. 5), the resulting net cost per stroke remained constant at 0.044 ml O_2 kg^{-1} $stroke^{-1}$. Consequently, each swimming stroke performed by the seal had a predictable effect on the oxygen reserves of the animal, more so than the
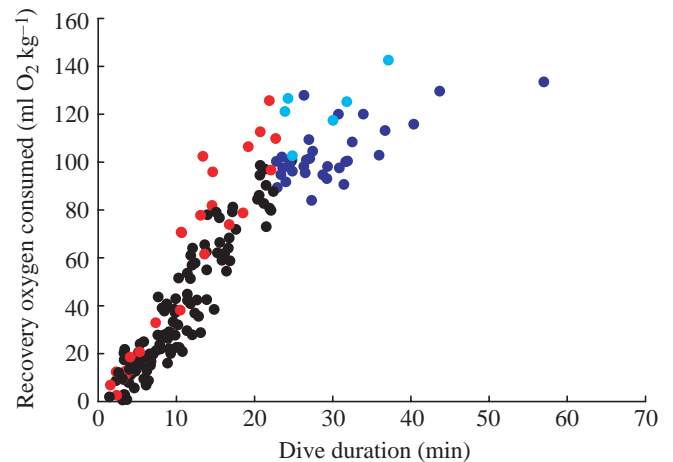

Fig. 6. The effects of behavior on recovery oxygen consumption in diving Weddell seals. Each point represents an individual dive for an animal as shown in Fig. 2B, now color coded for feeding behavior as determined from video sequences, and aerobic limits determined from blood [lactate] values. Aerobic and anaerobic dives for non-foraging seals are shown in black and dark blue circles, respectively. Post-dive oxygen consumption increased in foraging seals, and is indicated by red (aerobic dives) and light blue (anaerobic dives) circles.

duration of the dive because gliding can represent a large fraction of the total dive duration (Williams et al., 2000; Davis et al., 2001).

Similar analyses have been conducted for running animals, in which the cost of terrestrial locomotion has been attributed to cost of each step (Alexander and Ker, 1990; Kram and Taylor, 1990). However, the cost per stroke of diving Weddell seals was considerably less than reported for stride costs of running mammals. Using the same methods as Taylor et al. (1982), the total cost per stroke for Weddell seals was calculated by dividing the recovery oxygen consumption (ml O_2 kg^{-1}) by the number of strokes taken during the preceding dive, using a conversion factor of 20.1 J/ml O_2. Note that this value differs from the net cost per stroke presented above, and does not account for the oxygen consumed during gliding periods. The resulting value, 2.39 J kg^{-1} $stroke^{-1}$ for swimming Weddell seals, compares with 5.0 J kg^{-1} $stride^{-1}$ for running mammals (Taylor et al., 1982). For runners ranging in body mass over four orders of magnitude the metabolic energy consumed at equivalent speeds remained nearly constant. Likewise, total stroke costs varied little for five species of phocid seal (Fig. 7). The total cost per stroke ranged from 1.44 J kg^{-1} $stroke^{-1}$ for a 97 kg harp seal to 2.87 J kg^{-1} $stroke^{-1}$ for a 33 kg harbor seal.

The difference between step and stroke costs among mammals may be explained in part by the different physical forces that must be overcome during running and swimming (Dejours, 1987). Among runners, smaller plantar areas reduce the cost of overcoming gravitational and frictional forces during locomotion. Conversely, propulsive surfaces are often enlarged in aquatic mammals that must overcome
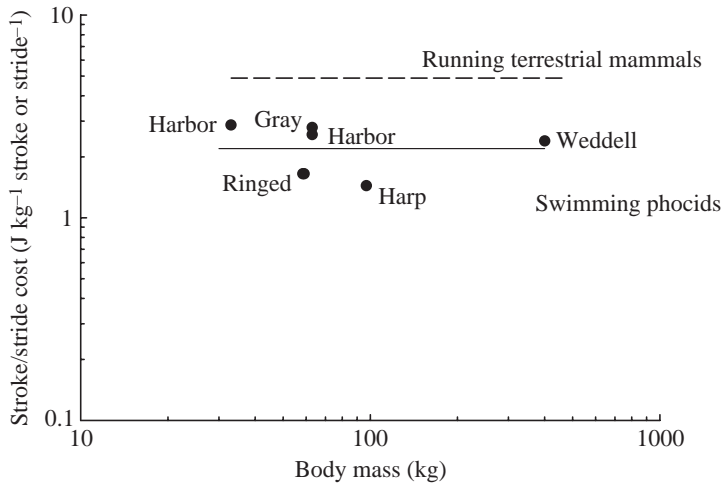
Fig. 7. Total cost of a stroke or stride in relation to body mass for swimming phocid seals and running mammals. Each point represents the mean stroke costs calculated from the oxygen consumption and stroke frequency of harbor (Davis et al., 1985), and gray, ringed and harp (Innes, 1984; Fish et al., 1988) seals swimming in a flume. Weddell seal data are from the present study. The solid line is the mean total cost per stroke for five species of swimming phocid seal. The dashed line is the mean cost per stride for running terrestrial mammals from Taylor et al. (1982).

hydrodynamic drag (Fish, 1993). The distance traveled per step (Kram and Taylor, 1990) or stroke (T. M. Williams, unpublished data) will also affect the energetic cost of running and swimming, respectively. In the present study, it was not possible to differentiate between large and small amplitude strokes, and a closer examination of the data from tail-mounted accelerometers may allow investigators to classify unique stroke types (e.g. accelerative, maintenance, braking, steering), each with a different energetic cost. Such analyses of these individual stroke types may allow us to further refine the locomotor costs associated with propulsive movements by large and small phocid seals.

The final component of the generalized energetic model is the energy required for prey warming, digestion and assimilation (Fig. 6). For the Weddell seals in this study, feeding resulted in a 44.7% increase in metabolic rate over a wide range of dive durations and distances traveled (Fig. 4). The pattern was similar to that described by Ponganis et al. (1993) for a juvenile Weddell seal presumed to be foraging on *Pleuragramma antarcticum*. It is unlikely that these increases were due to added locomotion associated with capturing fish as both resting and diving metabolic rates increased following feeding. Interestingly, the metabolic effect was apparent for dives in which fish were ingested as well as dives taking place as long as 5 h after fish ingestion (Fig. 3). This suggests that the digestion, assimilation and warming of prey elevate metabolism in foraging seals. Wilson and Culik (1991) have shown a similar response in another diving endotherm, the Adelie penguin. For these birds cold ingesta resulted in a marked energetic effect independent of the heat increment of feeding.

The high energetic demands associated with foraging suggest a selective advantage for aquatic mammals demonstrating high locomotor and assimilation efficiencies. By reducing the energy expended for travel and for processing prey, limited oxygen reserves could be extended and the duration of underwater hunting prolonged. Relatively little is known about reducing assimilation costs *per se,* although the timing and type of prey ingested has been shown to have an effect on total energetic cost in marine mammals (Costa and

Kooyman, 1984; Bowen et al., 2002), and may be regulated (Crocker at al., 1997). In comparison, several strategies enable swimmers to increase locomotor efficiency. Intermittent forms of swimming in particular have been shown to reduce the cost of forward movement in a wide variety of aquatic animals. Burst-and-coast swimming by fishes (Weihs, 1974; Fish et al., 1991), and porpoising (Au and Weihs, 1980), wave-riding (Williams et al., 1992) and prolonged gliding (Costa and Gales, 2000; Williams et al., 2000; Davis et al., 2001) by marine mammals lead to reduced locomotor costs. Gliding is an exaggerated from of intermittent propulsion that has recently been observed for many diving animals including Weddell seals, blue whales and elephant seals (Williams et al., 2000; Davis et al., 2001), bottlenose dolphins (Skrovan et al., 1999), right whales (Nowacek et al., 2001), Adelie penguins (Sato et al., 2002) and other diving birds (Lovvorn and Jones, 1991; Lovvorn et al., 1999). The change from constant to interrupted propulsion acts to reduce the total number of strokes required to complete a dive, and thus enables the animal to conserve limited oxygen stores during submergence (Williams, 2001).

Budgeting the number of strokes serves as such an energy conserving strategy for diving Weddell seals due to the relationship between recovery oxygen consumption and stroke count (Fig. 5). Maximum aerobic efficiency is achieved by traveling the greatest distance on the fewest number of strokes, a task that may be accomplished by taking advantage of buoyancy changes with depth and using intermittent propulsion (Williams et al., 2000; Sato et al., 2003). This relationship also provides a useful tool for assessing the energetics of diving for free-ranging seals. If, as in running animals (Alexander and Ker, 1990), activity is priced by each locomotor movement, then the cost of diving may be predicted from the sum of individual stroking costs.

Predicting foraging costs for a free-ranging marine predator

The underwater location and cryptic feeding behavior of marine mammals makes the determination of foraging energetics particularly challenging for this group. Over the past 30 years, a variety of approaches have been used to study the energetics of these animals at sea. These can be generally categorized as indirect measurements and time budget analyses in which field observations of behaviors are matched with metabolic rates determined in captivity (Butler and Jones, 1997; Costa, 2002). The former includes the dilution of

isotopically labeled water and the use of physiological variables as surrogates for metabolism. For example, breathing rates (Sumich, 1983; Kreite, 1995), heart rate (Williams et al., 1992; Boyd et al., 1995; Butler and Jones, 1997), and swimming speed (Kshatriya and Blake, 1988; Hind and Gurney, 1997) have been used to estimate the energetics of free-ranging marine mammals. However, several factors such as the effect of diving bradycardia on heart rate and the effect of prolonged gliding sequences on swimming speed can obscure the actual activity level of the animal, thereby rendering the use of these indirect measures inaccurate for some diving birds and mammals or for some types of dives.

Alternatively, the relationship between energetic cost and stroke count allows the energetic demands of a dive to be predicted from propulsive movements. For Weddell seals that are not foraging, or at least have not fed within 3 h of a dive the aerobic cost of a dive is described by the equation:

$$\text{Non-feed}V_{\text{O}_2\text{rec}} =$$
$$\text{BMR}t + \text{locomotor cost} = (9.98M_{\text{b}}^{-0.25})t + 0.04S_{\text{tot}}, \quad (9)$$

where $V_{\text{O}_2\text{rec}}$ is in ml O_2 kg^{-1}, M_{b} is body mass in kg, t is dive duration in min and S_{tot} is the total number of strokes taken. The BMR of mammals from Kleiber (1975) is 2.5 ml O_2 kg^{-1} min^{-1} for the seals in the present study. If the foraging behavior of the seal is monitored or if the animal has been known to feed, then the resulting aerobic cost will be approximately 44.7% higher (Figs 3, 6) than predicted by this equation. The cost of a foraging dive may be calculated by combining Equation 9 with the equation describing the effect of feeding (Equation 6):

$$\text{Feed}V_{\text{O}_2\text{rec}} = 16.19 + (12.08M_{\text{b}}^{-0.25})t + 0.05S_{\text{tot}}. \quad (10)$$

Because meal size, prey composition, and the time of feeding may affect the results (Costa and Williams, 1999), this is considered a preliminary estimate of the actual costs within 3 h of fish ingestion. Furthermore, seals exceeding aerobic diving limits will incur anaerobic costs in addition to the aerobic costs presented here.

This method enables energetic costs to be assessed for free-ranging animals in which direct energetic measurements are impossible and avoids the potential problems associated with using heart rate or swimming speed as predictors for metabolism (see McPhee et al., 2003). In addition, the relative cost of discrete behaviors (i.e. locating, chasing or traveling to prey) or segments of a dive (i.e. ascent, bottom or descent periods) can be estimated by counting the number of strokes performed during these periods.

In summary, the cost of foraging by Weddell seals entails many energetic components associated with locomotion and the ingestion of prey. The relative proportion of energy allocated to each of these components by a Weddell seal changes with the distance traveled on a foraging dive. For example, locomotor costs will increase proportionately on longer distance dives as the total number of strokes increases. Many questions remain regarding the effects of meal size and prey type on feeding costs, as well as variation in basal metabolism during prolonged submergence. However, by accounting for each of these costs and monitoring stroking mechanics, dive duration and feeding behavior, it is possible to estimate the aerobic demands of diving in free-ranging seals where the cryptic behavior and remote location prevent direct energetic measurements.

References

Acevedo-Gutierrez, A., Croll, D. A. and Tershy, B. R. (2002). High feeding costs limit dive time in the largest whales. *J. Exp. Biol.* **205**, 1747-1753.

Alexander, R. McN. and Ker, R. F. (1990). Running is priced by the step. *Nature* **346**, 220-221.

Andrews, R. D. (2002). The energetics of diving and the question of metabolic depression. *The Physiologist* **45**, 325.

Au, D. and Weihs, D. (1980). At high speeds dolphins save energy by leaping. *Nature* **284**, 548-550.

Bowen, W. D., Tully, D., Boness, D. J., Bulheier, B. M. and Marshall, G. J. (2002). Prey-dependent foraging tactics and prey profitability in a marine mammal. *Mar. Ecol. Prog. Ser.* **244**, 235-245.

Boyd, I. L., Woakes, A. J., Butler, P. J., Davis, R. W. and Williams, T. M. (1995). Validation of heart rate and doubly labeled water as measures of metabolic rate during swimming in California sea lions. *Funct. Ecol.* **9**, 151-160.

Butler, P. J. and Jones, D. R. (1997). Physiology of diving birds and mammals. *Physiol. Rev.* **77**, 837-899.

Castellini, M. A., Kooyman, G. L. and Ponganis, P. J. (1992). Metabolic rates of freely diving Weddell seals: Correlations with oxygen stores, swim velocity and diving duration. *J. Exp. Biol.* **165**, 181-194.

Charnov, E. L. (1976). Optimal foraging. The marginal value theorem. *Theor. Pop. Biol.* **9**, 129-136.

Costa, D. P. (2002). Energetics. In *Encyclopedia of Marine Mammals* (ed. W. F. Perrin, B. Wursig and J. G. M. Thewissen), pp. 387-394. San Diego: Academic Press.

Costa, D. P. and Gales, N. J. (2000). Foraging energetics and diving behavior of lactating New Zealand sea lions, *Phocarctos hookeri. J. Exp. Biol.* **203**, 3655-3665.

Costa, D. P. and Gales, N. J. (2003). Energetics of a benthic diver: Seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea. Ecol. Monogr.* **73**, 27-43.

Costa, D. P. and Kooyman, G. L. (1984). Contribution of specific dynamic action to heat balance and thermoregulation in the sea otter *Enhydra lutris. Physiol. Zool.* **57**, 199-203.

Costa, D. P. and Williams, T. M. (1999). Marine Mammal Energetics. In *Biology of Marine Mammals* (ed. J. E. Reynolds and S. A. Rommel), pp. 176-217. Washington DC: Smithsonian Institution Press.

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

Culik, B. M., Bannasch, R. and Wilson, R. P. (1994). External devices on penguins: how important is shape? *Mar. Biol.* **118**, 353-357.

Davis, R. W., Fuiman, L. A., Williams, T. M., Collier, S. O., Hagey, W. P., Kanatous, S. B., Kohin, S. and Horning, M. (1999). Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* **283**, 993-996.

Davis, R. W., Fuiman, L. A., Williams, T. M. and Le Beouf, B. J. (2001). Three-dimensional movements and swimming activity of a northern elephant seal. *Comp. Biochem. Physiol.* **129A**, 759-770.

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.

Dejours, P. (1987). Water and air physical characteristics and their physiological consequences. In *Comparative Physiology: Life in water and on land* (ed. P. Dejours, L. Bolis, C. R. Taylor and E. R. Weibel), pp. 3-11. Springer, NY: Fidia Research Series.

Dunstone, N. and O'Connor, R. J. (1979a). Optimal foraging in an amphibious mammal. I. The aqualung effect. *Anim. Behav.* **27**, 1182-1194.

Dunstone, N. and O'Connor, R. J. (1979b). Optimal foraging in an amphibious mammal. II. A study using principal component analysis. *Anim. Behav.* **27**, 1195-1201.

Elsner, R. (1986). Limits to exercise performance: Some ideas from comparative studies. *Acta Physiol. Scand.* **128 Suppl. 556**, 45-51.

Fedak, M. A., Rome, L. and Seeherman, H. J. (1981). One-step N_2 dilution technique for calibrating open-circuit O_2 measuring systems. *J. Appl. Physiol.* **51**, 772-776.

Fish, F. E. (1993). Influence of hydrodynamic design and propulsive mode on mammalian swimming energetics. *Aust. J. Zool.* **42**, 79-101.

Fish, F. E., Fegely, J. F. and Xanthopoulos, C. J. (1991). Burst-and-coast swimming in schooling fish (*Notemigonus crysoleucas*) with implications for energy economy. *Comp. Biochem. Physiol.* **100**, 633-637.

Fish, F. E., Innes, S. and Ronald, K. (1988). Kinematics and estimated thrust production of swimming harp and ringed seals. *J. Exp. Biol.* **137**, 157-173.

Fuiman, L. A., Davis, R. W. and Williams, T. M. (2002). Behavior of midwater fishes under the Antarctic ice: observations by a predator. *Mar. Biol.* **140**, 815-822.

Hind, A. T. and Gurney, W. S. C. (1997). The metabolic cost of swimming in marine homeotherms. *J. Exp. Biol.* **200**, 531-542.

Hurley, J. A. and Costa, D. P. (2001). Standard metabolic rate at the surface and during trained submersions in adult California sea lions (*Zalophus californianus*). *J. Exp. Biol.* **204**, 3273-3281.

Innes, H. S. (1984). Swimming energetics, metabolic rates and hind limb muscle anatomy of some phocid seals. PhD thesis, University of Guelph, Canada.

Kleiber, M. (1975). *The Fire of Life*. Huntington, NY: Robert E. Krieger Publishing Co.

Kooyman, G. L., Kerem, D. H., Campbell, W. B. and Wright, J. J. (1973). Pulmonary gas exchange in freely diving Weddell seals. *Resp. Physiol.* **17**, 283-290.

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 for preferred pathways from blood chemistry and behavior. *J. Comp. Physiol.* **138**, 335-346.

Kram, R. and Taylor, C. R. (1990). Energetics of running: a new perspective. *Nature* **346**, 265-267.

Kramer, D. L. (1988). The behavioral ecology of air breathing by aquatic animals. *Can. J. Zool.* **66**, 89-94.

Kreite, B. (1995). Bioenergetics of the killer whale, *Orcinus orca*. PhD thesis, University of British Columbia, Vancouver, Canada.

Kshatriya, M. and Blake, R. W. (1988). Theoretical model of migration energetics in the blue whale, *Balaenoptera musculus*. *J. Theor. Biol.* **133**, 479-498.

Lavigne, D. M., Innes, S., Worthy, G. A. J., Kovacs, K. M., Schmitz, O. J. and Hickie, J. P. (1986). Metabolic rates of seals and whales. *Can. J. Zool.* **64**, 279-284.

Lovvorn, J. R., Croll, D. A. and Liggins, G. A. (1999). Mechanical *versus* physiological determinants of swimming speeds in diving Brunnich's guillemots. *J. Exp. Biol.* **202**, 1741-1752.

Lovvorn, J. R. and Jones, D. R. (1991). Body mass, volume, and buoyancy of some aquatic birds and their relation to locomotor strategies. *Can. J. Zool.* **69**, 2888-2892.

McNab, B. K. (2000). The standard energetics of mammalian carnivores: Felidae and Hyaenidae. *Can. J. Zool.* **78**, 2227-2239.

McPhee, J. M., Rosen, D. A. S., Andrews, R. D. and Trites, A. W. (2003). Predicting metabolic rate from heart rate in juvenile Steller sea lions *Eumetopias jubatus*. *J. Exp. Biol.* **206**, 1941-1951.

Nowacek, D. P., Johnson, M. P., Tyack, P. L., Shorter, K. A., McLellan, W. A. and Pabst, D. A. (2001). Buoyant balaenids: The ups and downs of buoyancy in right whales. *Proc. R. Soc. Lond. B* **268**, 1811-1816.

Ponganis, P. J., Kooyman, G. L. and Castellini, M. A. (1993). Determinants of the aerobic dive limit of Weddell seals: Analysis of diving metabolic rates, postdive end tidal PO_2's, and blood and muscle oxygen stores. *Physiol. Zool.* **66**, 732-749.

Qvist, J., Hill, R. D., Schneider, R. C., Falke, K. J., Liggins, G. C., Guppy, M., Elliot, R. L., Hochachka, P. W. and Zapol, W. M. (1986). Hemoglobin concentrations and blood gas tensions of free-diving Weddell seals. *J. Appl. Physiol.* **61**, 1560-1569.

Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B. and Naito, Y. (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *J. Exp. Biol.* **206**, 1461-1470.

Sato, K., Naito, Y., Kato, A., Niizuma, Y., Watanuki, Y., Charrassin, J. B., Bost, C.-A., Handrich, Y. and Le Maho, Y. (2002). Buoyancy and maximal diving depth in penguins: do they control inhaling air volume? *J. Exp. Biol.* **205**, 1189-1197.

Scholander, P. F. (1940). Experimental investigation on the respiratory function in diving mammals and birds. *Hvalradets Skrifter.* **22**, 1-131.

Skrovan, R. C., Williams, T. M., Berry, P. S., Moore, P. W. and Davis, R. W. (1999). The diving physiology of bottlenose dolphins (*Tursiops truncatus*) II. Biomechanics and changes in buoyancy at depth. *J. Exp. Biol.* **202**, 2749-2761.

Stephens, D. W. and Krebs, J. R. (1986). *Foraging Theory*. Princeton, NJ: Princeton University Press.

Sumich, J. L. (1983). Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, *Eshrichtius robustus*. *Can. J. Zool.* **61**, 647-652.

Taylor, C. R., Heglund, N. C. and Maloiy, G. M. O. (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 1-21.

Taylor, C. R., Karas, R. H., Weibel, E. R. and Hoppeler, H. (1987). Adaptive variation in the mammalian respiratory system in relation to energetic demand. II. Reaching the limits to oxygen flow. *Respir. Physiol.* **69**, 7-26.

Taylor, C. R., Maloiy, G. M. O., Weibel, E. R., Langman, V. A., Kamau, J. M. Z., Seeherman, H. J. and Heglund, N. C. (1980). Design of the mammalian respiratory system. III. Scaling maximum aerobic capacity to body mass: wild and domestic mammals. *Resp. Physiol.* **44**, 25-37.

Weihs, D. (1974). Energetic advantages of burst swimming of fish. *J. Theor. Biol.* **48**, 215-229.

Williams, T. M. (2001). Intermittent swimming by mammals: A strategy for increasing energetic efficiency during diving. *Amer. Zool.* **41**, 166-176.

Williams, T. M., Davis, R. W., Fuiman, L. A., Francis, J., Le Boeuf, B., Horning, M., Calambokidis, J. and Croll, D. A. (2000). Sink or Swim: Strategies for cost efficient diving by marine mammals. *Science* **288**, 133-136.

Williams, T. M., Friedl, W. A., Fong, M. L., Yamada, R. M., Sedivy, P. and Haun, J. E. (1992). Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. *Nature* **355**, 821-823.

Williams, T. M., Friedl, W. A. and Haun, J. E. (1993). The physiology of bottlenose dolphins (*Tursiops truncatus*): Heart rate, metabolic rate and plasma lactate concentration during exercise. *J. Exp. Biol.* **179**, 31-46.

Williams, T. M., Haun, J., Davis, R. W., Fuiman, L. A. and Kohin. S. (2001). A killer appetite: Metabolic consequences of carnivory in marine mammals. *Comp. Biochem. Physiol.* **129A**, 785-796.

Williams, T. M., Shippee, S. F. and Rothe, M. J. (1996). Strategies for reducing foraging costs in dolphins. In *Aquatic Predators and their Prey* (ed. S. P. R. Greenstreet and M. L. Tasker), pp. 4-9. Oxford: Fishing News Books, Blackwell Science Ltd.

Wilson, R. P. and Culik, B. M. (1991). The cost of a hot meal: Facultative specific dynamic action may ensure temperature homeostasis in post-ingestive endotherms. *Comp. Biochem. Physiol.* **100A**, 151-154.

Wilson, R. P., Grant, W. S. and Duffy, D. C. (1986). Recording devices on free-ranging marine animals: Does measurement affect foraging performance? *Ecology* **67**, 1091-1093.

Zar, J. H. (1974). *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall, Inc.