FORAGING ENERGETICS AND DIVING BEHAVIOR OF LACTATING NEW ZEALAND SEA LIONS, *PHOCARCTOS HOOKERI*

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Summary

The New Zealand sea lion, *Phocarctos hookeri*, is the deepest- and longest-diving sea lion. We were interested in whether the diving ability of this animal was related to changes in its at-sea and diving metabolic rates. We measured the metabolic rate, water turnover and diving behavior of 12 lactating New Zealand sea lions at Sandy Bay, Enderby Island, Auckland Islands Group, New Zealand (50°30′S, 166°17′E), during January and February 1997 when their pups were between 1 and 2 months old. Metabolic rate (rate of CO_2 production) and water turnover were measured using the ^{18}O doubly-labeled water technique, and diving behavior was measured with time/depth recorders (TDRs). Mean total body water was $66.0±1.1\%$ (mean ± S.D.) and mean rate of CO_2 production was $0.835±0.114\,\mathrm{ml\,g^{-1}\,h^{-1}}$, which provides an estimated mass-specific field metabolic rate (FMR) of $5.47±0.75\,\mathrm{W\,kg^{-1}}$. After correction for time on shore, the at-sea FMR was estimated to be $6.65±1.09\,\mathrm{W\,kg^{-1}}$, a value 5.8 times the predicted standard metabolic rate of a terrestrial animal of equal size.

The mean maximum dive depth was $353±164\,\mathrm{m}$, with a mean diving depth of $124±36\,\mathrm{m}$. The mean maximum dive duration was $8.3±1.7\,\mathrm{min}$, with an average duration of $3.4±0.6\,\mathrm{min}$. The deepest, $550\,\mathrm{m}$, and longest, $11.5\,\mathrm{min}$, dives were made by the largest animal ($155\,\mathrm{kg}$).

Our results indicate that the deep and long-duration diving ability of New Zealand sea lions is not due to a decreased diving metabolic rate. Individual sea lions that performed deeper dives had lower FMRs, which may result from the use of energetically efficient burst-and-glide locomotion. There are differences in the foraging patterns of deep and shallow divers that may reflect differences in surface swimming, time spent on the surface and/or diet. Our data indicate that, although New Zealand sea lions have increased their O_2 storage capacity, they do not, or cannot, significantly reduce their at-sea metabolic rates and are therefore likely to be operating near their physiological maximum.

Key words: New Zealand sea lion, *Phocarctos hookeri,* Hooker's sea lion, field metabolic rate, doubly labelled water, time/depth recorder, foraging energetics, diving physiology, diving behaviour, foraging ecology.

Introduction

The diving patterns of freely diving, air-breathing vertebrates result from an interaction between the animal's behavior and its physiological capability (Castellini et al., 1985; Kooyman, 1989; Ponganis et al., 1993). The resulting diving behavior, while being constrained by physiological and anatomical adaptations, generally reflects the distribution, abundance, depth and energy content of the prey (Costa, 1991a,b, 1993a).

Remote recorders have resulted in a wealth of information on the diving behavior of freely living marine mammals and seabirds (Kooyman, 1989; Costa, 1993b; Boyd and Croxall, 1996). These data reflect a wide range of foraging strategies among this group and have led to a discussion of the primary determinants of these strategies (Kooyman et al., 1980, 1983; Kooyman, 1989; Costa, 1993b; Boyd and Croxall, 1996). The diving capability of a marine mammal is determined by its total metabolic stores and the rate at which they are used (Kooyman, 1989). These metabolic stores can be separated into aerobic and anaerobic components. The aerobic component of diving metabolism is thought to be the major determinant of diving ability (Kooyman et al., 1980, 1983; Kooyman, 1989; Ponganis et al., 1993, 1997). The aerobic dive limit (ADL) is experimentally defined as the diving duration beyond which blood lactate levels increase above resting levels.

Lactating New Zealand sea lions, *Phocarctos hookeri*, have been reported to be the deepest- and longest-diving otariid (Gales and Mattlin, 1997). They typically dive for 3.9 min (median 4.3 min) and routinely attain depths of 123 m, with a maximum depth of 474 m. Some females routinely dive to depths of 187 m, with mean dive durations of 4.7 min. This

diving pattern is characterized by almost continuous dives, most of which are to the benthos. Unexpectedly, an unusually high proportion (44 %) of dives exceed the theoretical ADL. Aerobic diving is the most efficient way to dive because it provides the greatest cumulative submerged time and the shortest inter-dive interval (Kooyman, 1989; Houston and Carbone, 1992; Ydenberg and Clark, 1989).

Gales and Mattlin (1997) hypothesized that the New Zealand sea lion is physiologically better equipped for prolonged, continuous diving than other otariids and/or that the availability of prey is such that the diving behavior reflects the sea lions' physiological limit in a marginal foraging environment. It was subsequently found that New Zealand sea lions have the largest blood volume, and therefore oxygen-storage capacity, of any otariid, but it was still insufficient to account for the long-duration dives typical of this species (Costa et al., 1998). Measurements of swimming velocity in diving New Zealand sea lions showed that deep and shallow divers had similar surface intervals and that deep divers had higher descent rates than shallow divers. Further, these profiles indicated that deep divers employed burst-and-glide locomotion and that these animals were gliding over a substantial portion of the descent phase of the dive (Crocker et al., 2000). The goal of the present study was to determine whether New Zealand sea lions are physiologically better equipped for prolonged, continuous diving than are other otariids. Here, we test the hypothesis that the diving ability of New Zealand sea lions is in part due to a reduction in oxygen utilization during diving that would be reflected by a lower at-sea metabolic rate.

Materials and methods

Fieldwork was conducted at Sandy Bay, Enderby Island, Auckland Islands Group, New Zealand (50°30′S, 166°17′E) during January and February 1997. Enderby Island is the site of the second largest of the *Phocarctos hookeri* (Gray) rookeries (approximately 400–500 pups per year) (Gales and Fletcher, 1999) and is the best site for capture and eventual recapture of lactating females. Measurements of foraging energetics and diving behavior were completed on females during their summer breeding season when their pups were between 1 and 2 months old. Metabolic rate (rate of CO_2 production) and water turnover were measured on 12 females during periods when they were fasting onshore suckling their pups and foraging at sea using the ^{18}O doubly-labeled water method (Lifson and McClintock, 1966; Nagy, 1980; Nagy and Costa, 1980; Costa, 1987; Speakman, 1997).

The selection of experimental animals was based on the females appearing healthy, being seen to be suckling a pup and representing a range of body masses. Pup sexes were represented equally in the experimental group. Captures were made using a specially designed hoop net (Furhman Diversified, TX, USA) constructed from soft, strong, knotless mesh with a multi-layered head end to reduce the vision of the animal (but still allow free breathing) and a hole at the apex of

the net through which the sea lion's nose protruded. Once in the net, the net handle was removed, the sea lion was physically restrained by two handlers, and a rubber mask was placed over its nose. The anesthetic gas Isoflurane was delivered with oxygen to the mask *via* a field portable vaporizer (Acoma MK III, Japan), and the sea lion was usually anesthetized within 2 min (Gales and Mattlin, 1998). The sea lion was then placed on a restraint frame and weighed using a 250 kg capacity digital scale (Dyna-Link MSI-7200, Measurement Systems International, Seattle, WA, USA) suspended from an aluminum tripod to within ±0.2 kg. Standard body length and girth were measured to the nearest centimeter. Once restrained, blood (20 ml) was drawn from the lateral gluteal vein for measurement of isotope background specific activity, followed by an intraperitoneal injection of 140 ml of sterile saline that consisted of 10 % $H_2^{18}O$ and 4.92 MBq of tritiated water (HTO). Females were then released and recaptured 3–4 h later, when a 20 ml blood sample was collected to measure equilibrated isotope concentrations. In most cases, females were recaptured twice over the following 10 day period, as soon as practical after returning from a foraging trip, and a 20 ml blood sample was taken and body mass recorded. The presence or absence of an individual at the colony was determined from a VHF radio transmitter glued to the pelage of the sea lion using standard telemetry techniques.

Simultaneously with the isotopic measurements, time/depth recorders (TDRs) were deployed on the females to assess diving behavior. Two types of TDR were used; MK3e (N=3) and MK6 (N=9) (Wildlife Computers, Redmond, WA, USA). The MK3e TDRs are housed in a 149 mm long, 26.5 mm diameter titanium tube and weigh 136 g. They are able to record depths of up to 1000 m. The MK6 TDRs are encased in an ovoid plastic housing 69 mm×57 mm×35 mm, weigh 80 g and can measure depth to either 250 m or 500 m. Prior to deployment, each piece of equipment was glued to a piece of neoprene material cut to the same size as the unit's base. This wet-suit base was then glued to the dorsal pelage of the sea lion using a two-part epoxy glue (Araldite 2017, Ciba-Geigy, Cambridge, UK). Because of the shape of the MK IIIe TDRs, they could not be glued but were anchored to the neoprene with three pre-sewn plastic cable ties and two stainless-steel hose clamps. The TDRs were set to sample every 5 s. The dive records were first normalized using Wildlife computers Zero Offset Correction program, and the subsequent dive record was analyzed using Wildlife Computers Dive Analysis software. A dive had to exceed 2 m in depth to qualify as a dive, and only dives greater than 6 m were used in the analysis.

Energetics data

Total body water (TBW) was determined by the initial dilution of $H_2^{18}O$ (Nagy and Costa, 1980). Final TBW was calculated as the final mass of the animal multiplied by the initial TBW/mass ratio. The specific activity of tritium was determined by scintillation spectrometry of triplicate samples of 300 μl of pure water (distilled from the serum samples) in 10 ml of Ecolight cocktail (ICN Costa Mesa, CA, USA)

Table 1. *Measurement interval, mass, time at sea, water space, water influx and metabolic rate of New Zealand sea lions*

Female (pup sex)	Mass		Total body water			Measurement interval (days)	Time at sea (days)	H_2O influx $(ml\,kg^{-1}\,day^{-1})$	CO$_2$ production			FMR $(W\,kg^{-1})$
	Initial (kg)	Final (kg)	^{18}O		HTO				Nagy $(ml\,g^{-1}\,h^{-1})$	Speakman $(ml\,g^{-1}\,h^{-1})$	Difference (%)	
			(l)	(%)	(l)							
E-39 (F)	126.4	136.2	83.8	66.3	87.8	8.6610	5.9792	162	0.677	0.568	−16	4.44
E-40 (M)	83.4	85.4	55.3	66.3	57.9	5.7354	3.7097	125	1.083	0.967	−11	7.10
E-41 (M)	107.0	111.8	71.0	66.4	73.8	5.8889	4.7159	167	0.833	0.705	−15	5.46
E-42 (M)	106.0	107.4	69.4	65.5	71.4	7.6958	4.7812	120	0.841	0.726	−14	5.51
E-43 (M)	121.1	126.6	80.9	66.8	83.0	6.5375	3.8438	107	0.771	0.676	−12	5.05
E-52 (F)	107.2	103.8	69.0	64.3	70.5	7.6208	4.2569	97.3	0.787	0.671	−15	5.16
E-53 (F)	120.6	119.0	81.0	67.2	83.6	4.9764	3.6389	149	0.840	0.700	−17	5.51
E-55 (M)	103.6	115.0	67.7	65.4	69.3	5.0438	3.9060	155	0.877	0.771	−12	5.75
E-56 (F)	105.8	113.0	69.1	65.3	69.6	6.1042	4.6319	142	0.767	0.654	−15	5.03
E-58 (F)	116.6	121.2	76.5	65.6	77.8	7.1250	5.4069	133	0.835	0.718	−14	5.47
E-59 (F)	147.4	162.2	100.2	68.0	105.1	7.0694	4.7951	120	0.709	0.633	−11	4.65
E-61 (M)	91.6	95.6	59.2	64.7	61.8	6.8639	5.1986	143	0.999	0.881	−12	6.55
Mean	111.4	116.4	73.6	66.0	76.0	6.6102	4.5720	134	0.835	0.723	−14	5.47
S.D.	16.7	19.8	12.0	1.1	12.7	1.1126	0.7308	23	0.114	0.108	2	0.75

HTO, tritiated water; FMR, field metabolic rate; F, female; M, male.

The values for total body water are given for both ^{18}O dilution and HTO dilution. However, percentage total body water is for ^{18}O space only.

The two values for the rate of CO_2 production result from the use of equations of Nagy (1980) or the two-pool model of Speakman (1997).

FMR is derived using the equations of Nagy (1980).

(Ortiz et al., 1978). The specific activity of $H_2^{18}O$ was determined by mass ratio spectrometry (Metabolic Solutions, Nashua, NH, USA) of pure water distilled from serum samples. CO_2 production was calculated using equation 3 of Nagy (1980), which assumes an exponentially changing body water pool. This equation does not include corrections for isotopic fractionation effects; no equations are available for correcting simultaneously fractionation effects and changing water volumes. For comparison, CO_2 production was also calculated using the two-pool model of Speakman (1997). Water influx was calculated using equations 5 and 6 of Nagy and Costa (1980) assuming an exponentially changing body water pool. Given that the diet of New Zealand sea lions is not well known, we used a conversion factor from California sea lions, *Zalophus californianus*, of $23.6\,kJ\,l^{-1}\,CO_2$ for converting CO_2 production to energy consumption. This assumes that all the fat and protein contained in the diet are oxidized and that the diet is composed of 80.3 % water, 1.3 % fat and 16.7 % protein and that the energy content is $3.75\,kJ\,g^{-1}$ (Costa et al., 1990).

Field metabolic rate (FMR) data collected over the entire measurement interval included variable amounts of onshore FMR. Data were normalized to estimate FMR while at sea by correcting for the proportion of time and, hence FMR, spent onshore. Time onshore was calculated from the TDR records. In two cases, TDR records were not available (animals E-55, E-39) and the attendance pattern was determined from the transmitters attached to the animals to monitor their presence or absence from the rookery. The presence or absence of the animals was monitored by scanning the study area for the presence of all deployed frequencies with a Telonics TR-2 receiver (Mesa, AZ, USA) four times each day at 07:00, 12:00, 18:00 and 22:00 h. As there are no measurements of onshore FMR for this species, it was estimated to be 2.5 times the predicted standard metabolic rate (SMR) from Kleiber (1975). The only comparable measurements of onshore metabolic rate of a lactating female otariid was 2.5 times SMR for Antarctic fur seals *Arctocephalus gazella* and northern fur seals *Callorhinus ursinus* (Costa and Trillmich, 1988). At-sea FMR was then calculated for each female by solving the following relationship for at-sea FMR:

$$measured\ FMR = (onshore\ FMR)(\%\ time\ onshore) + (at\text{-}sea\ FMR)(\%\ time\ at\ sea). \quad (1)$$

Means are given ±1 S.D. Unless stated otherwise, differences between means were tested using a two-sample *t*-test, and relationships were tested using least-squares linear regression analysis.

Results

Foraging energetics

Metabolic rate measurements were completed on all 12 animals that had variable periods at sea and onshore. Mass changes, body water, metabolic rate and water influx data for these animals are presented in Table 1. Values were on average 13.6 % lower when FMR was calculated using the two-pool equation of Speakman (1997) than using the equation of Nagy (1980). Time spent at sea and onshore, FMRs calculated for animals while at sea and dive data are provided in Table 2.

Table 2. *Mass change, dive variables and field metabolic rate data corrected to represent only the time at sea for female New Zealand sea lions*

| Female | Mass change (kg) | Number of trips to sea | Time at sea (days) | Mean dive variables | | | | Total dive number | Dive rate (dives h⁻¹) | Diving time | | Total distance travelled (m) | Travel speed (m h⁻¹) | FMR at sea (W kg⁻¹) |
				Depth (m)	Duration (min)	Surface (min)	Bottom (min)			(h)	(% at sea)			
E-39	9.8	2	5.9792	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	5.20
E-40	2.0	3	3.7097	ND	4.3	3.2	ND	696	7.82	49.88	56.0	ND	ND	9.31
E-41	4.8	2	4.7159	140	3.0	4.6	0.8	894	7.90	44.42	39.2	323 809	2861	6.11
E-42	1.4	2	4.7812	92	3.0	3.5	1.6	1038	9.05	51.72	45.1	355 156	3095	7.12
E-43	5.5	2	3.8438	111	4.0	2.7	2.3	825	8.94	54.97	59.6	369 490	4005	6.65
E-52	−3.4	2	4.2569	69	2.6	2.5	1.1	1202	11.77	51.88	50.8	295 338	2891	6.96
E-53	−1.6	1	3.6389	99	3.3	2.6	1.7	887	10.16	49.42	56.6	323 248	3701	6.50
E-55	11.4	1	3.9060	97	2.6	3.3	0.8	(465)	9.98	ND	43.3	ND	2722	6.59
E-56	7.2	3	4.6319	180	4.1	6.3	1.5	645	5.80	44.08	39.6	327 660	2947	5.72
E-58	4.6	2	5.4069	165	3.6	9.8	0.9	582	4.49	34.42	26.5	245 411	1891	6.32
E-59	14.8	2	4.7951	155	3.4	8.6	1.0	568	4.94	32.55	28.3	229 915	1998	5.61
E-61	4.0	2	5.1986	135	3.8	3.9	1.7	976	7.82	61.17	49.0	422 736	3388	7.72
Mean	4.6	2.0	4.4441	124	3.4	4.6	1.3	831	8.06	47.45	44.9	321 418	2950	6.65
S.D.	5.3	0.6	0.6095	36	0.6	2.5	0.5	209	2.27	8.85	11.0	59 783	665	1.09

FMR, field metabolic rate; ND, no data.

There are no diving data for E-39 because she lost her time/depth recorder (TDR). There are no depth data for E-40 because she routinely exceeded the depth capability of the TDR The TDR of E-55 stopped collecting data after 2 days, so these data are taken as representative of her entire trip to sea.

Dive pattern

Ten complete and one partial diving record were obtained from the 12 sea lions, yielding a total sample of 11 341 dives. One unit stopped collecting data after 2 days at sea (E-55), and another unit detached from the animal while it was at sea (E-39). One animal (E-40) reached the maximum resolution (236 m) of the attached TDR on 5 % of its dives, and data on dive depth for this animal were therefore deleted from the analysis. The mean maximum dive depth was 353 ± 164 m, with a mean diving depth of 124 ± 36 m. The deepest single dive was 550 m and the longest was 11.50 min, both by the largest animal in our study E-59. The mean maximum dive duration was 8.3 ± 1.7 min, with an average duration of 3.4 ± 0.6 min. The dive data for each animal are provided in Table 2, along with concurrently collected at-sea metabolic rates.

A significant limitation of using FMR measurements derived from doubly-labeled water is that they integrate the time/energy budget over the entire trip to sea. Therefore, the only comparable behavioral data are integrated metrics such as mean dive depth, mean duration, etc. For this reason, the analysis of diving behavior was limited to mean indices of behavior over the entire trip to sea. A more complete analysis of the diving behavior of this species can be found in Gales and Mattlin (1997) and Crocker et al. (2000). Individual sea lions exhibited different diving patterns in terms of mean dive depth, duration and indices of diving effort (Table 2). Dive duration increased significantly with dive depth ($r^2=0.46$, $P=0.032$) (Fig. 1). While there was no significant correlation between dive depth and time spent at the bottom of a dive ($r^2=0.03$, $P=0.65$) (Fig. 1), the mean surface interval increased
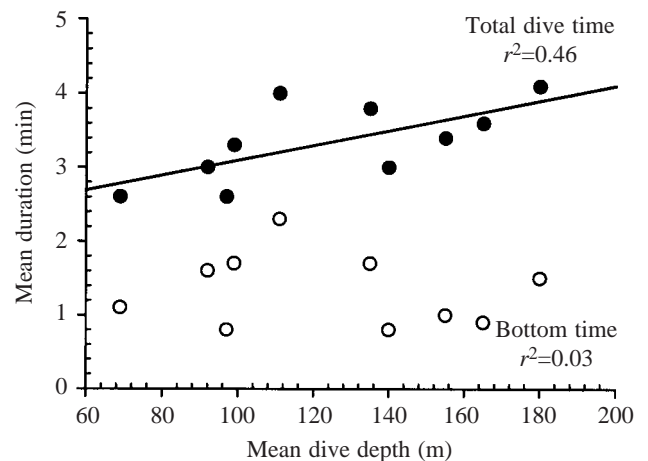

Fig. 1. Mean dive duration ($r^2=0.46$, $P=0.032$) and mean bottom time ($r^2=0.03$, $P=0.65$) as a function of mean dive depth for each animal.

significantly as animals made deeper dives ($r^2=0.66$, $P=0.005$) (Fig. 2A). The mean surface interval was more dependent on mean dive depth than on either dive duration ($r^2=0.04$, $P=0.56$) or bottom time ($r^2=0.20$, $P=0.19$). The deeper the dive, the more time spent on the surface with significantly less time at sea spent diving ($r^2=0.45$, $P=0.006$) (Fig. 2B). Surprisingly, body mass had little effect on diving behavior: there was no significant relationship between body mass and mean dive depth ($r^2=0.20$, $P=0.44$), duration ($r^2=0.02$, $P=0.66$), bottom time ($r^2=0.01$, $P=0.78$) or mean surface interval ($r^2=0.28$, $P=0.10$).
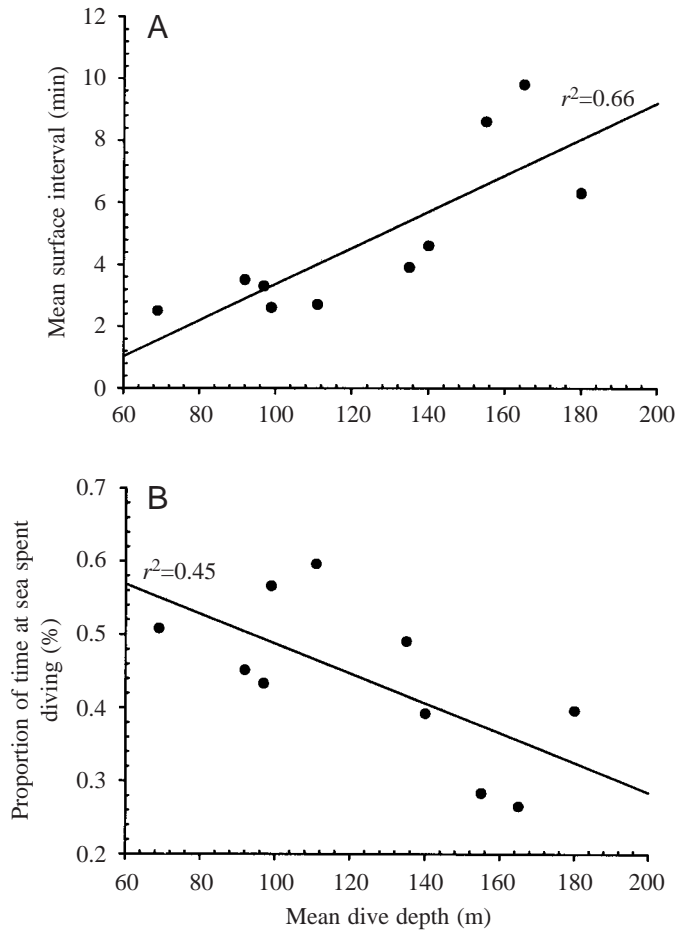
Fig. 2. (A) Mean time spent on the surface between dives as a function of each animal's mean dive depth (r^2=0.66, P=0.005). (B) The relative proportion of time that each animal spent diving while at sea as a function of each animal's mean dive depth (r^2=0.45, P=0.006).

Fig. 3. (A) Mean dive effort (m h^{-1}) as a function of each animal's mean dive depth. The distance covered was calculated as the total vertical distance covered during the descent and ascent plus the distance covered at the bottom of the dive (r^2=0.20, P=0.19). (B) The mean dive rate (dives h^{-1}) plotted as a function of each animal's mean dive depth (r^2=0.88, P<0.001).

Given that deep divers spent more time at the surface with less time diving, it is not surprising that mean dive rate decreased with increasing dive depth (r^2=0.88 P<0.001). However, there was no significant relationship between dive rate and metabolic effort in terms of at-sea FMR (r^2=0.09, P=0.38). An index of dive effort that takes into account both the rate and absolute depth of the dive can be calculated from the rate of vertical distance covered in the water column as a function of time (Arnould et al., 1996). However, this metric is only applicable to divers that make spiked dives, which are dives that have no bottom time and no horizontal swimming. As New Zealand sea lions spend a considerable time at the bottom of a dive, we estimated the horizontal distance covered at the bottom of the dive by multiplying the bottom time by the mean swimming speed. New Zealand sea lions have a mean swimming speed of 1.64 m s^{-1} at the bottom of a dive (Crocker et al., 2000). Using this index, there was no significant relationship between dive effort and dive depth (r^2=0.20, P=0.19) (Fig. 3A).
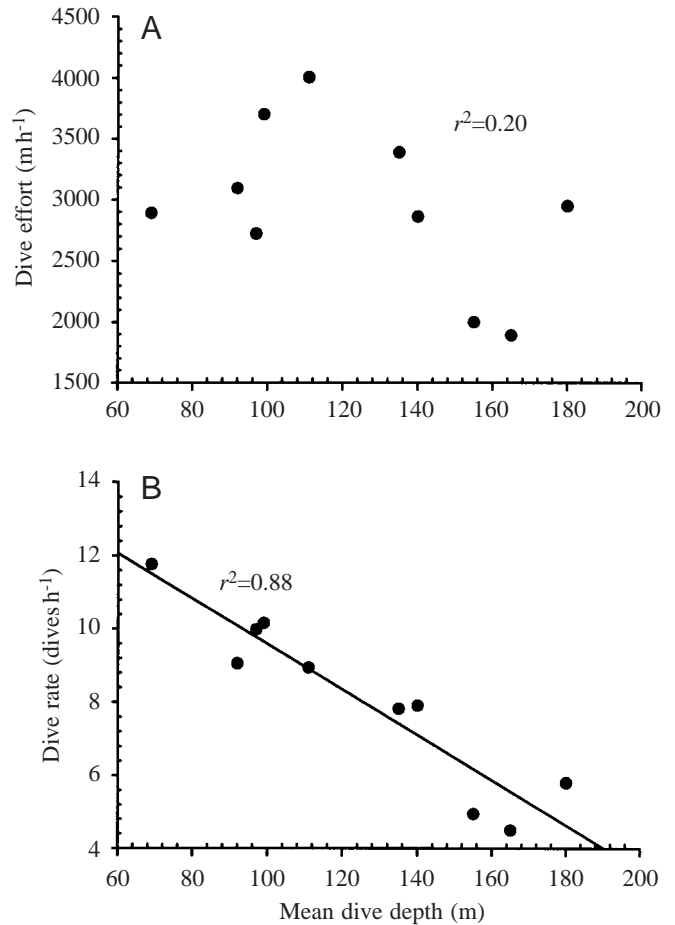
Given the differences in diving behavior between deep- and shallow-diving sea lions, we might expect differences in their rate of energy expenditure. The relationship between mass-specific FMR and mean dive depth for all sea lions was not significant (r^2=0.26, P=0.078; Fig. 4A), but it was highly significant (r^2=0.71, P=0.003) when the data from one of the smaller females (E-61) with the highest FMR was removed from the analysis. This point fell outside the 99% confidence interval for the regression and can be considered an outlier. In contrast, there were no correlations between FMR and dive effort (r^2=0.22, P=0.17), dive rate (r^2=0.09, P=0.38), bottom time (r^2=0.14, P=0.30), dive duration (r^2=0.1, P=0.35) or mean surface interval (r^2=0.24, P=0.13). However, there was a significant correlation between FMR and the proportion of time spent at sea diving (r^2=0.38, P=0.042) (Fig. 4B).

Discussion

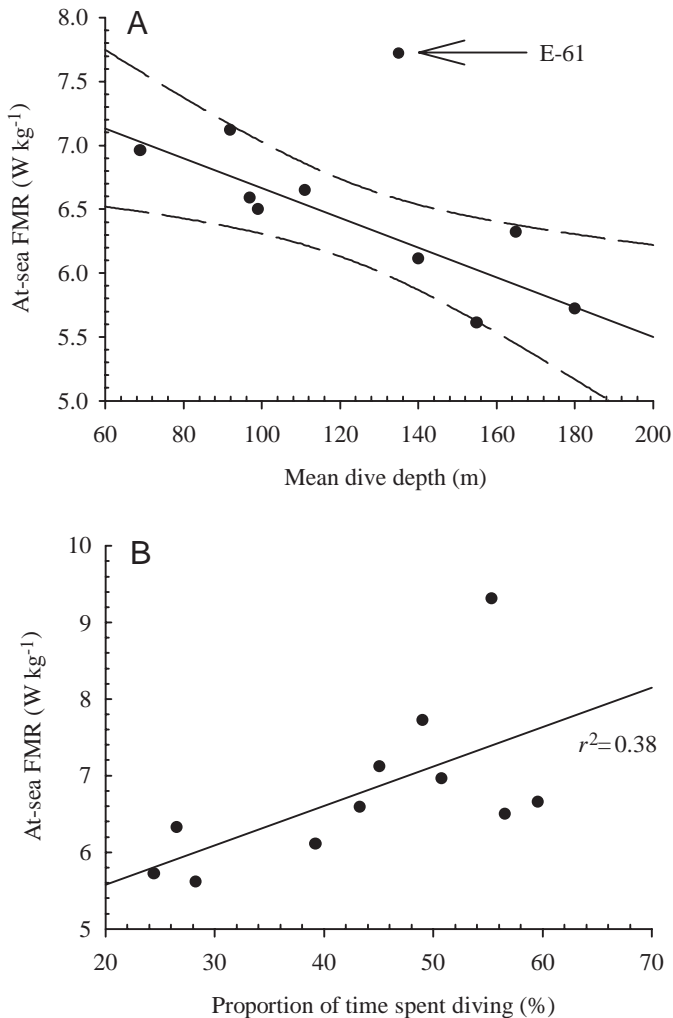The most striking observation relevant to the diving physiology of New Zealand sea lions is the profound role of

Fig. 4. (A) Mass-specific field metabolic rate (FMR) while at sea *versus* mean dive depth for each animal. The trend was almost significant with all data included ($r^2=0.26$, $P=0.078$) and was highly significant (solid line) when one of the smaller animals, E-61, was removed from the sample ($r^2=0.71$, $P=0.003$). The dashed lines represent the 99% confidence interval for the regression. Note that animal E-61 is outside the confidence interval and can therefore be considered an outlier. (B) Field metabolic rate (FMR) while at sea *versus* proportion of time at sea spent diving ($r^2=0.38$, $P=0.042$).

Fig. 5. The ratio of the mean time spent at the surface to mean dive duration as a function of mean dive depth for each animal ($r^2=0.47$, $P=0.029$).

A disproportionate increase in mean surface interval relative to mean dive duration in New Zealand sea lions is consistent with a requirement to spend more time on the surface to clear lactic acid. One of the disadvantages of anaerobic metabolism during diving is that, while a diver may increase the duration of a single dive, the total accumulated time spent under water is reduced because the animal must spend proportionately more time at the surface clearing lactic acid. New Zealand sea lions follow this prediction: the ratio of mean surface interval to mean dive duration increased with increasing dive depth ($r^2=0.47$, $P=0.029$) (Fig. 5).

It is also possible that deep divers spend more time on the surface for reasons unrelated to their diving metabolism. If deep-diving New Zealand sea lions eat large prey, they might need to return to the surface to consume them, whereas shallow divers could feed on small prey, consuming them entirely under water. Differences in the foraging behavior of diving birds and mammals have been observed for prey that are located at different depths in the water column (Costa, 1991a).

Diving metabolic rate

An important component of the dive response is a reduction in metabolic rate, which allows more efficient utilization of oxygen reserves (Scholander et al., 1942). Our initial hypothesis was that New Zealand sea lions would have a reduced diving metabolic rate and that this would result in a correspondingly lower at-sea FMR. However, the at-sea FMR of New Zealand sea lions was 5.8 times the predicted basal rate of a terrestrial animal of equal size, well within the 4.8–7 times BMR previously reported for Australian sea lions *Neophoca cinerea*, California sea lions, Northern fur seals and Antarctic fur seals (Fig. 6) (Costa, 1993a). This result leads us to reject the hypothesis that New Zealand sea lions have a greater diving capacity because of reductions in their diving metabolic rate. Given the variability in FMR observed for this species, one might predict that longer-diving sea lions would exhibit a reduced at-sea FMR. The data do not support this hypothesis: there was no correlation between FMR and dive duration

dive depth on dive pattern and foraging energetics. Our data indicate that the mean surface interval increased as the mean dive depth increased (Fig. 2A), while the overall amount of time spent diving declined (Fig. 2B). There are a number of possible explanations for this observation. One is that as sea lions dive deeper they are unable to maintain aerobic metabolism and must incorporate some component of anaerobic metabolism during the dive, thus increasing mean surface time. When Weddell seals *Leptonychotes weddelli* exceed the aerobic threshold, the post-dive surface interval increases disproportionately faster than dive duration (Kooyman et al., 1980, 1983). This greater surface interval is required to clear the lactic acid accumulated during the dive.
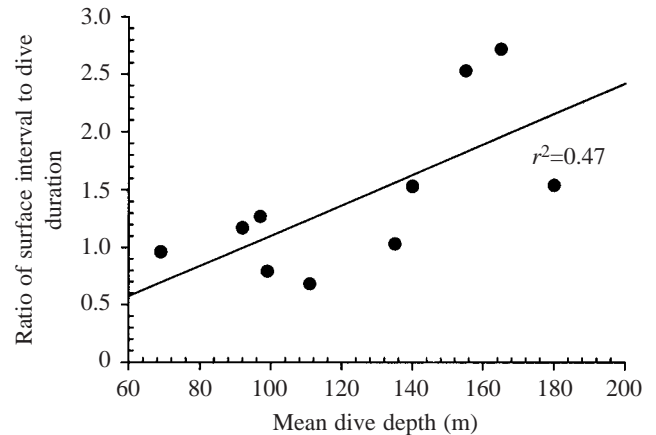
Fig. 6. The at-sea field metabolic rate (FMR) of New Zealand sea lions plotted relative to values available for other otariids. Values are mean ± S.D. Data for other otariids are from Costa et al. (1989a,b, 1990) and Trillmich (1996). The linr for predicted standard metabolic rate (BMR) is for terrestrial mammals (Kleiber, 1975). Ca sea lion, California sea lion (*N*=7); Ant fur seal, Antarctic fur seal (*N*=21); No fur seal, Northern fur seal (*N*=10); Aust sea lion, Australian sea lion (*N*=16); NZ sea lion, New Zealand sea lion (*N*=12).
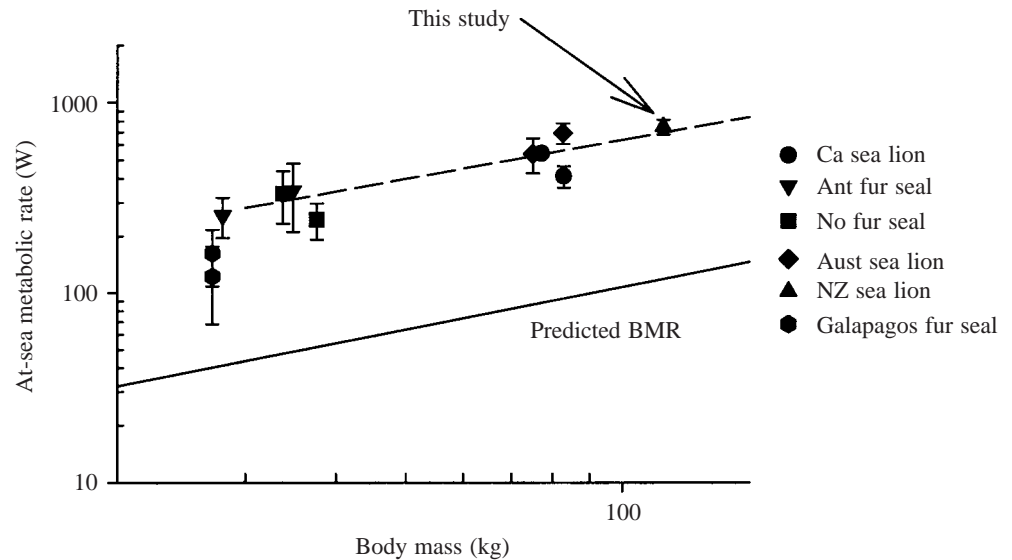
(r^2=0.1, *P*=0.35) or bottom time (r^2=0.14, *P*=0.30). This does not preclude variations in metabolic rate that may have occurred within individual dives, but it does preclude a consistent reduction in metabolic rate as a means of increasing mean dive duration.

The time spent at the bottom of a dive was independent of depth in New Zealand sea lions. This was achieved by an increase in the mean duration of dives (Fig. 1) coupled with an increased rate of descent in deeper dives. Measurements of swimming speed using swim velocity/depth recorders on New Zealand sea lions confirmed that deep divers descend faster than shallow divers (Crocker et al., 2000). How, then, is it possible for deep-diving sea lions to descend faster during a dive and yet maintain a lower metabolic rate? New Zealand sea lions employ a burst-and-glide form of locomotion (Crocker et al., 2000). At the start of the dive, they use their pectoral flippers and accelerate rapidly. After an initial series of strokes, they then glide and increase speed as they descend. An example of this diving pattern can be seen in Fig. 7. This pattern was confirmed by attaching a video camera to the back of freely ranging sea lions. The video images clearly showed an initial period of powered swimming followed by free gliding until the animal reached the bottom (N. J. Gales and B. Buhlier, unpublished data). A lower metabolic rate would be consistent with deep-diving sea lions spending a greater proportion of their dive gliding, whereas shallow divers may spend more time actively swimming. A biomechanical analysis suggests that gliding during descent, along with the associated changes in lung volume, allows bottlenose dolphins *Tursiops truncatus* to conserve energy during deep dives (Skrovan et al., 1999). Similarly, Williams et al. (2000) found that four species of marine mammal diving deeper than 80 m increased their dive duration by prolonging the gliding phase during the descent. They also found that Weddell seals reduced their rate of oxygen consumption by between 9.2 and 56.9 % by increasing the gliding phase during the descent.
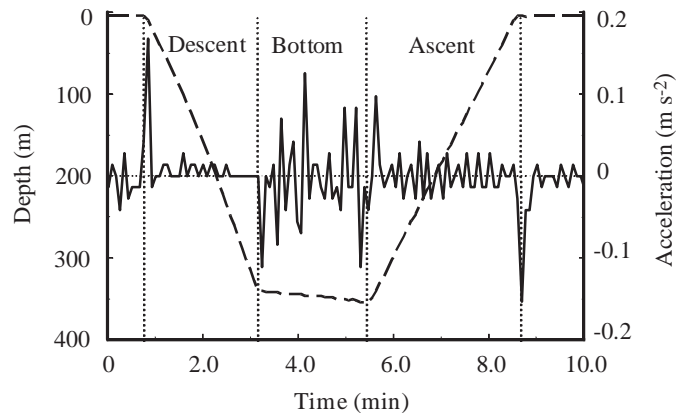

Fig. 7. A representative dive of a New Zealand sea lion recorded with a swim-velocity time/depth recorder. Dive depth is shown as a dashed line and acceleration (calculated from swimming velocity) as a solid line. The dotted vertical lines show the beginning and end of the descent, the bottom portion and the ascent phases of the dive. The descent phase of the dive has an initial burst of acceleration followed by very small accelerations compared with the other phases of the dive. See Crocker et al. (2000) for details of data collection.

An alternative hypothesis for the lower FMR of deeper-diving sea lions is that deep divers are not working as hard, as indicated by the lower proportion of time at sea spent diving together with the greater time spent at the surface (Fig. 2). However, our data do not support this hypothesis. Even though deep divers make fewer dives per unit time (Fig. 3B), their diving effort is similar to that of shallow divers (Fig. 3A). This is indicated by a lack of correlation between FMR and dive rate (r^2=0.09, *P*=0.38), dive effort (r^2=0.22, *P*=0.17) or time at the surface (r^2=0.24, *P*=0.13). In contrast, there was (with the one outlier animal removed) a highly significant correlation between FMR and mean dive depth (Fig. 4A, r^2=0.71, *P*=0.003). These observations lend further support to the hypothesis that deeper-diving individuals have a decreased

FMR as a result of using an efficient form of locomotion that relies on an initial burst followed by gliding to depth.

Aerobic dive limit

Given the considerable variation in diving pattern observed in this species, we might expect to see consistent differences in metabolic rate and diving pattern among individuals. Deep-diving individuals spent more time at the surface than shallow divers (Fig. 2A), but the FMR of deep divers was lower than that of shallow divers (Fig. 4A). This suggests that deep-diving sea lions had lower metabolic rates, but still operated at a level that required a greater anaerobic component than shallow-diving individuals. The ADL of each animal can be determined by dividing the O_2 store by the animal-specific FMR in Table 2. The O_2 store was estimated from measurements of blood volume (Costa et al., 1998) coupled with estimates of the muscle and lung oxygen stores following the method of Gentry et al. (1986) and Davis and Kanatous (1999). Briefly, this method calculates the blood oxygen store as the sum of arterial and venous oxygen using the equations:

$$\text{arterial } O_2 = 0.33 V_b (0.95 - 0.20 \text{ saturation}), \quad (2)$$

$$\text{venous } O_2 = 0.66 V_b (\text{arterial content} - 5 \text{ vol\%}), \quad (3)$$

where 0.33 is the proportion of arterial blood, 0.66 is the proportion of venous blood, V_b is blood volume (ml), 0.95–0.20 saturation is the amount of oxygen extracted during a dive assuming an oxygen capacity of $23.0\,\text{ml}\,100\,\text{g}^{-1}$ (Lenfant et al., 1970) and (arterial content minus 5 vol%) is the amount of oxygen extracted during a dive (Kooyman et al., 1983). Muscle oxygen stores were estimated using the equation:

$$\text{muscle } O_2 = [\text{Mb}] \times 1.34 \times m \times 0.3, \quad (4)$$

where [Mb] is myoglobin concentration $(3.2\,\text{g}\,100\,\text{g}^{-1})$ (Lenfant et al., 1970), m is body mass, $1.34\,\text{ml}\,O_2\,\text{g}^{-1}$ is the amount of oxygen stored in the myoglobin and 0.3 is the proportion muscle mass in the body (Kooyman et al., 1983). Diving lung oxygen stores were estimated using the equation:

$$\text{lung } O_2 = V_i \times m \times 0.15 F_{O_2}, \quad (5)$$

where V_i is diving lung volume, $0.50(0.10 m^{0.96})$ (in l) (Kooyman, 1989), F_{O_2} is the fractional oxygen content of air in the lungs and $0.15 F_{O_2}$ is the oxygen extracted from the air in the lungs (Kooyman et al., 1971).

It is important to note that at-sea FMR is an average rate that integrates the variable costs of surface swimming, diving and resting, and the actual diving metabolic rate could therefore be higher or lower. The FMR, O_2 stores, calculated (cADL), mean dive duration and the ratio of observed dive duration to the cADL are presented in Table 3. These data support the hypothesis that individual animals exhibit different physiological responses while diving. For example, sea lions E-59, E-55, E-52 and E-41 carried out dives that were very close to the cADL, while other individuals, E-40, E-43 and E-61, routinely exceeded their cADL in one animal (E-40) by 2.6-fold. Further inspection of the data in Table 3 reveals that
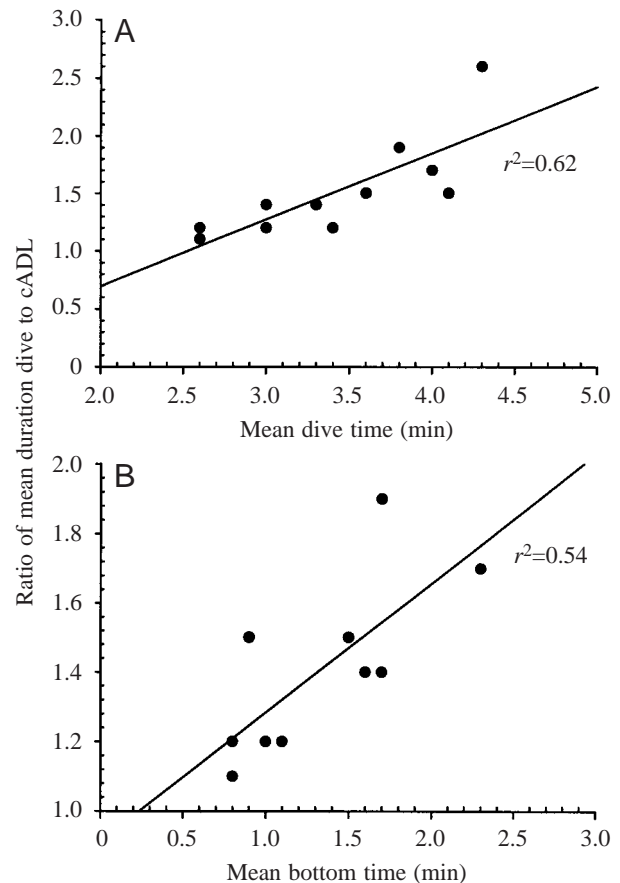

Fig. 8. The ratio of mean dive duration to calculated aerobic dive limit (cADL) for each animal *versus* (A) mean dive duration (r^2=0.62, P=0.004) and (B) mean bottom time (r^2=0.54, P=0.016).

as dive duration and bottom time increase so does the ratio of observed dive duration to cADL (r^2=0.62, P=0.004 for dive duration; r^2=0.54, P=0.016 for bottom time) (Fig. 8), whereas there is no relationship between this ratio and mean dive depth (r^2=0.07, P=0.47). This is surprising because it does not support the hypothesis that deep diving is achieved by incorporating anaerobic metabolism. Further, it implies that differences in the diving pattern of shallow and deep divers were due to differences in the type of prey consumed, which may vary with respect to size, energy content and/or how or where the prey was processed (handling time).

The efficacy of calculating ADL is this way is supported by measurements of aerobic thresholds in freely diving trained California sea lions (Ponganis et al., 1997). These authors found that increased formation of lactic acid corresponded with dives lasting greater than 2.3 min. The predicted ADL of these animals was based on estimates of body oxygen stores coupled with FMRs derived from doubly-labeled water measurements on wild adult female California sea lions (Costa et al., 1990). ADLs calculated in this way yielded predicted ADLs of between 1.8 and 2.0 min, whereas ADLs calculated from metabolic rates estimated from flume studies yielded much longer ADLs of 3–3.5 min. Although ADLs calculated from

Table 3. *The calculated aerobic dive limit derived for each sea lion on the basis of their estimated body oxygen stores and at-sea field metabolic rate*

Female	Mass (kg)	FMR (ml O$_2$ min^{-1})	O$_2$ stores (ml)	cADL (min)	Mean dive duration (min)	Ratio of dive duration to cADL	Surface time (%)	Swimming speed (m s^{-1})
E-40	84.4	2394	4001	1.7	4.3	2.57	43.4	1.66
E-41	109.6	2035	5186	2.5	3.0	1.18	10.5	1.81
E-42	106.7	2315	5058	2.2	3.0	1.37		
E-43	123.9	2510	5870	2.3	4.0	1.71	23.4	1.63
E-52	105.5	2236	5001	2.2	2.6	1.16	8.9	1.65
E-53	119.8	2373	5679	2.4	3.3	1.38	34.4	1.57
E-55	109.3	2193	5181	2.4	2.6	1.10		
E-56	109.4	1907	5186	2.7	4.1	1.51	51.5	1.89
E-58	118.9	2290	5636	2.5	3.5	1.42		
E-59	154.8	2644	7338	2.8	3.4	1.23		
E-61	93.6	2199	4437	2.0	3.8	1.88	34.4	1.71
Mean	112.3	2281	5325	2.3	3.4	1.48	29.5	1.70

cADL, calculated aerobic dive limit; FMR, field metabolic rate.
Measured dive duration is given for comparison along with the ratio of mean dive duration to cADL.
Data on % time spent resting on the surface and average swim speed are from Crocker et al. (2000).

doubly-labeled water measurements underestimated the actual ADL by 13–22%, they were far closer than ADLs calculated using flume studies, which overestimated the actual ADL by 43–57%. If the same correction applies to New Zealand sea lions, anaerobic metabolism would only be expected in those animals that had cADLs greater than 1.3 times the predicted value. If this were the case, many of our animals routinely dived aerobically (E-41, E-52, E-55 and E-59), while others routinely dived outside their ADL and must have included an anaerobic component in their diving metabolism (E-40, E-42, E-43, E-53, E-56, E-58 and E-61). Furthermore, the animals that spent the greatest proportion of their time on the surface inactive were those that exceeded the cADL by the greatest amount (Table 3).

Comparison with other species

Comparable data on diving pattern and energetics are only available from the Antarctic fur seal *Arctocephalus gazella* (Arnould et al., 1996; Costa et al., 2000). In contrast to New Zealand sea lions, Antarctic fur seals make shallow short dives, routinely diving to mean depths of only 19 m, and remain

submerged for 1.13 min (Table 4). Given such shallow dives, it is not surprising that at-sea FMR did not vary with dive duration or depth in fur seals. Unlike New Zealand sea lions, FMR in Antarctic fur seals increased with increasing trip duration and declined as the proportion of time spent diving and diving effort increased. Arnould et al. (1996) suggested that, for fur seals, a reduced diving effort and lower relative time spent diving indicated that the animals spent more time swimming between dense prey patches and thus spent less time per patch, but caught more prey for their effort (Boyd, 1996; Boyd et al., 1995). The energy cost of swimming is greater than that of diving, so individuals that spend more time transiting between patches expend more energy (Arnould et al., 1996). In contrast, the at-sea FMR of New Zealand sea lions increased as the proportion of time spent diving increased, reflecting the consequences of the deep diving pattern of this animal. New Zealand sea lions spent 2–4 times more time at sea diving with a diving effort that was 4–7 times greater than that observed for Antarctic fur seals (Table 4). Antarctic fur seals spend more time surface-swimming, so this should be a greater factor in determining their at-sea FMR.

Table 4. *Comparison of the present data from New Zealand sea lion females with data collected on female Antarctic fur seals foraging at Cape Shirreff, Livingston Island (Costa et al., 2000), and female fur seals foraging from Bird Island, South Georgia (Arnold et al., 1996)*

	Body mass (kg)	Dive depth (m)	Dive duration (min)	At-sea FMR (W kg^{-1})	At-sea FMR (W kg$^{-0.75}$)	Dive rate (h^{-1})	Diving time (% at sea)	Dive effort (m h^{-1})
Antarctic fur seal								
Cape Shirreff	33.7	19	0.9	9.73	23.4	6.13	9.77	233
Bird Island	36.8	12.7	1.13	6.66	16.4	13	20.4	469
New Zealand sea lion	112.3	124	3.4	6.65	21.6	8.06	44.9	2950

FMR, field metabolic rate.

These differences may also reflect the differences between animals that have highly patchy but dense prey resources (Antarctic fur seal) *versus* benthic foragers with a more evenly distributed (less patchy) prey resource (New Zealand sea lion). Nonetheless, comparisons of mass-adjusted FMRs between New Zealand sea lions and Antarctic fur seals indicate that, overall, they have surprisingly similar rates of energy expenditure while at sea, even though their swimming and diving patterns are so strikingly different. These similarities imply that otariids operate within a narrow range of FMRs. Differences in how fur seals and sea lions budget their energy expenditure are important; fur seals invest in travel between high-value patches that are near the surface, while sea lions invest in diving effort because their resources are spread out on the benthos.

The deep and long-duration diving ability of New Zealand sea lions is not due to a decreased diving metabolic rate, but rather to reliance in part on increased oxygen stores. Individual sea lions that performed deeper dives had lower FMRs that probably were due to reliance on burst-and-glide locomotion that reduced the cost of locomotion. Differences in the foraging pattern that correlate with the depth of the dive may be related to differences in diet. Lastly, our data indicate that, although New Zealand sea lions have increased their O_2 storage capacity, they have not or cannot significantly reduce their at-sea metabolic rates and are therefore likely to be operating near their physiological maximum.

References

Arnould, J. P. Y., Boyd, I. L. and Speakman, J. R. (1996). The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. *J. Zool., Lond.* **239**, 769–782.

Boyd, I. L. (1996). Temporal scales of foraging in a marine predator. *Ecology* **77**, 426–434.

Boyd, I. L. and Croxall, J. P. (1996). Dive durations in pinnipeds and seabirds. *Can. J. Zool.* **74**, 1696–1705.

Boyd, I. L., Reid, K. and Bevan, R. M. (1995). Swimming speed and allocation of time during the dive cycle in Antarctic fur seals. *Anim. Behav.* **50**, 769–784.

Castellini, M. A., Murphy, B. J., Fedak, M. A., Ronald, K., Gofton, N. and Hochachka, P. W. (1985). Potentially conflicting metabolic demands of diving and exercise in seals. *J. Appl. Physiol.* **58**, 392–399.

Costa, D. P. (1987). Isotopic methods for quantifying material and energy intake of free-ranging marine mammals. In *Approaches to Marine Mammal Energetics* (ed. A. C. Huntley, D. P. Costa, G. A. J. Worthy and M. A. Castellini), pp. 43–66. Lawrence: Allen Press.

Costa, D. P. (1991a). Reproductive and foraging energetics of high latitude penguins, albatrosses and pinnipeds – implications for life history patterns. *Am. Zool.* **31**, 111–130.

Costa, D. P. (1991b). Reproductive and foraging energetics of pinnipeds: implications for life history paterns. In *Behaviour of Pinnipeds* (ed. D. Renouf), pp. 300–344. London: Chapman & Hall.

Costa, D. P. (1993a). The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. In *Marine Mammals: Advances in Behavioural and Population Biology*, vol. 66 (ed. I. L. Boyd), pp. 293–314. Symposium of the Zoological Society of London: Oxford University Press.

Costa, D. P. (1993b). The secret life of marine mammals: novel tools for studying their behavior and biology at sea. *Oceanography* **6**, 120–128.

Costa, D. P., Antonelis, G. P. and De long, R. L. (1990). Effects of El Niño on the foraging energetics of the California sea lion. In *Effects of El Niño on Pinnipeds* (ed. F. Trillmich and K. Ono), pp. 156–165. Berlin: Springer Verlag.

Costa, D. P., Croxall, J. P. and Duck, C. D. (1989a). Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology* **70**, 596–606.

Costa, D. P., Gales, N. J. and Crocker, D. E. (1998). Blood volume and diving ability of the New Zealand sea lion, *Phocarctos hookeri*. *Physiol. Zool.* **71**, 208–213.

Costa, D. P., Goebel, M. E. and Sterling, J. T. (2000). Foraging energetics and diving behavior of the Antarctic fur seal, *Arctocephalus gazella* at Cape Shirreff, Livingston Island. Seventh SCAR Biology Symposium (in press).

Costa, D. P., Kretzmann, M. and Thorson, P. H. (1989b). Diving pattern and energetics of the Australian sea lion, *Neophoca cinerea*. *Am. Zool.* **29**, 71A.

Costa, D. P. and Trillmich, F. (1988). Mass changes and metabolism during the perinatal fast: a comparison between Antarctic and Galapagos fur seals. *Physiol. Zool.* **61**, 160–169.

Crocker, D. E., Gales, N. J. and Costa, D. P. (2000). Swimming speed and foraging strategies of New Zealand sea lions, *Phocarctos hookeri*. *J. Zool., Lond.* (in press).

Davis, R. W. and Kanatous, S. B. (1999). Convective oxygen transport and tissue oxygen consumption in Weddell seals during aerobic dives. *J. Exp. Biol.* **202**, 1091–1113.

Gales, N. J. and Fletcher, D. J. (1999). Abundance, distribution and status of the New Zealand sea lion, *Phocarctos hookeri*. *Wildl. Res.* **26**, 35–52.

Gales, N. J. and Mattlin, R. H. (1997). Summer diving behavior of lactating New Zealand sea lions, *Phocarctos hookeri*. *Can. J. Zool.* **75**, 1695–1706.

Gales, N. J. and Mattlin, R. H. (1998). Fast, safe, field-portable gas anesthesia for otariids. *Mar. Mammal. Sci.* **14**, 355–361.

Gentry, R. L., Costa, D. P., Croxall, J. P., David, J. H. M., Davis, R. W., Kooyman, G. L., Majluf, P., McCann, T. S. and Trillmich, F. (1986). Synthesis and conclusions. In *Fur seals: Maternal Strategies on Land and at Sea* (ed. R. L. Gentry and G. L. Kooyman), pp. 220–264. Princeton, NJ: Princeton University Press.

Houston, A. L. and Carbone, C. (1992). The optimal allocation of time during the diving cycle. *Behav. Ecol.* **3**, 256–265.

Kleiber, M. (1975). *The Fire of Life: An Introduction to Animal Energetics*. Huntington: R. E. Krieger Publishing Co.

Kooyman, G. L. (1989). Diverse divers: physiology and behavior. In

Zoophysiology Series, vol. 23 (ed. K. Johansen and D. S. Farner). Berlin: Springer-Verlag.

Kooyman, G. L., Castellini, M. A., Davis, R. W. and Maue, R. A. (1983). Aerobic dive limits of immature Weddell seals. *J. Comp. Physiol.* B **151**, 171–174.

Kooyman, G. L., Kerem, D. H., Campbell, W. B. and Wright, J. J. (1971). Pulmonary function in freely diving Weddell seals, *Leptonychotes weddelli*. *Respir. Physiol.* **12**, 271–82.

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.* B **138**, 335–346.

Lenfant, C., Johansen, K. and Torrance, J. D. (1970). Gas transport and oxygen storage capacity in some pinnipeds and the Sea Otter. *Respir. Physiol.* **9**, 277–286.

Lifson, N. and McClintock, R. (1966). Theory of use of the turnover rates of body water for measuring energy and material balance. *J. Theor. Biol.* **12**, 46–74.

Nagy, K. A. (1980). CO_2 production in animals: analysis of potential errors in the doubly labeled water method. *Am. J. Physiol.* **238**, R466–R473.

Nagy, K. A. and Costa, D. P. (1980). Water flux in animals: analysis of potential errors in the tritiated water method. *Am. J. Physiol.* **238**, R454–R465.

Ortiz, C. L., Costa, D. P. and LeBoeuf, B. J. (1978). Water and energy flux in fasting weaned elephant seal pups (*Mirounga angustirostris*). *Physiol. Zool.* **51**, 166–178.

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 P_{O_2}'s and blood and muscle oxygen stores. *Physiol. Zool.* **66**, 732–749.

Ponganis, P. J., Kooyman, G. L., Winter, L. M. and Starke, L. N. (1997). Heart rate and plasma lactate responses during submerged swimming and trained diving in California sea lions, *Zalophus californianus*. *J. Comp. Physiol.* **167**, 9–16.

Scholander, P. F., Irving, L. and Grinnell, S. W. (1942). Aerobic and anaerobic changes in seal muscles during diving. *J. Biol. Chem.* **142**, 431–440.

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.

Speakman, J. R. (1997). *Doubly Labelled Water: Theory and Practice*. London: Chapman & Hall.

Trillmich, F. (1996). Parental investment in pinnipeds. In *Advances in the Study of Behavior*, vol. 25, *Parental Care*: *Evolution, Mechanisms and Adaptive Significance* (ed. J. S. Rosenblatt and C. T. Snowdon), pp. 533–577. San Diego, London: Academic Press, Inc.

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

Ydenberg, R. C. and Clark, C. W. (1989). Aerobiosis and anaerobiosis during diving by western grebes: an optimal foraging approach. *J. Theor. Biol.* **139**, 437–449.