

# Physiological effects on dive patterns and foraging strategies in yearling Weddell seals (*Leptonychotes weddellii*)

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**Abstract:** Fifteen yearling Weddell seals (*Leptonychotes weddellii*) were captured, measured, weighed, blood sampled, and fitted with time–depth recorders, and released to determine if diving behavior was related to physical condition. Upon recovery of the time–depth recorders, dives were classified into four types based on shape, using cluster analysis. Based on maximum depth, two groups were further subdivided, for a total of seven types. The mean and maximal dive depth, duration, and frequency were determined for each yearling for all dive types combined and for each type separately. Stepwise regression and ANOVA techniques were used to test the relationship between diving behavior and physiological and morphometric measurements. In general, half of the variation in the pooled diving behavior could be explained by body-size differences. Larger yearlings made longer and shallower dives than smaller yearlings. Dive patterns indicated that large yearlings foraged primarily on small shallow-water prey items, while small yearlings concentrated on energy-rich deep-water prey. However, the interpretation of diving behavior, foraging locations, and diet that resulted from analyzing individuals and dive types was very different from that based on average diving behavior. This argues against generalizing variation among individuals and using only average diving behavior when describing marine mammal dive patterns.

**Résumé :** Quinze Phoques de Weddell (*Leptonychotes weddellii*) de 1 an ont été capturés, mesurés, pesés, échantillonnés et munis d'un appareil enregistreur de la profondeur et de la durée, puis libérés; le but de l'opération était de déterminer si le comportement de plongée est relié à la condition physique. Sur récupération des appareils, une analyse de regroupements nous a permis de classifier les plongées en quatre types d'après leur forme. D'après la profondeur maximale, deux de ces groupes ont été subdivisés, ce qui a donné lieu à sept types. Les profondeurs moyennes et maximales des plongées, leur durée et leur fréquence ont été déterminées pour chaque animal pour tous les types de plongée combinés et pour chaque type séparément. Une procédure de régression pas à pas croissante et une analyse de variance ont servi à éprouver la relation entre le comportement de plongée et des mesures physiologiques et morphométriques. En général, la moitié de la variation dans le comportement de plongée évaluée en tenant compte de tous les types pouvait s'expliquer par des différences de taille corporelle. Les plus gros phoques faisaient des plongées plus longues et moins profondes que les plus petits phoques. Les patterns de plongée semblaient indiquer que les plus gros phoques se nourrissaient surtout de petites proies en eau peu profonde, alors que les plus petits phoques concentraient leurs efforts pour attraper des proies d'eau profonde, riches en énergie. Cependant, l'interprétation des comportements de plongée, des points de recherche de nourriture et du régime alimentaire en tenant compte des dives des individus et des divers types de plongées dans les analyses différait fortement des conclusions obtenues à partir du comportement de plongée moyen. Il est donc essentiel de tenir compte des résultats individuels et de ne pas se limiter au seul comportement de plongée moyen pour décrire les patterns de plongée chez les mammifères marins.

[Traduit par la Rédaction]

## Introduction

Since the development of time–depth recorders (TDRs), the free-ranging diving behavior of many marine mammal species has been examined. The majority of these studies have focused

on average and maximal dive ability (Lydersen and Kovacs 1993; Castellini et al. 1992; Riedman 1990; Kooyman 1989; Le Boeuf et al. 1988, 1989; Gentry and Kooyman 1986; Croxall et al. 1985). Variation in diving behavior among individuals within a species has been addressed far less often, and the focus has often been on differences between groups of animals, such as males and females, animals at different life-history stages, or animals under different environmental regimes (Boyd et al. 1994; Slip et al. 1994; DeLong and Stewart 1991; Hindell et al. 1991; Costa et al. 1989; Feldkamp et al. 1989; Kooyman et al. 1983; Kooyman 1975). Generally, behavioral differences have been attributed to the factor that varied, and variation among individuals within these "homogeneous" groups was not explored. Behavioral differences among individuals of similar ages and under similar conditions have been discussed only recently (Testa 1994; McConnell et al. 1992; Hindell et al. 1991; Goebel et al.

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1990), but still the observed variation was often attributed to known differences in foraging location or diet.

The root cause of the variation among individuals has been hard to explain, and recently attempts have been made to link variation in diving behavior to physiological differences. This technique has been successfully employed to explain differences in diving capacity between species and among individuals of different age, condition, or sex within species (Boness et al. 1994; Slip et al. 1994; Thorson and Le Boeuf 1994; Ponganis et al. 1993; Hindell et al. 1992; Kooyman et al. 1983). However, small-scale physiological differences, such as those found between animals of similar ages and condition, have rarely been linked to observed differences in diving behavior. As a result, it has been difficult to assess the role played by physiology in determining the "normal" diving behavior of individuals and the significance of variation among similar individuals.

Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound offer the opportunity to test hypotheses about the role played by physiology in individual variation in diving behavior. Weddell seals have been studied extensively and their diving behavior and physiology are well understood. They live in a relatively simple ecosystem and their diet is limited to a few prey species (Castellini et al. 1992; Green and Burton 1987; Plötz 1986). In addition, during summer there is little fluctuation in light levels (Castellini et al. 1992). Work on Weddell seal physiology has revealed that age, mass, body oxygen stores, condition, and sex all potentially affect diving patterns (Burns and Testa 1997; Burns and Castellini 1996; Ponganis et al. 1993; Kooyman et al. 1980, 1983). Furthermore, many studies of diving behavior have led to the development of techniques to classify dives, and permit reasonable inferences to be drawn about the purpose of different dive types (Schreer and Testa 1996; Testa 1994; Bengtson and Stewart 1992; Le Boeuf et al. 1992; Hindell et al. 1991; Kooyman 1968). This knowledge may allow differences in average dive characteristics to be attributed to differences in certain types of dives. In addition, it might be possible to relate these differences back to the condition of the animals themselves. Because this study was an attempt to understand behavioral differences within a group of relatively similar animals, we controlled for as many factors as possible. All yearlings were approximately the same age ( $\pm 3$  weeks) and apparently healthy and foraging. In addition, yearlings were instrumented in the same area ( $\pm 5$  km) and at the same time of year. Still, there remained significant variation among individuals in all measures of diving behavior and physiology.

The goals of this study were (i) to quantify the diving behavior of yearling Weddell seals, (ii) to assess the differences in diving behavior among individuals, and (iii) to relate observed differences in individuals' diving behavior to their physiological status.

## Materials and methods

### Animal capture and handling

During the austral springs of 1992, 1993, and 1994, 15 yearling Weddell seals (10 males, 5 females) were captured by manual restraint in McMurdo Sound, Antarctica ( $77^{\circ}45'S$ ,  $166^{\circ}30'E$ ), so that physiological measurements could be taken and diving behavior monitored. When first captured, the seals were weighed with a hanging electronic scale (accuracy  $\pm 0.1$  kg). Seals were manually

restrained while morphometric measurements were taken, a blood sample was drawn, and a TDR (Wildlife Computers, Woodinville, Wash., U.S.A., Mark 5 or 6) was attached to the mid-dorsal pelage with Devcon™ 5-min epoxy adhesive. Seals were released as soon as the epoxy hardened. The seals were recaptured 3–10 days later and the TDRs retrieved.

In addition to mass, the axial girth (AG; girth just behind the foreflippers) and total length (TL; tip of nose to tip of tail) of each seal was measured (accuracy  $\pm 3$  cm). A regression equation based on data collected from 20 yearlings in McMurdo Sound between 1977 and 1995 was used to predict mass from AG and TL (predicted mass =  $21.93 + 4.28 \times 10^{-5} (AG^2 \times TL)$ ; Castellini and Kooyman 1990; Hofman 1975). The residuals from this regression were treated as an index of relative mass (RMI) for the subset of yearlings ( $n = 15$ ) that carried TDRs. However, this measure is not necessarily indicative of blubber content (B.S. Fadely, personal communication).

At the time of first capture, a 20-mL blood sample was drawn from the pelvic venous plexus into heparinized Vacutainer® collection tubes using 18 or 20 gauge needles. Blood samples were held in an insulated container to avoid freezing and processed within 1 h. Hematocrit (Hct) was determined in duplicate using a battery-operated field microhematocrit centrifuge (Compur M1100; samples were spun at  $5400 \times g$  for 3.5 min). Hemoglobin content (Hb) was determined spectrophotometrically using methanocyanide (Sigma Chemicals Kit 525-A) and plasma lactate and glucose concentrations were determined using a YSI Model 2300 Stat glucose/L-lactate autoanalyzer. The methods used to determine the ketone body concentration and plasma specific gravity have been previously described (Castellini et al. 1990; Castellini and Costa 1990).

### Dive data

The TDRs were programmed to sample depth (resolution 2 or 3 m) every 10 s during the course of the deployment. Dive data collected by the TDRs were decoded using programs provided by Wildlife Computers (ZOC, DA), and the depth and duration of all dives were determined. Because the sampling interval and depth resolution of the TDRs provided an insufficient representation of short and shallow dives, only dives that exceeded 30 s and 12 m were considered for further analysis in this report (Schreer and Testa 1995, 1996; Wilson et al. 1995; Boyd 1993).

Dives were classified subsequently by shape, based on the methods of Schreer and Testa (1995, 1996). The depth values for each dive (a series of depths over time, starting and ending with depth equal to zero) were interpolated so that each dive was represented by 100 depths, and dives were then standardized so that the maximum depth was 1 and the remaining depths scaled less than 1. The mean value for every 10 depths was calculated to reduce the number of data points and to smooth the dive profiles. Ten corresponding means for each dive enabled the shapes of all dives, regardless of their maximum depth or duration, to be compared.

A *k*-means clustering algorithm (Proc FASTCLUS; SAS Institute Inc. 1990) was also used to assess the number of dive types and categorize the dives. To determine the number of groups (clusters) within a data set,  $R^2$  and pseudo *F* statistic values from cluster analysis were compared over the number of clusters. Inflections within these curves may indicate a suitable number of clusters (Proc CLUSTER and Proc FASTCLUS; Schreer and Testa 1995; SAS Institute Inc. 1990; Calinski and Harabasz 1974). This procedure was first performed on all of the data and subsequently on three subsamples to test for stability. A second ad hoc procedure was used for determining a suitable number of dive types, following Schreer et al.<sup>2</sup>

<sup>2</sup> J.F. Schreer, R.J. O'Hara Hines, and K.M. Kovacs. Classification of dive profiles: a comparison of statistical clustering techniques and unsupervised artificial neural networks. Submitted for publication.

Briefly, the mean dive shapes for 2–10 clusters were plotted and analyzed visually. A suitable number of groups was determined as the point at which any additional separations created only redundant or unstable dive types (i.e., two or more groups with very similar shapes, or groups that occurred at one clustering level but not at subsequent levels). After classifying the data into suitable groups by shape, maximum-depth histograms were calculated for each dive type to determine if any further categorization could be accomplished. Differences in average dive depth, duration, and frequency by dive type were tested by one-way ANOVA. Post-hoc comparisons of means were made using Tukey's HSD method with significance at  $p < 0.05$ .

For each individual yearling and for all yearlings combined, the mean dive depth (m) and duration (min) were calculated. This was done for all dives combined and for dives separated by type. In addition, the dive depth and duration that were exceeded by only 5% of dives were calculated (as Burns and Castellini 1996). This measure of maximum ability was used instead of the actual maximum in order to control for the effects of extremely rare events. In the calculation of dive frequency (average number of dives per day), a seal-day was taken to run from 4:00 p.m. to 3:59 p.m. rather than from midnight to midnight, because seals were generally active at night and were most likely to be hauled out in the afternoon (Thomas and DeMaster 1983). Frequencies were calculated using dive data only from seal-days for which there was complete TDR coverage. Dive frequency was calculated for all dive types combined and for each dive type. In addition, the proportion of dives of each type was determined for all full seal-days separately and then averaged. This was done for each yearling and for all yearlings combined.

### Individual and physiological effects

One-way parametric ANOVA procedures were used to determine if there was significant ( $p < 0.05$ ) variation among individuals in mean dive depth, duration, or frequency. Post-hoc comparisons using Tukey's (HSD) multiple comparison of means procedure were carried out to determine if observed differences were significant and to identify groups of individuals. This procedure was used to test for variation among individuals with all dive types combined and within each dive type.

Dive parameters (mean and maximum depth, duration, and frequency) were regressed against year, mass, RMI, sex, Hct, Hb, plasma glucose, lactate, specific gravity (a measure of hydration state), and ketone body concentration (an indication of fasting) to determine if individual variation in overall diving behavior (all dive types pooled) was due to morphological and (or) physiological differences. AG and TL were not included in the regression analyses because they were significantly correlated ( $p < 0.05$ ) with mass. A stepwise linear regression procedure with forward selection ( $F$  to enter = 4.0) was used to determine if any of the independent variables were significant predictors of diving behavior. All dependent variables except dive frequency were normally distributed, as assessed with the Wilk–Shapiro statistic and visually by a rankit plot (Zar 1984). Dive frequency was square-root transformed to approximate the normal distribution.

Similarly, the effect of the measured morphological and physiological parameters on the dive parameters for each type of dive was tested with regression analysis. The mean and maximum dive depth and duration and the mean dive proportion and frequency for each dive type were regressed against individual mass, RMI, sex, Hct, Hb, plasma glucose, lactate, specific gravity, and ketone body concentration. As for the pooled data, normality was assessed with a rankit plot and the Wilk–Shapiro statistic (Zar 1984). To achieve normality, dive frequency was square-root transformed and dive proportion (by type) square-root and arcsine transformed ( $p' = \sqrt{\arcsin(\sqrt{p + 0.01})}$ ). Correlation analysis was also used to assess the relationship between dive parameters and morphometric measurements.

### Diel effects

The effect of time of day on dive frequency was assessed using circular statistics (Batschelet 1981). For all individuals combined, and for each individual, the frequency distribution of dives was tested for uniformity using Rayleigh's test. If the distribution of dives was determined to be non-uniform ( $p < 0.05$ ), the mean dive time and the 95% confidence interval were determined. The Watson–Williams test of heterogeneity was used to determine if the mean value (in all cases where the mean was not uniformly distributed by hour) differed by individual. Heterogeneity was accepted if  $p < 0.05$ . The same procedure was used to test for diel variation within each dive type. First, the effect of time on dive type was determined for all yearlings as a group, then the pattern for each individual yearling was examined. However, the mean dive time was not determined if a seal made fewer than 10 dives of that type.

The effect of time of day on dive depth and duration was tested using periodic regression techniques (Batschelet 1981). The dependent variable was either the average or maximum dive depth or duration for each hour of each day that the seals carried a TDR. Regression was run on the data from all seals pooled and for each seal individually. The period was assumed to be 24 h and a cosine function was fitted to the data. Depth and duration were judged to exhibit significant diel fluctuation if both the first-order trigonometric polynomial coefficients ( $\cos \omega t$  and  $\sin \omega t$ ) were significant ( $p < 0.05$ ) and the  $r^2$  value was greater than 10%.

## Results

### General dive behavior

Even controlling for as many parameters as possible (age, date, capture location), there was significant variation in the condition of the yearlings in this study (Table 1). There were also significant differences among individual seals in the number of dives per day and the average dive depth and duration, as determined by one-way ANOVA ( $p < 0.001$  in all cases). Yearling Weddell seal dives averaged  $120.3 \pm 67.1$  (SD) m in depth and  $8.83 \pm 1.49$  min in duration and yearlings dove  $57 \pm 23$  times per day. However, mean dive depth ranged from 43 to 250 m, mean duration from 6.7 to 11.5 min, and mean frequency from 24 to 112 dives/day. Post-hoc comparison of mean depth, duration, and frequency revealed several overlapping groups of individuals for which the means were not significantly different (Fig. 1). Yet the groups determined from mean depth were not the same as the groups determined from mean duration (12 overlapping groups that contained 3–7 individuals each) or average dive frequency (3 overlapping groups).

Individual differences in diving behavior did not appear to be determined by the location of TDR deployment. Figure 2 shows the capture locations for the 15 yearling Weddell seals that were fitted with TDRs between 1992 and 1994. Actual dive locations were not known. Yearlings were fairly mobile, changed haulout locations between TDR deployment and retrieval (the greatest distance moved was 33.6 km), and rarely remained within the study area (approximately 160 km<sup>2</sup>) for more than a week. In addition, all but 2 yearlings made dives in excess of 100 m, and mean dive depths for animals tagged at the same location often differed by more than 100 m. As half of the yearlings in both 1992 and 1994 were shallow divers and half deep divers, study year was judged to have an insignificant effect. However, it is possible that both tagging location and year influenced diving in ways that we were unable to detect.

**Table 1.** Capture history and morphological data for the 15 Weddell seal yearlings that carried TDRs in McMurdo Sound, Antarctica.

ID No.	Sex	Dates	Mass (kg)	Length (cm)	Girth (cm)	RMI
9791	M	Oct. 14–20, 1992	119.2	155	124	–4.73
9836	M	Nov. 2–9, 1992	141.7	152	133	4.69
10095	M	Oct. 15–20, 1992	145	172	128	2.46
10112	F	Oct. 20–25, 1992	155.5	184	130	0.48
10113	M	Oct. 20–25, 1992	138.1	155	125	12.51
10149	F	Oct. 25–29, 1992	135	156	124	10.41
10150	M	Oct. 25–29, 1992	169.4	163	142	6.8
10420	M	Nov. 27 – Dec. 2, 1992	119.4	163	122	–6.37
10289	F	Nov. 7–12, 1993	—	163	152	—
10558	M	Oct. 29 – Nov. 6, 1994	92.6	149	117	–16.63
10574	M	Oct. 29 – Nov. 6, 1994	95.1	155	115	–14.56
10618	M	Oct. 31 – Nov. 6, 1994	107	144	111	9.13
10667	M	Nov. 19–27, 1994	140.8	162	133	–3.78
10839	F	Nov. 8–15, 1994	144.6	178	130	6.08
10900	F	Nov. 8–12, 1994	149.6	171	149	–34.82

Of all the physiological and morphometric measurements taken, only measures of body size explained a significant proportion of the variation in diving behavior. For yearlings in this study, mass explained 48% of the variation in mean dive depth (mean depth =  $-1.71 \times \text{mass} + 343$ ), 33% of the variation in mean dive duration (mean duration =  $0.04 \times \text{mass} + 3.83$ ), and 49% of the variation in mean dive frequency (mean frequency =  $-0.66 \times \text{mass} + 146$ ). As mass increased, depth and dive frequency tended to decrease and dive duration to increase (Fig. 3). Measures of body size (mass, RMI) were also the only variables that accounted for individual variation in the maximal (95% cumulative frequency) dive depth and duration. Larger animals made longer and shallower dives, with mass accounting for 82% of the variation in maximum dive duration (maximum duration =  $0.12 \times \text{mass} - 1.79$ ), but only 22% of the variation in maximum dive depth (maximum depth =  $-2.49 \times \text{mass} + 558.85$ ). Blood-chemistry parameters showed little individual variation and were not correlated with dive parameters (HCT  $58.9 \pm 2.0\%$ , Hb  $25.60 \pm 1.15 \text{ g\%}$ , lactate  $6.4 \pm 0.9 \text{ mM}$ , glucose  $7.1 \pm 0.3 \text{ mM}$ , ketone bodies  $0.179 \pm 0.088 \text{ mM}$ , specific gravity  $1.022 \pm 0.002 \text{ g/mL}$ ).

Rayleigh's test for uniformity revealed that seals did not dive uniformly throughout the day ( $p < 0.001$ ) and that dives were most frequent in the early morning (Fig. 4). However, the 95% confidence interval was large (5 a.m.  $\pm$  6 h) and the Watson–Williams test of heterogeneity indicated significant individual variation in the time of peak dive activity ( $F = 79.66$ ,  $p < 0.0001$ ). Most seals concentrated their diving activity in the hours between midnight and 6 a.m., but yearlings 9791 and 10289 dove more often before midnight and 3 seals (10618, 10113, and 10839) showed no diel variation in dive activity. There was no significant relationship between the time of day when individuals dove most frequently and the mean or maximum depth or duration, overall dive frequency, or any physiological measure.

While diel trends were evident in mean dive depth and duration when all individuals were combined (Fig. 4), these trends were not significant (periodic regression analysis,  $p > 0.05$ ). However, when the dive patterns of each seal

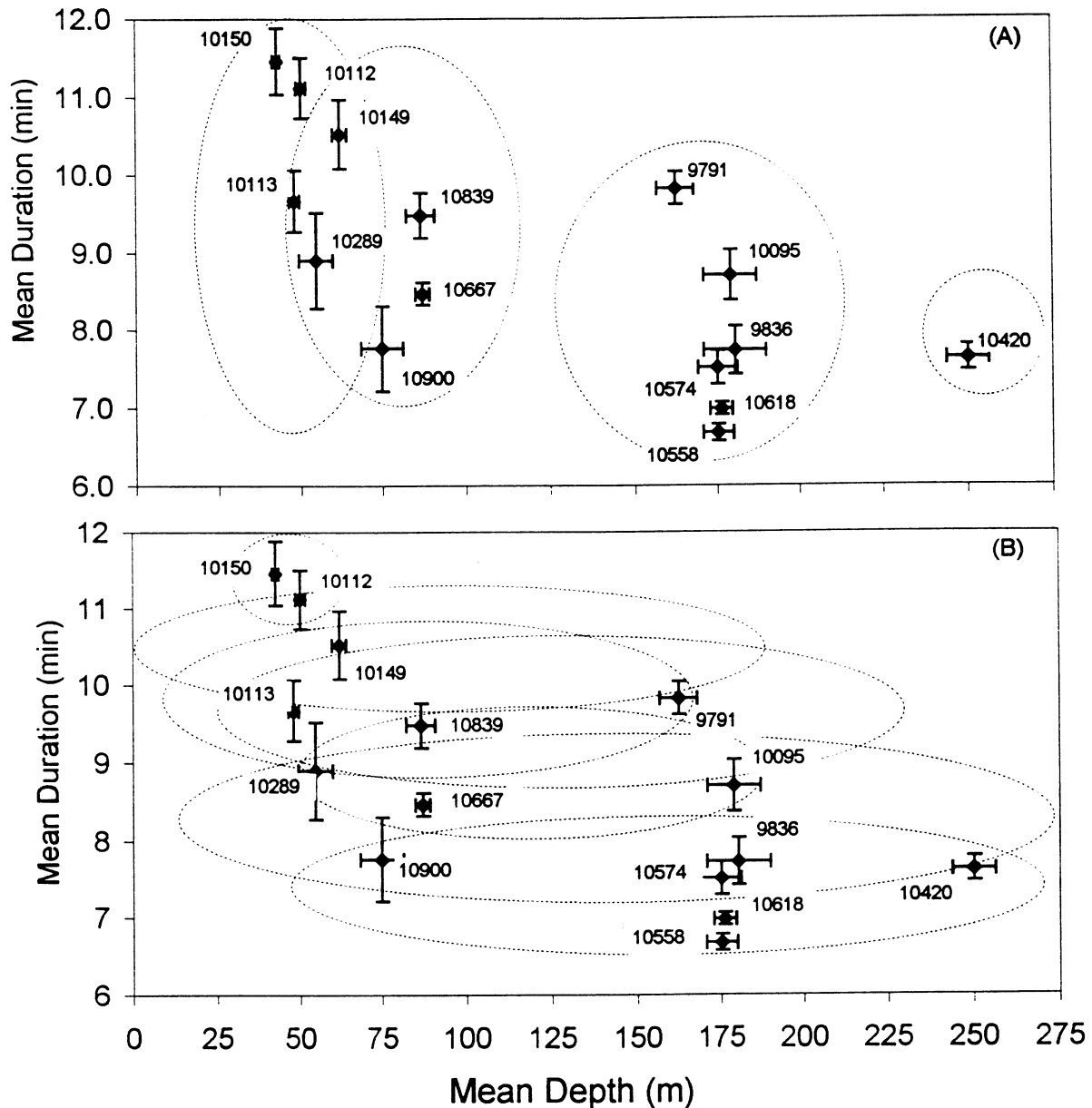
were analyzed separately, 6 yearlings did show some significant diel variation in these measures (yearlings 9791, 9836, 10113, 10420, 10667, and 10839). There was no difference in the average dive depth or duration between these yearlings and those that did not show any diel variation in diving behavior ( $t$  test,  $p > 0.05$ ), and the amount of variation accounted for by time of day was less than 50% in all cases but one (75% of the variation in maximal duration of dives made by yearling 10420 was due to time of day). The deepest and longest dives of these yearlings occurred at midday and the diel pattern was more evident in depth than in duration.

### Dive types

The results of cluster analyses performed on all the data and the subsamples indicated that four clusters (dive shapes) were an appropriate number for this data set: "slow ascent," "slow descent," "U-shaped," and "square" (Fig. 5). Note that the distribution of depths in slow-ascent dives are skewed right and those in slow-descent dives skewed left. Following this analysis, maximum-depth histograms were calculated for each dive type to determine if any further categorization could be accomplished. As the histograms for slow-descent and slow-ascent dives were distributed unimodally with depth, no further categorization was warranted. However, the maximum-depth histograms for square and U-shaped dives were multimodal, which indicated that the data could be further classified. U-shaped dives were therefore divided into three groups: less than 60 m (shallow U), between 60 and 230 m (mid-depth U), and deeper than 230 m (deep U). Square dives were divided into two groups: shallower than 30 m (shallow square) and deeper than 30 m (deep square).

Table 2 summarizes the diving behavior of Weddell seal yearlings. Deep U and deep square dives were the most common, while shallow U and shallow square dives were the least common. The results of one-way ANOVA indicated that not all dive types differed in mean depth, duration, frequency, or proportion (Table 2). Shallow U and shallow square dives differed only in shape, while both deep U and deep square, and mid-depth U and slow-ascent dives differed only in mean depth. Four dive types, slow ascent, mid-depth U,

**Fig. 1.** Relationship between mean ( $\pm$  SE) dive depth and duration. Dashed circles indicate the different overlapping groups in which the mean depth (A) or duration (B) did not differ significantly ( $p < 0.05$ , Tukey's HSD). Individual yearlings are identified by ID No.



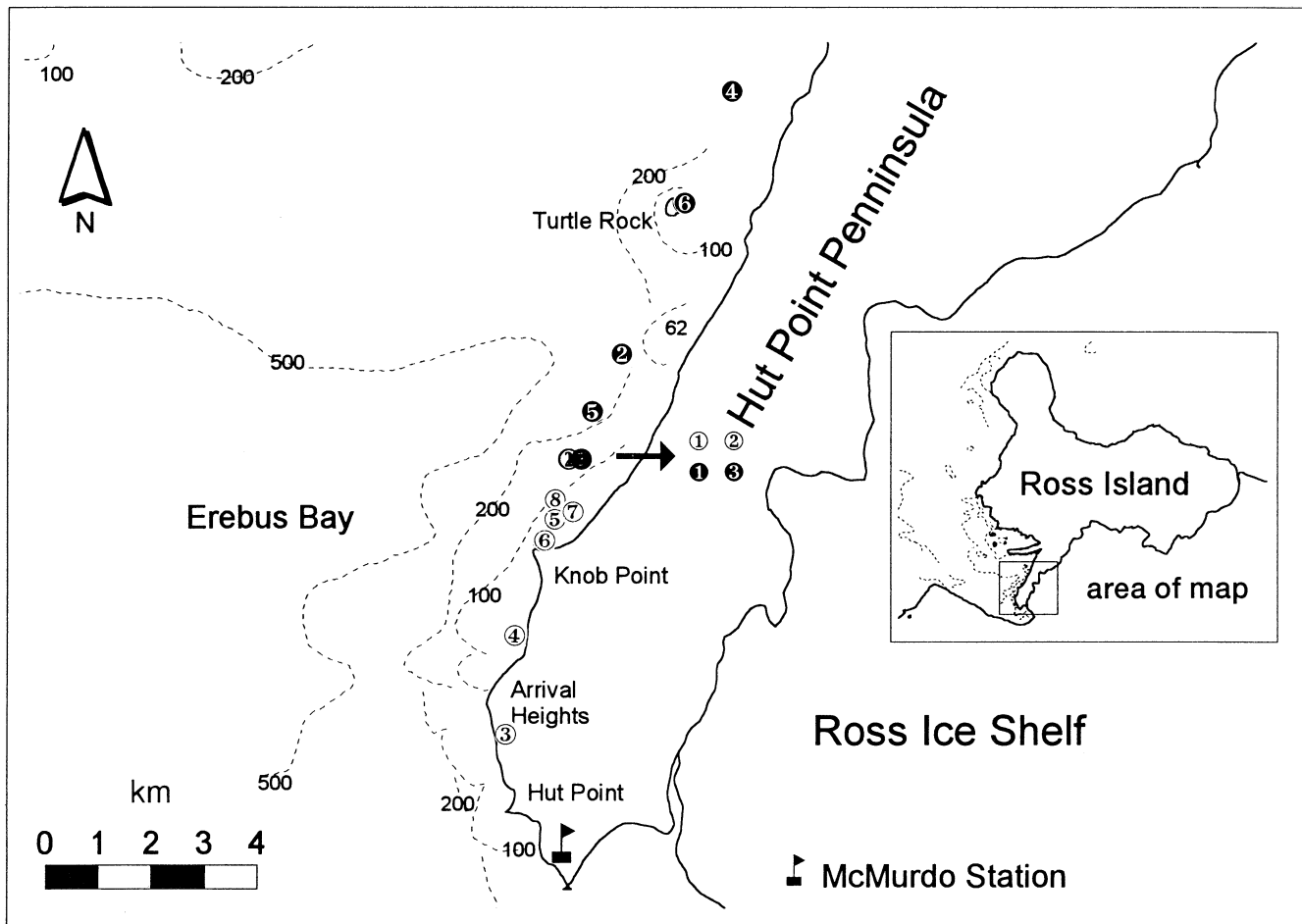
deep U, and deep square, had similar mean durations. Similarity between dive types in mean depth, duration, or frequency was possible because dive types were based initially on shape and not depth or duration.

Dives of all types except deep square were distributed non-uniformly throughout the day (Rayleigh's test,  $p < 0.05$ ), and the time of peak occurrence differed by type ( $F = 128.26$ ,  $p < 0.0001$ ). While slow-ascent dives occurred primarily before midnight (10:45 p.m.  $\pm$  1:00 h), all other types occurred most frequently in the early morning, with overlap in their 95% confidence intervals between the hours of 2 a.m. and 6 a.m. (Table 3). Uniformity of dive time by type was tested for within each individual seal. For more than half the seals, slow-descent, shallow U, and shallow square dives were distributed uniformly throughout the day. Slow-ascent, mid-depth U, deep U, and deep square dives were more often

distributed non-uniformly (Table 3). The proportion of dive types that showed no variation in frequency of occurrence throughout the day differed by individual seal and ranged from 0 to 100%. For example, there was no diel pattern in dive frequency for any dive type for seal 10112, while seal 9836 showed diel variation in all dive types. For the other 13 seals, the proportion of dive types that were non-uniformly distributed throughout the day varied from 33 to 75%.

There was diel variation in mean dive depth and duration for each type of dive for all yearlings combined (Fig. 6). However, when the yearlings were treated separately, some showed diel patterns in the average or maximum depth of dives of certain types, while others did not. In general, when a pattern was present, dives were deeper and longer during the middle of the day and the difference was more pronounced in depth than in duration.

**Fig. 2.** Yearling locations at either TDR deployment or recovery. Solid circles indicate deep divers (mean depth > 100 m) and open circles shallow divers (mean depth < 100 m). Ocean depth (m) is indicated by the bathymetric (broken) lines. Yearling 9836 was captured to the north at Cape Evans (77°34.5'S, 166°04.8'E). The arrow points to an expanded view of the four animals that were tagged in close proximity to each other.



Shallow divers: ① 10112 ② 10113 ③ 10149 ④ 10150 ⑤ 10289 ⑥ 10667 ⑦ 10839 ⑧ 10900  
 Deep divers: ① 9791 ② 10618 ③ 10095 ④ 10420 ⑤ 10558 ⑥ 10574

There was significant variation among individuals in mean dive depth, duration, frequency, and proportion within and between dive types (one-way ANOVA by type,  $p < 0.05$  in all cases) (Fig. 7). Mean dive duration varied by individual for all dive types, while mean dive depth, frequency, and proportion varied by individual for all types except shallow U. Variation among individuals could be explained only partially by differences in seal size. In all instances, stepwise regression procedures demonstrated that mass and (or) RMI were the only measured variables that influenced diving behavior. However, while mass and (or) RMI were often significant, they explained more than half of the variation in diving behavior for only some dive types and measures (Table 4). Mean dive duration was positively correlated with body size for all dive types except shallow square, whereas the frequency and proportion of all dive types except deep square were negatively correlated with mass or RMI.

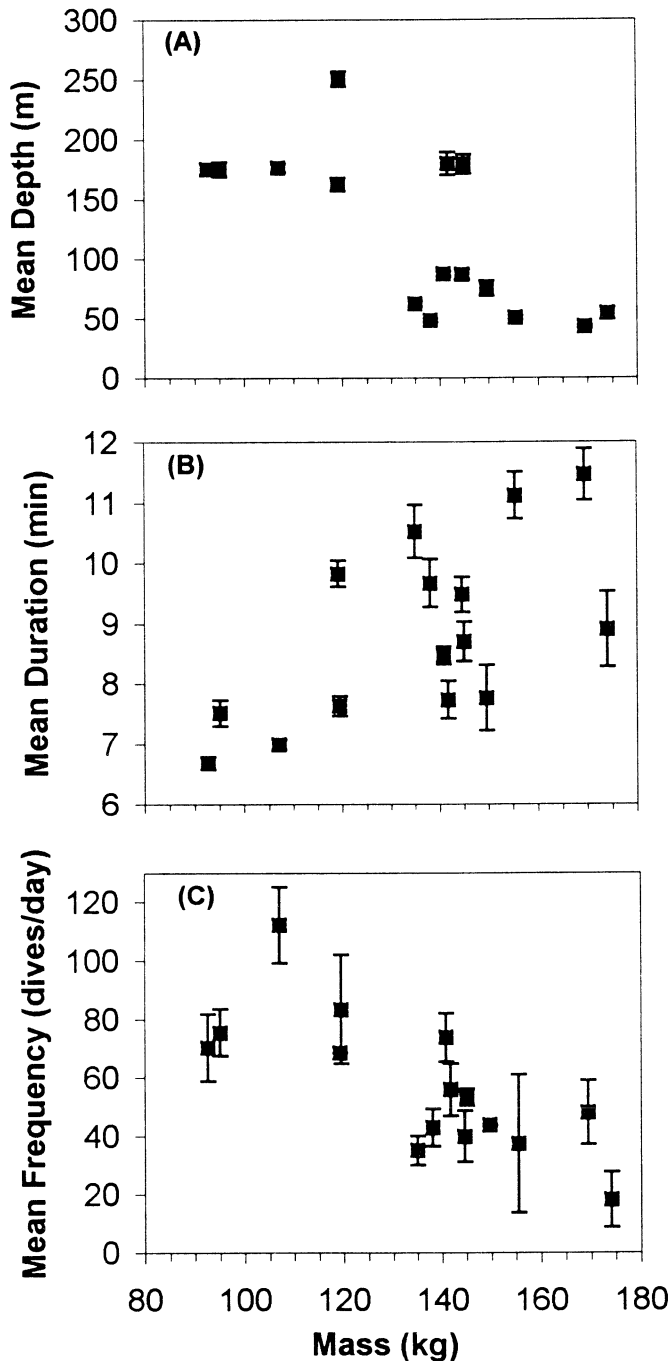
Correlation analysis revealed that many of the differences in mean diving behavior could be attributed to differences in the proportions of square and U-shaped dives. As the proportion of deep square dives increased, the proportion of deep U dives decreased, mean dive depth and frequency declined, and mean dive duration increased ( $p < 0.05$ ) (Table 5). In fact, most of the shallow-diving seals (mean depth < 100 m) did not make any deep U dives, and they all made significantly more deep square dives than did the deep divers (Fig. 8).

## Discussion

### Dive behavior and physiology

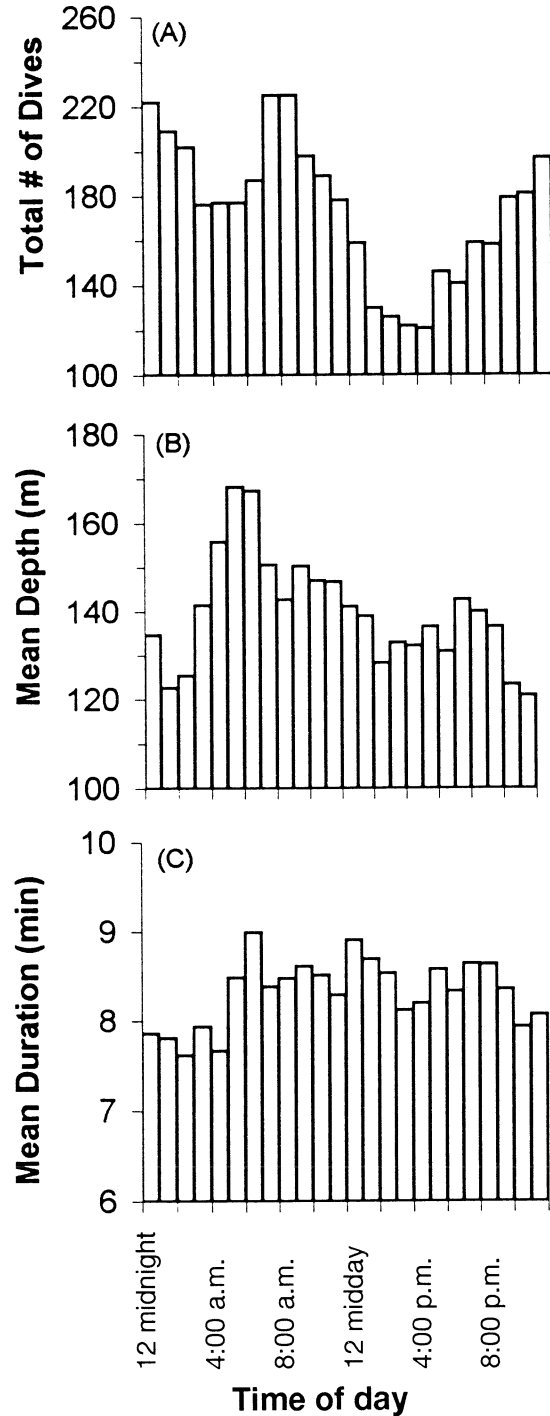
Despite the fact that all the seals in this study were apparently healthy yearlings diving in the same area and at the same time of year, there was significant variation among indi-

**Fig. 3.** The relationship between mass and mean ( $\pm$ SE) dive depth (A), duration (B), and frequency (C) for the 15 yearling Weddell seals in this study. Regression equations are given in the text.



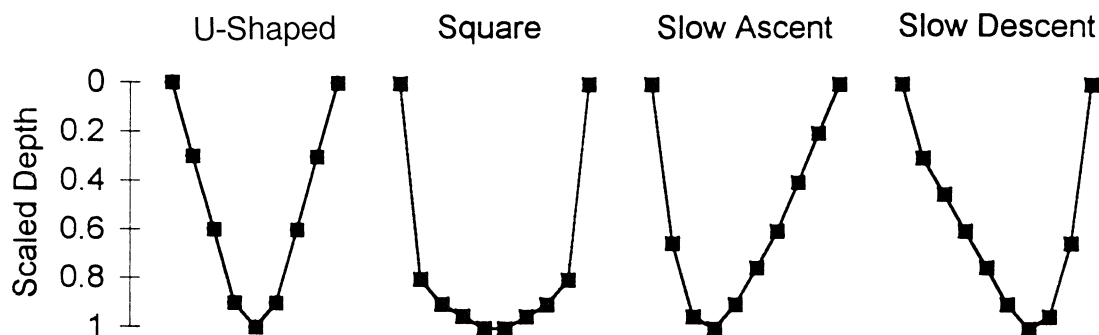
viduals in both physiological and behavioral measures. While the dive patterns were not expected to be identical because the large sample size permitted the detection of small differences, the variation was greater than anticipated, both in the average dive data and once dive types were identified and treated separately. Of all parameters measured, body mass, as opposed to direct physiological measures, accounted for the largest component of the variability. Differences in body size were correlated with dive depth, duration, and frequency,

**Fig. 4.** Diel variation in the total number of dives (A), mean dive depth (B), and duration (C) for all yearlings combined.



and the pattern observed in overall diving behavior was the same as that seen within each dive type. Generally, mean dive depth, frequency, and proportion of total dives by type decreased with increasing mass, and dive duration increased. The only exception to this pattern was that larger yearlings made more deep square dives, as measured by both dive frequency and proportion.

While the relationship between behavior and mass was not always strong (Table 4;  $r^2$  ranged from 0.19 to 0.72), few

**Fig. 5.** The shapes of the four main dive types, determined by cluster analysis.**Table 2.** Dive depth, duration, frequency, and proportion (percentage of total dives) (mean  $\pm$  SE) for each of the seven types of dives made by Weddell seal yearlings in McMurdo Sound, Antarctica.

	Shallow U (n = 263)	Shallow square (n = 353)	Slow ascent (n = 510)	Slow descent (n = 593)	Mid-depth U (n = 806)	Deep square (n = 902)	Deep U (n = 1003)
Depth (m)							
Mean	25 $\pm$ 0.9	14.5 $\pm$ 0.4	132.4 $\pm$ 3.1*	45.6 $\pm$ 1.8*	150 $\pm$ 1.5*	62.4 $\pm$ 0.4*	304.3 $\pm$ 0.4*
Maximum	60	30	384	326	231	405	480
Group	a	a	cd	ab	d	bc	e
Duration (min)							
Mean	2.5 $\pm$ 0.2*	2.3 $\pm$ 0.1*	8.9 $\pm$ 0.2*	4.5 $\pm$ 0.2*	9.4 $\pm$ 0.1*	9.7 $\pm$ 0.1*	10.0 $\pm$ 0.1*
Maximum	19.9	12.5	30.7	27.8	29.9	24.8	25.5
Group	a	a	b	a	b	b	b
Frequency (dives/day)							
Mean	3 $\pm$ 0.3	2.4 $\pm$ 0.3	7.5 $\pm$ 1*	7.3 $\pm$ 0.7*	12 $\pm$ 1.8*	12.9 $\pm$ 1.7*	14.7 $\pm$ 2.6*
Maximum	12	12	39	22	55	55	73
Group	a	a	ab	ab	bc	bc	c
Proportion (%)							
Mean	6 $\pm$ 1	5.7 $\pm$ 0.6	11.5 $\pm$ 1.4*	13.9 $\pm$ 1.6	17 $\pm$ 2	26.9 $\pm$ 3.3*	19 $\pm$ 3.2*
Maximum	18.2	21.8	46.9	54.6	60	85.7	84.2
Group	a	a	ab	ab	b	c	bc

**Note:** Dive types with the same group code have mean values that do not differ significantly (Tukey's HSD post-hoc comparison of means,  $p < 0.05$ ). Groups were determined using one value for each yearling.

\*Significant variation between individual means ( $p < 0.05$ ).

other marine mammal studies have linked individual differences in average diving behavior to physiology. In general, these studies compared animals of different ages or sex and showed that while physiology could constrain the range of possible behaviors, its effect on routine behavior was more limited (Burns and Testa 1997; Burns and Castellini 1996; Le Boeuf et al. 1996; Boyd et al. 1994; Kooyman et al. 1983). The fact that measures of body size accounted for up to 72% of the behavioral variation suggests that the diving behavior of yearling Weddell seals is fairly sensitive to physiological, or at least morphological, constraints.

Dive duration is the measure of diving behavior expected to be most sensitive to variation in body size. It has been demonstrated repeatedly that as body mass increases, mass-specific oxygen stores increase and metabolic rate and transport costs decrease (Thorson and Le Boeuf 1994; Ponganis et al. 1993; Davis et al. 1985; Schmitz and Lavigne 1984). As a result, larger animals are able to remain submerged longer and have longer aerobic dive limits (Kooyman et al. 1980, 1983). This was the pattern observed in all the yearlings and for all dive types. As mass increased, dive

duration (mean and maximum) increased as well. However, in contrast to the causal relationship between mass and dive duration, it is unlikely that body size directly constrained dive depth or frequency, so the correlation between these factors is harder to explain.

It is possible that the inverse relationship between yearling mass and dive frequency resulted from a combination of the duration limitations faced by the small, deep-diving yearlings and the mathematical relationship between dive duration and frequency. As average dive duration decreases, the total number of dives possible within a given time increases. Therefore, the increase in dive frequency seen in smaller seals could have been solely a result of their shorter average dive duration. However, the large variation in total time spent diving (1.18–15.27 h/day) both within and among individual seals was unrelated to mass, and dive frequency and duration were not significantly correlated. This, in combination with the fact that mass accounted for 49% of the variation in mean dive frequency when all types were combined, and between 25 and 50% of the variation in the frequency of each dive type, argues against a strict mathe-



**Table 3.** Diel variation in dive frequency by dive type.

Dive type	No. of dives	Mean time	Proportion of yearlings with diel cycle	Time of peak activity
Slow ascent	510	10:40 p.m. $\pm$ 5:34 h <sup>‡</sup>	8/11 (73)	8:06 p.m. – 3:44 a.m.
Slow descent	547	4:18 a.m. $\pm$ 6:30 h <sup>‡</sup>	5/12 (42)	10:15 p.m. – 3:32 a.m.
Shallow U	203	5:43 a.m. $\pm$ 7:50 h <sup>†</sup>	1/9 (11)	5:58 a.m.
Mid-depth U	806	11:12 p.m. $\pm$ 8:29 h*	7/11 (64)	7:23 p.m. – 4:45 a.m.
Deep U	1003	5:48 a.m. $\pm$ 6:23 h <sup>‡</sup>	6/7 (86)	12:17 a.m. – 5:00 a.m.
Shallow square	213	5:18 a.m. $\pm$ 7:24 h*	3/10 (30)	1:43 a.m. – 5:17 a.m.
Deep square	902	2:30 a.m. $\pm$ 10:10 h	8/12 (66)	7:03 p.m. – 3:29 a.m.

**Note:** The mean time  $\pm$  the 95% confidence interval is shown for all yearlings combined. The number of yearlings with a diel cycle of dive activity is reported as the fraction (and proportion) of total yearlings which made dives of that type. The time of peak activity is the range of mean values for the yearlings with non-uniform frequency distributions. Numbers in parentheses are percentages.

\*Non-uniform at  $p < 0.05$ .

†Non-uniform at  $p < 0.01$ .

‡Non-uniform at  $p < 0.001$ .

mathematical explanation. In addition, because dive proportion was not directly related to mean dive duration or frequency, there was no reason to suspect that up to 52% of the variation in the proportion of different dive types could be explained by mass.

An alternative explanation of the relationship between dive frequency and mass relies on optimal foraging theory. Dives consist of three components: travel to the foraging depth, bottom time, and travel back to the surface. As a result, for a given duration, deeper dives have less bottom time in which seals can find and capture prey than do shallower ones. Thus, deeper diving seals must either dive more often, swim to depth faster, or increase the duration of each dive in order to have equivalent total bottom time (Houston and Carbone 1992; Kramer 1988). However, the mean dive duration for yearlings in this study was 8.8 min, a value surprisingly close to their calculated aerobic dive limit (ADL) of 8.5–9.9 min (Burns and Castellini 1996). This suggests that the smaller, deep-diving yearlings were unable to increase their mean dive duration without significantly increasing the proportion of anaerobic dives, and instead had to rely on increasing dive frequency to increase bottom time. The question of why the smaller yearlings tended to dive to greater depths remains.

### Dive types

To understand why the smaller yearlings dove, on average, much deeper than did the larger yearlings, we attempted to determine the purpose of the dive types identified by cluster analysis and maximum-depth histograms. This was done by examining the profile of the dive and comparing the shape with that of dives made by adult Weddell seals and other phocid species. However, it is important to note here that the purpose of the dives is inferred, and not directly known.

*Shallow U and shallow square* dives differed only in shape, and were the shallowest, shortest, and least common types in both frequency and proportion. While overall these dives occurred most often in the early morning, few individuals showed diel variation in dive frequency, and there was no pattern in dive depth or duration with time of day. Because the dives were so short and shallow, it is unlikely

that they represented any directed foraging activity. Instead, shallow U and square dives probably represented social activity or travel between neighboring breathing holes, two activities that occur throughout the day.

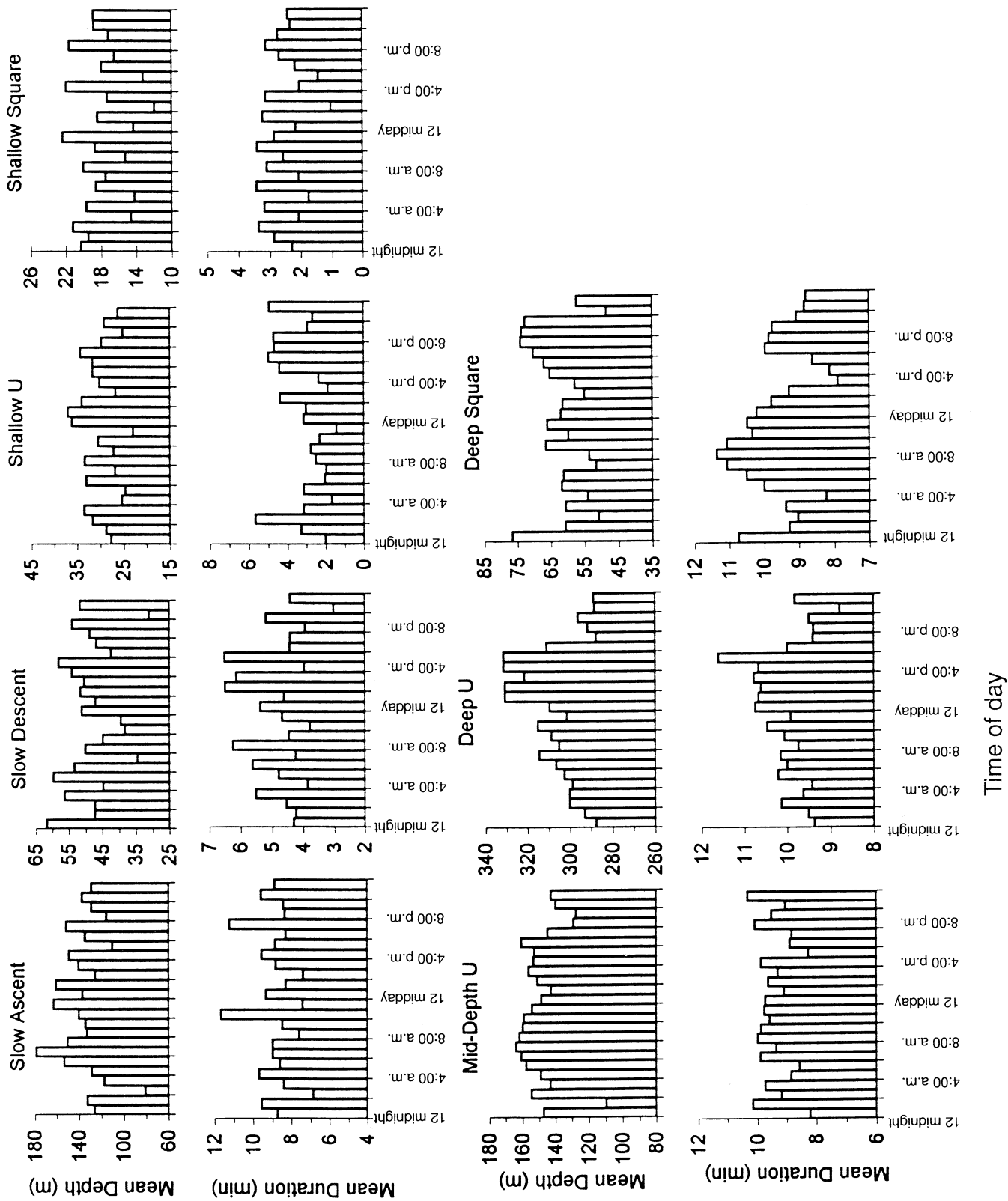
*Slow-descent* dives were also fairly short, shallow dives that occurred most often in the early morning hours. The slow-descent dives made by yearlings appeared to be similar to (proposed) resting/sleeping or food processing dives made by elephant seals (Asaga et al. 1994; Le Boeuf et al. 1992; Hindell et al. 1991). However, their short duration suggests that these dives are similar to, although shorter than, exploratory dives made by adult Weddell seals in which the seal slowly descended along the sea floor bottom looking for prey and then quickly surfaced to begin another search (Schreer and Testa 1996). Alternatively, these dives, together with the shallow U and shallow square dives, might represent orientation, rest, or social activities (Kooyman 1968).

*Slow-ascent* dives made by yearlings were similar to slow-ascent dives made by adult Weddell seals near the end of foraging bouts. Adult slow-ascent dives are thought to represent processing dives or unsuccessful foraging dives where the seal slowly ascends while collecting cues for subsequent dives (Schreer and Testa 1996). In yearlings, the diel variation in dive frequency, depth, and duration, in combination with the long duration of these dives, suggests that slow-ascent dives are similarly associated with foraging behavior.

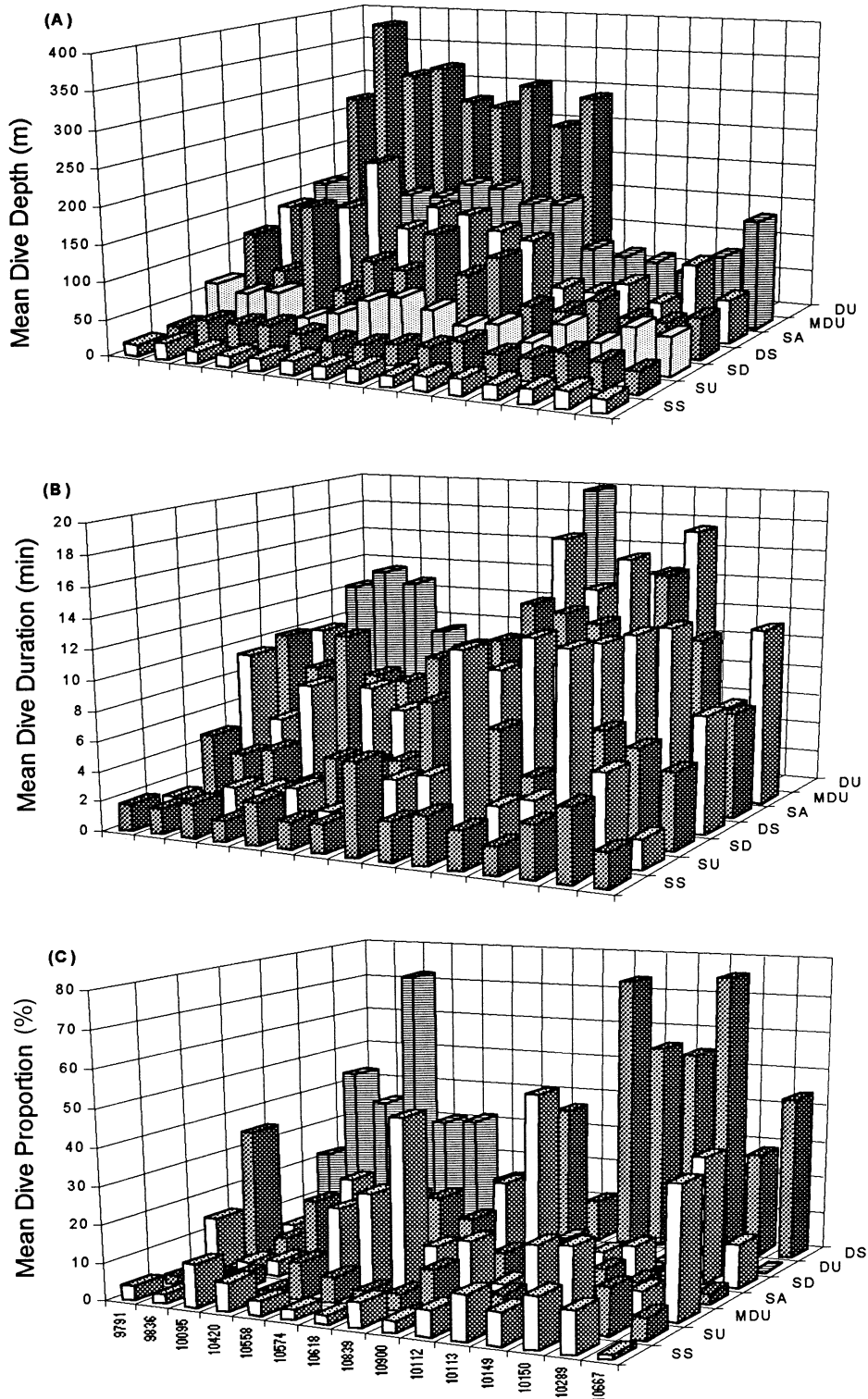
*Mid-depth and deep U-shaped* dives appeared similar to the pelagic foraging (square) and exploration (V-shaped) dives made by adult Weddell seals (Schreer and Testa 1996). Alternatively, deep U dives could represent pelagic foraging and mid-depth U traveling or searching dives, as has been suggested for similarly shaped dives made by grey and elephant seals (Slip et al. 1994; Le Boeuf et al. 1992; Thompson et al. 1991). However, like slow-ascent dives, mid-depth and deep U dives averaged approximately 10 min in duration. This suggests that seals making these dives were attempting to maximize their time at depth while remaining (on average) just within their calculated ADL, a strategy that seems more suited to foraging than traveling.

*Deep square* dives also had a mean duration close to the yearling ADL, but they were much shallower than all other

Fig. 6. Diel variation in mean dive depth and duration for each of the seven dive types for all yearlings combined.



**Fig. 7.** Mean dive depth (A), duration (B), and proportion (C) of total dives per day for each dive type and yearling. Dive types are as follows: SS, shallow square; SU, shallow U; MDU, mid-depth U; SA, slow ascent; SD, slow descent; DU, deep U; DS, deep square. Individual yearlings are identified by ID No.



dives of similar duration. Square dives have been interpreted as benthic foraging dives in elephant seals, grey seals, and adult Weddell seals (Schreer and Testa 1996; Sjöberg et al. 1995; Le Boeuf et al. 1992; Hindell et al. 1991; Thompson et al. 1991). However, in adult Weddell seals, square dives

were much deeper and longer than those reported here, and were thought to represent a mix of benthic and pelagic foraging (Schreer and Testa 1996). As 90% of the deep square dives of yearlings occurred at depths of less than 100 m, and there was little diel variation in depth, duration, or fre-

**Table 4.** Morphometric factors that significantly influenced dive parameters for yearling Weddell seals in McMurdo Sound, Antarctica.

Dive type	Mean depth (m)	Maximal depth (m)	Mean duration (min)	Maximal duration (min)	Frequency (dives/day)	Proportion (% of dives by type)
Slow ascent	-1.19 mass $r^2 = 0.27$		+0.09 mass $r^2 = 0.43$	+0.18 mass $r^2 = 0.5$	-0.16 mass $r^2 = 0.32$	-0.3 mass $r^2 = 0.3$
Slow descent			+0.04 mass $r^2 = 0.19$		-0.25 RMI $r^2 = 0.52$	-0.6 RMI $r^2 = 0.46$
Shallow U	+0.21 mass $r^2 = 0.48$		+0.11 mass $r^2 = 0.36$	+0.18 mass $r^2 = 0.45$	-0.04 RMI $r^2 = 0.31$	
Mid-depth U	-0.81 mass -1.2 RMI $r^2 = 0.53$	-1.5 mass $r^2 = 0.34$	+0.13 mass $r^2 = 0.35$	+0.15 mass $r^2 = 0.38$	-0.16 mass $r^2 = 0.25$	-0.3 mass $r^2 = 0.19$
Deep U		+2.4 RMI $r^2 = 0.31$	+0.12 mass -0.13 RMI $r^2 = 0.72$	+0.16 mass $r^2 = 0.4$	-0.64 mass $r^2 = 0.41$	-0.7 mass $r^2 = 0.31$
Shallow square	+0.09 RMI $r^2 = 0.21$	+0.19 RMI $r^2 = 0.27$				
Deep square			+0.07 mass $r^2 = 0.25$	+0.15 mass $r^2 = 0.5$	+0.36 mass $r^2 = 0.5$	+0.8 mass $r^2 = 0.52$

**Note:** Regression analysis is based on the average value for each yearling. Empty cells indicate that none of the morphometric or physiological parameters measured had a significant effect on the dive parameter.

**Table 5.** Correlation coefficients between mass (kg), mean dive depth (m), duration (min), and frequency (number of dives/day) for all dive types combined, and the mean daily proportion (percentage) of dives of each type made by yearling Weddell seals.

	Mass	Mean depth	Mean duration	Mean frequency	Percentage					
					Slow ascent	Slow descent	Shallow U	Mid-depth U	Deep U	Shallow square
Mean depth	-0.67									
Mean duration	0.70	-0.72								
Mean frequency	-0.68	0.70	-0.67							
Percentage										
Slow ascent	-0.55	—	—	—						
Slow descent	—	—	—	—	—					
Shallow U	—	—	—	—	—	0.70				
Mid-depth U	—	—	—	0.61	—	—	—			
Deep U	—	0.94	-0.60	—	—	—	—	—		
Shallow square	—	—	0.64	—	—	—	—	-0.58	—	
Deep square	0.72	-0.84	0.87	-0.65	-0.56	—	—	—	-0.67	—

**Note:** A dash indicates that there was no significant correlation ( $p > 0.05$ ).

quency, it seems probable that the square dives made by yearlings were primarily shallow benthic foraging dives. It seems unlikely that these were traveling dives because seals that made many U-shaped dives made few square dives, and seals that made predominantly deep square dives made very few "foraging" dives of other types (see Fig. 8, Table 5).

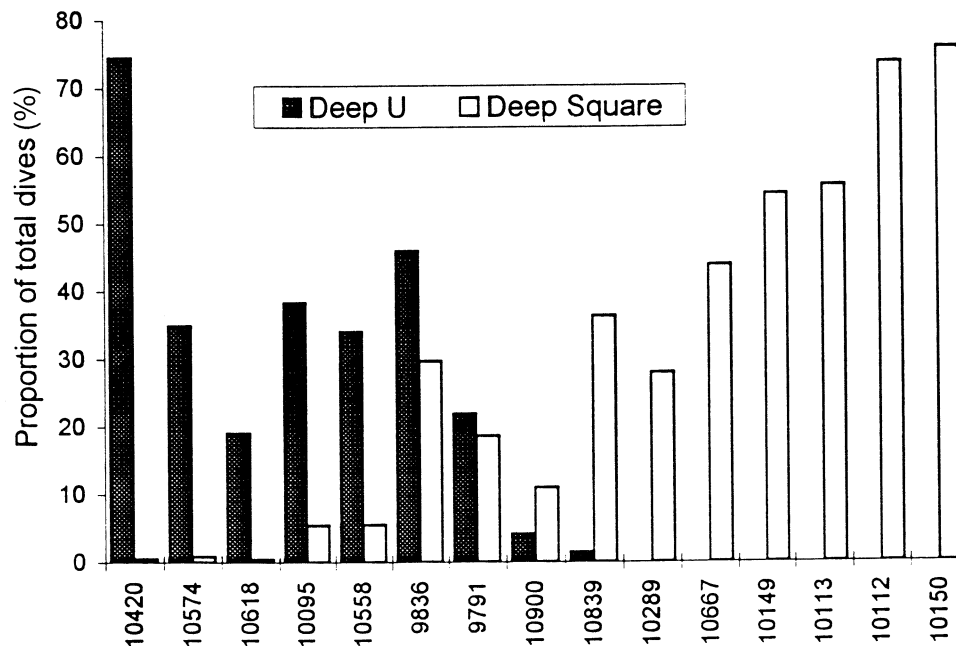
In general, the dives made by yearling Weddell seals were similar to those made by adults. However, because of their smaller size, yearlings' dives tended to be both shallower and shorter than adults' dives. Three of the dive types made by yearlings, shallow U, shallow square, and slow-ascent, seemed to represent a combination of social, traveling, and processing dives. These dives were routinely less than 5 min in length and fairly shallow, and their depth and duration changed little throughout the day. On average,  $26.2 \pm 14.5\%$  (combined percentage) of the dives made by yearlings were classi-

fied as shallow U, shallow square, and slow-descent dives. The remaining diving activity ( $73.8 \pm 14.5\%$ ) could be interpreted as foraging behavior. The absence of large diel fluctuations in the depth or duration of most dives probably resulted from the near constant light levels during this study. This agrees with previous studies in McMurdo Sound which have shown that the amount of diel variation in dive parameters changed with the seasons and was least evident in the austral summer (Burns and Testa 1997; Testa 1994; Castellini et al. 1992).

**Implications for behavioral strategies**

Further analyses revealed that differences in the proportion of the two main foraging dives, deep square and deep U, largely determined the mean diving behavior. The decrease in mean dive depth (all dives combined) associated with

Fig. 8. Mean daily proportions of total deep square and deep U dives for all yearlings. Individual yearlings are identified by ID No.



increased mass was caused by an increase in the proportion of deep square dives and a decrease in the proportion of slow-ascent and deep U dives. Similarly, because seals that made more square dives made fewer dives overall, the decrease in dive frequency associated with increased mass was also linked to the proportion of these two dive types. As deep square dives are thought to represent benthic foraging and deep U dives pelagic foraging, from this analysis it appears that within Erebus Bay during the summer, larger yearlings foraged mainly in the shallow-water benthic community, while smaller yearlings concentrated their foraging predominantly in the pelagic ecosystem.

The diet of Weddell seals consists primarily of small fishes, cephalopods, invertebrates, and the occasional large Antarctic cod (*Dissostichus mawsoni*) (Castellini et al. 1992; Green and Burton 1987; Plötz 1986; Testa et al. 1985; Dearborn 1965). In McMurdo Sound, most studies have shown that the Antarctic silverfish (*Pleuragramma antarcticum*) forms the bulk of the diet and benthic fishes and other prey items are much less common (Castellini et al. 1992; Green and Burton 1987; Testa et al. 1985). While the Antarctic silverfish, cod, and cephalopods are predominantly found at midwater, the smaller ice fishes (*Trematomus* spp., *Pagothenia borchgrevinki*) inhabit the undersurface of the sea ice and shallow benthic areas (Ekau 1990; Macdonald et al. 1987; Eastman 1985). Little else is known about prey availability or abundance within the study area. It seems probable that the shallow-diving yearlings that made predominantly deep square dives were concentrating on benthic nototheniids, while the deeper divers were foraging mainly on pelagic species. If this was the case, the deep-diving yearlings were foraging on a much more energy-dense (kcal/g) prey base than were the shallow divers (Friedrich and Hagen 1994; Castellini et al. 1992). Similar patterns have been observed in other species whose diet and mean dive depth were both known to differ: in general, deeper diving individuals

foraged on more energy-dense prey or expended less energy while foraging (Goebel et al. 1990; Costa and Gentry 1986).

While differences in summer foraging depths and diet could result if the larger yearlings were excluding smaller individuals from shallow foraging grounds, previous studies have suggested that the inshore areas where adults congregate become food depleted during the summer breeding season (Testa et al. 1985). Thus, while food may be easier to reach in the benthic areas, it may be both richer in energy and easier to find in the pelagic zone. In fact, most Weddell seal studies have indicated that nonbreeding animals concentrate their diving and foraging activity in deep water, and have suggested that the nearshore aggregations seen during the breeding season are temporary (Schreer and Testa 1996; Testa 1994; Castellini et al. 1992; Kooyman 1968). Even during the summer, yearlings are more commonly found outside of Erebus Bay in regions of deeper water (Testa 1987; Stirling 1969; Kooyman 1968), and all yearlings in this study were fairly mobile and soon left the area.

Despite differences in depth, all types of foraging dives lasted approximately 10 min, which suggests that both deep- and shallow-diving yearlings faced similar constraints on duration. Individual yearlings from both groups exceeded their calculated ADL 16–79% of the time, much more frequently than did free-diving adult Weddell seals (5–8%: Kooyman et al. 1980). Even if the calculated ADL significantly underestimated the actual ADL (as has been suggested for younger pups; Burns and Castellini 1996), these findings strongly suggest that young, growing yearlings are often required to “push” their physiological limits in order to increase their bottom time and meet their energy-intake needs. As discussed earlier, perhaps shallow-diving yearlings were able to make fewer dives overall because a greater proportion of the dive time was spent at the foraging depth. Yet, the fact that shallow dives were no shorter than pelagic dives suggests that the dives had a low energy return rate and

long search and handling times. Pelagic foraging yearlings probably exploited a more energy-dense prey resource, but as their time at depth was limited as a result of the longer travel times, they had less time for prey search and capture and therefore needed to make more dives in order to obtain enough food. Still, the costs of living at the edge of the physiological envelope are probably high for both deep- and shallow-diving yearlings: juvenile survival rates are significantly lower than those of adults (Hastings 1996; Testa 1987). As of January 1997, none of the animals in this study have been resighted as subadults, so the fitness consequences of the two strategies cannot be evaluated. However, as both strategies can be maintained in the population only if they have similar fitness consequences, it seems likely that the differences in foraging strategy reflect individual preferences for different areas, or behavior tailored to different physiological limitations.

This study has shown that there can be large variations in diving behavior within an apparently homogeneous group of animals, and that physiological variables such as mass can be correlated with behavioral patterns in unexpected ways. While approximately half of the variation in diving behavior can be explained by differences in body size, a significant amount of variation remains unexplained by the variables measured here. This residual variation has significant implications for marine mammal diving behavior studies, for it suggests that we cannot reliably link diving behavior with individual traits or condition. In addition, this study demonstrates that average diving behavior is not sufficient for comparing behavior or understanding foraging strategies. The interpretation of yearling diving behavior, foraging locations, and diet that resulted from separating individuals and dive types was different from that based on the average diving behavior. Together these findings argue against ignoring variation among individuals when describing dive patterns or comparing the diving behavior of different sex and age groups. Finally, this study suggests that all yearlings, whether foraging in deep or shallow water, are required to push their physiological limits in order to forage effectively.

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(revised 1985) of the National Institutes of Health, the current laws of the United States of America, and the principles and guidelines of the Canadian Council on Animal Care.

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