

# The development of diving behavior in juvenile Weddell seals: pushing physiological limits in order to survive

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**Abstract:** In juvenile phocids, the successful transition from nursing to independent foraging is contingent upon the development of adequate diving skills within the limited time between weaning and the depletion of body reserves. Yet, because juvenile seals are unable to remain submerged for as long as adults, owing to their smaller size, higher metabolic rates, and lowered oxygen stores, their behavioral options are likely constrained. To determine how such limitations might influence foraging strategies, we studied the development of diving behavior and physiology in Weddell seal (*Leptonychotes weddellii*) juveniles, using a combination of time–depth recorders, satellite-linked dive recorders, and morphological and physiological measurements (mass and blood chemistry). Time–depth recorder data indicated that the average depth, duration, and frequency of dives made by pups increased rapidly in the period from birth through weaning, but slowed soon thereafter. While preweaning increases in these parameters were correlated with seal age, postweaning increases in dive capacity were gradual and were probably the result of slower changes in mass and body composition. In weaned pups and yearlings, dive frequency and time underwater increased with age and (or) mass. Despite their smaller size and lower absolute energy requirements, the amount of time juveniles spent in the water was similar to that spent by adults. However, because juveniles were unable to remain submerged as long as adults and because most foraging dives were deep, juveniles were unable to spend an equivalent amount of time at the foraging depths. This difference was evident even though juveniles dove much closer to their anaerobic threshold than did adults. These findings support the hypothesis that the foraging efficiency of younger seals is reduced relative to that of adults, owing to physiological and morphological constraints on aerobic dive duration, and suggests that low juvenile survival might result from behavioral constraints.

**Résumé :** Chez les jeunes phocidés, la transition entre la période d'allaitement et la quête de nourriture autonome dépend de l'acquisition d'aptitudes adéquates à plonger dans la période critique entre le sevrage et le déclin des réserves énergétiques. Cependant, parce que les juvéniles sont incapables de rester submergés aussi longtemps que les adultes à cause de leur taille plus petite, leur taux de métabolisme plus élevé et leurs réserves d'oxygène moins grandes, leurs options en matière de stratégies comportementales sont probablement restreintes. Pour déterminer comment de telles contraintes peuvent influencer les stratégies de quête de nourriture, nous avons étudié l'évolution du comportement de plongée et de la physiologie chez de jeunes Phoques de Weddel (*Leptonychotes weddellii*) au moyen de plusieurs méthodes combinées, utilisation d'appareils enregistreurs de la profondeur et de la durée, d'appareils enregistreurs de plongée liés à un satellite, prise de mesures morphologiques et physiologiques (masse, chimie du sang). Les appareils enregistreurs de la profondeur et de la durée ont montré que la profondeur, la durée et la fréquence moyennes des plongées augmentent rapidement entre la naissance et le sevrage, mais diminuent ensuite peu après. Alors que l'augmentation de ces paramètres avant le sevrage est en corrélation avec l'âge chez les juvéniles, l'augmentation de la capacité de plongée après le sevrage est graduelle et résulte probablement des variations moins rapides de la masse et de la composition corporelle. Chez les jeunes phoques sevrés et les phoques de 1 an, la fréquence des plongées et le temps passé sous l'eau augmentent en fonction de l'âge et (ou) de la masse. En dépit de leur plus petite taille et de leurs besoins énergétiques absolus moins importants, les juvéniles passent autant de temps dans l'eau que les adultes. Cependant, parce que les juvéniles sont incapables de rester submergés aussi longtemps que les adultes et comme la plupart des plongées de quête de nourriture se font en eau profonde, les juvéniles sont incapables de passer autant de temps aux profondeurs où ils pourraient trouver leur nourriture. La différence est flagrante, même si en plongée les jeunes se rapprochent beaucoup plus de leur seuil anaérobie que les adultes. Ces résultats confirment l'hypothèse selon laquelle l'efficacité de la recherche de nourriture chez les jeunes phoques est moins grande que celle des adultes à cause des contraintes physiologiques et morphologiques qui conditionnent la durée des plongées aérobies et indiquent que la survie plus faible des juvéniles peut être attribuable à des contraintes comportementales.

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## Introduction

Knowledge of the mechanisms by which neonatal mammals acquire the tools necessary to become competent predators is crucial to our understanding of how physiological processes influence behavioral strategies. While such questions can be addressed in many species, the study of how pinniped neonates become marine predators offers several unique and significant advantages. All pinnipeds are born on land or ice and, during the first days post partum, there is little to distinguish newborn pinnipeds from other mammalian young. In fact, most pinniped pups are unwilling to enter the water for several days following birth, and many demonstrate little aquatic activity prior to weaning (for review see Riedman 1990). Even in those species whose pups are aquatically active soon after birth, such as harbor, bearded, ringed, and Weddell seals, there is little apparent foraging until after weaning (Lydersen and Hammill 1993; Muelbert and Bowen 1993; Lydersen et al. 1994; Corpe 1996; Burns and Testa 1997; Burns and Schreer 1999). Thus, at weaning, pups of all species must learn to swim–forage successfully before the energy stores they acquired during lactation are depleted. As the success of this transition can affect both juvenile survivorship and population levels (Eberhardt and Siniff 1977; Merrick et al. 1987), understanding the physiological and ecological factors that affect juvenile diving capacity and behavior is extremely important.

Work on Weddell seals and other pinnipeds has revealed that marine mammals possess a suite of physiological adaptations that allow them to make deep and long dives: they have increased the amount of oxygen that can be carried to depth and have reduced the rate at which it is used. Large oxygen stores in the blood and muscle result from large blood volume, elevated hematocrit and hemoglobin, large muscle mass, and high concentrations of myoglobin in the muscle, while diving oxygen use rates are minimized through regulation of heart rate, metabolic rate, body temperature, and selective vasoconstriction (Kooyman et al. 1980, 1983; Qvist et al. 1986; Kooyman 1989; Castellini 1991; Fedak and Thompson 1993; Thorson and Le Boeuf 1994; Butler and Jones 1997). Because the maximum dive duration that can be accomplished before the balance of metabolism becomes anaerobic (the aerobic dive limit or ADL) is determined by metabolic rate and body oxygen stores, it is possible to relate individual- and species-specific behavioral differences to these two physiological parameters. Indeed, among species that exhibit different behavioral patterns, those that must dive deepest or longest in order to forage successfully have the largest oxygen stores and the lowest use rates (Kooyman et al. 1980, 1983; Castellini 1991; Thorson and Le Boeuf 1994; Butler and Jones 1997; Merrick and Loughlin 1997; Horning and Trillmich 1997b).

For adult pinnipeds, physiological limitations on maximal oxygen stores and minimal use rates proscribe the boundaries of diving abilities. However, these limitations are generally thought to have little impact on routine activity patterns. While oxygen stores and tissue pH and metabolite levels can quickly return to pre-dive levels following aerobic dives, recovery can take in excess of an hour after dives that greatly exceed the anaerobic threshold (Kooyman et al. 1980; Castellini et al. 1988; Burns and Castellini 1996). As a result, marine mammals are generally thought to better maximize

their time at the foraging depths by making multiple aerobic dives, rather than a few extremely long anaerobic dives (Kooyman et al. 1980; Dolphin 1988; Butler and Jones 1997). Indeed, for most species for which we have good estimates of the ADL, anaerobic dives appear to be rare.

In contrast with adults, physiological limitations have recently been shown to have a larger impact on juvenile diving behavior (Kooyman et al. 1983; Thorson and Le Boeuf 1994; Burns and Castellini 1996; Burns et al. 1997; Horning and Trillmich 1997a, 1997b). Juveniles face additional constraints, because the physiological factors that limit dive duration are highly correlated with animal size and age. Smaller individuals are first disadvantaged, because metabolic rate scales as  $\text{mass}^{0.75}$  and oxygen stores scale as  $\text{mass}^{1.0}$ , which combine to cause the ADL to scale as  $\text{mass}^{0.75}$ . In addition, young growing individuals have higher mass-specific metabolic rates and, possibly, also, smaller mass-specific body-oxygen stores. Finally, young pups do not appear to be as able to regulate heart rate, respiration, vasoconstriction, or body temperature as well as adults, which may further elevate diving metabolic rates (Kodama et al. 1977; Schmitz and Lavigne 1984; Schmidt-Nielsen 1990; Rea and Costa 1992; Cherepanova et al. 1993; Ponganis et al. 1993; Thorson and Le Boeuf 1994; Castellini et al. 1994; Burns and Castellini 1996; Butler and Jones 1997). In combination, body size and developmental constraints appear to limit the diving capacity of juveniles and therefore delineate a much smaller range of possible dive behaviors (Thorson and Le Boeuf 1994; Burns and Castellini 1996; Horning and Trillmich 1997a, 1997b). This limitation warrants consideration when interpreting the behavioral ecology of juvenile marine mammals, especially in species that forage at deep depths, such as Weddell seals.

There are four primary ways in which juvenile marine mammals might compensate for their reduced breath-hold capacity. First, juveniles might rapidly acquire the physiological and morphological attributes necessary to make long dives; second, juveniles might forage on prey that is easier to catch or found at shallower depths or in different areas than adult prey; third, juveniles might expend more effort foraging by diving more frequently or spending more time in the water than adults; and finally, juveniles might increase the average duration of their dives by increasing the number or proportion of long or anaerobic dives. This last strategy would be beneficial, despite increased recovery times, if the minimum dive duration necessary for prey capture approximated the ADL or if juveniles could extend their ADL on long dives by dramatically reducing their metabolic rate (Fedak and Thompson 1993; Butler and Jones 1997). While such behavioral modifications have often been suggested, only recently has there existed sufficient data from within a single population of marine mammals to rigorously examine which, if any, of these potential strategies are employed by young animals.

This paper will examine each of these four hypotheses using data collected in McMurdo Sound, Antarctica, from Weddell seal adults, yearlings, and pups. Because Weddell seal pups dive actively from about 4 weeks of age onward, they offer a unique opportunity for studying the development of diving behavior, both during the nursing period and post weaning (Kooyman 1968; Thomas and DeMaster 1983;

**Table 1.** Seal age and size and summarized information on tag deployment.

	Age range	<i>N</i> (individuals)	Mass range (kg)	Tag type	Study season	<i>N</i> (dives)
Nursing pups <sup>a</sup>	4–8 weeks	36	52.5–134.0	TDR	Nov.–Jan. 1992–1994	11 295
Weaned pups <sup>a</sup>	9–13 weeks	16	61.6–120.0	TDR	Jan.–Feb. 1992–1994	14 661
	14–32 weeks	19	61.7–113.0 <sup>b</sup>	SLTDR	Jan.–June 1992–1994	42 890
Yearlings	51–54 weeks	15	92.6–169.4	TDR	Oct.–Dec. 1992–1994	4 182
Adult females	6–13+ years	8	320–417 <sup>b</sup>	SLTDR	Feb.–Sept. 1990–1991	49 778

<sup>a</sup>Seals carried TDRs multiple times.

<sup>b</sup>At initial tag deployment.

Burns and Castellini 1996; Burns and Testa 1997). In addition, there is a significant body of information on the biology, diving behavior, ecology, and physiology of all age-classes to use for comparative purposes.

## Methods

This study was carried out in Erebus Bay, McMurdo Sound, Antarctica (77°45'S, 166°30'E). The physiological and behavioral data presented here were collected as part of two large research projects. One examined the development of diving behavior and physiology in pups (animals < 1 year old; Burns and Castellini 1996; Burns and Testa 1997) and yearlings (animals born the previous year; Burns et al. 1997), while the second studied the diving behavior of adult females (animals older than 6 years; Testa 1994). All animal handling, data collection, and analysis methods are presented in more depth in the papers originally reporting the studies.

### Animal handling

Between 1992 and 1994, 36 individual Weddell seal pups (17 males and 19 females) carried time–depth recorders (TDRs) for 3- to 7-d periods every other week from the time they were 4 weeks old until they were 13 weeks old (Burns and Testa 1997). Satellite-linked time–depth recorders (SLTDRs; 0.5 W, Service Argos platform transmitter terminals, manufactured by Wildlife Computers, Woodinville, Wash.); Wildlife Computers, SDR-T6; Service Argos PTTs) were deployed on 19 of these pups once they were weaned (Burns et al. 1999). Over this same time period, TDRs were also deployed on 15 yearling seals (10 males and 5 females) (Burns et al. 1997). The diving behavior of reproductively mature adult females (6 years or older) comes from a study conducted in McMurdo Sound in 1990 and 1991, in which 8 females were successfully outfitted with SLTDRs (Testa 1994) (Table 1). All TDR data were collected during the austral summer months of November through January, while all SLTDR data come from late summer through winter (January through September).

All juvenile seals (pups and yearlings) were measured (length and girth) and weighed ( $\pm 0.1$  kg) at each handling. For those adult females that were not weighed, mass was estimated based on length and girth measurements using standard regression techniques (Castellini and Kooyman 1990). All animal ages were known from tagging records (Testa and Siniff 1987). Weddell seal pups are weaned at approximately 6–7 weeks of age and undergo a short postweaning fast (Rea 1995). For the purposes of this study, pups of 8 weeks or less were termed nursing pups and those older than 8 weeks were considered weaned and nutritionally independent. All yearlings were tagged as newborn pups in the previous year and all adult females were reproductively mature.

### Dive data

The TDRs deployed on pups and yearlings monitored depth every 10 s when wet, had a depth resolution of 3 m, and a maximum depth of 500 m. Like the TDRs, the SLTDRs deployed on pups

sampled depth every 10 s during dives, had a depth resolution of 3 m, and a maximum depth of 500 m. However, these data were compressed for transmission, so that data received were the number of dives in each of 6 depth and duration bins (80-m and 4-min intervals). Mean dive depth and duration were then estimated from these counts (Burns and Testa 1997; Burns and Castellini 1998). SLTDRs deployed on adult females in 1990 and 1991 transmitted the maximum depth and total duration of each dive and sampled at a 60-s frequency and with a 3 m depth resolution (Testa 1994).

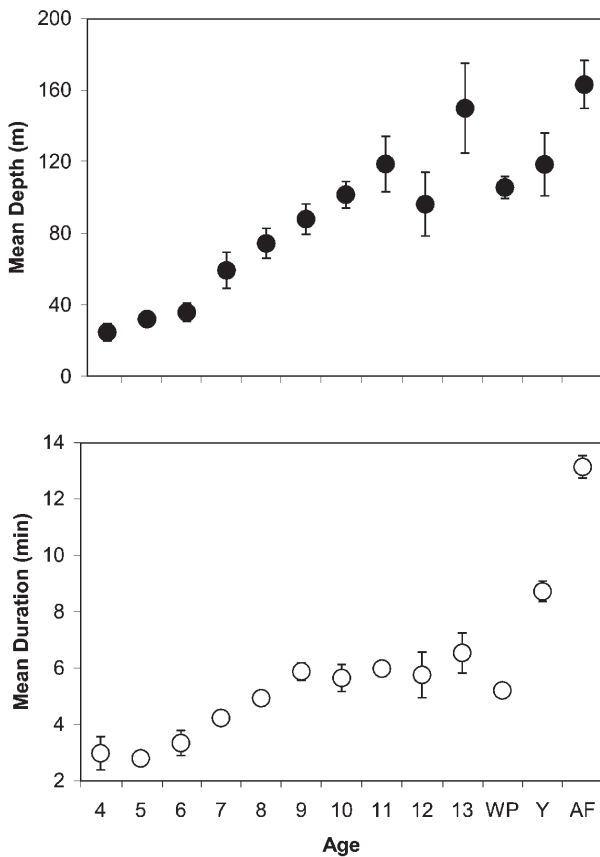
Data from both the TDRs and SLTDRs were downloaded by computer and processed with software from Wildlife Computers. Owing to erroneous drift of the zero depth in the TDR and possible effects of wave action, a depth of twice the resolution of the TDR (6 m) was considered to be representative of the surface, and a depth of twice this (12 m) was considered to be indicative of a dive. Therefore, for all pups and yearlings outfitted with TDRs, only dives with a maximum depth greater than 12 m and a duration of 1 min were analyzed. For adults outfitted with SLTDRs, the minimum duration required for a dive to be analyzed was set at 1 min. Setting the duration cutoff at 2 or 3 min increased the average dive duration by less than 50 s, and so the shortest possible cutoff was used to be as comparable with juveniles as possible. For all animals, the mean dive depth and duration values are those from each dive averaged over all dives for each seal at each age. Similarly, average dive frequency is the average number of dives per day grouped by individual and age.

For pups and yearlings outfitted with TDRs and adult females outfitted with SLTDRs, the total amount of time spent diving (depth > 12 m) was determined for individual seals by summing the duration of all dives each day. For pups outfitted with SLTDRs, time underwater was estimated for each seal at each age by multiplying the mean number of dives in each duration bin by the bin midpoint (Burns and Castellini 1998). Mean time underwater (MTUW) was calculated as the average value for all seals within each age group. It has previously been shown that for young Weddell seals the bin midpoint is a reasonable approximation of the mean duration of dives within the bin (Burns and Castellini 1998). However, for all seals, this metric will underestimate the total time spent in the water, because it does not take into account time spent at or near the surface at depths below the cutoff resolution of the instruments (i.e., 12 m).

The amount and proportion of time that seals spent at the bottom of each dive was also estimated. To do this, the amount of time that seals spent at or below 80% of the maximum depth of the dive was calculated using Dive Analysis software. Once the total bottom time (BT) was determined for each dive, the proportion of the total dive time spent at the bottom (PBT) was calculated (bottom time/total dive duration). Because this value is determined for each dive, it does not represent the proportion of dive time that is spent above or below a certain depth. To control for potential differences in these parameters due to dive depth, the mean BT and percent BT were computed for each individual (at each age) for all dives within 50 m depth intervals, and these values were also compared.



**Fig. 1.** Dive depth and duration (mean  $\pm$  SE) for pups between 2 and 13 weeks of age ( $n = 36$ ), weaned pups outfitted with SLTDR tags (WP;  $n = 19$ ), yearlings (Y;  $n = 15$ ), and adult females (AF;  $n = 8$ ).



While dive frequency and time underwater were used to assess dive effort, to assess differences in foraging efficiency (FE) across age-classes we calculated FE following Ydenberg and Clark (1989):

$$FE = \frac{\text{bottom time}}{\text{dive duration} + \text{postdive surface interval}}$$

For these calculations, the postdive surface interval (PDSI) was determined by Dive Analysis software and was limited to durations shorter than 20 min (95% of all PDSIs < 20 min). Efficiencies were calculated for each dive and averaged for each animal. Values were then compared across age classes using ANOVA methods. To determine how dive depth and duration influenced efficiency, average values were calculated for dives within 50-m and 1-min categories and these values were compared across age-classes.

For animals in each age class, the ADL was estimated in three ways. The diving lactate threshold (DLT), as per Butler and Jones (1997), was determined from postdive lactate levels as reported in the literature, while the calculated ADL (cADL) was determined as  $ADL = \text{total body oxygen stores (TBO}_2) / \text{diving (or resting) metabolic rate}$  (Kooyman et al. 1980, 1983; Ponganis et al. 1993; Burns and Castellini 1996). Whenever possible, age-specific values for these parameters were used in determining the cADL. In addition, we estimated the ADL from the inflection point in the curve relating mean PDSIs to dive duration (here referred to as the pdADL) (Yeager and Ultsch 1989; Burns and Castellini 1996). The proportion of dives greater than each of these ADL estimates was then calculated for each seal, and then averaged for animals within each age class.

Correlations between dive behavior and animal age or mass were assessed using stepwise linear regression techniques. Significance was assumed if both  $p < 0.05$  and  $r^2 > 0.10$ . Comparisons among groups were performed using one-way ANOVA methods. Differences among individual groups were tested post hoc using Tukey's HSD method, and significance was assumed at  $p < 0.05$ . Because individual pups were represented in each age category by different numbers of records, to avoid pseudoreplication problems, one sample from each pup was randomly selected for each statistical comparison in the TDR records and 4 samples were randomly selected from each pup in the SLTDR records. For all analyses, pup age was in weeks and mass in kilograms.

#### Animal diet and foraging locations

The diet of Weddell seals of different ages was determined through scat analysis (prey hard parts; 189 scats collected over 5 years), tissue stable-isotope ratio analysis ( $\delta^{13}C$ ,  $\delta^{15}N$  isotope ratios; 42 blood samples and 6 different potential prey species), and analyses of actual diving behavior (dive depth, duration, and frequency, as well as the time–depth profile or shape of each dive; Burns et al. 1998; Burns and Schreer, 1999). Foraging locations were determined from animal positions (latitude and longitude), as determined by land or aerial survey or by Argos satellite position fixes (Testa 1994; Burns et al. 1999).

## Results

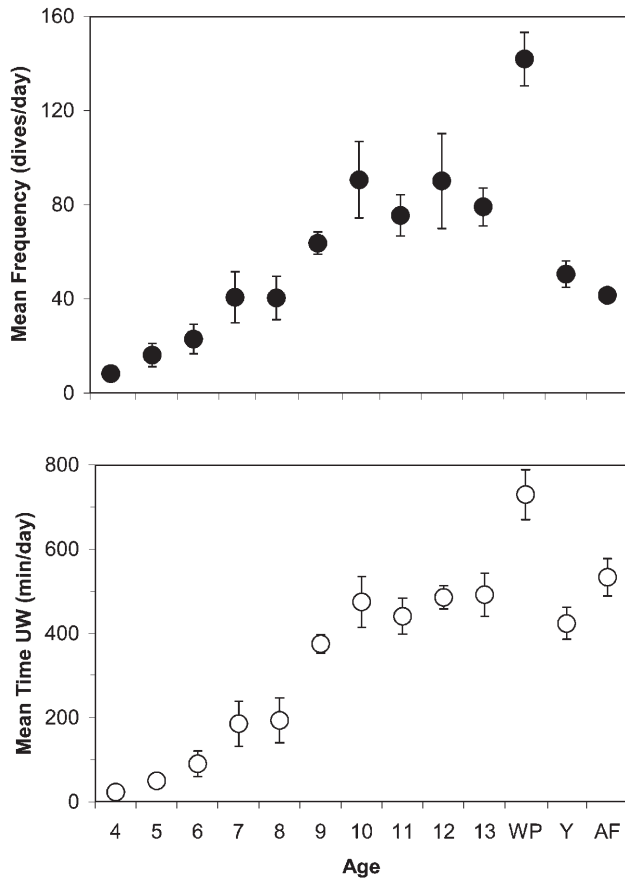
### Dive depth and duration

Mean dive depth and duration increased significantly with pup age during the nursing period but did not vary significantly with age or mass once pups were weaned (Fig. 1). For nursing pups (2–8 weeks old), age accounted for 45% of the variation in mean depth and 52% of the variation in mean duration but mass was not a significant predictor of behavior (mean depth =  $-31.6 + 13.2 \times \text{age}$ ; mean duration =  $-0.10 + 0.64 \times \text{age}$ ;  $p < 0.05$ ). However, once pups were weaned (9–13 and 14–32 weeks old), there was no significant relationship between mass or age and dive depth or duration. Unfortunately, because no mass data was available once pups were outfitted with SLTDR tags, it was impossible to determine if the absence of age effects was due to differences in individual growth rates. However, in yearlings, mean dive duration was positively correlated with mass (mean duration =  $3.03 + 0.41 \times \text{mass}$ ,  $r^2 = 0.49$ ,  $p < 0.002$ ). There was no correlation between mass and dive duration in adult females. Overall, the mean depth of dives ( $105.8 \pm 8.2$  m) made by weaned pups approached that of yearlings ( $118.5 \pm 17.6$  m) and adults ( $163.1 \pm 13.4$  m) but their mean dive duration remained much shorter ( $5.82 \pm 0.24$ ,  $8.72 \pm 0.36$ , and  $13.14 \pm 0.40$  min, respectively). Because physiological constraints were more likely to be evident in duration than depth, all remaining analyses focus on temporal variables (dive duration, frequency, and BT).

### Dive effort

Daily dive frequency and MTUW was significantly correlated with age and mass in nursing pups (dive frequency =  $-13.9 - 0.30 \times \text{mass} + 12.9 \times \text{age}$ ,  $r^2 = 0.41$ ,  $p < 0.01$ ; MTUW =  $-221.0 + 58.25 \times \text{age}$ ,  $r^2 = 0.40$ ,  $p < 0.001$ ). However, once pups were weaned there was no further increase in dive frequency or time underwater. In yearlings, dive frequency declined with mass ( $131.2 - 0.59 \times \text{mass}$ ,  $r^2 = 0.38$ ,  $p = 0.009$ ) but MTUW did not. Surprisingly, larger adult

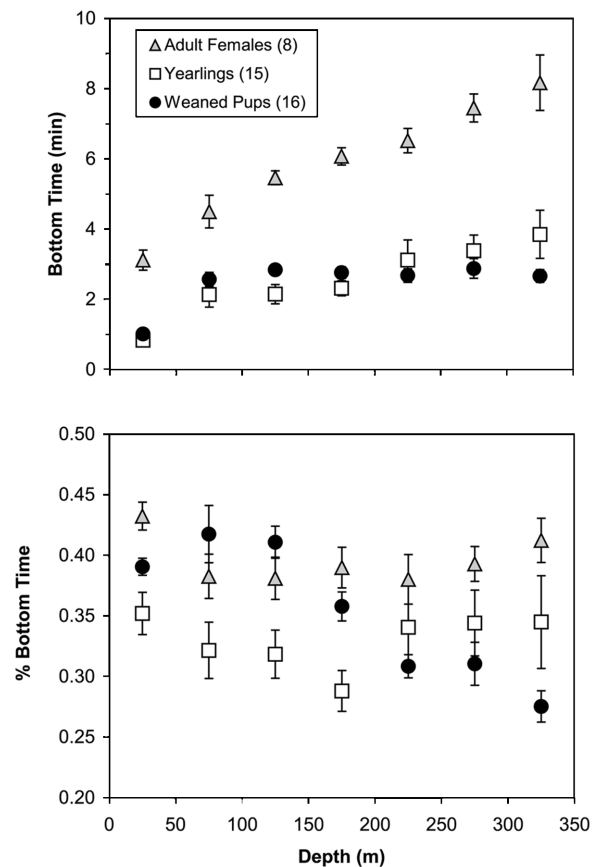
**Fig. 2.** Differences in daily dive frequency and time (mean  $\pm$  SE) underwater among age groups. Ages and sample sizes are as given in Fig. 1.



females made fewer dives and spent less time underwater than smaller individuals (dive frequency =  $134.4 - 0.26 \times$  mass,  $r^2 = 0.89$ ,  $p < 0.001$ ; MTUW =  $1606.5 - 2.94 \times$  mass,  $r^2 = 0.72$ ,  $p = 0.000$ ). Overall, the dive frequency of SLTDR-tagged weaned pups ( $142 \pm 11$  dives/d) was significantly greater than that of younger weaned pups ( $72 \pm 7$  dives/d), yearlings ( $51 \pm 6$  dives/d), and adults ( $42 \pm 3$  dives/d) (one-way ANOVA,  $p < 0.05$ ). In addition, SLTDR-tagged weaned pups spent more time underwater each day ( $729.5 \pm 59.3$  min/d) than did younger weaned pups ( $411.7 \pm 50.4$  min/d), yearlings ( $423.9 \pm 37.9$  min/d), and adults (range 368–721 min/d) (one-way ANOVA,  $p < 0.01$ ; Fig. 2).

In nursing pups, the amount of time spent at the bottom of dives increased with animal age but the PBT did not (BT =  $-0.25 + 0.27 \times$  age,  $r^2 = 0.45$ ,  $p = 0.001$ ; PBT =  $37.10 \pm 1.82\%$ ). However, there was no similar increase for weaned pups between 9 and 13 weeks of age (BT =  $2.37 \pm 0.1$  min; PBT =  $40.05 \pm 1.84\%$ ). Because of data collection differences, these values could not be calculated for older weaned pups outfitted with SLTDRs. While larger yearlings spent more time at the bottom of dives on both absolute and proportionate scales (BT =  $-2.25 + 0.043 \times$  mass,  $r^2 = 0.55$ ,  $p = 0.001$ ; PBT =  $3.12 + 0.27 \times$  mass,  $r^2 = 0.48$ ,  $p = 0.003$ ), there was no correlation between mass and BT in adult females (BT =  $6.16 \pm 0.18$  min; PBT =  $39.68 \pm 0.76\%$ ). On average, absolute BT increased across age classes (one-way ANOVA,  $p < 0.01$ ) but the PBT remained constant (one-way

**Fig. 3.** Differences in bottom time and percent bottom time (mean  $\pm$  SE) among weaned pups (outfitted with TDRs), yearlings, and adults. The number of animals within each age-class is indicated.



ANOVA,  $p > 0.05$ ). However, when the absolute and proportionate amount of time spent at the bottom of dives was compared among age classes within 50 m depth categories, it was clear that smaller animals were able to spend less time at depth than were older animals. In addition, as depth increased, adults were able to increase their BT and maintain the PBT, while pups and yearlings were not (Fig. 3).

#### Foraging efficiency

For nursing pups, FE increased with age but not with mass (FE =  $10.90 + 1.85 \times$  age,  $r^2 = 0.11$ ,  $p = 0.004$ ). In contrast, yearling FE increased with mass (FE =  $2.60 + 0.17 \times$  mass,  $r^2 = 0.44$ ,  $p = 0.004$ ). There was no correlation between FE and age or mass in weaned pups outfitted with TDRs or in adult females ( $30.86 \pm 1.52$  and  $31.06 \pm 0.78$ , respectively). On average, the mean FE of yearlings ( $26.17 \pm 1.0$ ) was lower than that of weaned pups and adults (one-way ANOVA,  $p < 0.01$ ). However, the manner in which depth and duration impacted FE differed among age-classes (Fig. 4). In yearlings and adults, FE increased with dive depth, but in weaned pups it declined once dives exceeded 150 m. Surprisingly, 26.7% of dives made by pups exceeded this value and so were accompanied by lowered FE. For all three age classes, FE increased as dive duration increased and then declined in the longest of dives. This decline occurred once dives exceeded 8 min for weaned pups,

**Table 2.** The mean dive duration and the three estimates of the ADL for Weddell seals within each age-class.

	<i>N</i> (individuals)	Avg. mass (kg)	Mean duration (min)	DLT (min)	cADL <sup>a</sup> (min)	pdADL (min)
Weaned pups <sup>b</sup>	17	96.5±3.0	5.67±0.02	6 <sup>c</sup>	8.0	7
Yearlings	15	132±6.0	7.27±0.07	10 <sup>d</sup>	12	13
Adult females	8	359.8±9.5	12.73±0.03	20 <sup>e</sup>	21.4	22

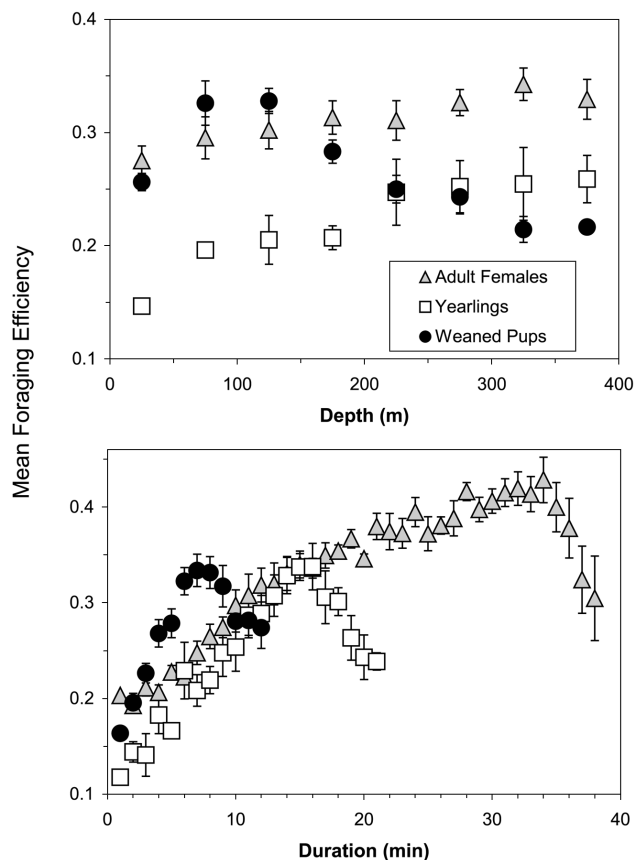
<sup>a</sup>Calculated according to Ponganis et al. (1993) and Burns and Castellini (1996) with the following modifications: weaned pups: Hct (hematocrit) = 60%, Hb (hemoglobin) = 25 g/dL, Mb (muscle myoglobin) = 3.5 g%; yearlings: Hct = 64%, Hb = 27 g/dL; adults: Hct = 67%, Hb = 27.9 g/dL. New Hct and Hb values are from Rea (1995) and J.M. Burns (unpublished data).

<sup>b</sup>Includes only those between 9 and 13 weeks of age.

<sup>c</sup>Three seals (Burns and Castellini 1996).

<sup>d</sup>Two seals (Kooyman et al. 1983).

<sup>e</sup>Four seals (Kooyman et al. 1980).

**Fig. 4.** Changes in foraging efficiency (mean ± SE) with dive depth and duration for weaned pups (9–13 weeks old), yearlings, and adults.

16 min for yearlings, and 34 min for adults. The proportion of dives that were longer than this cutoff differed by age-class: 19.8% of dives made by weaned pups were longer than 8 min, while only 4.2% of yearling dives were longer than 16 min, and fewer than 0.5% of adult dives were longer than 34 min.

#### Aerobic dive limit

Table 2 reports the values of the various ADL estimates for pups, yearlings, and adults used in this study. They include DLT, cADL, and pdADL (Fig. 5). The comparison of these values with the mean dive duration for weaned pups (9–13 weeks of age), yearlings, and adults clearly indicates

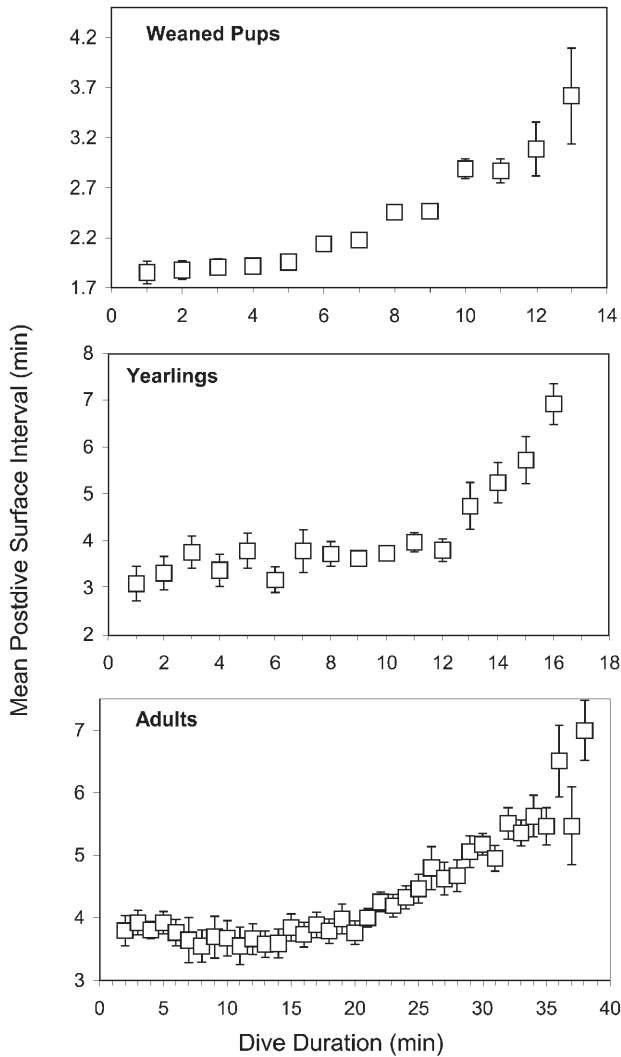
that the proportion of free ranging dives that exceeded these estimates differed by age group (Fig. 6). In all cases, the difference between the ADL and the mean dive duration for juveniles (<2 min) was much smaller than for adults (>5 min), which suggests that younger seals were operating at much closer to their anaerobic threshold than adults. The difference between the cADL and mean dive duration did not change significantly with animal mass for weaned pups, yearlings, or adults.

#### Discussion

Initially, four hypotheses were presented to explain how juvenile Weddell seals might deal with their physiological constraints on dive depth and duration. From these analyses, it appears that both weaned pups and yearlings do manage their time underwater differently from adults, and that the modifications are in direct response to physiological constraints on dive duration and the resultant limitation on foraging behaviors. These findings were not surprising. Research on many different marine mammals has made it clear that juveniles are faced with physiological limitations that can and do impact their diving behavior (Thorson and Le Boeuf 1994; Burns and Castellini 1996; Corpe 1996; Gazo 1996; Burns et al. 1997, 1999; Merrick and Loughlin 1997; Horning and Trillmich 1992a, 1997b). However, our understanding of how physiological limitations impact the foraging behavior and success of juveniles and how juveniles might compensate for these limits has been slower coming, and this is one of the few studies that have addressed behavioral and physiological aspects at the same time (Le Boeuf et al. 1996; Horning and Trillmich 1997a, 1997b). While initial theoretical models predicted that juveniles would alter their foraging behavior in the face of depth and duration constraints not experienced by adults, support for differential foraging patterns has been largely absent. Indeed, while selective foraging on (presumably) easier to catch prey items and (or) those found at shallower depths by Weddell seal juveniles was first suggested by (Lindsey 1937; Bertram 1940), this work and other recent studies have failed to reveal sufficient age-related variation to support the hypothesis that juveniles in McMurdo Sound follow this strategy.

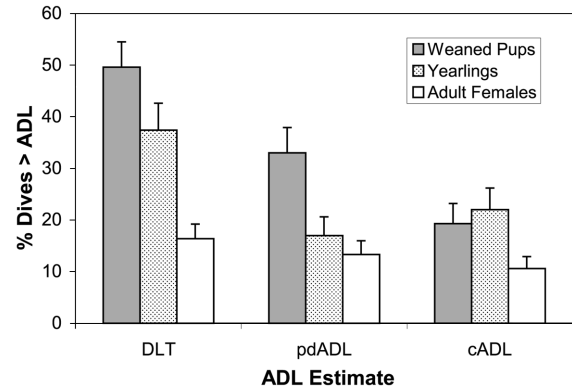
Instead, Weddell seals of all ages appear to forage on similar prey items. The vast majority of bones and hard parts recovered from the scats of pups, yearlings, and adults were from *Pleuragramma antarcticum*, the Antarctic silverfish,

**Fig. 5.** Increases in the postdive surface interval (mean  $\pm$  SE) with increasing dive duration in weaned pups between 9 and 13 weeks of age, yearlings, and adults.



and otoliths suggested that all seals concentrated on fishes of similar size (Burns et al. 1998). In addition, stable-isotope ratio analyses and behavioral classification based on time-depth profiles also suggested that all animals foraged on similar prey species (Schreer and Testa 1996; Burns et al. 1998; Burns and Schreer 1999). While some juveniles appeared to concentrate their foraging in the benthic ecosystem, the majority of foraging dives made by adults, yearlings, and weaned pups were to depths in excess of 100 m. As *P. antarcticum* dominates the McMurdo Sound ecosystem and occurs predominantly at depths greater than 100 m (Hubold 1984; Eastman 1985; Kellermann 1986), these analyses support the conclusion that all age classes forage on similar species. These findings further suggest that juveniles of pinniped species that are highly specialized foragers, or that exist in species-poor environments, may be constrained to forage on the same prey as adults. While telemetry studies suggest that newly weaned Weddell seal juveniles attempt to avoid intraspecific competition by dispersing from the pupping colony earlier and along slightly different routes than adults (Burns et al. 1999), pups clearly

**Fig. 6.** The proportion (mean  $\pm$  SE) of free ranging dives made by weaned pups (9–13 weeks old), yearlings, and adults that exceeded the ADL, which is estimated from postdive lactate levels (DLT), increases in the postdive surface intervals (pdADL), and calculated from body oxygen stores and metabolic rate estimates (cADL).



relied on methods other than dietary shifts to compensate for their lower dive capacity.

As physiological limitations on dive depth and duration are primarily due to an individual's age and mass (Kooyman et al. 1983; Lydersen and Hammill 1993; Thorson and Le Boeuf 1994; Horning and Trillmich 1997b), perhaps the easiest way for juvenile marine mammals to minimize the impact of mass-dependent physiological limitations is to quickly outgrow them. Rapid age-related gains in mass and the physiological mechanisms associated with diving accompany increases in mean dive depth and duration, and early onset of these changes has been noted, especially in the more precocial phocids (Lydersen and Hammill 1993; Castellini et al. 1994; Lydersen et al. 1994; Rea 1995; Burns and Castellini 1996; Burns and Testa 1997). In combination, physiological (oxygen stores and metabolic rates) and morphological (absolute size) maturation increases the ability of animals to remain submerged. However, in juvenile Weddell seals, rapid and significant increases in dive depth and duration were only prevalent from birth through weaning, during which time pups were both growing and maturing rapidly. During this period, pups increased in mass fourfold, and physiological processes related to diving such as heart rate, vasoconstriction, and metabolic control approached adult values (Rea 1995; Burns and Castellini 1996). In addition, hematocrit, hemoglobin and muscle myoglobin levels all increased during the lactation period. Still, weaned pups were smaller, had lower mass-specific body-oxygen stores, and higher mass-specific metabolic rates than adults (Elsner et al. 1977; Kooyman et al. 1983; Castellini et al. 1988; Rea 1995; Burns and Castellini 1996; J.M. Burns, unpublished data). As a result, although weaned pups were able to dive to the depths necessary to forage on *P. antarcticum*, they could not remain at these depths for long.

As their dive duration did not reach that of adults within the first year, juvenile Weddell seals were clearly still limited in their diving capacities by their smaller size, smaller oxygen reserves, and higher metabolic rate. How then were they able to successfully forage on the same prey resources as adults? From these analyses, it appears that weaned Weddell seal pups compensated for their inability to remain



at depth by increasing their trips to depth. As dive frequency has been used as a metric for diving effort (Costa et al. 1989; Goebel et al. 1990; Boness et al. 1994; Boyd et al. 1994; Thorson and Le Boeuf 1994), our finding that weaned pups made almost twice as many dives as yearlings and adults suggests that pups expended greater effort diving than did older animals. Time underwater, another metric of diving effort, also suggested that weaned pups were expending significantly more effort than expected. Indeed, the amount of time both weaned pups and yearlings spent underwater was similar to that spent by adults, despite their smaller body size and lower absolute energy requirements. The high dive frequency seen in weaned pups is not a result of a greater proportion of nonforaging or social dives, as dive shape and time–depth profile analyses indicate that the proportion of foraging dives for weaned pups, is similar to that for yearlings and adults (40–60% of total dives: Schreer and Testa 1996; Burns et al. 1997; Burns and Schreer 1999). In combination, these findings suggest that smaller animals were not able to obtain as much food per dive or per unit of time underwater as were older animals. Similarly, juvenile harbor seals are thought to spend more time actively searching for food, but with less success at catching prey, than older animals (Lesage et al. 1998).

Greater dive effort, as indexed by dive frequency and time underwater, is probably a result of the limitations pups face with respect to the amount and proportion of time they can spend at depths in excess of 100 m. While more than half of all dives made by weaned pups were deeper than 100 m, both travel and bottom-time estimates indicate that weaned pups and yearlings had less than 3 min to spend at this depth searching for food, a value considerably less than the 5–9 min available to adults. In addition, once dives exceeded 100 m, pups were unable to increase their time at depth, and so the fraction of time pups could spend foraging during deeper dives declined. This limitation was likely mainly due to body size, as larger yearlings were able to spend both more time and a greater percentage of their time at the foraging depths.

This constraint on the amount of time that smaller and younger animals were able to spend at the bottom of dives was reflected in the FE of pups. While the diving and FE of weaned pups was similar to that of adults for shallow and short dives, FE increased with depth and duration for adults but declined markedly as dives got longer and deeper for juveniles. As a result, older animals were able to achieve and maintain higher efficiencies over a wider range of depths and durations than younger and smaller individuals. This decline in FE with increased depth and duration is significant, as approximately a third of all pup dives were deeper than 150 m and longer than 6 min, and most foraging dives (as identified by bout analysis and dive shape) were at least this long and deep (Burns and Schreer 1999). Thus pups, in contrast with yearlings and adults, were likely to face constraints on their FE in the course of routine behavioral patterns. Similarly, larger northern elephant seal and Galapagos fur seal juveniles were able to exploit food resources that were unavailable to smaller and younger individuals (Le Boeuf et al. 1996; Horning and Trillmich 1997b).

The final way in which young seals could alter their diving behavior to compensate for their smaller size and shorter

dive capacity is by increasing the proportion of anaerobic dives. While increasing the proportion of anaerobic dives is generally thought of as disadvantageous, because lactic acidosis increases the necessary surface recovery time and reduces the total amount of time that an animal can spend diving (Kooyman et al. 1980; Castellini et al. 1988; Ydenberg and Clark 1989), this strategy appears to have been used extensively by juvenile Weddell seals. Not only did both weaned pups and yearlings dive much closer to their anaerobic threshold than adults, they also appeared to make considerably more anaerobic dives than adults. Even the most liberal of the ADL estimates indicates that juveniles do not have the duration “cushion” of adults. These findings suggest that minimizing surface time is not as important to juveniles as spending time at foraging depths, and indicate that these young animals are pushing a physiological limit in order to forage successfully. Further support for this hypothesis comes from the fact that when juveniles made dives that were longer than their ADL, these dives were accompanied by increased surface recovery times and elevated postdive lactate levels. This indicates that juveniles were not increasing their dive time by further reducing diving metabolic rate, as has been hypothesized for the extremely long dives of grey and elephant seals (Hindell et al. 1992; Thompson et al. 1993; Boyd and Croxall 1996).

The conclusion that juvenile Weddell seals make more anaerobic dives, or frequently dive close to their anaerobic threshold, has several implications. Dives longer than the ADL generally require that accumulated lactic acid be processed, either during surface recovery or during subsequent shorter dives (Kooyman et al. 1980; Castellini et al. 1988; Fedak and Thompson 1993). While true, this interpretation overlooks the fact that, because the initial upswing in the postdive lactate level curve has a relatively shallow slope, dives that are only slightly longer than the ADL place a very small lactic acid load on the individual seal (Kooyman et al. 1980; Burns and Castellini 1996; Ponganis et al. 1997). It may be that, by allowing lactic acid to build up over the course of several “slightly” anaerobic dives, animals can “work” this region of the curve and therefore delay recovery behaviors. Such a strategy would be extremely advantageous for animals that had just located a deep but abundant prey patch or for juveniles that cannot comfortably reach the necessary foraging depths. Indeed, recent analysis of foraging dive bouts made by weaned pups suggest that once pups locate a foraging patch, they make a series of dives to that depth. These dives are often longer than all but the cADL, and average between 6.5 and 8 min. As these bouts progress, PDSIs increase slightly, and bouts are often followed by rest periods at the surface (Burns and Schreer 1999; J.M. Burns, unpublished data). Delayed processing of lactate has now been directly measured and (or) inferred from the dive records of marine birds, pinnipeds, and whales (Kooyman et al. 1980; Castellini et al. 1988; Fedak and Thompson 1993; Thompson et al. 1993; Burns and Castellini 1996; Ponganis et al. 1997; Shaffer et al. 1997). Thus, while it has long been recognized that the ADL is not a fixed point but a fluid number, these more recent findings suggest that animals may tailor their behavioral response to anaerobic dives in accordance with the degree to which the ADL is exceeded and with the amount of lactic acid accumulated. This ability,



while valuable to all age groups, appears to play a critical role in allowing juveniles to forage effectively despite their smaller size.

In addition, for both weaned pups and yearlings, FE continued to increase with increasing dive duration past the inflection point in the PDSI curves, and it was not until dives were approximately 25% longer than the ADL that declines in FE were observed. Dives slightly longer than the ADL were an important component of the behavioral repertoire of juvenile seals, as approximately 28% of all dives made by weaned pups occurred between the duration at which the mean PDSI increased and the mean FE decreased. Yearlings made fewer of these longer dives, as only 12% of their dives were between 12 and 16 min. This suggests that such "slightly" anaerobic dives may be frequently utilized by juveniles in order to increase foraging success at the deeper depths where their main prey is found. While a similar increase in FE past the ADL was observed for adults, the rare nature of these longer dives suggests that adults do not often utilize this strategy. Alternatively, it may be that the relatively short PDSIs observed in weaned pups allows them to better utilize this strategy, owing to their apparent ability to rapidly reload oxygen reserves (Kramer 1988; Houston and Carbone 1992).

In summary, these analyses clearly show that juvenile Weddell seals modify their diving behavior to compensate for their smaller size and dive duration constraints. Modifications are evident in three main spheres. First, pups mature rapidly, and quickly increase their diving skills. However, age effects are only dominant until pups are foraging successfully, after which time, mass appears to play a more important role in setting physiological limitations on dive duration. Second, juveniles tend to dive more frequently, so the amount of time they spend underwater is similar to that of adults. They do this despite lower absolute food requirements, which suggests that foraging success may be lower than in older animals. Indeed, at the deeper foraging depths, and for dives of longer duration, young pups have a lower FE than do adults and yearlings. The decline in the FE curves for dives deeper than 150 m or 8 min suggests that dives beyond these limits are only achieved through an increase in surface recovery time or a decrease in BT, both of which were observed. In combination with the lower average dive duration and the smaller amount of time at foraging depths, it appears that juveniles are required to make more anaerobic dives and to spend more time diving close to their anaerobic threshold in order to maximize their FE and success.

These differences in diving behavior have several implications for the survivorship of young Weddell seals and, by extrapolation, for other young marine mammals. To compensate for their smaller size, young Weddell seals spend more time in the water, which in turn likely increases their risk of predation and their total energy expenditure (Smith 1965; Mikhalev et al. 1981; Boyd et al. 1997; Burns and Castellini 1998). Despite this, they are unable to achieve the same amount of foraging and BT as older larger animals. In combination, these factors may help explain several population-biology findings. As is the case for many marine mammals, the 1-year survival of juveniles is extremely low, averaging about 43%, roughly half that of adults (Testa 1987; Hastings

1996). Second, survivorship for pups and yearlings appears dependent on their reaching certain mass thresholds: the chance of a pup surviving its first year declines dramatically for animals weaned at less than about 90 kg, and no yearlings of less than this mass have ever been sighted (Hastings 1996). In combination, it appears that physiological and morphological limits impact both the diving behavior of juvenile Weddell seals and, possibly, even their survival. Juveniles that do survive, appear to do so by growing quickly and then pushing their physiological limits in many of the ways initially predicted.

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