ENERGETICS OF A BENTHIC DIVER: SEASONAL FORAGING ECOLOGY OF THE AUSTRALIAN SEA LION, *NEOPHOCA CINEREA*

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Abstract. This research examines the foraging energetics and diving behavior of the Australian sea lion, *Neophoca cinerea*. We examine whether the foraging ecology of the Australian sea lion is typical for an animal that has evolved to exploit benthic habitats. Such a strategy is in marked contrast to those utilized by some seabirds and other pinnipeds that feed in the midwater, where travel and search components of the time at sea become more important. Onshore and at-sea field metabolic rates (FMR) were measured using doubly labeled water in lactating sea lions at Kangaroo Island, South Australia, during the winter of 1988 (early lactation, breeding season 1) and the summer of 1990 (early lactation, breeding season 2). Dive behavior was also measured with dataloggers during these seasons, as well as in the summer of 1991 (late lactation, breeding season 2). The foraging behavior of *Neophoca cinerea* indicated that it works hard to exploit benthic habitats in the waters around its breeding site. Sea lions maximized time spent at or near the benthos, with 61% of each dive and 35% of their time at sea being spent at the deepest 20% of the dives. The dive pattern was characterized by almost continuous diving when at sea, with 57.9% of their time at sea spent at depths ≥ 6 m, and dive rates of 10.7 dives/h. Mean surface intervals (1.0–1.9 min) accounted for only 42% of mean dive durations (2.2–4.1 min). Mean dive depths ranged from 41.5 m to 83.1 m, with maximum dives ranging from 60 m to 105 m. The energetic costs of this strategy are high when compared with those of other otariids: the mean at-sea FMR was 7.05 $\pm$ 0.99 W/kg. We report seasonal variability in foraging energetics and dive behavior that is likely to be sensitive to regional oceanography, the maintenance costs of female sea lions and their offspring, and the distribution and behavior of their prey. Further, we note that Australian sea lions are functionally adapted to benefit from benthic foraging strategies because their larger size and insulating blubber convey an advantage over the generally smaller sympatric fur seals that would have a decrease in air/fur insulation with compression at deeper depths and would experience greater water infiltration of the fur with longer dives.

Key words: aerobic dive limit; Australian sea lion; benthic foraging; diving behavior; doubly labeled water; foraging ecology; foraging energetics; fur seals; interannual variability; Neophoca cinerea; *sea lions; seasonality.*

INTRODUCTION

Foraging strategies of air-breathing marine vertebrates develop as dynamic relationships among energetic requirements, environmental characteristics, and functional performance (e.g., swimming speed, duration of breath holding, and depth of dives) (Kooyman 1989, Costa 1991, 1993). Thus, each marine predator must decide how, when, and where, within a three-dimensional water space, to acquire its prey. Within this context there appear to be two distinct foraging strategies employed by air-breathing marine predators: benthic and epipelagic (midwater) feeding. Functional characteristics define the differences between these approaches. If the prey that is being sought exists on, or near, the benthos, then searching for prey does not commence until the animal has already invested the cost of transport to the deepest point of the dive. By contrast, epipelagic feeders target prey that move within the water column and the entire dive can contribute to the search effort. Consequently, compared to epipelagic feeders, benthic divers spend more time submerged, a greater proportion of each dive at the deepest component of the dive, and more commonly utilize or exceed their available oxygen stores (aerobic dive limit, ADL).

A variety of species exemplify this pattern in nature by utilizing both benthic and epipelagic strategies: Blue-eyed Shags, *Phalacocorax atriceps* (Croxall et al. 1991), North Atlantic Cormorants, *Phalacrocorax carbo* and Shags, *Phalacrocorax aristotelis*, (Gremillet et al. 1998), Rockhopper Penguins, *Eudyptes chrysocome* (Tremblay and Cherel 2000), King Penguins, *Aptenodytes patagonicus* (Cherel et al. 1996), Emperor Penguins, *Aptenodytes forsteri* (Kirkwood and Robert-

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son 1997, Rodary et al. 2000), and northern fur seals, *Callorhinus ursinus* (Loughlin et al. 1987, Goebel et al. 1991). Other marine vertebrates tend to specialize and exhibit predominately epipelagic or benthic foraging. The family Otariidae (fur seals and sea lions) provides a good example of this. Fur seals typically demonstrate a diurnal epipelagic foraging strategy (Gentry and Kooyman 1986, Feldkamp et al. 1989, Ponganis et al. 1990, 1992, Goebel et al. 1991, Boyd and Croxall 1992, Boyd et al. 1994, 1995, Harcourt et al. 1995, Horning and Trillmich 1997, 1999, Mattlin et al. 1998, Boyd 1999, Georges et al. 2000). Sea lions, particularly those in the southern hemisphere, more commonly feed at or near the benthos with little or no diurnal variation (Werner and Campagna 1995, Gales and Mattlin 1997, Thompson et al. 1998). Although the energetic and physiological parameters of each species, along with geographical and stochastic variations in three-dimensional prey distribution and behavior, lead to some exceptions and variations to these models, they provide a framework to examine the determinants of otariid foraging strategies.

An essential component of understanding foraging strategies is the measurement of energetic cost in relation to foraging behavior. In only two species of penguin and in two species of otariids have there been concurrent measurements of diving behavior with metabolic cost: King Penguins (Kooyman et al. 1992), Adelie Penguins, *Pygoscelis adeliae* (Chappell et al. 1993), Antarctic fur seals, *Arctocephalus gazella* (Arnould et al. 1996, Costa et al. 2000), and New Zealand sea lions, *Phocarctos hookeri* (Costa and Gales 2000). Differences between benthic and epipelagic foraging strategies were well illustrated in the otariid studies. Antarctic fur seals made shallow, short, nocturnal dives, routinely diving to mean depths of only 19 m and remaining submerged for 1.1 min (Arnould et al. 1996, Costa et al. 2000). In contrast, the New Zealand sea lions made deep, long dives to depths of well over 100 m for mean durations of 3.4 min. Field metabolic rate (FMR) in Antarctic fur seals increased with trip duration and declined as diving effort and the percentage of time spent diving increased. Not surprisingly, for such a shallow diver, FMR did not vary with dive duration or depth (Arnould et al. 1996). In contrast, the FMR of New Zealand sea lions increased as the percentage of time spent diving increased (New Zealand sea lions spent 2–4 times more time at sea diving), but it did not vary with trip duration (Costa and Gales 2000).

Variations in FMR that correspond to diving pattern may well reflect the differences between animals that forage on highly patchy but dense prey resources (Antarctic fur seal) vs. benthic foragers with a more predictable and less patchy prey resource (New Zealand sea lion). Because swimming near the surface is more costly than swimming through the water column (Costa and Williams 2000), fur seals trade off the benefits of exploiting concentrated prey patches with the costs of travel in order to search for them (Boyd et al. 1995, Boyd 1996). Conversely, sea lions balance their energy budget by maximizing their time at the benthos (bottom time of the dive) where prey are available. Despite the different strategies, comparison of mass-adjusted FMRs between New Zealand sea lions and Antarctic fur seals indicates that, overall, they had similar rates of energy expenditure while at sea. These similarities imply that otariids may operate within a narrow range of FMRs (Costa and Gales 2000).

The Australian sea lion is particularly interesting because it represents an outlier within the behavioral range of the otariids. This rare endemic, which numbers ~10 000 animals (Gales et al. 1994), is a non-annual, nonsynchronous, colonial breeder. The typical breeding season is 17.6 mo long and occurs at different times of year at different colonies (Higgins 1993, Higgins and Gass 1993, Gales et al. 1994, Gales and Costa 1997). Gales et al. (1994) and Gales and Costa (1997) hypothesized that this reproductive strategy evolved principally because the animals live in an area where marine resources are limited, but show little seasonal fluctuations. Studies of the foraging energetics of this species would be essential to further examine this hypothesis.

In the present study, we measured the seasonal foraging energetics and diving behavior of the Australian sea lion (*Neophoca cinerea*) and compared these data with those previously published for other otariids to test where this species fits within the benthic vs. epipelagic foraging patterns. We then considered the ecological implications of their foraging strategies. This paper provides the first investigation of the foraging energetics and dive behavior of the Australian sea lion and the first investigation of any otariid to examine seasonal variation in both of these parameters.

MATERIALS AND METHODS

Study area

Fieldwork was conducted at Seal Bay, Kangaroo Island, South Australia (35°41′ S, 136°53′ E; Fig. 1) during the austral winter of July–August 1988 (early lactation, breeding season 1) and the austral summers of February 1990 (early lactation, breeding season 2) and 1991 (late lactation, breeding season 2). Approximately 180 pups are born in the Seal Bay region each breeding season. Although this is a relatively small pup production by the standards of most polygynous pinnipeds, it is the fourth largest for this endemic species (Gales et al. 1994). Because a managed tourism industry has operated at this colony for many years, with up to 100 000 people per annum visiting the sea lions at the main Seal Bay haul-out beach, the sea lions at this colony are tolerant of human intrusions. The adjacent breeding areas (separated from the haul-out beach by rocky headlands) are off limits to tourists and
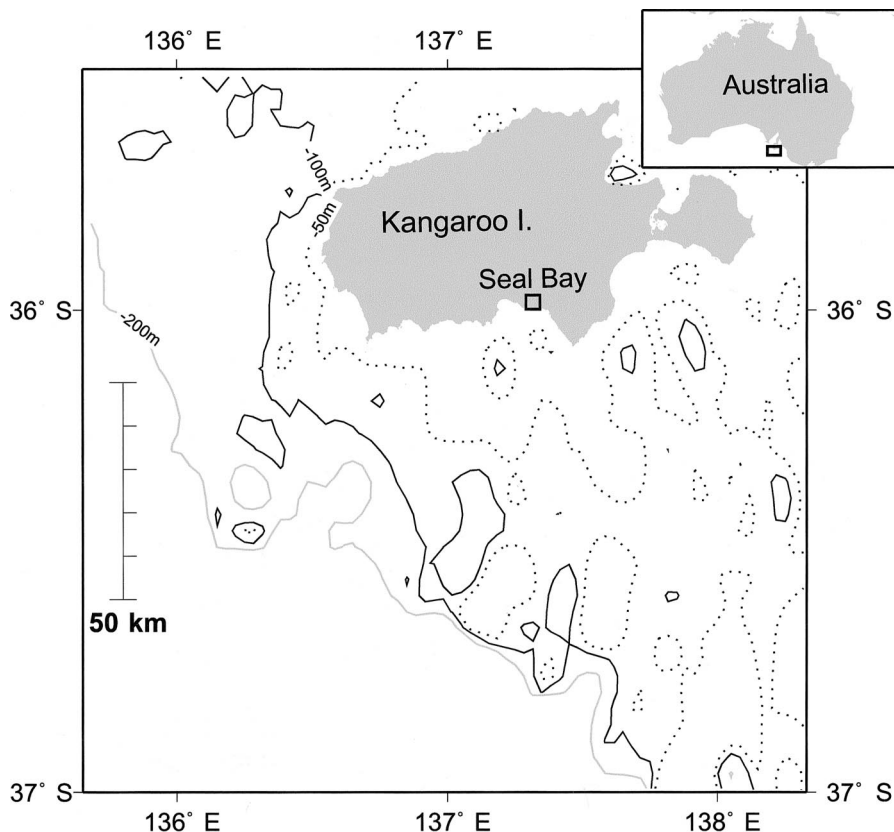
FIG. 1.   Map of Kangaroo Island, South Australia, showing the location of the Seal Bay study site along with the surrounding bathymetry. The extensive continental shelf off the Seal Bay Colony represents the area where the sea lions were foraging and is delineated by the 50-m (dotted), 100-m (solid), and 200-m (solid gray) contour lines.

represent an ideal location in which to study this species. The climate at this location is bi-seasonal, characterized by hot, dry summers and mild, wet, temperate winters. The local maritime environment consists of shallow on-shelf waters (mainly <120 m), that sustain a relatively low biological productivity (Pearce 1991).

Experimental procedure

During 1988 and 1990, at-sea (foraging) metabolism (CO_2 production) and water turnover were measured on 16 lactating sea lions (eight per season), and measured on shore, fasting (resting) metabolism in four lactating sea lions (two per season) using the doubly labeled water method (Lifson and McClintock 1966, Nagy 1980, Nagy and Costa 1980, Costa and Gentry 1986, Costa 1987, Costa et al. 1989, Speakman 1997). Concurrent with these measurements, at-sea foraging behavior was measured with time depth recorders. During 1991, only measurements of dive behavior were collected on six sea lions.

Experimental animals were selected by searching for apparently healthy females, representing a range of body masses, seen to be suckling a pup for which the parturition date was known (Higgins 1990). These pups were identified either from flipper tags or from tem-

porary pelage marks created with hair dye. When possible, females that had been ashore for at least one day, and were therefore predicted to depart on a foraging trip within 24 h, were selected. At Seal Bay, females usually depart after 1–2 d of suckling their pup (Higgins and Gass 1993). Females were captured using a specially designed hoop net (Furhman Diversified, Seabrook, Texas, USA) made from soft, strong, knotless mesh with a multilayered head end that reduces the vision of the animal but allows free breathing. Once the sea lion was in the net, the net handle was removed and the sea lion was physically restrained and placed onto a specially constructed restraint board, similar to that described by Gentry and Holt (1982). During restraint, blood (20 mL) was drawn from the lateral gluteal vein for determination of isotope background specific activity, followed by an intraperitoneal injection of between 60 and 75 mL of 15% oxygen-18 water ($H_2^{18}O$) and 2.2 MBq tritiated water (HTO) in 3 mL of sterile saline. Body mass was measured with a hanging electronic balance (±0.1 kg). After injection, females were placed in a holding cage to allow the injected isotopes to equilibrate in the body water space. An additional 10–20 mL blood sample was collected 3 h

TABLE 1. Measurement interval, mass, time at sea, water influx, and metabolic rate of Australian sea lions.

| Cow no. | Pup | | Cow body mass | | | Total body water | | | Measurement interval (d) |
	Sex	Age (d)	Initial (kg)	Final (kg)	Mean (kg)	^{18}O (L)	^{18}O (%)	HTO (L)	
A) Winter 1988									
11-88	M	57	91.1	89.1	90.1	62.2	68.2%	63.5	5.99
14-88	M	39	92.1	95.6	93.9	63.0	68.4%	64.3	4.87
18-88	?	?	77.2	76.8	77.0	52.4	67.8%	53.5	4.94
AD-88	M	30	100	88.7	94.4	60.2	60.2%	61.5	8.84
C2-88	M	45	68.5	65.3	66.9	44.4	64.8%	45.3	9.08
E-88	F	80	77.8	67.9	72.9	50.9	65.4%	52.0	6.77
K-88	M	63	85.4	81.7	83.6	56.7	66.4%	57.9	3.85
P-88	F	45	83.9	95.6	89.8	55.2	65.8%	56.4	2.92
V2-88	M	14	84	69.1	76.6	51.3	61.1%	52.4	2.96
AL-88	M	2	77.3	69.8	73.6	53.4	69.1%	54.6	5.88
Winter 1988 mean		42	83.7	80.0	63.5	63.5	65.4%	56.1	5.61
1 SD		24	9.1	11.8	9.9	6.1	2.9	5.9	2.17
B) Summer 1990									
138-90	M	23	57.1	62.5	59.8	40.2	70.3%	40.7	5.84
AD-90	F	39	87.0	91.0	89.0	58.8	67.6%	61.2	2.94
51-90	F	38	64.8	68.0	66.4	44.8	69.1%	43.5	7.20
AK-90	F	30	86.0	90.5	88.3	58.1	67.5%	62.5	6.12
C2-90	M	24	75.5	77.0	76.3	50.4	68.3%	51.6	3.64
141-90	F	13	71.0	76.5	73.8	49.0	68.9%	48.4	4.93
139-90	M	25	80.0	83.2	81.6	50.8	63.5%	52.3	3.63
102-90	F	89	62.0	66.0	64.0	40.2	64.8%	41.7	2.90
C2-90	...	...	75.4	75.5	75.5	50.3	68.3%	51.5	2.96
106-90	F	82	77.0	74.5	75.8	51.4	66.8%	52.4	1.96
Summer 1990 mean		40	73.6	76.5	75.0	49.4	67.5%	50.6	4.21
1 SD		27	9.9	9.6	9.7	6.4	2.0	7.4	1.71

Note: Ellipses indicate that no data were available.
† Calculations from Nagy (1980) and Speakman (1997).
‡ Field metabolic rate (FMR) was calculated using both the equations from Nagy (1980) that correct for changes in total body water only and the two-pool model of Speakman (1997) that corrects for errors associated with isotope fractionation only. At-sea FMR is the FMR calculated using the equations from Nagy (1980) and then correcting for the percentage of time spent on shore.

after injection to determine isotope concentrations at the start of the experimental period.

Simultaneous with the isotopic measurements, time depth recorders (TDRs) were deployed on the females to assess diving behavior (Costa 1988). Wildlife Computers (Redmond, Washington, USA) Mk 3 TDRs were used to measure diving pattern. A radio transmitter (Advanced Telemetry Systems, Bethel, Minnesota, USA) was attached to the TDR by a stainless steel hose clamp. A plastic spacer was placed between the TDR and a metal plate, and these were held together with a hose clamp. The metal plate was then glued to the pelage on the female's mid-dorsal area using a marine epoxy resin (Ten-set Evercoat, Anaheim, California, USA). The MK3 TDRs were housed in a 149 mm long, 26.5 mm diameter aluminum tube and weighed 136 g. They were capable of recording depths to 250 m with 2-m resolution. TDRs were set to sample depth every 10 s. The arrival and departure of females were then monitored with a scanning telemetry receiver (Telonics, Mesa, Arizona, USA) interfaced to an Esterline Angus strip chart recorder (Esterline Angus, Rochester, New York, USA). Females were recaptured as soon as possible after returning from a foraging trip. Upon re-

capture, body mass was recorded, blood samples were taken, and the TDR was retrieved.

Data analysis: energetics

Total body water (TBW) was determined by the initial dilution of HTO and $H_2^{18}O$ (Nagy and Costa 1980). TBW determined by dilution of $H_2^{18}O$ was used in calculations of CO_2 production, with the exception of 1988 data. In 1988, TBW and was only determined by the initial dilution of HTO and was then adjusted by 2.13% to account for the overestimate in water space by HTO compared to $H_2^{18}O$ (Table 1). Final TBW was calculated as the final mass times the initial TBW water : mass ratio.

Tritium specific activity was determined by scintillation spectrometry of triplicate aliquots of 300 µL pure water (vacuum distilled from the serum samples) in 10 mL of Betaphase liquid scintillation cocktail (Westchem, San Diego, California, USA). The specific activity of $H_2^{18}O$ was determined by mass ratio spectrometry (1988 by Global Geochemistry, Canoga Park, California, USA; 1990 Metabolic Solutions, Nagog, Massachusetts, USA) of pure water distilled from plasma samples. CO_2 production was calculated using Eq.

TABLE 1. Extended.

Time at sea (%)	H$_2$O (mL·kg^{-1}·d^{-1})	CO$_2$ production†		Field metabolic rate‡		
		Nagy (mL·g^{-1}·h^{-1})	Speakman (mL·g^{-1}·h^{-1})	Nagy (W/kg)	Speakman (W/kg)	At sea (W/kg)
47.8%	119.6	0.747	0.625	4.90	4.10	7.48
46.3%	96.0	0.744	0.654	4.88	4.29	7.53
36.9%	106.0	0.823	0.708	5.39	4.64	8.52
40.2%	78.2	0.600	0.491	3.93	3.22	6.89
44.3%	96.4	0.786	0.665	5.15	4.36	7.91
40.3%	87.8	0.678	0.546	4.44	3.58	7.40
38.4%	85.6	0.763	0.651	5.00	4.27	8.05
54.0%	120.6	0.784	0.709	5.14	4.65	7.41
0.0%	8.2	0.355	0.298	2.57	2.16	
0.0%	7.6	0.360	0.317	2.61	2.30	
43.5%	98.8	0.741	0.631	4.85	4.14	7.65
5.7%	15.6	0.071	0.076	0.46	0.50	0.50
55.7%	135.3	0.927	0.823	6.08	5.39	7.53
68.0%	163.2	0.891	0.764	5.84	5.01	7.03
72.3%	164.4	0.775	0.631	5.08	4.14	6.11
65.4%	100.0	0.726	0.656	4.76	4.30	6.04
72.4%	131.3	0.733	0.613	4.80	4.02	5.83
76.4%	96.4	0.664	0.578	4.35	3.79	5.26
69.4%	145.9	0.695	0.580	4.56	3.80	5.67
82.5%	180.4	1.153	1.016	7.56	6.66	8.21
0.0%	7.7	0.390	0.353	2.83	2.56	
0.0%	15.7	0.371	0.333	2.69	2.41	
70.3%	139.6	0.821	0.708	5.38	4.64	6.46
7.9%	30.2	0.163	0.152	1.07	1.00	1.02

3 of Nagy (1980), which assumes an exponentially changing body water pool. For comparison, CO$_2$ production was also calculated using the two-pool model presented in Speakman (1997). Water influx was calculated using Eqs. 5 and 6 in Nagy and Costa (1980), assuming an exponentially changing body water pool. Given that the diet of Australian sea lions is not well known, we used a conversion factor determined for California sea lions of 23.6 kJ/L CO$_2$ to convert CO$_2$ production to energy consumption. This assumes that all of the fat and protein contained in the diet is oxidized, and that fat metabolism yields 26.81 kJ/L CO$_2$ produced and protein metabolism yields 22.97 kJ/L CO$_2$ (Costa 1987). The composition of the diet of California sea lions is 80.3% water, 1.3% fat, 16.7% protein, and 3.75 kJ/g energy (Costa et al. 1990). We assumed that the four animals that did not go to sea were fasting and were exclusively metabolizing fat. For these animals, an energy conversion factor of 26.81 kJ/L CO$_2$ was used.

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 portion of time and, hence, FMR spent on shore. Time on shore was calculated as the portion of the measurement interval where the animal's radio signal was detected or data on arrival and departure were taken from the TDR record. Onshore FMR for each animal was taken as the mass-corrected rate determined from mean values for the four females that did not go to sea.

In order to calculate at-sea FMR (and thus remove the onshore metabolic component) the data were normalized by plotting FMR data (containing both onshore and at-sea components) as a function of the percentage of time spent at sea (Fig. 2). A least squares linear regression was then calculated for summer and winter data separately. The regression equations were used to predict the FMR for each animal at their respective percentage of time spent at sea. The difference (residual) between the predicted and actual FMR was then added to the extrapolated FMR where the animals had spent all of their time at sea (Fig. 2; Costa et al. 2000).

Data analysis: diving behavior

Wildlife Computers Dive Analysis software (Redmond, Washington, USA) was used for analysis. Dives <6 m were considered to be nonforaging dives primarily associated with travel or rest and were not analyzed. Because the resolution of the instruments was 2 m, this stratification removed potential resolution errors. The maximum depth considered to be at the surface was 4 m. Bottom time was defined as the time the sea lion spent at depths exceeding 80% of the maximum depth of the dive. Rates of descent and ascent were
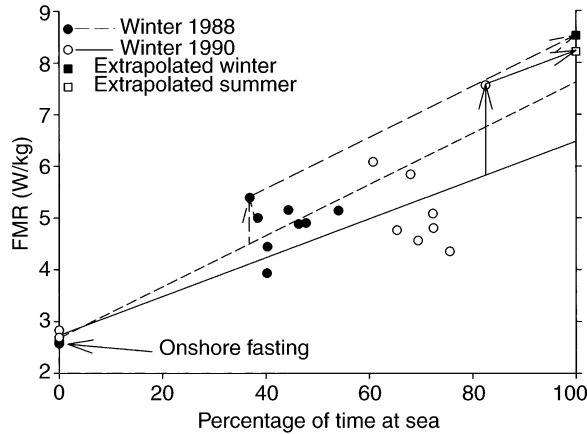
FIG. 2. Relationship between field metabolic rate (FMR) measured during winter 1988 and summer 1990 and percentage of time at sea for lactating Australian sea lions. Least-squares linear regressions for the two seasons are shown. Estimates for at-sea FMR were calculated by adding the residual of each animal's FMR value to the value predicted if animals spent 100% of their time at sea. The two arrows demonstrate this extrapolation for two points (winter 1988 and summer 1990). Note that the data points at 0% of time at sea represent animals that spent all of their measurement period fasting on shore.

calculated from the start point of the dive to the beginning of the bottom time and the end point of bottom time to the end point of the dive, respectively. Surface interval was measured as the time between dives of ≥ 6 m. Foraging trips were characterized by almost continuous diving with very few surface intervals exceeding ~30 min. These few, longer intervals were contained within the uppermost percentile of surface intervals and seemed to separate the major bouts of diving. They were presumably associated with travel or extended rest. Consequently, because we are interested in analyzing the interdive intervals for the majority of dives, intervals greater than the 99th percentile were excluded from analysis for the summary statistics data. All surface interval data were analyzed for all other parameters.

Time at sea was determined from dive records and was measured from when the animal entered the water to when it subsequently hauled out. These measurements were corroborated with telemetry records and direct observations of the animals ashore. The percentage of time spent diving was defined as the percentage of time at sea that the animal spent at depths of ≥ 6 m. As a further measure of foraging effort, we determined the minimum distance that the sea lion must have traveled per hour to execute all dives. This was achieved by summing the doubled maximum depths for each dive and dividing the result by the hours.

Estimates of minimum distance traveled to modal and maximum dive depths were made by measuring the distance to the closest equivalent depth from marine chart AUS 346 dated 1997 (Australian Hydrographic

Office, Wollongong, New South Wales, Australia; Fig. 1). Depth soundings south of Kangaroo Island are not comprehensive; thus, these data are only indicative.

Data analysis: combined energetics and dive data

In some cases, we were not able to obtain dive records for trips in which energetic measurements were collected (individuals P-88 and 14-88; AD-90), or for only one of several trips completed during the energetic measurement (AD-88; 51-90, 138-90). In these cases, the dive data from the most recent complete trip of that animal were used. Statistical analysis was carried out using SigmaStat 2.0 (SPSS 1997). Means were compared using a two-sample t test for normally distributed data and a Wilcoxon signed-ranks test when data failed a test for normality. Trends were tested using linear regression analysis. Differences or trends were considered significant when $P \leq 0.05$.

Aerobic dive limit calculations

Individual specific aerobic dive limit calculations (cADL, measured in minutes) were determined for sea lions in 1988 and 1990 by dividing each animal's total O_2 stores by its specific FMR, measured by doubly labeled water:

$$cADL = \text{available } O_2 \text{ stores/FMR.}$$

There were no data on FMR in 1991 to make this calculation. It is important to note that at-sea FMR integrates the costs of surface swimming, diving, and resting; therefore, the actual metabolic rate during diving could be higher or lower (Culik et al. 1996). Costa et al. (2001) report a total oxygen store for Australian sea lions of 47 mL O_2/kg, derived from measurements of blood volume, hemoglobin and myoglobin concentrations in this species, and from allometric estimates of muscle mass and lung volume.

RESULTS

Foraging energetics

Metabolic rate measurements were completed on 19 animals (1988, $n = 10$; 1990, $n = 9$). Two animals (C2-88, C2-90, and AD-88, AD-90) were sampled in both years. Three sea lions (AL-88, V2-88, 106-90) did not go to sea and were used for measurements of onshore fasting metabolism (Fig. 2). In 1990, one animal (C2-90) remained on shore prior to foraging at sea and we obtained a blood sample after three days of fasting on shore, after which she subsequently completed a normal foraging trip. We thus obtained both onshore fasting and at-sea feeding metabolic rates for this animal. Mean onshore FMR was 2.68 ± 0.11 W/kg. This is 2.3 times the predicted basal metabolic rate (BMR) for a terrestrial animal of an equivalent size (Kleiber 1975). At-sea FMR was 7.05 ± 0.99 W/kg for both years, a value that is 6.2 times the predicted BMR of an equally sized terrestrial animal. Mass change, water

TABLE 2. Energetic and dive parameters of lactating Australian sea lions compared across three seasons.

Parameter	Winter 1988	Summer 1990	Summer 1991
Pup age (d)	51	40*	417*
Overall FMR (W/kg)	4.85	5.38	...
At-sea FMR (W/kg)	7.65*	6.46*	...
Total body water (%)	65.9	67.5	...
Water influx (mL·kg^{-1}·d^{-1})	99**	140**	...
Mass change (%)	−2.25*	5.55*	...
Mass (kg)	84.5	72.9	...
Trip duration (d)	1.50**	2.30**	2.86
Dive depth (m)	68*	52*	67*
Dive duration (min)	3.4	2.97*	3.55*
Surface interval (min)	1.59	1.3	1.45
Bottom time (min)	1.92	1.85	2.08
Descent rate (m/s)	1.71*	1.44*	1.36
Ascent rate (m/s)	1.64*	1.41*	1.32
Dive effort (m/h)	1238	1226	1376
Time diving at sea (%)	52.7	58.6	60.7
Dive rate (no. dives/h)	9.23*	11.87*	10.30*

Note: Ellipses indicate that no data were available.
 * $P < 0.05$; ** $P < 0.01$.

space, metabolic rates, and water influx data for all animals are presented in Table 1.

Relative mass change increased significantly with increasing water influx in 1988 ($P = 0.035$, $r^2 = 0.30$) and for 1988 and 1990 combined ($P = 0.027$, $r^2 = 0.55$), but was not significant in 1990. Relative mass change was significantly increased with increased trip duration in 1990 ($P = 0.012$, $r^2 = 0.82$). For both years combined, water influx (which can be used as a proxy of food intake; Costa 1987) significantly increased as trip duration increased ($P = 0.009$, $r^2 = 0.44$). There was a trend between the at-sea FMR and the trip duration for both years combined ($P = 0.052$, $r^2 = 0.28$). Surprisingly, there was no relationship between FMR and water influx or between FMR and relative mass change. In 1990, FMR was significantly correlated with pup age (FMR, $P = 0.030$, $r^2 = 0.57$), as was water influx ($P = 0.040$, $r^2 = 0.53$).

We examined seasonal effects on energy expenditure between winter (1988) and summer (1990), controlling for stage of lactation (early lactation in both years). At-sea FMR was significantly greater during winter than summer ($P = 0.01$, $t_{14} = -2.962$), whereas water influx ($P = 0.004$, $t_{14} = 3.384$), relative mass change ($P = 0.025$, $t_{14} = 2.51$), and trip duration ($P = 0.006$, $t_{12} = 3.372$) were significantly lower in winter. Table 2 presents a summary of seasonal relationships across a wide range of energetics and diving behavior parameters.

Dive behavior

Dive records were obtained for only four of eight animals that went to sea in 1988 and seven of eight animals that went to sea in 1990. All six animals that were sampled for diving behavior in 1991 returned records.

Trips to sea were characterized by almost continuous diving, with few extended surface intervals. Diving occurred at all times of day and night, without any apparent diurnal pattern in any year (Fig. 3). Typical dive shapes for 1988 and 1990, shown in Fig. 4, reveal a pattern of apparent benthic diving. This interpretation is made on the basis that (1) a substantial percentage of each dive was spent at the bottom of the dive, (2) consecutive dives were to strikingly similar depths, (3) there was a lack of diurnal variation, and (4) the depths were consistent with those of the adjacent shelf waters. During a foraging trip, the maximum dive depths appeared to track the benthos (Fig. 5).

While at sea, the sea lions spent 57.9% of their time diving (≥ 6 m), accomplishing an average of 10.7 dives/h. Based on available bathymetric charts, we calculated that on any given foraging trip, sea lions traveled at
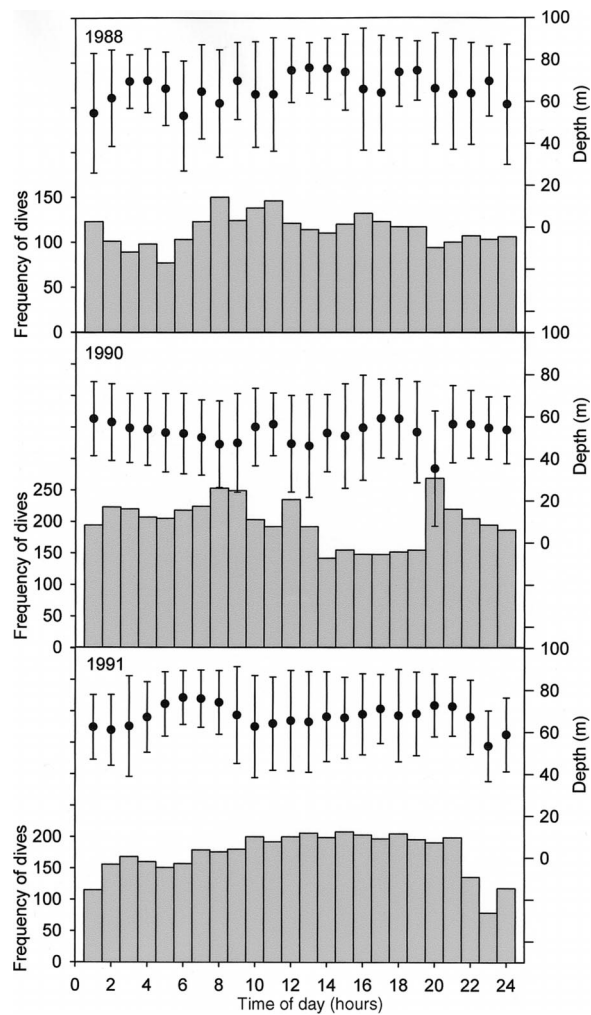

FIG. 3. No significant diurnal pattern existed between the frequency distribution of dives (histogram) and dive depths (mean ± 1 SD) of lactating sea lions for the field seasons in 1988, 1990, and 1991. Time of day is based on a midnight (0 = 0000 hours) to midnight (24 = 2400 hours) schedule.
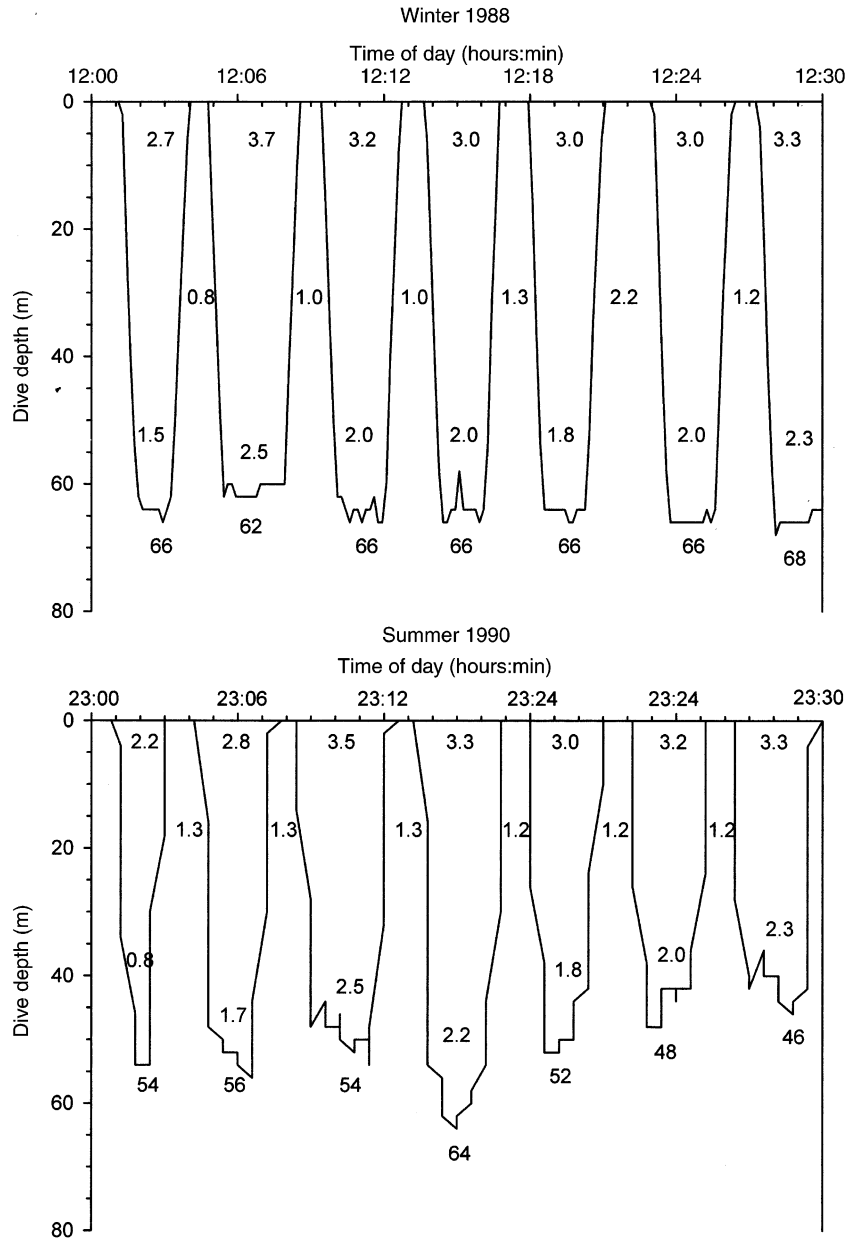
Fig. 4. An illustration of a time scale of dive depth for typical dives for an individual sea lion C2 in winter 1988 (C2-88) compared with summer 1990 (C2-90). Each dive is annotated with dive duration in minutes (number at the top and within each dive), bottom time in minutes (number at the bottom and within each dive), maximum dive depth in meters (number below each dive), and surface interval in minutes (number between dives).

least an average of 25 km (range 8–42 km) to areas in order to achieve modal dive depths and traveled 37 km (range 21–56 km) to areas where maximum dives were undertaken (Table 3). The mean dive depth for all sea lions was 61 m, with an average maximum depth of 86 m. The deepest dive was 105 m. The average dive duration was 3.3 min, with a mean maximum duration of 6 min. The longest dive lasted 8.3 min. On average, the sea lions spent 61% of each dive as bottom time. The surface interval (mean = 1.4 min) was only 42% of the mean dive duration (Table 4).

Analysis of mean dive statistics from all years revealed that dive duration was significantly correlated with dive depth ($P = 0.002$, $r^2 = 0.49$), bottom time ($P = 0.0001$, $r^2 = 0.83$; Fig. 6), and dive rate ($P = 0.028$, $r^2 = 0.28$). Dive depth was not correlated with bottom time or surface interval, but was correlated with dive rate ($P = 0.001$, $r^2 = 0.57$); deeper diving sea lions made fewer dives per hour. Mean bottom time was not correlated with mean surface interval, but was correlated with the percentage of time spent diving ($P = 0.030$, $r^2 = 0.28$). Dive rate was correlated with
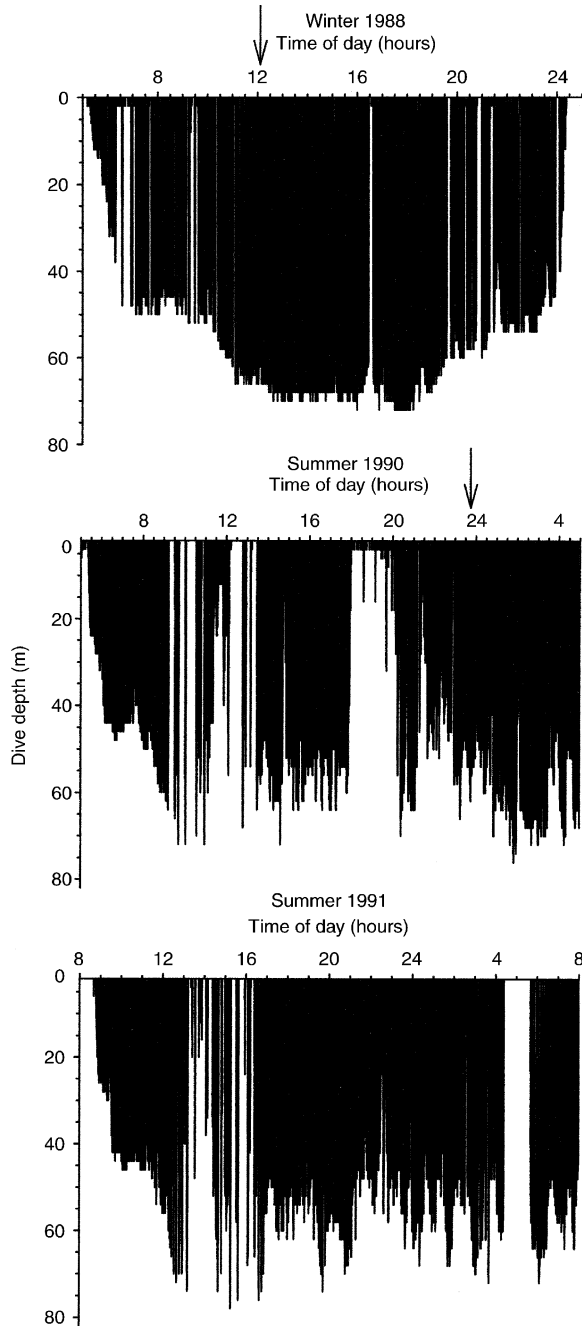
FIG. 5. An illustration of dive patterns for an individual sea lion C2 for the three field seasons (C2-88 winter 1988, C2-90 summer 1990, C2-91 summer 1991) using a more condensed time scale than in Fig. 4. The dive pattern for winter 1988 represents all dives during a trip to sea and demonstrates how maximum dive depths appear to track the increasing and then decreasing depths as the animal leaves and returns to the breeding location. Dive patterns for the other two seasons are dives for incomplete trips to sea. Arrows mark the time at which the dives illustrated in Fig. 4 were selected. Hours of the day are as in Fig. 3 (8 = 0800 hours).

female mass ($P = 0.011$, $r^2 = 0.53$); larger females made fewer dives per hour. Female mass did not correlate with any other dive behavioral parameter.

Differences were also apparent using the mean seasonal dive statistics. Here we made comparisons between 1988 and 1990 for seasonal differences (controlled for lactation stage; i.e., with no significant difference in pup age between 1988 and 1990), and between 1990 and 1991 for lactation stage differences (controlled for season; i.e., both experiments were conducted in the summer month of February). During winter, animals dived deeper ($P = 0.034$, $t_9 = 2.501$) and made fewer dives per hour ($P = 0.018$, $t_9 = 2.877$) than in summer. Mean rates of descent ($P = 0.04$, $t_9 = 2.397$) and ascent ($P = 0.043$, $t_9 = -2.358$) were also greater in winter than in summer. Additionally, diving behavior varied with stage of lactation. During early lactation, sea lions dived more frequently ($P = 0.027$, $t_{11} = 2.550$), more shallowly ($P = 0.017$, $t_{11} = -2.802$), and made shorter dives ($P = 0.047$, $t_{11} = 2.241$) than during late lactation.

Foraging energetics and dive behavior

For 1988 and 1990 combined, there was no significant relationship between at-sea FMR and dive duration, bottom time, percentage of time diving, surface interval, dive rate, or effort. The FMR to dive depth relationship approached significance ($P = 0.069$, $r^2 = 0.32$). Water influx, which is an index of prey consumption, was significantly correlated with percentage of time spent diving ($P = 0.021$, $r^2 = 0.46$; Fig. 7). During 1988, water influx was significantly correlated with mass change ($P = 0.0351$, $r^2 = 0.55$).

Aerobic dive limit

The cADLs for the sea lions in this study had a range of 1.9–3.0 min, with a mean of 2.3 min. Mean dive durations exceeded these cADLs in all but one case (individual 141-90) by a mean of 38%. On average, 79.4% of the sea lions' dives exceeded their cADL (Table 5, Fig. 8).

During winter (1988), the percentage of dives that exceeded the cADL of the sea lions was significantly greater than in the summer (1990; Mann-Whitney Rank Sum Test, $P = 0.006$, $t = 38$). The percentage of dives that exceeded cADL was highly correlated with bottom time ($P = 0.0013$) and significantly correlated with depth ($P = 0.045$, $r^2 = 0.38$).

DISCUSSION

The foraging pattern of the Australian sea lion is consistent with that of a typical benthic hunter; dives are long, relatively deep, to consecutively similar depths, show no diurnal pattern, and maximize bottom time (at least half of the dive is spent near maximum depth). Seasonal and lactational variation in foraging behavior and energetics are evident. The diet of the Australian sea lion supports the interpretation of ben-

TABLE 3. Time at sea, number of dives, percentage of time diving, dives per hour, minimum dive distance per hour, and estimates of the minimum distance traveled to modal and maximum dive depth for lactating Australian sea lions.

Cow no.	Time at sea (h)	No. dives	Diving time (%)	No. dives/h	Dive distance/h (m)	Modal dive depth (km)	Maximum dive depth (km)
						Minimum distance	
AD-88	85.2	818	53.4	9.6	1186	23	38
C2-88	73.4	804	55.8	10.9	1209	22	24
P-88	69.3	655	63.8	9.4	1571	34	56
14-88	66.0	459	37.6	7.0	986	35	42
138-90	84.8	990	55.1	11.7	1302	42	46
AD-90	67.1	622	60.9	9.3	1230	21	44
C2-90	63.2	753	55.5	11.9	1150	15	27
102-90	57.1	673	60.6	11.8	1350	24	36
139-90	44.8	579	63.7	12.9	1079	16	19
141-90	21.3	250	43.3	11.7	1243	24	27
51-90	67.0	924	71.1	13.8	1226	8	21
106-91	62.2	682	64.1	11.0	1583	41	49
141-91	74.6	743	59.2	10.0	1353	27	31
158-91	58.9	589	58.6	10.0	1504	31	49
114-91	94.3	932	61.9	9.9	1534	27	59
167-91	49.7	481	65.6	9.7	1160	23	31
C2-91	66.4	744	54.7	11.2	1119	16	24
Mean	65.0	688.1	57.9	10.7	1281	25	37
1 SD	16.8	187.4	8.1	1.6	178	9	12

thic feeding, with a diet including octopus, cuttlefish, squid, lobster (*Jasus* sp.), benthic elasmobranchs, and a variety of demersal teleosts (King 1983, Gales and Cheal 1992, Ling 1992).

Benthic hunters need to maximize the time they spend at the benthos. At the scale of the single dive, this requires the utilization of strategies and mechanisms that minimize the time and cost of transport to and from the water surface. At the scale of a foraging trip, an animal must maximize the percentage of its overall time at sea spent diving relative to time spent surface swimming (Boyd 1996, Costa and Williams 2000). Consistent with this, Australian sea lions invest almost 60% of their time at sea diving, during which they dive at a rate of 10.7 dives/h. Bottom time accounts for 35% of the time at sea (60.1% of each dive). An important component of the Australian sea lion's benthic foraging strategy is to maintain bottom time independent of depth. This is achieved by increasing the overall duration of the dive as the animal forages deeper (Fig. 7). Similar benthic diving patterns have also been described in other marine predators. Among

TABLE 4. Summary statistics for dive depth, duration, bottom time, surface interval, and descent and ascent rates for lactating Australian sea lions.

Cow no.	Depth (m)					Duration (min)				
	Mean	1 SD	Median	Mode	Maximum	Mean	1 SD	Median	Mode	Maximum
AD-88	61.7	20.5	68	72	86	3.3	1.2	3.5	3.8	6.2
C2-88	54.9	16.8	60	68	76	3.0	0.9	3.2	3.2	5.2
P-88	83.1	21.2	88	84	104	4.1	1.0	4.2	4.0	6.7
14-88	70.9	25.8	82	82	90	3.2	1.1	3.5	3.3	5.2
138-90	56.1	23.6	54	90	96	2.8	1.1	3.0	3.2	6.0
AD-90	66.2	16.9	68	66	92	3.9	1.2	4.2	4.2	6.5
C2-90	47.4	15.7	50	50	78	2.8	0.9	2.8	2.8	4.7
102-90	57.2	21.9	64	76	84	3.1	1.1	3.3	3.3	5.5
139-90	41.5	18.2	50	52	60	2.9	1.2	3.2	3.5	6.0
141-90	52.2	27.0	74	76	78	2.2	1.7	2.7	0.5	5.0
51-90	44.5	9.2	44	42	66	3.1	0.7	3.1	3.0	5.2
106-91	70.1	23.4	82	88	102	3.4	1.0	3.5	4.0	6.8
141-91	68.0	15.3	76	77	80	3.6	0.7	3.5	3.5	7.0
158-91	75.1	17.7	80	80	102	3.5	0.7	3.5	3.3	5.5
114-91	77.6	19.0	81	77	105	3.8	1.0	3.8	4.0	8.3
167-91	59.9	14.8	63	72	80	4.1	0.9	4.2	4.5	6.8
C2-91	49.9	14.0	52	52	76	2.9	0.9	3.0	3.0	5.7
Mean	61.0		67	71	86	3.3		3.4	3.4	6.0
1 SE	12.1		14	14	13	0.5		0.5	0.9	0.9

this group, some species demonstrate almost exclusive benthic foraging. For example, the southern sea lion, which dives to the same mean depths, spends a similar percentage of its time at sea on, or close to, the benthos (29%) (54.7% of each dive), as well as diving at similar rates (11–19/h) and having a similar percentage (53%) of submerged time (Werner and Campagna 1995, Thompson et al. 1998). Another example is the deeper diving New Zealand sea lion, which compensates for the additional cost of traveling to the deeper benthos by utilizing additional strategies for defending bottom time (22% of time at sea, 50.6% of each dive; Gales and Mattlin 1997, Costa and Gales 2000, Crocker et al. 2001), such as a faster descent (25% greater than for Australian sea lions) achieved through ''burst and glide'' locomotion (Crocker et al. 2001). This allows faster transit times in deeper dives without increases in energy expenditure (Costa and Gales 2000). Such a mechanism may also be utilized by Australian sea lions that had faster transit rates during deeper dives.

Two fur seal species are also regular benthic feeders. The Australian fur seal (*Arctocephalus pussilus doriferus*) feeds almost exclusively on the benthos (Arnould and Hindell 2001), whereas its conspecific, the South African fur seal (*Arctocephalus pussilus pussilus*), feeds exclusively in the water column (Gentry and Kooyman 1986). The northern fur seal switches between bouts of benthic and epipelagic foraging within and between foraging trips (Gentry and Kooyman 1986, Goebel et al. 1991).

Benthic diving patterns have also been observed for some sea birds. For example, the Blue-eyed Shag spends 42.7% of its foraging time underwater, dives at a rate of 5.1 dives/h, and bottom time is 47% of each dive (Croxall et al. 1991). Great Cormorants spend 40% of their time at the bottom of the dive (Gremillet et al.
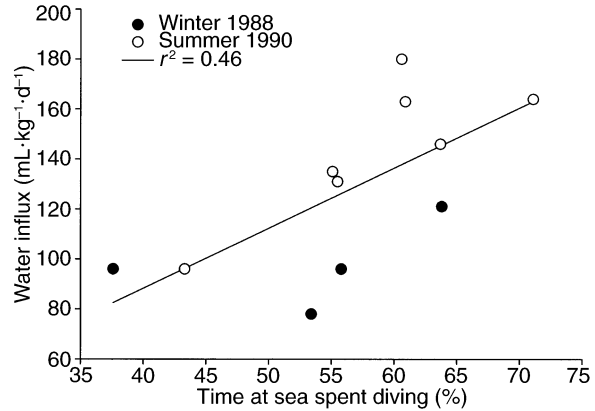

FIG. 6. The relationship between the percentage of time that lactating Australian sea lions spent diving in winter 1988 and summer 1990 and the water influx ($mL \cdot kg^{-1} \cdot d^{-1}$). A highly significant least-squares linear regression was fitted to the combined data for both years ($P = 0.02$, $r^2 = 0.46$).

1999), whereas Emperor Penguins spend 35% of their time as bottom time (Rodary et al. 2000). Rockhopper Penguins spend 66.7% of each dive as bottom time (Tremblay and Cherel 2000). As was the case with the New Zealand sea lion, much of this variation is associated with water depth; the deeper diving animals (Emperor Penguins and shags) spend more time in transit.

These strategies for maximizing bottom time can also be advantageous to midwater feeders in circumstances in which prey concentrate at particular and predictable depths, such as the deep scattering layer. In such cases, the usual epipelagic strategy of searching for prey in transit is less profitable. The distinction is that the prey-rich layers move in a diurnal pattern, and this is reflected in the variation in dive depths of the

TABLE 4. Extended.

| Bottom time (min)					Surface interval (min)					Mean rate (m/s)	
Mean	1 SD	Median	Mode	Maximum	Mean	1 SD	Median	Mode	Maximum	Descent	Ascent
2.2	0.9	2.3	2.3	5.0	1.7	2.3	1.3	0.0	20.0	1.6	1.5
2.1	0.8	2.0	2.0	4.3	1.5	1.5	1.2	1.0	14.3	1.7	1.7
2.6	0.8	2.7	2.7	5.2	1.3	1.2	1.3	1.3	12.8	1.8	1.7
2.0	0.8	2.2	2.2	3.8	1.3	1.5	1.2	1.3	23.3	1.7	1.7
1.7	1.0	1.7	0.0	5.3	1.4	1.3	1.2	0.0	11.7	1.6	1.4
2.5	1.1	2.5	2.7	5.0	1.6	2.2	1.3	1.3	22.3	1.4	1.3
1.6	0.7	1.7	1.8	3.5	1.2	1.8	1.0	1.0	23.7	1.1	1.4
1.8	0.9	1.8	1.8	4.0	1.1	0.9	1.0	1.0	6.8	1.4	1.4
2.0	1.1	2.3	2.5	5.3	1.0	0.9	1.0	0.0	5.8	1.4	1.2
1.2	1.2	1.2	0.0	3.7	1.9	1.2	1.7	1.3	8.0	1.8	1.7
2.1	0.6	2.2	2.0	4.2	1.0	0.5	1.0	1.0	3.7	1.3	1.5
2.0	0.8	2.0	2.2	5.2	1.5	1.1	1.3	1.2	8.7	1.4	1.5
2.1	0.7	2.0	2.3	5.0	1.5	1.4	1.3	1.0	15.3	1.4	1.3
2.0	0.6	2.0	1.8	3.7	1.5	1.4	1.3	1.2	16.0	1.6	1.4
2.0	0.9	2.0	2.0	6.3	1.6	2.2	1.3	1.2	34.3	1.4	1.2
2.7	0.8	2.7	2.5	4.8	1.4	1.5	1.2	1.2	14.2	1.3	1.2
1.7	0.7	1.7	1.7	4.5	1.1	1.1	1.0	1.0	11.7	1.1	1.3
2.0		2.1	1.9	4.6	1.4		1.2	0.9	14.9	1.5	1.4
0.4		0.4	0.8	0.8	0.2		0.2	0.5	7.9	0.2	0.2
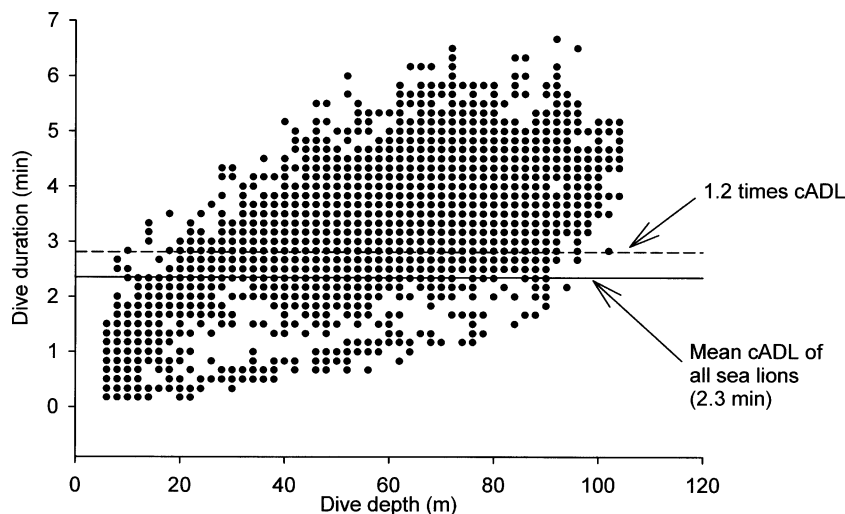
FIG. 7. The relationship between dive duration and dive depth for all dives by lactating Australian sea lions recorded in winter 1988 and summer 1990 ($n = 7527$). The mean calculated aerobic dive limit (cADL) for the sea lions is shown as a solid line to demonstrate that the majority of dives exceeded the cADL (79.4%). The dashed line is the mean cADL corrected for the likely 20% underestimate of ADL from Ponganis et al. (1997).

predators. Diurnal patterns are not a feature of benthic foragers.

Predator avoidance is also an advantage of continuous benthic diving because the amount of time spent at the surface is minimized. The great white shark (*Carcharodon carcharias*), an important predator of Australian sea lions (Ling 1992), typically attacks its prey from below (Klimley 1994). Thus, maximizing time at the bottom would decrease the sea lions' susceptibility to shark attack. Northern elephant seals show a similar diving pattern in arriving and departing from their rookeries, where white sharks are also important predators. LeBoeuf and Crocker (1996) have suggested that predator avoidance is an important factor in the development of this diving pattern.

Physiology of benthic diving

A measure of the tendency of this benthic foraging strategy to push the physiological capacity of Australian sea lions can be seen by the degree to which each animal exceeds its cADL. In order to defend bottom time by increasing dive duration (independent of depth), this species exceeds its cADL in almost 80% of dives and seemingly pushes its ability beyond what we might predict possible. The lack of relationship between surface interval and dive duration is at odds with the accepted theory of a postdive increase in surface interval, typically required to clear anaerobic metabolites that are accumulated when animals exceed their aerobic limits (Kooyman 1989). This paradox might indicate that our calculation of cADL is too low. Al-

TABLE 5. Body mass, field metabolic rate (FMR), estimated O_2 stores, cADL (calculated aerobic dive limit for individuals), mean dive duration, ratio of mean dive duration to cADL, and percentage of dive durations greater than cADL for lactating Australian sea lions.

| Cow no.	Mass (kg)	FMR (W)	FMR (mL O_2/min)	O_2 stores (mL)	cADL (min)	Duration (min)	Dive cADL	Dives >cADL (%)
14-88	93.9	707	2113	4411	2.09	3.24	1.55	87.6
AD-88	94.4	650	1942	4434	2.28	3.33	1.46	86.4
C2-88	66.9	529	1581	3144	1.99	3.04	1.53	91.1
P-88	89.8	665	1987	4218	2.12	4.05	1.91	95.0
138-90	59.8	450	1345	2811	2.09	2.84	1.36	80.1
AD-90	89.0	626	1870	4183	2.24	3.93	1.76	93.4
51-90	66.4	406	1213	3121	2.57	3.09	1.20	82.5
C2-90	76.3	444	1327	3584	2.70	2.75	1.02	57.0
141-90	73.8	388	1159	3466	2.99	2.20	0.74	46.8
139-90	81.6	463	1383	3835	2.77	2.94	1.06	66.3
102-90	64.0	525	1569	3008	1.92	3.08	1.61	87.7
Mean	77.8	532	1590	3656	2.34	3.14	1.38	79.4
1 SD	12.6	113	337	594	0.36	0.52	0.35	15.8
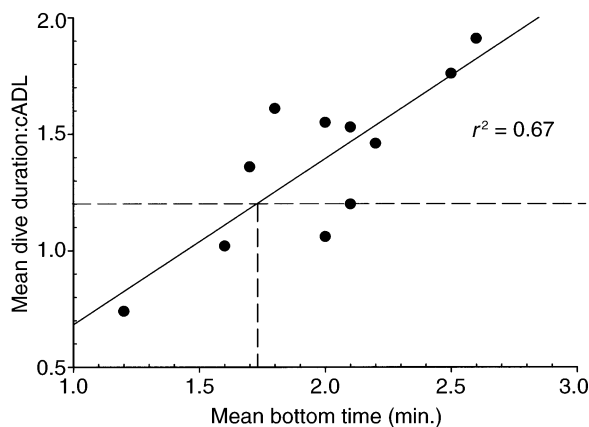
FIG. 8. The ratio between mean dive duration and cADL shows a linear increase with mean bottom time ($r^2 = 0.69$, $P < 0.01$). The dashed horizontal line is where the mean dive duration : cADL ratio exceeds 1.2 (allowing for 20% underestimate of ADL [Ponganis et al. 1997]). The vertical dashed line shows that this ratio exceeded 1.2 in dives with bottom times greater than 1.7 min.

though we recognize problems with this calculation and with interspecies comparisons (where ADL is calculated, not measured), our cADL estimates are based on measurements of blood volume, muscle myoglobin and hemoglobin concentrations, and at-sea FMR for this species (Costa et al. 2001). In measurements in which actual lactate levels were measured for diving California sea lions, Ponganis et al. (1997) determined that actual ADL was ~1.2 times the cADL derived using the same methodology employed here. Even if we inflated our cADL by a similar factor, the mean dive duration of seven of the 11 animals significantly exceed this parameter, making a compelling case for the argument that Australian sea lions are working at the upper limit of their physiological capability.

An alternative explanation is that the sea lions dramatically decrease their metabolic rate while diving, with a compensatory increase in their metabolic rate while on the surface. Such a mechanism has been proposed for King Penguins by Culik et al. (1996). Following the approach of Culik et al. (1996), we calculated the diving metabolic rate necessary for each animal to dive aerobically, given its oxygen stores and its observed dive duration. These data were then used to calculate the postdive surface FMR that would have resulted. We combined these data with the amount of time spent underwater and on the surface after a dive to calculate a postdive FMR. Three of the animals dived within their aerobic dive limits and were not included in these calculations. For the remaining eight animals, the diving metabolic rate would have been, on average, 4.2 times the predicted BMR, whereas the postdive surface FMR would have been 11.7 times predicted BMR, with some animals having a postdiving FMR as high as 13–14 times BMR (individuals 14-88, C2-88, AD-90). These levels are well above the 9.3 BMR that

Culik et al. (1996) estimated for surface recovery periods in King Penguins, and are likely to be well above the maximum metabolic capacity of a sea lion. A recent study has shown that trained, captive California sea lions can reduce their metabolism during submergence (Hurley and Costa 2001). This mechanism may occur in Australian sea lions and may have led us to underestimate their cADL. However, it still appears likely that these animals are exceeding, or at least operating at the upper limit of, their aerobic dive limit. This feature is common to benthically diving seabirds and marine mammals (Costa et al. 2001, Schreer et al. 2001). Nonetheless, the only way to test this hypothesis is to measure postdive lactate levels in freely diving Australian sea lions.

Because diving ability is a function of body mass (Kooyman 1989, Boyd and Croxall 1996, Schreer and Kovacs 1997, Costa and Williams 2000), it would be interesting to know how juvenile Australian sea lions contend with the challenge of making a living in this environment. The long dependency period of pups (15 mo; Higgins 1993) may be associated with their need to learn a repertoire of foraging skills sufficient to allow them to reach a critical mass for nutritional independence (Gales and Costa 1997). Studies addressing the ontogeny of diving in this species would be instructive.

Given the continuous diving behavior, the general cline of increasing and then decreasing depths during a foraging trip, and the lack of extensive travel to foraging grounds, it is reasonable to speculate that Australian sea lions are exploiting a sparse and evenly distributed resource. In contrast, mid-water diving species tend to dive in bouts, which is interpreted as exploiting a prey patch; the time between bouts is spent surface swimming, resting, or grooming (Boyd 1996). In the case of the Antarctic fur seal, surface travel between prey patches and the associated searching are a major component of the overall cost of the foraging trip (Arnould et al. 1996, Boyd 1996).

The fact that sea lions utilize blubber for thermal regulation, in contrast to fur seals, which use a layer of air in their fur, confers an advantage for long duration and repetitive dives. In contrast to air in fur, the insulating quality and buoyancy of blubber do not vary with depth and do not require grooming. It is not surprising, therefore, to see fur seals more highly represented among the epipelagic feeders and sea lions more commonly exploiting benthic habitats. In seabirds, which are smaller than marine mammals, the relative cost of increased buoyancy is likely to be greater (Gremillet and Wilson 1999). Both fur seals and seabirds will incur increased thermal costs as the insulating air layer is lost with increasing depth.

When at-sea FMR is normalized for body mass, the Australian sea lion has a rate equivalent to that of the benthic-feeding New Zealand sea lion, is higher than the mid-water feeding California sea lion, and falls within the high end of the range reported for fur seals

Table 6. Comparison of dive behavior and energetics for nine species of otariids.

Species[†]	Body mass (kg)	Dive depth (m)	Dive duration (min)	At-sea FMR W/kg	At-sea FMR W/kg[0.75]	No. dives/h	Dive time at sea (%)	Dive effort (m/h)
Galapagos fur seal[1,13]	27	26	<2.0	5.00	12.3	5.6	24	···
Antarctic fur seal								
Cape Sherriff[2]	33.7	19	0.9	9.73	23.4	6.13	9.77	233
Bird Island[3]	36.8	12.7	1.13	6.66	16.4	13	20.4	469
New Zealand fur seal[4]	36.4	53	2.2	···	···	···	···	···
Australian fur seal[5]	77.7	58	2.9	···	···	8.3	40.7	997.0
Northern fur seal[1,6]	35.7	68	2.2	8.16	19.9	1.5	26.0	···
Australian sea lion[7]	**69.3**	**61**	**3.3**	**7.05**	**20.3**	**10.7**	**57.9**	**1281**
New Zealand sea lion[8]	114.1	121	3.38	6.9	22.6	7.6	43.5	1772
California sea lion[9,12]	81.5	31–98	1.5–2.8	5.94	17.8	8.4	33	···
Southern sea lion[10]	126	61	3.1	···	···	11–19	52.7	···
Northern sea lion[11]	273	15–28	1.2–1.6	···	···	10.5–15.8	···	···

Note: Ellipses indicate that no data were available.

† Sources of data (as indicated by superscript numbers): (1) Gentry et al. (1986); (2) Arnould et al. (1998); (3) Costa et al. (2000); (4) Mattlin et al. (1998); (5) Arnould and Hindell (2000); (6) Costa and Gentry (1986); (7) present study; (8) Costa and Gates (2000); (9) Feldkamp et al. (1989); (10) Werner et al. (1995); (11) Merrick and Loughlin (1997); (12) Costa et al. (1990); (13) Trillmich and Kooyman (2001).

(Table 6). At first, this is surprising, given the long duration and high rate of diving in Australian sea lions. A lower mass-specific metabolic rate may have been advantageous. However, benthic diving may be energetically expensive because considerable effort may be required to pursue and acquire prey. Furthermore, Australian sea lions spend very little time resting on the surface compared to many other otariids.

We found no clear pattern between diving behavior and foraging costs. Arnould et al. (1996) showed relationships between dive effort (time at sea, percentage of time at sea spent diving, and rate of diving) and energetic costs (at-sea FMR) in the Antarctic fur seal. In contrast, for the same species over a single season, Costa et al. (2001) found no relationships. In the New Zealand sea lion, the only dive behavior parameter to correlate significantly with energetic cost was mean dive depth (Costa and Gales 2000). In the present study, the relationship between dive depth and at-sea FMR approached significance ($P = 0.07$, $r^2 = 0.32$). Because mean dive depths varied so little for the Australian sea lions and the sample size of the deeper diving sea lions measured in winter was small, it is not surprising that the relationship was not strong.

During winter, sea lions dived deeper, but at a lower rate, had a higher metabolic rate, exceeded their cADL to a greater degree, had a lower water influx, lower mass change, shorter trip duration, and more rapid dive descent and ascent rates than in summer (Table 2). This could be interpreted as prey being harder to find or catch during winter. Changes in water flux may reflect a lower rate of prey intake, a change in prey type, and/ or a change in the water : nutritional content of the prey (as the lipid content of prey increases, its water content declines). Previous work suggests that otariids do not drink seawater when feeding (Costa 1987). The rela-

tionship that we report between the percentage of time diving and water influx is therefore suggestive that increased foraging effort leads to an increase in prey acquisition. In winter, sea lion mass gain was correlated with the prey consumed (water influx). Although we were not able to determine if the foraging areas varied between seasons, there was no significant difference in the distances to water depths of modal and maximum diving depths between seasons.

Variation in the foraging energetics of Australian sea lions may be related to seasonal oceanography. Oceanographic influences on a benthically feeding species might be expected to be weaker than those on a midwater feeding species. Nevertheless, oceanography is likely to affect the distribution, behavior, and recruitment of benthic and demersal prey, and hence their predators. In the Kangaroo Island region, the Leeuwin current is known to have a maximum influence during winter as its seasonally strongest flow meanders down Australia's west coast and eastward across the Great Australian Bight (Fig. 1), is augmented by the predominantly southwesterly winds. Kangaroo Island, which is close to the extant eastern limit of the distribution of the Australian sea lion, is also the eastern limit of the Leeuwin current in winter (Pearce 1991). The Leeuwin current impedes cool upwellings of relatively more productive waters along the continental shelf edge. During summer, the weaker flowing Leeuwin current is effectively blocked by the predominantly southeasterly winds (Pearce 1991), and some upwelling events occur along the shelf edge, south of Kangaroo Island and elsewhere in South Australia (Schahinger 1987). This seasonal oceanography may account for some of the seasonal differences in energetics and diving behavior observed.

Comparisons of dive behavior between early and late lactation revealed that the females dived deeper, longer, and at a lower rate in late lactation. Dive duration has been shown to increase later in gestation for New Zealand fur seals and Northern elephant seals (LeBoeuf et al. 1989, Mattlin et al. 1998). It is unclear whether the greater mean dive duration reflects an increased physiological capability associated with pregnancy, an adjustment to meet the greater demand of provisioning the growing fetus and the older pup (in the case of the otariid), or seasonal effects on prey distribution and abundance.

Ecological implications

Thus far we have presented a discussion of a relatively rare species that exploits its nearby benthic resources. We have outlined some functional features that confer an advantage for a benthic foraging strategy and have compared these to those of the epipelagic foragers. The Australian sea lion is sympatric over much of its range with the New Zealand fur seal, a predominately epipelagic forager (Harcourt et al. 1995, Mattlin et al. 1998). Over the past decade, these fur seals have experienced spectacular population growth (Shaughnessy et al. 1994, Gales et al. 2000). This is in marked contrast to an apparent stability or even decline in the population size of the Australian sea lion (Gales et al. 2000). It is compelling to consider whether the underlying cause for this dichotomy is associated with their disparate foraging strategies. This pattern of contrasting demographic trends is mirrored, to a greater or lesser extent, by the other benthically foraging sea lions (southern sea lions and New Zealand sea lions), which are sympatric with epipelagic foraging fur seals (South American fur seal *Arctocephalus australis*, and New Zealand fur seal, respectively). It is likely that both the New Zealand and Australian sea lion populations have always been low in relation to fur seal numbers (Gales et al. 1994, Childerhouse and Gales 1998, Gales and Fletcher 1999), and thus the population differences are unlikely to be an historic artifact.

Such dichotomous trends between sympatric epipelagic and benthically foraging endotherms appear to have parallels within the penguins. Those that feed predominantly on the benthos (Gentoo [*Pygoscelis papua*], Rockhopper, and Yellow-eyed Penguins [*Spheniscus hookeri*]) typically have low populations in areas where their epipelagic sympatrics, which include Macaroni (*Eudyptes chrysolophus*), Adelie (*Pygoscelis adeliae*), Royal (*Eudyptes schlegi*), and Chinstrap (*Pygoscelis antarctica*) Penguins, maintain large, and in some cases expanding, populations (Lishman 1985, Croxall et al. 1988, 1993, Hindell 1989, Williams et al. 1992*a*, *b*, Hindell et al. 1996, Hull et al. 1997, Croxall and Davis 1999).

It is apparent that the cost of specializing in benthic prey is to limit available foraging habitat. Epipelagic habitats are generally more extensive and thus confer greater carrying capacity. A compounding dilemma for specialist benthic foragers is that of juvenile survival during the period when their body mass constrains access to the benthos. One implication might be that juvenile survival is a major determinant in the demographic trends that we observe in this group.

Our findings support the hypothesis that Australian sea lions are adapted to utilize a low-productivity, aseasonal marine environment (Gales et al. 1994, Gales and Costa 1997). Australian sea lions offer a window into the interactions among foraging ecology, habitat specialization, and demographic consequences.

Literature Cited

Arnould, J. P. Y., I. L. Boyd, and J. R. Speakman. 1996. The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. Journal of Zoology **239**: 769–782.

Arnould, J. P. Y., and M. A. Hindell. 2001. Dive behaviour, foraging locations, and maternal attendance patterns of Australian fur seals (*Arctocephalus pusillus doriferus*). Canadian Journal of Zoology **79**:35–48.

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

Boyd, I. L. 1999. Foraging and provisioning in Antarctic fur seals: interannual variability in time–energy budgets. Behavioral Ecology **10**:198–208.

Boyd, I. L., J. P. Y. Arnould, T. Barton, and J. P. Croxall. 1994. Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. Journal of Animal Ecology **63**:703–713.

Boyd, I. L., and J. P. Croxall. 1992. Diving behaviour of lactating Antarctic fur seals. Canadian Journal of Zoology **70**:919–928.

Boyd, I. L., and J. P. Croxall. 1996. Dive durations in pinnipeds and seabirds. Canadian Journal of Zoology **74**: 1696–1705.

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

Chappell, M. A., V. H. Shoemaker, D. N. Janes, S. K. Maloney, and T. L. Bucher. 1993. Energetics of foraging in breeding Adelie Penguins. Ecology **74**:2450–2461.

Cherel, Y., V. Ridoux, and P. G. Rodhouse. 1996. Fish and squid in the diet of King Penguin chicks, *Aptenodytes pa-*

tagonicus, during winter at sub-Antarctic Crozet Islands. Marine Biology **126**:559–570.

Childerhouse, S., and N. J. Gales. 1998. Historical and modern distribution and abundance of the New Zealand sea lion *Phocarctos hookeri*. New Zealand Journal of Zoology **25**:1–16.

Costa, D. P. 1987. Isotopic methods for quantifying material and energy intake of free-ranging marine mammals. Pages 43–66 *in* A. C. Huntley, D. P. Costa, G. A. J. Worthy, and M. A. Castellini, editors. Approaches to marine mammal energetics. Allen Press, Lawrence, Kansas, USA.

Costa, D. P. 1988. Methods for studying the energetics of freely diving animals. Canadian Journal of Zoology **66**:45–52.

Costa, D. P. 1991. Reproductive and foraging energetics of pinnipeds: implications for life history patterns. Pages 300–344 *in* D. Renouf, editor. Behaviour of pinnipeds. Chapman and Hall, London, UK.

Costa, D. P. 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. Pages 293–314 *in* I. L. Boyd, editor. Marine mammals: advances in behavioural and population biology. Symposium of the Zoological Society of London, Oxford University Press, Oxford, UK.

Costa, D. P., G. P. Antonelis, and R. L. De Long. 1990. Effects of El Niño on the foraging energetics of the California sea lion. Pages 156–165 *in* F. Trillmich and K. Ono, editors. Effects of El Niño on pinnipeds. Springer-Verlag, Berlin, Germany.

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

Costa, D. P., and N. J. Gales. 2000. Foraging energetics and diving behavior of lactating New Zealand sea lions, *Phocarctos hookeri*. Journal of Experimental Biology **203**:3655–3665.

Costa, D. P., N. J. Gales, and M. E. Goebel. 2001. Aerobic dive limit: how often does it occur in nature? Comparative Biochemistry and Physiology Part A **129**:771–783.

Costa, D. P., and R. L. Gentry. 1986. Free-ranging energetics of northern fur seals. Pages 79–101 *in* R. L. Gentry, and G. L. Kooyman, editors. Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, New Jersey, USA.

Costa, D. P., M. E. Goebel, and J. E. Sterling. 2000. Foraging energetics and diving behavior of the Antarctic fur seal, *Arctocephalus gazella* at Cape Shirreff, Livingston Island. Pages 77–84 *in* W. Davisons, C. Howard-Williams, and P. Broady, editors. Antarctic ecosystems: models for wider ecological understanding. New Zealand Natural Sciences Press, Christchurch, New Zealand.

Costa, D. P., and T. M. Williams. 2000. Marine mammal energetics. Pages 176–217 *in* J. Reynolds and J. Twiss, editors. The biology of marine mammals. Smithsonian Institution Press, Washington, D.C., USA.

Crocker, D. E., N. J. Gales, and D. P. Costa. 2001. Swimming speed and foraging strategies of New Zealand sea lions, *Phocarctos hookeri*. Journal of Zoology **254**:267–277.

Croxall, J. P., D. R. Briggs, A. Kato, Y. Naito, Y. Watanuki, and T. D. Williams. 1993. Diving pattern and performance in the Macaroni Penguin *Eudyptes chrysolophus*. Journal of Zoology (London) **230**:31–47.

Croxall, J. P., and L. S. Davis. 1999. Penguins: paradoxes and patterns. Marine Ornithology **27**:1–12.

Croxall, J. P., R. W. Davis, and M. J. O'Connell. 1988. Diving patterns in relation to diet of Gentoo and Macroni Penguins at South Georgia. Condor **90**:157–167.

Croxall, J. P., Y. Naito, A. Kato, P. Rothery, and D. R. Briggs. 1991. Diving patterns and performance in the Antarctic

Blue-eyed Shag *Phalacrocorax atriceps*. Journal of Zoology (London) **225**:177–200.

Culik, B. M., K. Putz, R. P. Wilson, D. Allers, J. Lage, C. A. Bost, and Y. LeMaho. 1996. Diving energetics in King Penguins (*Aptenodytes patagonicus*). Journal Experimental Biology **199**:973–983.

Feldkamp, S. D., R. L. Delong, and G. A. Antonelis. 1989. Diving patterns of California sea lions, *Zalophus californianus*. Canadian Journal of Zoology **67**:872–883.

Gales, N. J., and A. J. Cheal. 1992. Estimating diet composition of the Australian sea-lion (*Neophoca cinerea*) from scat analysis: an unreliable technique. Wildlife Research **19**:447–456.

Gales, N. J., and D. P. Costa. 1997. The Australian sea lion: a review of an unusual life history. Pages 78–87 *in* M. Hindell and C. Kemper, editors. Marine mammal research in the southern hemisphere. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Gales, N. J., and D. J. Fletcher. 1999. Abundance, distribution and status of the New Zealand sea lion, *Phocarctos hookeri*. Wildlife Research **26**:35–52.

Gales, N. J., B. Haberley, and P. Collins. 2000. Changes in the abundance of New Zealand fur seals, *Arctocephalus forsteri*, in Western Australia. Wildlife Research **27**:165–168.

Gales, N. J., and R. H. Mattlin. 1997. Summer diving behaviour of lactating New Zealand sea lions, *Phocarctos hookeri*. Canadian Journal of Zoology **75**:1695–1706.

Gales, N. J., P. D. Shaughnessy, and T. E. Dennis. 1994. Distribution, abundance and breeding cycle of the Australian sea lion, *Neophoca cinerea* (Mammalia: Pinnipedia). Journal of Zoology **234**:353–370.

Gentry, R. L., and J. R. Holt. 1982. Equipment and techniques for handling northern fur seals. NOAA Technical Report **NMFS SSRF-758**. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.

Gentry, R. L., and G. L. Kooyman. 1986. Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, New Jersey, USA.

Georges, J.-Y., Y. Tremblay, and C. Guinet. 2000. Seasonal diving behaviour in lactating subantarctic fur seals on Amsterdam Island. Polar Biology **23**:59–69.

Goebel, M. E., J. L. Bengtson, R. L. DeLong, R. L. Gentry, and T. R. Loughlin. 1991. Diving patterns and foraging locations of female northern fur seals. U.S. National Marine Fisheries Service Fishery Bulletin **89**:171–180.

Gremillet, D., G. Argentin, B. Schulte, and B. M. Culik. 1998. Flexible foraging techniques in breeding Cormorants *Phalacrocorax carbo* and Shags *Phalacrocorax aristotelis*: benthic or pelagic feeding? Ibis **140**:113–119.

Gremillet, D., and R. P. Wilson. 1999. A life in the fast lane: energetics and foraging strategies of the Great Cormorant. Behavioral Ecology **10**:516–524.

Gremillet, D., R. P. Wilson, S. Storch, and Y. Gary. 1999. Three-dimensional space utilization by a marine predator. Marine Ecology Progress Series **183**:263–273.

Harcourt, R. G., A. M. Schulman, L. S. Davis, and F. Trillmich. 1995. Summer foraging by lactating female New Zealand fur seals *Arctocephalus forsteri* off Otago Peninsula, New Zealand. Canadian Journal of Zoology **73**:678–690.

Higgins, L. V. 1990. Reproductive behavior and maternal investment of Australian sea lions. Dissertation. University of California, Santa Cruz, California, USA.

Higgins, L. V. 1993. The nonannual, nonseasonal breeding cycle of the Australian sea lion, *Neophoca cinerea*. Journal of Mammalogy **74**:270–274.

Higgins, L. V., and L. Gass. 1993. Birth to weaning: parturition, duration of lactation and attendance cycles of the

Australian sea lion (*Neophoca cinerea*). Canadian Journal of Zoology **71**:2047–2055.

Hindell, M. A. 1989. The diet of gentoo penguins *Pygoscelis papua* at Macquarie Island—winter and early breeding season. Emu **89**:71–78.

Hindell, M. A., G. G. Robertson, and R. Williams. 1996. Resource partitioning in four species of sympatrically breeding penguins. Pages 196–215 *in* P. I. N. Dann and P. Reilly, editors. The penguins: ecology and management. Second International Penguin Conference, Cowes, Victoria, Australia, August 1992. Surrey Beatty, Chipping Norton, New South Wales, Australia.

Horning, M., and F. Trillmich. 1997. Ontogeny of diving behaviour in the Galapagos fur seal. Behaviour **134**:1211–1257.

Horning, M., and F. Trillmich. 1999. Lunar cycles in diel prey migrations exert a stronger effect on the diving of juveniles than adult Galapagos fur seals. Proceedings of the Royal Society of London, Biological Sciences Series B **266**:1127–1132.

Hull, C. L., M. A. Hindell, and K. Michael. 1997. Foraging zones of royal penguins during the breeding season, and their association with oceanographic features. Marine Ecology Progress Series **153**:217–228.

Hurley, J. A., and D. P. Costa. 2001. Standard metabolic rate at the surface and during trained submersions in adult California sea lions (*Zalophus californianus*). Journal of Experimental Biology **204**:3273–3281.

King, J. E. 1983. Seals of the world. British Museum of Natural History, London, UK.

Kirkwood, R., and G. Robertson. 1997. The foraging ecology of female Emperor Penguins in winter. Ecological Monographs **67**:155–176.

Kleiber, M. 1975. The fire of life. Krieger Publishing, New York, New York, USA.

Klimley, A. P. 1994. The predatory behavior of the white shark. American Scientist **82**:122–133.

Kooyman, G. L. 1989. Diverse divers: physiology and behavior. Springer-Verlag, Berlin, Germany.

Kooyman, G. L., Y. Cherel, Y. Le Maho, J. P. Croxall, P. H. Thorson, V. Ridoux, and C. A. Kooyman. 1992. Diving behavior and energetics during foraging cycles in King Penguins. Ecological Monographs **62**:143–163.

LeBoeuf, B. J., and D. E. Crocker. 1996. Diving behavior of elephant seals: implications for predator avoidance. Pages 193–205 *in* P. Klimley, editor. Great white shark: the biology of *Carcharodon charcharias*. Academic Press, San Diego, California, USA.

LeBoeuf, B. J., Y. Naito, and A. C. Huntley. 1989. Prolonged, continuous, deep diving by northern elephant seals. Canadian Journal of Zoology **67**:2514–2519.

Lifson, N., and R. McClintock. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. Journal of Theoretical Biology **12**:46–74.

Ling, J. 1992. *Neophoca cinerea*. Mammalian Species Number 392:1–7. American Society of Mammalogists, Allen Press, Lawrence, Kansas, USA.

Lishman, G. S. 1985. The food and feeding ecology of Adelie Penguins (*Pygoscelis ageliae*) and Chinstrap Penguins (*P. antarctica*) at Signy Island, South Orkney Islands. Journal of Zoology (London) **205**:245–263.

Loughlin, T. R., J. L. Bengtson, and R. L. Merrick. 1987. Characteristics of feeding trips of female northern fur seals. Canadian Journal of Zoology **65**:2079–2084.

Mattlin, R. H., N. J. Gales, and D. P. Costa. 1998. Seasonal dive behaviour of lactating New Zealand fur seals (*Arctocephalus forsteri*). Canadian Journal of Zoology **76**:350–360.

Merrick, R. L., and T. R. Loughlin. 1997. Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. Canadian Journal of Zoology **75**:776–786.

Nagy, K. A. 1980. CO_2 production in animals: an analysis of potential errors in the doubly-labeled water technique. American Journal of Physiology **238**:R466–R473.

Nagy, K. A., and D. P. Costa. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. American Journal of Physiology **238**:R454–R465.

Pearce, A. F. 1991. Eastern boundary currents of the Southern Hemisphere. Journal of the Royal Society of Western Australia **74**:35–45.

Ponganis, P. J., R. L. Gentry, E. P. Ponganis, and K. V. Ponganis. 1992. Analysis of swim velocities during deep and shallow dives of two northern fur seals, *Callorhinus ursinus*. Marine Mammal Science **8**:69–75.

Ponganis, P. J., G. L. Kooyman, L. M. Winter, and L. N. Starke. 1997. Heart rate and plasma lactate responses during submerged swimming and trained diving in California sea lions, *Zalophus californianus*. Journal of Comparative Physiology **167**:9–16.

Ponganis, P. J., E. P. Ponganis, K. V. Ponganis, G. L. Kooyman, R. L. Gentry, and F. Trillmich. 1990. Swimming velocities in otariids. Canadian Journal of Zoology **68**:2105–2112.

Rodary, D., W. Bonneau, Y. Le Maho, and C. A. Bost. 2000. Benthic diving in male Emperor Penguins, *Aptenodytes forsteri* foraging in winter. Marine Ecology Progress Series **207**:171–181.

Schahinger, R. B. 1987. Structure of coastal upwelling events observed off the south-east coast of South Australia during February 1983–April 1984. Australian Journal of Marine and Freshwater Research **38**:439–459.

Schreer, J. F., and K. M. Kovacs. 1997. Allometry of diving capacity in air-breathing vertebrates. Canadian Journal of Zoology **75**:339–358.

Schreer, J. F., K. M. Kovacs, and R. J. O'Hara Hines. 2001. Comparative diving patterns of pinnipeds and seabirds. Ecological Monographs **71**:137–162.

Shaughnessy, P. D., N. J. Gales, T. E. Dennis, and S. D. Goldsworthy. 1994. Distribution and abundance of New Zealand fur seals, *Arctocephalus forsteri*, in South Australia and Western Australia. Wildlife Research **21**:667–695.

Speakman, J. R. 1997. Doubly labeled water: theory and practice. Chapman and Hall, London, UK.

SPSS. 1997. SigmaStat. Version 2.03. SPSS, Chicago, Illinois, USA.

Thompson, D., C. D. Duck, B. J. McConnell, and J. Garrett. 1998. Foraging behaviour and diet of lactating female southern sea lions (*Otaria flavescens*) in the Falkland Islands. Journal of Zoology **246**:135–146.

Tremblay, Y., and Y. Cheryl. 2000. Benthic and pelagic dives: a new foraging behaviour in Rockhopper Penguins. Marine Ecology Progress Series **204**:257–267.

Trillmich, F., and G. L. Kooyman. 2001. Field metabolic rate of lactating Galapágos fur seals (*Arctocephalus galapagoensis*): the influence of offspring age and environment. Comparative Biochemistry and Physiology **A129**:741–749.

Werner, R., and C. Campagna. 1995. Diving behaviour of lactating southern sea lions *Otaria flavescens* in Patagonia. Canadian Journal of Zoology **73**:1975–1982.

Williams, T. D., D. R. Briggs, J. P. Croxall, Y. Naito, and A. Kato. 1992*a*. Diving pattern and performance in relation to foraging ecology in the Gentoo Penguin, *Pygoscelis papua*. Journal of Zoology (London) **227**:211–230.

Williams, T. D., A. Kato, J. P. Croxall, Y. Naito, D. R. Briggs, S. Rodwell, and T. R. Barton. 1992*b*. Diving pattern and performance in nonbreeding Gentoo Penguins (*Pygoscelis papua*) during winter. Auk **109**:223–234.