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THE DEVELOPMENT OF DIVING BEHAVIOR AND
PHYSIOLOGY IN JUVENILE WEDDELL SEALS
(LEPTONYCHOTES WEDDELLII) IN MCMURDO
SOUND, ANTARCTICA

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

In Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By
Jennifer Moss Burns, B.S., M.S.

Fairbanks, Alaska

August 1997

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THE DEVELOPMENT OF DIVING BEHAVIOR AND PHYSIOLOGY IN JUVENILE WEDDELL SEALS (LEPTONYCHOTES WEDDELLII) IN MCMURDO SOUND, ANTARCTICA

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ABSTRACT

The development of diving behavior and physiology in juvenile Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica was studied in order to determine the effects of age, body size, and condition on diving ability. During the austral summers of 1992, 1993, and 1994, the diving behavior of 39 pups and 15 yearlings was monitored using time depth recorders (TDRs). In addition, 26 pups were equipped with satellite-linked time depth recorders (SLTDRs) to track fall and winter diving behavior. Blood samples and morphological measurements were taken at each handling.

Pups began to dive within two weeks of birth, and the mean dive depth, duration, and number of dives per day increased significantly over the next 10 weeks. During this period, the ability of pups to regulate physiological processes related to diving increased, as did their aerobic dive limit (ADL). Whereas diving behavior was determined primarily by age rather than mass in young pups, age had little effect on the diving behavior of pups older than 2 months (as determined from SLTDR records). Because seals were not handled after SLTDR deployment, the effects of mass could not be directly modeled in these pups. However, in yearlings, the ADL, and approximately 50% of the variation in dive behavior could be explained by differences in body size.

Most dive parameters differed by time of day, and deeper and longer dives were more frequent in the afternoon period. The diel pattern was consistent with the hypothesis that pups were foraging throughout the day on vertically migrating prey species. In yearlings, dive patterns suggested that large individuals foraged primarily on shallow water prey, while smaller animals concentrated on deeper prey such as Antarctic silverfish.

Tracking studies revealed that juveniles were capable of long distance movements, but suggested that they remained closer to the coastline than adults. The absence of obvious differences in dive behavior between regions suggested that juveniles were foraging on similar prey throughout the Ross Sea. While scat analyses confirmed this hypothesis, tissue stable isotope ratios suggested that some juveniles were feeding on different prey, or in different areas than adults.
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<td>Aerobic dive limit</td>
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<td>AG</td>
<td>Axial Girth</td>
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<td>BMR</td>
<td>Basal metabolic rate</td>
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<td>C:N</td>
<td>Carbon to nitrogen ratio</td>
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<td>CO</td>
<td>Cardiac output</td>
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<td>δ^{13}C</td>
<td>Standardized $^{13}$C:$^{12}$C ratio</td>
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<td>δ^{15}N</td>
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<td>DMR</td>
<td>Diving metabolic rate</td>
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<td>GPS</td>
<td>Global positioning system</td>
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<td>Hb</td>
<td>Hemoglobin</td>
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<td>HCT</td>
<td>Hematocrit</td>
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<td>HR</td>
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<td>i.m.</td>
<td>Intramuscular</td>
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<td>LC</td>
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<td>Meters</td>
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<td>min</td>
<td>Minute</td>
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<td>Mb</td>
<td>Myoglobin</td>
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<td>No dive records</td>
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Thanks also go to Dr. Ward Testa, who one February day walked into my office at the Marine Mammal Laboratory, NOAA, and offered me a position as a doctoral student at UAF on a project that was better than I could ever imagine. I am grateful for his encouragement in the lab and field, and his continual prodding to think about the bigger picture, and in more ecological and evolutionary terms.

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Preface

Most chapters in this thesis have been submitted for publication or are already published. These chapters were submitted with my advisors Dr. Castellini and/or Dr. Testa as co-authors. Chapters 6 and 7 were also co-authored by colleagues whose help was essential to the project's success. However, the entirety of the work presented in each chapter of this thesis is my own.

I first presented the information in Chapter 2 as a talk at the Scientific Committee for Antarctic Research's sixth international biology symposium. It was subsequently published in the symposium volume *Antarctic Communities*, which was edited by B. Battaglia, J. Valencia and D.W.H. Walton (1997, Cambridge University Press, London, pp 328-334). The article was co-authored with Dr. Ward Testa, who, along with the field research team of Amal Ajmi, John Blake, Michael Castellini, Brian Fadely, Janey Fadely, Kelly Hastings, Steve Lewis, Lome Rea, Brad Scotton and Kate Wynne (polar heroes all) helped collect this data.

Chapter 3, co-authored with Dr. Michael Castellini, has been published in the Journal of Comparative Physiology B (1996, v166, pp 473-483). This project was conceived while sitting in a fish hut in McMurdo Sound waiting for a gale to pass, and would not have happened without Dr. Castellini's enthusiastic 'why not, let's try it' attitude. His support and experience working with Weddell seals using the isolated hole protocol (and fixing generators at 3 am) made this research possible. Special thanks also go to Drs. Tania Zenteno-Savin and Lome Rea for staying up all night to collect blood samples from sometimes 'difficult' seals.

Chapter 4 was co-authored with Dr. Castellini, and has been submitted to Marine Mammal Science. This work originated from discussions with many researchers who work with both types of tags. In particular, thanks go to Dr. Ward Testa, Kathy Frost, Erich Follmann, and Melinda Braun.

Chapter 5 was co-authored with both Dr. Castellini and Dr. Testa, and has been submitted to Journal of Zoology (London). The manuscript is the result of the field efforts of the entire 'sealheads' team: John Blake, Mike Castellini, Brian Fadely, Janey Fadely, Tom Gelatt, Kelly Hastings, Rob Jensen, Steve Lewis, Lome Rea, Brad Scotton, Ward Testa, Kate Wynne, and Tania Zenteno Savin, all of whom were willing to be covered with epoxy and puppy pesto so that I could obtain this data. Special thanks to those who stayed late in the 1992-93 season to deploy the tags on pups. In addition, profuse thanks go to Lloyd Lowry and Robert DeLong from the Alaska Department of Fish and Game for helping me analyze the seal location data and digitize the regional maps.
Chapter 6 has been accepted to the Canadian Journal of Zoology with Jason Schreer and Dr. Castellini as co-authors. This manuscript includes the analysis of dive types using techniques developed by Jason as part of his M.S. thesis research. I would also like to thank Lorrie Rea for providing me with the blood chemistry data, and Brian Fadely for helping me develop the body condition index used in this chapter. Help handling the rambunctious yearlings came from all the ‘sealheads’, with special thanks to Kelly and Brian who helped ‘restrain’ Spot.

Chapter 7 has been submitted to Polar Biology as a manuscript co-authored by Steven Trumble, Mike Castellini and Ward Testa. Dr. Testa was responsible for the yearly scat collection and Steven Trumble and Max Hoberg identified prey remains. Help with field collection of scats and tissues came from ‘sealheads’ past and present, and stable isotope analysis was performed by Amy Hirons and Norma Haubenstock. Andrew Trites helped me finally complete this project by letting me use the elutriator system at the Vancouver Aquarium.
Chapter 1. Introduction

The diving behavior of marine mammals has received considerable attention since it was realized that some pinnipeds could make dives in excess of one hour long and to depths of greater than 1500 m (for review: Boyd and Croxall 1996, Riedman 1990). However, research interests have now shifted from determining maximal dive capabilities to better understanding the behavioral ecology and diving physiology of different species (for review: Riedman 1990, Kooyman 1989, Gentry and Kooyman 1986). This change results from, and has been accompanied by, rapid development in the methods used to monitor and understand marine mammal diving behavior and physiology. While the first marine mammal dives were simply timed with a stopwatch and their depth monitored by a dye coated pressure tube (Kooyman 1965), current computerized tags allow animal movements in depth and time to be followed over periods that range from days to months. Using today's technology, animal location, water temperature, ambient light levels, swim speed, and heart rate are just a few of the variables that can be monitored in free-diving marine mammals (Bengtson 1993, Costa 1993, Priede and French 1991, Hill 1986, Kooyman et al. 1983a). The ability to collect these types of data from large numbers of individual animals has helped explain variation in diving behavior within and between species.

It is now clear that a wide variety of environmental and ecological factors can influence marine mammal diving behavior and foraging strategies. In general, it appears that marine mammals optimize their foraging success by concentrating their dives in areas where prey are localized due to physical or biological factors, and that animal movements and dive patterns are often related to factors known to influence the availability of preferred prey items. Many pinnipeds appear to concentrate their foraging in areas of high productivity, such as at the edge of continental shelves or near temperature or current discontinuities (McConnell et al. 1992, Boyd and Amborn 1991, Goebel et al. 1990). Changes in light levels, prey availability, and the caloric content of the prey have been linked to differences in the characteristics of individual dives, dive bouts, and foraging trips (Boyd et al. 1994, Costa et al. 1989, Brown and Mate 1983). Diving patterns suggest that some animals optimize foraging by concentrating on the most energy rich prey, while others concentrate on the most available prey (Lydersen and Kovacs 1993, Goebel et al. 1990, Croxall et al. 1985). Within the polar regions, the extent of fast and pack ice is known to influence species distribution and individual dive patterns, while in more temperate areas, the
availability of suitable haul out sites near foraging areas can also influence species distributions (Bengtson and Stewart 1992, Gentry and Kooyman 1986, Laws 1984, Stirling 1977).

In addition to an increased understanding of how environmental and ecological factors influence diving behavior, significant progress has been made in understanding the mechanisms that allow marine mammals to make long and deep dives. While initial laboratory experiments suggested that all dives were supported by anaerobic metabolism and accompanied by dramatic reductions in heart rate, metabolic rate, and peripheral perfusion (Scholander 1940, Irving 1939), more recent studies have revealed that most dives are aerobic in nature. Increased tissue and circulating oxygen stores, efficient swimming mechanics, and diving metabolic rates that approach resting levels allow most marine mammals to maintain aerobic metabolism in the absence of freely available atmospheric oxygen during diving (for review: Castellini 1991, Kooyman 1989, 1985). Differences in these physiological variables among individuals and species have been clearly linked to variation in the diving behavior (Thorson and Le Boeuf 1994, Lydersen and Hammill 1993b, DeLong and Stewart 1991, Hindell et al. 1991, Kooyman 1985).

While there now exists an extensive body of literature on the diving behavior and physiology of marine mammals, surprisingly little is focused on neonates or juveniles (Homing and Trillmich 1997, Le Boeuf et al. 1996, Stewart et al. 1996, Lydersen et al. 1994, Thorson and Le Boeuf 1994, Lydersen and Hammill 1993a,b). In fact, the ontogeny of diving behavior and physiology has only recently received attention, despite indications that juvenile marine mammals are faced with a suite of disadvantages which may cause their behavior and ecology to differ significantly from that of adults. All pinnipeds are born on land or ice and during the first days post-partum there is little to distinguish newborn pinnipeds from any other mammalian neonate. In fact, most pinniped neonates are unwilling to swim for several days following birth, and if inadvertently submerged, may drown or die from exposure (Schreer et al. 1996, Le Boeuf and Condit 1983). Until weaning, many phocid pups rarely enter the water, and little aquatic activity is noted (for review: Riedman 1990). After weaning, pups must quickly learn to swim, dive, and forage successfully before the energy stores they acquired during lactation are depleted. Juvenile marine mammals also have disproportionately higher metabolic rates and lower body oxygen stores, which reduce dive capacity (Homing and Trillmich 1997, Thorson and Le Boeuf 1994, Lydersen and Hammill 1993a, Rea and Costa 1992). Thus, young marine mammals must quickly make the transition from a terrestrial to aquatic existence, and do so in the face of physiological and behavioral limitations not faced by adults.
As the success of this transition can affect both juvenile survivorship and population levels (Merrick et al. 1987, Eberhardt and Siniff 1977), understanding both the physiological and ecological factors that affect juvenile diving behavior is extremely important, and is the main focus of this research. In this dissertation, I will address hypotheses about how age, body size, and physiology effect the development of diving behavior in juvenile Weddell seals (*Leptonychotes weddelli*, Lesson). I will also examine the effects that time of day, season, and individual variation have on diving patterns, and draw inferences about foraging and dispersal tactics. Juvenile Weddell seals in McMurdo Sound, Antarctica, provide an excellent opportunity to study the ontogeny of diving behavior and physiology in a large phocid because the animals live in a relatively undisturbed environment, there is a significant body of information on the biology, diving behavior and physiology of adults, pups can be easily handled repeatedly throughout the lactation and post-weaning periods, and methods for assessing the health, condition, and diet have already been developed.

This introductory chapter will provide a background for the chapters that follow by providing information on the diving physiology of marine mammals and the biology and ecology of Weddell seals. Following the presentation of these data, I will further detail the scope of this project, and outline the main hypotheses tested.

DIVING PHYSIOLOGY

Marine mammals are able to routinely make extremely long and deep dives, and to travel, eat, sleep, and digest food all while separated from freely available atmospheric oxygen. However, while initial studies of diving marine mammals suggested that all dives resulted in dramatic decreases in oxygenation state and increased anaerobic metabolism, more recent studies of marine mammal diving physiology have revealed that the absence of atmospheric oxygen does not imply that oxygen is unavailable to working tissues (Castellini 1991, Kooyman 1985). In fact, when studying the physiology of freely diving marine mammals, two things become immediately clear: there are large physiological changes during diving as a result of the discontinuous breathing pattern, and that, for the most part, these changes do not appear to disturb the metabolic integrity of the animal (Castellini 1991, Castellini et al. 1988, Davis et al. 1985). It has even been suggested that at the level of cellular respiration, diving marine mammals generally maintain a steady, aerobic state (Hochachka 1992).

To do this, marine mammals have a suite of physiological adaptations designed to increase oxygen stores, and decrease oxygen use rates. Blood volume, hemoglobin (Hb), hematocrit
(HCT), and muscle myoglobin (Mb) levels are higher than in terrestrial mammals of similar size and allow large amounts of oxygen to be stored in the blood and tissues (Castellini 1991, Kooyman et al. 1981). In addition, most marine mammals are able to increase HCT during diving to maximize blood oxygen levels, thus increasing delivery to tissues and prolonging their aerobic capacity (Qvist et al. 1986, Kooyman 1985). The effects of increased blood viscosity associated with high HCT are reduced by large spleens which act as blood cell storage tanks when animals are not diving (Castellini and Castellini 1993, Zapol 1987). To compensate for lung collapse at depth, lung oxygen stores are significantly reduced in importance (Castellini 1991, Falke et al. 1985). However, because body oxygen stores can only be increased to a point before function is compromised, conservation of oxygen becomes important in diving mammals.

Changes in metabolic rate (MR), heart rate (HR), cardiac output (CO), and the redistribution of blood flow away from non-essential organs and those tissues with internal oxygen stores are the major adaptations that enable marine mammals to conserve oxygen during diving (Castellini and Kooyman 1989, Castellini 1985). In phocids, such shifts reduce whole body diving metabolic rates (DMR) to close to resting levels (Ponganis et al. 1993, Castellini et al. 1992b, Kooyman et al. 1980). However, it is important to remember that whole body DMRs are an integration of the MRs of many different tissues; some such as those in working muscles, increase during diving, while others may decline. In addition, shifts in MR, HR, and CO during diving can occur in association with impending surfacing, the need to replenish muscle oxygen stores, or processes associated with capture and digestion of prey (Cherepanova et al. 1993, Castellini et al. 1992b, Hill et al. 1987).

Increased oxygen stores and lowered MRs only serve to prolong an animal’s ability to remain aerobic during diving bouts. During all dives, tissue oxygen stores are depleted, and byproducts of respiratory acidosis accumulate (Castellini 1991, Kooyman et al. 1981). These effects are most noticeable when, during a dive, the balance of metabolism shifts from aerobic to anaerobic generation of energy. While aerobic dive activity is fueled mainly by fat oxidation, anaerobic activity relies entirely on the reduction of glucose to lactate (Davis 1983, Hochachka and Murphy 1979). As a result, lactic acid levels in the tissue increase and pH declines (Castellini 1991, Qvist et al. 1986). Because of the reduced CO and vasoconstriction, circulating metabolite levels are relatively stable during dives (Guppy et al. 1986, Qvist et al. 1986). However, following dives that rely heavily on anaerobic metabolism, an increase in circulating plasma lactate levels is observed (Zapol et al. 1989, Kooyman et al. 1983b, 1980). This increase is used to define the aerobic dive limit (ADL) of marine mammals (Ponganis et al. 1993, Kooyman et al. 1983b,
Following dives that greatly exceed the ADL, the return to pre-dive pH and metabolite levels can take in excess of an hour (Kooyman et al. 1983b, 1980). Such recovery is thought to occur mainly at the surface during extended rest intervals, but may also take place during subsequent aerobic dives (Fedak and Thompson 1993, Kooyman et al. 1980). In either case, marine mammals are thought to better maximize their time at depth by making multiple aerobic dives, rather than a few extremely long, anaerobic dives (Kooyman et al. 1980).

Because total body oxygen stores are proportional to body mass, whereas metabolic rates scale to mass\(^{0.75}\), the ADL is thought to scale to mass\(^{0.25}\) (Gentry and Kooyman 1986, Kooyman et al. 1980, Kleiber 1961). This places smaller individuals or species at a disadvantage in comparison to larger ones with respect to optimal aerobic dive duration and immediately places juveniles at a disadvantage in comparison to adults. However, young juveniles face a second, and potentially more significant constraint. Several studies have shown that young pups and juveniles are born with poorly developed body cardiovascular control, low total body oxygen stores, and high resting metabolic rates (Homing and Trillmich 1997, Castellini et al. 1994, Thorson and Le Boeuf 1994, Castellini et al. 1992b, Rea and Costa 1992). As a result, the aerobic capacity of young animals is reduced in comparison to adults (Kooyman et al. 1983b), not only because of the allometric relationship between oxygen stores and use rates, but because of developmental constraints. This reduction in dive ability is significant, and is an important aspect to consider when interpreting the behavioral ecology of juvenile marine mammals.

**WEDDELL SEAL BIOLOGY AND ECOLOGY**

Weddell seals are large phocids which inhabit the fast and pack ice surrounding the Antarctic Continent (Laws 1984). In McMurdo Sound, Antarctica (77.7°S 166°E), Weddell seals congregate near tidal cracks in the fast ice where females give birth to a single pup between late October and mid-November (Kaufman et al. 1977, Stirling 1969). At these traditional breeding colonies, females nurse their pups while males defend underwater breeding territories (Hill 1987, Kaufman et al. 1977, Siniff et al. 1975). Pups weigh approximately 25 kg at birth, but gain weight quickly and often exceed 100 kg when weaned approximately six weeks later (Hill 1987, Bryden et al. 1984). Pups will not willingly enter the water until they are older than one week, and if submerged, may drown before being able to exit through tidal cracks or breathing holes (Schreer et al. 1996, Thomas and DeMaster 1983a). However, by two weeks of age, pups are better coordinated, and initial forays into the water are observed. As lactation progresses, pups spend increasing amounts of time swimming and diving, but it is not known if pups are accompanied by their mothers on these dives, or if they supplement their milk diet with prey (Hill 1987, Bryden et
al. 1984, Thomas and DeMaster 1983b, Tedman and Bryden 1979, Kooyman 1968). Weaning is relatively abrupt, and adult females soon disperse from the breeding colonies (Testa 1994, Castellini et al. 1992a, Tedman and Bryden 1979). Following weaning, pups generally lose weight and may undergo a short, functional fast (Rea 1995). When pups begin to gain weight several weeks post-weaning, the absolute gain is probably small: yearling Weddell seals, although leaner, are of approximately the same size and weight as pups. Significant increases in mass occur mainly after year one, and by six years of age, adults can exceed 400 kg (Castellini et al. 1992a, Testa et al. 1989).

By the end of the austral summer, most of McMurdo Sound is open water and the majority of the seals have dispersed from the breeding colonies (Testa 1987, Stirling 1969, Kooyman 1968). Weaned pups and juvenile Weddell seals are rarely seen within the McMurdo Sound area after mid-January, and sighting patterns suggest that immature Weddell seals either remain outside of the traditional colonies, or emigrate from their natal areas for several years (Hastings 1996, Testa 1987, Stirling 1969, Kooyman 1968). Sighting probabilities of juvenile Weddell seals remain significantly lower than those of adults until the animals recruit into the breeding population at approximately six years of age (Hastings 1996, Testa 1987, Testa and Siniff 1987). The reason for this dispersal and age segregation is not known, but it may serve to decrease intraspecific competition for forage species.

Such a reduction in competition may be important for juvenile Weddell seals because of the types of prey available within McMurdo Sound and the Ross Sea. In these areas, adult Weddell seals feed primarily on a small, mid-water fish, *Pleuragramma antarcticum*, and secondarily on several fish species, squids, octopods, and crustaceans (Castellini et al. 1992a, Green and Burton 1987, Plötz 1986, Dearborn 1965). The majority of these prey items are thought to occur predominantly below 100 m, which correlates well with adult foraging patterns, as dives average approximately 250 m and 10 min (Schreer and Testa 1996, Testa 1994). Given the reduced aerobic capacity and dive ability of young seals, it seems probable that the adult diet is difficult for juveniles to obtain soon after weaning. However, while initial work on the diet of juvenile Weddell seals suggested that pups undergo a transitional period during which they forage primarily on crustaceans, there is little evidence to support this within McMurdo Sound (Thomas and DeMaster 1983b, Kooyman 1968, Bertram 1940, Lindsey 1937). If little resource partitioning exists between adults and juveniles, it is possible that lower juvenile foraging efficiencies may partially account for their higher mortality rates. Studies addressing the effects of age and mass...
on the development of juvenile diving behavior and foraging strategies are necessary in order to better understand those factors which influence survival.

Another important factor to consider is the effects that light level fluctuations have on foraging and diving behavior. Weddell seals in the Ross Sea inhabit a region where the sun does not set from late October to late February, or rise between late April and late August, and where, for most of the year, daily light level fluctuations are small in comparison to seasonal shifts (Castellini et al. 1992a). Diel changes in the mean depth and duration of dives made by adult Weddell seals during the spring and summer have been linked to the light cycle, and used to draw inferences about foraging strategies (Schreer and Testa 1996, Testa 1994, Castellini et al. 1992a, Kooyman 1981). During the dark winter months, these patterns break down, and foraging dives show little depth variation throughout the day (Testa 1994, Kooyman 1975). However, it is not known if these changes are a result of shifts in the prey availability, prey behavior, or preferred foraging tactics of the seals. The role of diel and seasonal variation in the dives of pups or juveniles has not previously been studied, but may yield important information about the degree of overlap between the foraging strategies of juveniles and adults.

SCOPE OF THE STUDY

The main goals of this dissertation are to determine the effects of age, body size, and condition on the development of diving behavior and physiology in Weddell seal pups and juveniles. In order to do this I monitored the free ranging dive behavior of Weddell seal pups and juveniles, and attempted to relate observed changes in dive parameters to both shifts in individual condition as pups aged, and to changes in the surrounding environment.

Chapter 2, "Developmental changes and diurnal and seasonal influences on the diving behavior of Weddell seal (Leptonychotes weddellii) pups" examines the effects of age, mass, time of day, and season on the dive behavior of seals between two weeks and six months of age, and compares the diving behavior of these pups to that of year-old seals. Inferences about the foraging behavior of pups and yearlings are drawn from patterns of dive behavior and mass change. Because this chapter was accepted for publication before the SLTDR data from the 1993 and 1994 field seasons were available, only data from the SLTDRs deployed in 1992 are included in this Chapter.

In chapter 3 "Physiological and behavioral determinants of the aerobic dive limit in Weddell seal (Leptonychotes weddellii) pups" the effects of age and mass on physiological processes
related to diving are tested in three young pups. Here, attention is focused on the development with age of diving metabolic rate, body oxygen stores, and physiological control mechanisms. In this study, I relate the ontogeny of diving physiology to changes in free ranging dive behavior, and assess how to best determine the actual aerobic dive limit (ADL) of juvenile marine mammals. This paper has been published in the Journal of Comparative Physiology B (1996, v166:473-483).

Chapter 4, "Dive data from satellite tags and time depth recorders: a comparison in Weddell seal pups" is a methods paper that discusses whether dive data collected from SLTDRs and TDRs can be considered comparable. Such an analysis was necessary because the two types of tags used in this study process and report dive data differently, and the direct comparison had never been made. This chapter also examines whether dive activity, time of day, or seal age affects the probability of receiving data from SLTDR tags, and assesses the accuracy of animal location and movement rates reported by SLTDRs. The conclusions drawn in Chapters 2 and 5 rely on the findings in this analysis.

Chapter 5, "Movements and diving behavior of weaned Weddell seal pups" looks at the effects of seal age, time of day, and location on the diving behavior of pups between two and seven months of age. I was particularly interested in determining the role of age in these older pups because studies on other phocids suggest that the importance of age in determining dive behavior declines rapidly after phocid pups are weaned and foraging on their own (Le Boeuf et al. 1996, Thorson and Le Boeuf 1994). As in Chapter 2, the effects of time of day were considered in an attempt to infer foraging behavior from dive records. Pup movement and dispersal patterns are reported and compared to those of adults in order to assess differences in habitat utilization or migration routes. This chapter includes all dive data collected from SLTDR tags over three years, and treats the data in a different fashion than was used in Chapter 2.

The extent and cause of individual variation in dive behavior, and the effects that this variation can have on the interpretation of dive records is examined in Chapter 6, "Physiological effects on individual dive patterns and foraging strategies in yearling Weddell seals." Correlations between individual dive behavior, mass, and metabolic chemistry are made in an attempt to determine if small differences in physiological factors within a relatively homogeneous group of animals are responsible for the observed differences in dive behavior. In addition, dive categorization techniques are used to make more detailed inferences about individual foraging behavior and strategies than is possible when all dives are grouped together.
In Chapter 7, "The diet of adult and juvenile Weddell seals in McMurdo Sound, Antarctica", the foraging behavior of Weddell seals is determined through analysis of collected scats and the stable isotope ratio in different seal tissues and prey items. Particular attention is paid to differences in the diet of adults and juveniles, and to inter-annual variation. The diet, as determined by these methods, is then compared with that inferred from dive behavior and the utility of the different techniques is discussed.

Chapter 8, "The ontogeny of Weddell seal diving behavior and physiology: ecological implications of phocid developmental patterns" presents the conclusions drawn from this research and provides a synthesis of our current understanding of the factors which influence phocid diving behavior and foraging strategies. This chapter emphasizes the effect that these changes can have on the behavioral ecology of juvenile Weddell seals, and suggests how these results might apply to the study of other phocid species. Future research directions and methods for determining how diving development and behavior might impact juvenile survivorship are also discussed.
LITERATURE CITED


Chapter 2: Developmental changes and diurnal and seasonal influences on the diving behavior of Weddell seal (*Leptonychotes weddellii*) pups.

ABSTRACT

The development of diving behavior of Weddell seal pups in McMurdo Sound, Antarctica, was monitored with time depth recorders (TDRs) during the austral springs and summers of 1992 and 1993. Pups (n = 17, 20) carried TDRs for periods of several days every second week between the ages of two and 13 weeks. To track diving behavior throughout the fall and winter, satellite-linked time depth recorders (SLTDRs) were deployed in January, 1993, on seven of the pups that had carried TDRs during 1992.

Pups began to dive within two weeks of birth. The number of dives per day, and the mean depth and duration of dives increased significantly over the first 13 weeks. During this period, dive behavior was determined primarily by pup age, although diel effects were apparent in dive frequency. The SLTDR records from pups between the ages of 11 and 32 weeks revealed diel effects in all measured parameters. The longest and deepest dives occurred during the afternoon period, night dives were short and shallow, and the morning and evening dives were intermediary. Dive frequency was highest during the night, and lowest during the afternoon. These effects predominated once the pups were older than three months.

Combined SLTDR and TDR data suggest possible seasonal trends in dive behavior, although the pattern was confounded by pup age. Mean dive depth and duration increased throughout the study only during the afternoon period, the hours of maximum light. In all other periods, dive depth and duration declined or remained constant. In combination, depth, duration, and frequency data suggest that dives were more shallow and less frequent later in the season in periods when light was limited. The diel and seasonal pattern in dive behavior is consistent with the hypothesis that pups are foraging throughout the day on vertically migrating prey species.

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INTRODUCTION

Many studies have documented the diving behavior of pinnipeds. Variations in dive behavior within and between species have been attributed to differences in foraging behavior, age, size, sex, season, and time of day (Thorson and Le Boeuf 1994, Castellini et al. 1992, Boyd et al. 1991, Feldkamp et al. 1989, Le Boeuf et al. 1986, Croxall et al. 1985, Testa et al. 1985, Kooyman et al. 1983, Kooyman 1975). Most studies have focused on the dive behavior of adults and juveniles; little work has been performed on young pups due to difficulties of instrument deployment on small individuals, and with recapture (Thorson and Le Boeuf 1994, Lydersen et al. 1992). However, because Weddell seal (Leptonychotes weddellii Lesson) pups are relatively large, and easy to approach and recapture both before and after weaning, they offer a unique opportunity to study the development of pup diving ability. In addition, the diving behavior of adult, juvenile and a few weaned Weddell seal pups has been documented (Castellini et al. 1992, Kooyman et al. 1983, Kooyman 1981, Kooyman 1968), and can be compared to that of the pups in this study. Understanding the development of pup diving ability is important for several reasons: differences in diving behavior at an early age may be linked to differential survival, diving behavior can provide clues about diet and foraging habits, and diving development might yield information on developmental physiology.

In McMurdo Sound, Antarctica, Weddell seals are born in October and November. Traditional colonies are generally in fast ice near tidal cracks which, in addition to breathing holes maintained by the seals, provide access to water (Testa et al. 1989, Kooyman 1981, Stirling 1977, Siniff et al. 1975). Pups weigh approximately 25 kg at birth, and at the end of the six week lactation period can exceed 100 kg (Castellini et al. 1992, Hill et al. 1986, Bryden et al. 1984). By two weeks of age, pups have begun to enter the water and they spend increasing amounts of time swimming and diving as lactation progresses (Hill 1987, Tedman and Bryden 1979). By the end of December pups are weaned and the fast ice has begun to thin and break up. By February much of the sound is open water and the majority of the seals have dispersed (Castellini et al. 1992). The maximum depth of McMurdo Sound is approximately 700 m, with depths greater than 200 m within 1 km of shore, making it unlikely that pup diving behavior is constrained by bathymetry while they remain in the sound. The short lactation period, rapid growth of the pups, and disappearance of their haul out substrate, suggests that the development of pup diving behavior is rapid.
Daylight patterns in the McMurdo Sound area are extreme. From October 21 until February 23, the sun never sets, and between April 23 and August 24, the sun never rises. While there is an absence of a typical light/dark cycle for eight months of the year, during the summer there is variation in the incident radiation due to the sun's angle, and during the winter the moon provides enough light to see distant features. There is no sunlight only during June and July (Castellini et al. 1992). During the spring and summer, adult Weddell seal dive behavior varies with time of day. Seals are generally on the surface during the day, and dives are concentrated in the crepuscular and night periods. The little information on diving patterns in the mid-winter months suggests that this pattern breaks down once the light levels stop fluctuating (Testa 1994, Castellini et al. 1992, Thomas and DeMaster 1983, Kooyman 1975). The role of diel and seasonal variation in the dives of pups or juveniles has not previously been studied. These effects, and those of age, were examined to determine the role of diurnal and seasonal variation in the development of pup diving behavior throughout lactation, and for several months post weaning.

METHODS

This study was conducted in McMurdo Sound, Antarctica (77°45'S, 166°30'E), during the austral summers of 1992 and 1993. Long-term tagging studies aided in adult and pup identification. Pup ages were known to within two days. Both male and female pups were studied (1992 n= 6,11; 1993 n=13,7). Time depth recorders (TDRs; Wildlife Computers, Woodinville, WA, USA, Mark 5 or 6) were deployed on individual pups for several days every two weeks to monitor the development of their diving behavior between the ages of two and 13 weeks. Seventeen pups carried TDRs during 1992 for a total of 60 deployments, and TDRs were deployed a total of 54 times on 20 pups in 1993. On average, pups carried TDRs four times in 1992 and three times in 1993. Until pups molted their lanugo pelage TDRs were carried on anklets consisting of a 4 cm wide, 3 mm thick neoprene rubber band fastened around the ankle with small corrosive bolts. The TDRs were attached to the anklet with Velcro and nylon ties. After the molt, TDRs were glued to the mid-dorsal pelage with an epoxy adhesive. Data collected from TDRs deployed in a similar fashion on four yearlings in 1992 is reported for comparison. TDRs monitored depth every 10 s when wet, had a depth resolution of 2 m, and a maximum depth of 500 m. Data from the TDRs consisted of a continuous time-line of depths.

To track dive behavior throughout the fall and winter, satellite-linked time depth recorders (SLTDRs) were deployed in January, 1993, on seven of the pups that had carried TDRs earlier in the season. The half-watt SLTDRs (Wildlife Computers, SDR-T6, Service Argos PTTs) were
attached to the mid-dorsal pelage with epoxy and netting. Like the TDRs, the SLTDRs sampled depth every 10 s during dives, had a depth resolution of 2 m, and a maximum depth of 500 m. However, due to transmission limitations, the SLTDRs placed all dives into one of 6 depth and duration bins (80 m and 4 min intervals) and transmitted the number of dives in each bin, rather than the actual depths and durations of dives. The data were transmitted to a polar orbiting satellite, and relayed to the University of Alaska via Service Argos (Fancy et al. 1988, Service Argos 1988). For analysis, all SLTDR recorded dives were given depth and duration values. The values assigned were determined by simultaneously collecting TDR and SLTDR dive data from individual weaned pups and yearlings, and calculating the mean depth and duration of those dives which fell within each histogram bin range. Additional information transmitted via Service Argos included status messages that reported the depth of the deepest dive in the previous 24 hours. The longest dive duration was not reported.

Data from both the TDRs and SLTDRs were downloaded by computer and processed with software from Wildlife Computers. The minimum depth for a dive to be analyzed was 12 m, and minimum duration was 30 s. In this analysis, the mean dive depth is the deepest depth of each dive averaged over all dives for each seal at each age (in weeks, rounded down) rather than the mean of the average depth of each dive. Average dive duration is the duration of 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. Weekly maximum dive depths are an average of the depths of the deepest dives made by each seal each day.

Diel effects were searched for by dividing the day into four equal periods: night (21:00-02:59), morning (03:00-08:59), afternoon (09:00-14:59), and evening (15:00-20:59). In part, this grouping of dive data by period was mandated by the need to compress data for transmission by the SLTDRs, but the times of the four periods were chosen to take into account the fluctuating daylight in McMurdo Sound and the known behavior of the seals. The average depth, duration, and frequency of dives was then calculated for each seal by period and deployment, and these values used in all analyses.

All comparisons were performed using multivariate linear regression, with age as a continuous variable, and year and period as categorical variables (STATISTIX software). Non-linear curve fitting was performed, but in all cases linear regression yielded the best fit. The null hypothesis assumed no difference in mean dive depth, duration, or frequency, by pup age, year, period or month. Significance for rejection of the null hypothesis was set at \( p < 0.05 \). Only equations from...
significant regressions are presented. Reported rates of increase in average dive depth, duration, or frequency are the slope coefficient from the best fit regression equation for the appropriate subset of data. Differences in rates were considered significant if the pertinent categorical variable was significant in the overall regression. All figures show the overall average dive depth, duration or frequency, grouped first by individual, then by period or year, as indicated.

RESULTS

Data from 58,500 dives were analyzed. In 1992, 10,188 pup dives and 1,810 yearling dives came from TDR records, and 29,920 from SLTDR records. In 1993, all 16,582 dives were collected by TDR. Dives were collected from TDRs between November and February, and from SLTDRs from January through May. No dives made by pups or yearlings ever exceeded the 500 m maximum resolution of the TDRs or the SLTDRs.

Mean depth, duration and frequency of dives made by pups between the ages of two and 13 weeks were mainly determined by the age of the pup, which accounted for 50-72% of the variation in dive behavior. However, the average depth and duration of dives was significantly greater in 1993 than in 1992, as were the weekly rates of increase (depth: 7.52 vs. 16.27 m/week; duration: 0.37 vs. 0.59 min/week). As a result, 1992 and 1993 dive depth and duration data were analyzed separately. There was no difference in the average dive frequency between 1992 and 1993, and these were combined for subsequent analysis (Figure 2.1). Because no significant difference in dive behavior existed between male and female pups in either 1992 or 1993, the sexes were combined.

Once the pups were older than three months, pup age (in weeks) accounted for little of the variation in dive behavior (data recorded by SLTDRs). There was no significant increase in the average dive depth and dive duration with increasing pup age from three to eight months, but average dive frequency was positively correlated with pup age. However, this correlation accounted for only 7% of the variation in dive frequency (Dive Frequency = 57.87 + 4.46*Pup Age, \( r^2 = 0.07, n=333, p < 0.001 \)).

In 1992, maximum dive depth increased with the age of pups across both the TDR and SLTDR record, but the rate of increase was significantly greater in the TDR record (TDR record: Maximum Depth = -46.56 + 21.15*Pup Age, \( r^2 = 0.67, n=52, p < 0.001 \); SLTDR record: Maximum Depth = 160.21 + 7.25*Pup Age, \( r^2 = 0.18, n=56, p < 0.001 \)).

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To determine if, in addition to pup age, dive behavior was influenced by time of day, period of day was added into the model as a categorical value. In both 1992 and 1993 for pups between the ages of two and 13 weeks, there were no significant differences in average dive depth or duration by period, so all periods were combined. Similarly, dive frequency (average number of dives per period) did not vary by period in either 1992 or 1993. In all cases, the absence of significant differences between periods in average dive depth, duration, and frequency, could be attributed to the large amount of individual variation between pups within each age class. As a result, there was little evidence for any consistent diurnal variation in the diving behaviour of pups younger than three months. For these pups, age, rather than time of day, appears to be the primary determinant of diving behaviour.

In contrast, once the pups were older than three months, the period of day had a significant effect on average dive depth, duration, and frequency as recorded by SLTDRs, and age had less influence. The average depth of dives was significantly different in each of the four periods. The deepest dives occurred in the afternoon, followed by the evening, morning, and night periods (Figure 2.2). The average depth of dives increased significantly with pup age only during the afternoon period (Average Depth = -11.7 + 7.59*Pup Age, $r^2=0.35$, n=70, $p < 0.001$), and was not correlated with pup age in the morning, afternoon, or evening periods. Maximum dive depths could not be analyzed by period because the time of the dive was not reported by the SLTDR.

Average dive duration of pups older than three months also varied by period, but not all periods were significantly different from each other. Dives in the night were shortest, followed by dives in the morning. The longest dives occurred in the afternoon and evening periods which were grouped because dive durations were not significantly different (Figure 2.2). Pup age was only a significant factor in the combined afternoon and evening period when dive duration increased slightly with pup age (Average Duration=4.05 + 0.07*Pup Age, $r^2=0.05$, n=151, $p = 0.004$).

Dive frequency showed the least variation by period. There were significantly more dives in the night and morning periods than in the afternoon or evening periods (Figure 2.2). Pup age was a significant factor in the combined night and morning period, when dive frequency increased slightly as pups aged (Average Frequency = 27.48 + 0.77*Pup Age, $r^2=0.03$, n=157, $p = 0.017$). There was no significant relationship between pup age and dive frequency in the afternoon period. The greatest increase in dive frequency with age occurred during the evening period (Average Frequency = -11.15 + 2.19*Pup Age, $r^2=0.37$, n=69, $p < 0.001$).
Analyses of seasonal trends were confounded by the overlap between calendar month and pup age. When month was treated as a categorical variable, the correlation between month and pup age was too large to separate the two effects. As a result, seasonal effects could only be searched for by using pup age as a proxy, and examining each of the periods separately. This technique revealed some interesting patterns. Once the pups were older than three months, average dive depths and durations were uncorrelated with pup age or month during morning, evening and night periods (see Figure 2.2). In contrast, both average depth and duration increased with pup age throughout the TDR and SLTDR records during the afternoon period. Despite the unusual light regime in McMurdo Sound, the afternoon period did receive some solar insolation during all of the SLTDR record. During the afternoon period, the rate of increase in average dive depth and duration as recorded by SLTDRs was not statistically different from the TDR records. Similarly, dive frequency continued to increase at a constant rate throughout the record only during the evening (Figure 2.3). During these periods, pup age accounted for greater than 40% of the variation in dive behavior.

In both the TDR and SLTDR recorded data, there were strong correlations between average dive depth and average dive duration. This correlation was greatest once the pups were older than three months, and was present in all periods of the SLTDR data. Table 2.1 shows the partial correlation values for average dive depth and duration, controlled for pup age. Because seal pups throughout the study spent a large proportion of their time on the surface, there was no clear correlation between dive duration and dive frequency.

**DISCUSSION**

The diving ability of Weddell seal pups developed rapidly during their first three months of life. During this period, pup age was the most important factor in determining the average depth and duration of dives. By the time pups were 13 weeks old their diving performance was still less than that of yearlings, although they were completely weaned and foraging on their own (Hill et al. 1986, Bryden et al. 1984). The differences in the rate of increase in average dive depth and duration by pup age between 1992 and 1993 could be a reflection of differences between the two years in pup growth rates or in ecological factors such as prey distribution. However, as dive frequency did not differ between the two years, it is more likely that the differences were tied to ecological rather than physiological causes. If 1992 pups were less capable divers than 1993 pups, then all three parameters should have been lower in 1992, which was not the case. One
such ecological cause could be differences in yearly prey distributions. Unfortunately, little is known about such variation in McMurdo Sound.

Time of day clearly played an important role in determining the dive behavior of Weddell seal pups. However, it did not appear as a significant factor in dive depth and duration until after the pups were older than three months, foraging on their own, and the sun had started to set. In these older pups, trends in all measured variables followed a similar pattern: dives were short, shallow and frequent during the night period, when light levels were lowest; and longest, deepest and least frequent during the afternoon period, when insolation was highest. The morning and evening periods when light levels changed rapidly, showed intermediate characteristics. The strength and continuity of this pattern throughout the study was somewhat unexpected, for McMurdo Sound does not have a typical light-dark cycle. However, even in May when the observations ceased, the afternoon period received some light, suggesting that dive patterns were influenced by insolation throughout the study.

The dive behavior of many pinniped species has been linked to the distribution of their prey (Boyd et al. 1991, Le Boeuf et al. 1986, Croxall et al. 1985), which supports the hypothesis that Weddell seal dives track their prey distribution. Unfortunately, while there is good information on the diet and dive behavior of adult and juvenile Weddell seals, there is little to no information on the ecology of their prey items in McMurdo Sound. Adult Weddell seals prey primarily on the Antarctic silverfish (*Pleuragramma antarcticum* Boulanger), and secondarily on several fish species, squid, octopods, and crustaceans (Castellini et al. 1992, Green and Burton 1987, Plötz 1986, Testa et al. 1985, Clarke and MacLeod 1982, Dearborn 1965). The few pup scats that we collected in McMurdo Sound contained otoliths from *Pleuragramma*, squid beaks, and crustacean parts, suggesting that pups forage on the same species as do adults. This is in contrast to early reports (Bertram 1940, Lindsey 1937) which suggest that weaned Weddell seal pups in other regions of Antarctica undergo a transitional period during which they prey primarily on crustaceans. Information on the ecology of these prey items comes from ice-free Antarctic waters outside of McMurdo Sound, where the majority of these species occur midwater, make diurnal vertical migrations, or are separated in size by depth (White and Piatkowski 1993, Kellermann 1986, Eastman 1985, Hubold and Ekau 1985). However, little information is available regarding their distribution or movements under ice or in the winter. Thus while both the diet and dive information suggest that Weddell seal adults, juveniles, and pups forage on similar prey, and that these species show some degree of vertical migration throughout the year, there is no direct evidence for such behavior.
In this study, the influence of season on Weddell seal dive behavior was difficult to determine. The correlation between pup age and season made it impossible to separate the two effects in all attempted statistical analyses. Although there was a steady increase in dive depth and duration throughout the TDR record, and during the afternoon period in the SLTDR record, after the pups were older than three months of age there was little significant change in dive behavior with age (or month) in any other period. Yet the lack of correlation between pup age and average dive depth, duration, and frequency in the morning, evening, and night periods might itself be a result of seasonal trends in light patterns. As light levels decline, vertically migrating prey might move closer to the surface. Seals foraging on these species could then capture their prey with shorter and shallower dives. As (until mid-May) the afternoon period has the highest light levels, seals may have to continue to dive deeply in this period in order to obtain sufficient food.

Increases throughout the record in dive depth and duration in the afternoon period, and in dive frequency during the morning, evening, and night, suggest that pup diving ability continues to develop through the first year. This is confirmed by comparing average afternoon dive depths and durations of pups at the end of the study (116 ± 13 m, 5.6 ± 0.5 min) to the overall averages for yearlings (200 ± 35 m, 8.69 ± 0.64 min), and adults (144 ± 83 m, 10.4 ± 2.9 min) (Castellini et al. 1992, this study). Additionally, the steady change in maximum dive depth by pups in this study indicates that both the frequency and depth of deep dives continues to increase. Clearly pups less than nine months of age have yet to develop the skills of yearling and adults. That pup dive depths are closer to adult values than are their dive durations suggests that the development of breath hold ability (oxygen stores), is slower than the development of the ability to reach great depths. Physiologically, this is expected. Smaller, younger seals have higher mass specific metabolic rates than adults and require more oxygen per unit mass for a given dive duration (Lavigne et al. 1986). Even juvenile Weddell seals (between 2 and 4 years old) have lower aerobic dive limits (ADL) than adults, (10-13 min vs 16-20 min) (Kooyman et al. 1983, Kooyman et al. 1980), indicating that increases in average dive duration continue for several years.

How, or if, the increase in aerobic capacity is developed after the pups are weaned has not yet been determined. Weaned pups are of approximately the same mass as yearlings, but may have a lower proportion of muscle mass (Rea and Costa 1992). This, along with differences in hematocrit, hemoglobin, and myoglobin content due to age, also might account for age-specific differences in the aerobic capacity. Assuming that pups swim at 1.5 m/s (an average swim speed
for many pinnipeds), a 400 m dive, requires 9 'minutes' of oxygen (Davis et al. 1985, Williams and Kooyman 1985). Pups can dive for this duration, but to make such a deep dive energetically feasible may require more time at that depth than they are capable of spending during an aerobic dive. Thus while there are no physiological reasons that pups should be unable to dive to 'adult' depths, they may not have sufficient oxygen stores to make such deep dives worth the effort. The strong correlation between depth and duration in both the TDR and SLTDR records corroborates this hypothesis.

The results of this study support several conclusions: that the development of diving behavior in Weddell seal pups is rapid, and that age is the primary determinant during the first three months. During this period of rapid development in diving ability, average maximum dive depth increased from 13 to 185 m, average dive duration from 1.7 to 7.6 min and average daily dive frequency from 5 to >500 dives/day. After the pups were three months old and foraging on their own, diving ability continued to improve, and diurnal influences on diving patterns became evident. While the role of seasonal effects was unclear, the pattern suggested agrees with that indicated by diurnal variation: shorter and shallower dives during periods and seasons when light is limited. In combination, these findings suggest that Weddell seals in McMurdo Sound forage on prey species that make diurnal vertical migrations under the ice. In addition, as similar variations in dive behavior are seen in adults, juveniles, and pups, it is likely that all ages forage on similar species.

ACKNOWLEDGMENTS

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Table 2.1: Partial correlation between average dive depth and duration.

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<th>Period</th>
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<th>Partial Correlation</th>
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<td>1992</td>
<td>Evening (3)</td>
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Figure 2.1: Mean dive depth (a), duration (b), and frequency (c) as recorded by TDR. Yearling values are shown for comparison. Error bars show standard error, n = 119.
Figure 2.2: Mean dive depth (a), duration (b), and frequency (c) by period, for those periods which differed significantly. Data collected from SLTDRs deployed on 7 pups in 1993. Yearling values are shown for comparison.
Figure 2.3: Mean dive depth (a), duration (b), and frequency (c) with pup age throughout the TDR and SLTDR records from 1992. Error bars show standard error. The least squared regression line fit for all the data is shown. Source = 1 for TDR data and 0 for SLTDR data.
LITERATURE CITED


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Chapter 3: Physiological and behavioral determinants of the aerobic dive limit in Weddell seal (*Leptonychotes weddellii*) pups

ABSTRACT

The aerobic dive limit (ADL), as defined by an increase in plasma lactate levels following dives, has to date only been determined in adult and juvenile Weddell seals (*Leptonychotes weddellii*). However, theoretical ADLs based on calculated total body oxygen (TBO$_2$) stores, estimated metabolic rates, and dive duration frequencies have been published for several species. Using data collected over the past three years in McMurdo Sound, Antarctica, the ADL of Weddell seal pups was determined by both the physiological and modeling methods. Time depth diving recorders (TDRs) deployed on 36 pups between two and 14 weeks of age allowed the ADL to be predicted from duration frequency histograms. The ADL was also calculated from estimates of TBO$_2$ stores and predicted diving metabolic rates (DMR). Finally, these two estimates were compared with ADLs determined by post-dive lactate levels in three pups between five and seven weeks old. The ADL of pups increased with age, but pup ADLs were still significantly shorter than those of yearlings and adults. In addition, the ADLs determined by the three methods were not equivalent for pups, yearlings, or adults, and indicate that care should be taken when modeling methods are used to estimate the ADL in other species. Changes in hematocrit (HCT), plasma glucose, and plasma lactate levels during and between rest, diving, and recovery in pups were compared to known values for juveniles and adults. Plasma metabolite levels were more highly regulated in older pups, and together with the increasing ADL, suggest that Weddell seal pups are not refined divers until after they are weaned, and that their diving ability continues to develop over several years.

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INTRODUCTION

The concept of the aerobic dive limit (ADL), the longest dive duration following which plasma lactate levels are not elevated above resting, has been used to place dive behavior within a physiological context. Dives shorter than the ADL are often referred to as more efficient, as they do not require extended recovery periods at the surface (Castellini et al. 1992b, Castellini and Kooyman 1989, Kooyman et al. 1980). Early studies on the diving behavior of Weddell seals (Leptonychotes weddellii) demonstrated that the ADL determined from post-dive lactate levels could also be predicted from the dive behavior itself, as generally less than 5% of adult and juvenile dives exceeded the measured ADL (Kooyman et al. 1983, 1980). In addition, the ADL could also be accurately estimated from calculations of the total body oxygen stores and the diving metabolic rate (DMR). As a result of the close agreement for adult and juvenile Weddell seals between the ADL determined from post-dive lactate levels, free ranging dive data, and calculated from total body oxygen (TBO₂) stores and metabolic rates (MR), these three techniques have often been thought of as interchangeable. However, only the measurement of post-dive lactate levels directly determines whether dives were aerobic or anaerobic.

Because determining post-dive plasma lactate levels in freely diving seals is difficult, (it has only been accomplished for Weddell seals diving in McMurdo Sound, Antarctica), many researchers have estimated the theoretical ADL for other species using one of the alternative techniques. DMRs have only rarely been measured, and are known to vary with dive type and duration (Ponganis et al. 1993, Castellini et al. 1992b, Kooyman et al. 1983, 1980). Yet, frequently, either DMRs of twice the basal metabolic rate (BMR) (from Kleiber 1961) or resting metabolic rates (RMR) are used with estimated TBO₂ stores to calculate the ADL (Lydersen et al. 1994, Slip et al. 1994, Lydersen and Hammill 1993a, Lydersen and Kovacs 1993, Hindell et al. 1992, Lydersen et al. 1992, Feldkamp et al. 1989, Le Boeuf et al. 1989). The proportion of monitored dives exceeding this calculated ADL is often reported as an indicator of inefficiency or, if the proportion is much greater, as unusual behavior (Slip et al. 1994, Hindell et al. 1992, Lydersen et al. 1992, Le Boeuf et al. 1988). Alternatively, the fact that less than 5% of the dives exceed the calculated ADL is sometimes taken as proof that the modeled ADL is correct, as had been shown for adult Weddell seals (Kooyman et al. 1983, 1980). Despite the widespread use of these estimation techniques, the validity of applying methods tested only on a few mature Weddell seals to seals of different ages or species has not been evaluated, even when large numbers of dives exceed the modeled ADL. In this study, the relationship between the three methods used...
to determine the ADL were examined, and the applicability of these techniques to young, developing, Weddell seal pups evaluated.

METHODS

There were two primary components to this study: the study of diving physiology and the determination of free ranging dive behavior. The methodology used in the experimental study of diving physiology follows that first described in Kooyman (1968), and later used by Kooyman et al. (1983, 1980), Qvist et al. (1986), Castellini et al. (1988), Zapol et al. (1989), and Ponganis et al. (1993). An isolated experimental dive site was created by drilling two 1 m diameter holes in the 3 m thick sea ice of McMurdo Sound in the Ross Sea, Antarctica (approximate location 166.25° E, 77.73° S). This site was sufficiently remote from any other holes or cracks in the ice such that seals released in the holes had to return to them to breathe. A hut with a trap door in the floor was set up over one hole for use as a field laboratory. The exterior hole was closed during experiments so that the seal was obligated to surface inside the laboratory, but was opened at the end of the trial to provide the seal with an exit to the sea ice.

Animal Handling

Four known-age Weddell seal pups (37 - 50 days old) were selected from the colony at Big Razorback Island in McMurdo Sound, Antarctica (166.48° E, 77.684° S) for use in the isolated hole dive experiment. Pups older than four weeks were chosen because by this age pups were routinely seen diving and resting alone. Pups were captured by manual restraint, weighed with a hanging electronic scale (accuracy ± 0.1 kg), and transported by sled to the experimental dive site. At the dive site, pups were anesthetized with a mixture of ketamine (0.1 mg/kg) and diazepam (0.25 ml/100 kg) given intramuscularly (i.m.). After Lidocaine (2 ml) was injected subdermally around the insertion site, two catheters were implanted approximately 10 cm apart in the intravertebral extradural vein and advanced approximately 50 cm. Once the catheters were in place, antibiotics (Keflin, 5 gm and Gentaved, 2 ml) were administered intravenously through a catheter. Each external catheter was approximately 1 m long, and ended in a float and 3-way valve. Catheters were held in place with neoprene pads glued to the fur with a cyano-acrylate adhesive (Loctite 422). This design allowed blood to be sampled while the seal was at the surface of the water. These blood sampling methods have been used extensively in Weddell seals (Castellini et al. 1988, Kooyman et al. 1983, 1980). While under anesthesia, a time depth recorder (TDR, Wildlife Computers Mark 5) was attached around a rear flipper with an anklet (Burns and Testa 1997). Upon full recovery from anesthesia, the trap door in the laboratory was opened, the seal was free to enter the water, and the experiment started.
At the end of the experiment, the laboratory trap door was closed, and the outside hole was opened. The seal then emerged onto the ice surface, where it was recaptured using manual restraint. The TDR and catheters were removed and the seal returned to the site of initial capture. Before release, a second injection of Gentaved (2 ml) was administered i.m. In all trials, the seal was in the water for no more than 14 hours, and was returned to Big Razorback Island within 24 hours of its initial capture. All pups handled prior to weaning were seen after the experiment with their mothers (identified by numbered flipper tags). One pup (22R) had been weaned prior to the experiment.

**Blood Collection and Analysis**

Blood was collected at the end of a dive by retrieving the floating catheter, clearing the line, and withdrawing a blood sample. The catheter was cleared of flush solution prior to blood collection by withdrawing greater than 3 ml fluid (catheter volume was less than 2 ml). The blood sample was then collected directly into heparinized vacutainers (Becton-Dickenson), or into heparinized syringes and immediately transferred into heparinized vacutainers. This process took approximately one minute, and all initial samples following dives were collected within 60 seconds of the seal surfacing. During long surface intervals blood was collected several times and the catheter flushed between each sample. When more than one sample was collected, the initial sample was considered the post-dive sample, and all subsequent samples considered recovery samples. The two main problems with repeatedly sampling blood through an external catheter in Antarctic waters were freezing and clotting. Both were prevented by flushing the catheter free of blood after each sample and filling the dead space prior to submergence with a 20% ETOH-saline solution, to which heparin (1000 U/l) had been added. However, post-dive lactate levels were collected from only three of the four pups, as both catheters in the first pup (21R) froze soon after entry into the water. Samples from pups 75R, 24R, and 22R were collected at rest, after dives, and during dive recovery.

Blood samples were stored on ice prior to centrifugation and separation of the plasma. Hematocrit (HCT) was determined in duplicate using a battery operated field micro-hematocrit centrifuge (Compur M1100, samples spun at 5400 x g (11500 rpm) for 3.5 min). The remaining blood was centrifuged and the plasma removed and frozen for later analysis. Samples were held in a liquid nitrogen cooled CryoPac shipper (-196°C) while in the field, and then transferred and stored at -80°C in McMurdo prior to initial analysis for plasma lactate and glucose concentrations. Plasma glucose and lactate concentrations were determined within one week of collection using
a YSI Model 2300 STAT glucose/L-lactate autoanalyzer. The remaining samples were transported to University of Alaska Fairbanks and stored at -80°C.

**Dive Data**

In the isolated hole dive experiments, once the seal was in the water and the experiment begun, the duration of all dives and surface events were recorded on a portable computer using a timing program written for QuattroPro. Time of sample collection was also recorded. Dive depth was determined once the TDR was recovered. The TDR sampled depth at 1 s intervals with a resolution of 2 m, and dive depths were determined using analysis software (3M) provided by Wildlife Computers.

**Free Ranging Dive Behavior:** Data on free ranging dive behavior was collected in 1992 and 1993 from 36 pups between the ages of two and 14 weeks old (19 males, 17 females) for a total of 119 records, and from 15 yearlings (10 males, 5 females). TDRs (Wildlife Computers Mark 5 or 6) were attached to a rear flipper with an anklet or glued dorsally to the fur (Devcon 5 minute epoxy). TDRs were removed 3-10 days after deployment, and pups carried TDRs multiple times (Burns and Testa 1997). TDRs sampled data at 10s intervals with a depth resolution of 2 or 3 m. Dives were decoded using programs provided by Wildlife Computers (ZOC, DA). Only dives which exceeded 30 s and 12 m were considered for further analysis in this report.

**ADL Determinations**

The ADL was determined in three ways: from the post-dive lactate levels collected in the isolated hole experiment, from behavioral dive data gathered by TDRs, and from calculations based on published estimates of TBO₂ stores and DMR.

**Physiological ADL:** The physiological ADL was determined from post-dive plasma lactate samples collected during the isolated hole experiments. The ADL duration was estimated using two different methodologies. First, the duration of the longest dive following which plasma lactate levels did not exceed the highest resting value was set as the classical lactate ADL, as defined by published methods (Kooyman et al. 1983, 1980). Alternatively, the ADL was estimated using line-fitting statistical procedures designed to detect physiological thresholds. In this process, the initial post-dive lactate level was regressed against dive duration using an iterative process that determined the two best fit linear regression lines which minimized the overall variance (Yeager and Ultsch 1989). Because the two lines were not constrained to share a joint point, the threshold value was taken as the dive duration intermediate between the last point of the first line and the
first point of the second line (Yeager and Ultsch 1989). This model was used to determine the
threshold value for the raw data, as well as for log-log and semi-log transformed data (Beaver et
al. 1985). In order to estimate the ADL of yearlings and adults statistically, post-dive plasma
lactate concentrations were determined by digitizing published figures (Kooyman et al. 1983,
1980).

The appropriateness of the two-line threshold model vs. a single line was assessed by comparing
the significance of the regression equations, the resultant $r^2$ values, and residual plots. In all
cases, two lines were judged to better fit the data than a single regression line. The threshold
value determined from these data sets is reported as the statistical estimate of the physiological
ADL.

Behavioral ADL: Behavioral ADLs were determined from the TDR records of all free ranging
pups and yearlings, as well as from the dive records of the three pups in the isolated hole
experiment. For each animal at each age, the dive duration that was exceeded by only 5% of the
dives was determined. The mean value for all seals in each age group was then termed the
behavioral ADL. The effect of mass, age, and sex on the behavioral ADL duration was assessed
using stepwise linear regression procedures (STATISTIX), with significance assumed at $p < 0.05$.

Calculated ADL: The calculated ADLs were determined as $ADL = \frac{TBO_2}{DMR}$. $TBO_2$ stores were
calculated based on mass specific values reported in the literature for blood volume, lung
oxygen stores, and muscle mass (Ponganis et al. 1993, Fujise et al. 1985, Kooyman and Sinnett
1982, Kooyman 1975, Kooyman et al. 1971, Lenfant et al. 1970), and data collected in this
project (Table 3.1). When possible, pup $TBO_2$ stores were estimated using values for subadult
rather than adult Weddell seals (Ponganis et al. 1993, Fujise et al. 1985). As the DMR of pups
has never been measured, it was approximated in these calculations by the RMR of four week
old Weddell seal pups of similar mass measured by Elsner et al. (1977).

The calculated ADL of yearlings and adults was determined using published estimates of their

Diving Metabolic Rates
We used our estimates of the ADL (classical, statistical, and behavioral) to back-calculate the
DMR of pups in this study according to the formula: $DMR = \frac{TBO_2\text{ stores}}{ADL}$. These estimates
were then compared to those from resting Weddell seal pups (Elsner et al. 1977) and to pups of
other species. All metabolic rates are presented as ml O₂/kg⁰.⁷⁵-min due to the large range in body mass (Kleiber 1961).

RESULTS

Isolated Hole Dive Experiment

The age, sex, mass, and dive data for the four pups used in isolated hole experiments are reported in Table 3.2. All pups were successfully anesthetized and catheterized, and dove normally once in the water. Pups were unable to exit the water due to the distance between the surface of the water and the floor of the laboratory (1 m). Dive bouts lasted from 26 to 167 min, followed by periods of rest and sleep in the water ranging from a few min to more than an hour. This pattern of bout diving is similar to that seen in TDR records from free ranging pup, juvenile, and adult Weddell seals (Castellini et al. 1992a). In comparison to free ranging pups of the same age, pups in the isolated hole made dives of similar mean duration, but shallower mean depth (Burns and Testa 1997).

Blood samples were collected at rest and following dives made by three pups. From those samples HCT, plasma lactate, and plasma glucose concentrations were determined. Changes with dive duration in post-dive lactate levels are shown in Figure 3.1, and post-dive HCT values in Figure 3.2. Plasma glucose levels did not change significantly as dive duration increased, and averaged 7.5 ± 0.4 mM for pup 75R, 8.2 ± 1.1 mM for 24R, and 7.2 ± 0.4 mM for 22R.

All three pups remained at the surface for extended periods after long dives which permitted multiple recovery blood samples to be drawn. During recovery from dives, HCT and plasma lactate levels declined steadily, while plasma glucose first increased and then decreased. Figure 3.3 illustrates an example of the pattern of changes in HCT, and plasma lactate and glucose concentrations seen during recovery after long dives. The long dives (> 8 min) in Figure 3.3 were made by pup 22R, and were characterized by an initial post-dive lactate level of greater than 3 mM, and HCT of 54 or higher. Plasma lactate, glucose, and HCT declined to resting values (approximately 1 mM, 7 mM, and 45%) over a 20 minute period. Recovery periods were shorter following shorter dives, or after dives with lower initial post-dive lactate and HCT levels. While neither pup 24R or 75R made dives as long as pup 22R, both showed similar recovery patterns following their longest dives.
ADL Determinations

Physiological ADL: The classical ADL for each pup was determined from the longest dive made in the isolated hole experiment following which plasma lactate levels were not elevated above the highest resting values (1.3 mM for pup 75R, 1.4 mM for 24R, and 1.3 mM for 22R). The ADL values were approximately 4 min for pups 75R and 24R (238 s and 252 s respectively), while 22R, the oldest pup, had a physiological ADL of approximately 5 min (280 s). The classic ADL for yearlings (10 min) and adults (22 min) was taken from the literature (Kooyman et al. 1983, 1980).

The ADLs estimated using the statistical method of regressing plasma lactate levels vs. dive time were similar to those determined by the classical method (Table 3.3). While the different data transformations produced slightly different ADL estimates, no one method was clearly the best. This is evident in Figure 3.4, which shows the physiological ADL determined by both classic and statistical methods for pup 22R. For all pups, the mean value of the statistical estimates differed from the classical estimate by less than one minute. For yearlings and adults, the mean statistical differed from the classical ADL by slightly more than a minute.

Behavioral ADL: The behavioral ADL, the dive duration which is only exceeded by 5% of dives (Kooyman et al. 1980), increased with age in both free ranging and experimental pups (Figure 3.5). The behavioral ADL determined for pups diving in the isolated hole was not significantly different from that of free ranging pups of the same age. The behavioral ADL of yearlings (14.8 ± 3.4 min) was determined from the free ranging dive behavior of yearlings in this study. The 26 min behavioral ADL of adults is an approximation from Kooyman et al. (1980).

To determine those factors responsible for the observed increase in the behavioral ADL of free ranging pups, the ADL was regressed against animal age and mass (52.5 to 134 kg). As mass was not significantly correlated with age (p = 0.47), these two factors were treated as independent. Across the entire range of age, 2 to 14 weeks, pup age accounted for approximately 57% of the variation in the behavioral ADL, while mass accounted for 4% (p < 0.05) (Figure 3.5). However, as pups aged, the relative impact of mass and age shifted. Age accounted for 45% of the variation in behavioral ADL of pre-weaned pups (age to 7 weeks) while mass was not significant. In weaned pups (older than 7 weeks), age accounted for 18% and mass for 32% of the variation in the behavioral ADL. In yearlings, mass accounted for 82% of the observed variation in the behavioral ADL (Figure 3.5). In all cases, larger and/or older seals had longer behavioral ADLs, and there was no difference by sex (p > 0.05).
Calculated ADL: The calculated ADL for pups decreased with increasing age (and decreasing mass), from 7.5 min in the pup 75R, to 7.3 min for 24R, to 7 min for the oldest pup 22R. The calculated ADL of pups was much lower than that of yearlings (9.3 ± 0.4 min) or adults (18 ± 1.0 min).

ADL Estimate Comparison: Table 3.4 clearly shows that the modeling methods used to estimate the ADL produce values that are not equivalent to the ADL determined from post-dive lactate levels in pups, yearlings, or adults. In pups, the ADL determined from post-dive lactate levels using both classical and statistical methods was shorter than the ADL estimated from behavioral data or calculated from TBO₂ stores and MRs. However, while both the physiological and behavioral ADL increased as the pups aged, the calculated ADL was longer for the fatter, younger pups.

While the magnitude of the differences between the ADL estimates will depend on the value accepted as 'real' it is important to note that for all animals (pups, yearlings, and adults) the behavioral ADL is markedly longer than that determined based on post dive lactate levels.

Diving Metabolic Rate Estimates
The DMR for pups estimated using their physiological and behavioral ADLs ranged from 25 to 59 ml O₂/kg⁰.⁷⁵ min, and, in general, decreased with age (Table 3.5). When compared to metabolic rates measured by respirometry for pups of other species, the values were 1 to 2 times higher than published rates, which ranged from a low of 10 to 20 ml O₂/kg⁰.⁷⁵ min for fasting northern elephant seal or harp seal pups swimming in a laboratory pool (Thorson and Le Boeuf 1994, Rea and Costa 1992, Worthy and Lavigne 1987) to a high of 25 ml O₂/kg⁰.⁷⁵ min for fasting ringed seal pups and nursing Weddell seal pups on land (Smith et al. 1991, Eisner et al. 1977).

The DMRs calculated for yearlings and adults from their ADL and TBO₂ stores were similar to those measured by respirometry.

DISCUSSION

Physiological Development
Several studies have shown that as pups age there are shifts in metabolic and physiological processes associated with increasing dive capacity. As northern elephant seals (Mirounga angustirostris) age, the duration of spontaneous apneas increase, while apneic heart rates and
metabolic rates decrease (Castellini et al. 1994, Thorson and Le Boeuf 1994, Rea and Costa 1992, Castellini et al. 1986). Older Weddell seal pups also appear to have greater cardiovascular control (pers. obs.). Along with an increased ability to regulate cardiorespiratory function, several studies have shown that older pups have lower resting and/or diving metabolic rates (Thorson and Le Boeuf 1994, Ponganis et al. 1993, Rea and Costa 1992, Elsner et al. 1977), and greater control over peripheral vasoconstriction (Cherepanova et al. 1993). In addition to declining rates of oxygen consumption, phocid post-weaning development is accompanied by the expansion of TBO$_2$ stores. Larger blood oxygen stores develop with age as a result of absolute increases in hemoglobin and HCT, as well as mass specific increases in blood volume (Rea 1995, Thorson and Le Boeuf 1994, Ponganis et al. 1993). Muscular stores of oxygen increase due to larger muscle mass and higher myoglobin content both in absolute and relative terms (Thorson and Le Boeuf 1994, Cherepanova et al. 1993, Lydersen and Hammill 1993a, Fujise et al. 1985). While changes in body composition and TBO$_2$ stores were not traced in this study, the measured post-dive lactate concentrations are an integration of both oxygen stores and utilization rates, and can be used as an indicator of physiological control.

The diving ability of Weddell seal pups, as measured by changes in average dive depth, duration, and frequency, has been shown to increase rapidly with age (Burns and Testa 1997). This study has indicated that the increase in dive ability with age is accompanied by an increase in the ability to regulate the metabolic processes associated with diving. In the two nursing pups (75R and 24R) almost all dives were followed by increased plasma lactate concentrations, and there was little evidence of HCT regulation. Dives of similar duration showed wide variation in measured HCT and plasma lactate values (see Figures 3.1 and 3.2), which suggests poor control of diving physiology and/or large variation in diving oxygen stores and MR. However, the one weaned pup (22R) showed much greater regulation of both plasma lactate and HCT during dives and recovery. The changes in plasma metabolites and HCT seen following dives in this pup were similar in pattern to those seen following dives and during recovery in adult and subadult seals (Zapol et al. 1989, Castellini et al. 1988, Qvist et al. 1986, Kooyman et al. 1980). Long dives resulted in maximal HCT levels and high plasma lactate concentrations. During recovery from presumably anaerobic dives, pup 22R rested at the surface as HCT and plasma lactate levels decreased. Following the longest dives, complete physiological recovery to resting plasma lactate and HCT values took approximately 20 min (see Figure 3.3), which is comparable to reported recovery times for adults (Zapol et al. 1989, Qvist et al. 1986). Similarly, for all pups and adults, shorter dives were followed by lower post-dive plasma lactate and HCT levels, and shorter recovery periods (Zapol 1989, Qvist et al. 1986, this study). These results suggest that
the period around weaning may mark a threshold point in the development by pups of physiological control mechanisms similar to those employed by adults.

**ADL Development**

The increase in dive capacity with age suggested by the blood metabolite data was also reflected by the changes in the ADL. While the scatter seen in post-dive lactate plots (Figure 3.1) made it difficult to precisely determine the physiological ADL for these young animals, classical and statistical methods produced estimates that differed by less than a minute. This indicates that there is little trouble identifying the inflection point in the lactate graphs. In addition, all methods suggested that the oldest pup had a longest ADL, and clearly identified the most important point: that all young pups have ADLs considerably shorter than juvenile or adult seals (Table 3.4). Moreover, the presence of statistically determinable threshold points for plasma lactate levels with respect to dive duration, supports the hypothesis that there is transition in the production or regulation of lactate during diving in pups similar to that in adults.

Changes in the behavioral ADL with pup age also indicated a rapid increase in dive ability. Prior to weaning, the behavioral ADL was most influenced by developmental stage (age), and mass, which influenced the behavioral ADL of older animals, had little impact. It was only after pups were weaned and foraging on their own that mass accounted for more than a third of the variation in the behavioral ADL. In young bearded (*Erignathus barbatus*), ringed (*Phoca hispida*) and elephant (*Mirounga angustirostris*) seals age also had a stronger impact on diving behavior than did mass (Lydersen and Hammill 1993b, Lydersen et al. 1994, Thorson and Le Boeuf 1994). The decrease in the calculated ADL with increased pup age results from the reliance on mass in the equations used to predict TBO₂ stores and DMR, and is believed to be inaccurate.

**Comparison of ADLs**

While the three methods of determining the ADL of Weddell seals did differ in their values, the estimates were within a few min of each other (see Table 3.4). Absolute and proportionate differences between the ADL estimates are not given, because the ‘true’ ADL is not a fixed number and was not unequivocally determined. However, while both the physiological and behavioral estimates suggested that age played an important role in determining the ADL, the calculated ADL, estimated in the absence of information about age specific body composition, TBO₂ stores, or DMR, was determined exclusively by mass. Differences between ADL’s in Table 3.4 indicate that both the duration of the estimated ADL, and the factors which influence it, can be affected by the method used, and suggests that an appropriate method for accurately
estimating the ADL in the absence of post dive lactate levels has yet to be determined. In the following discussion, the physiological ADL (without discriminating between the statistical or classical method) is accepted as the most accurate indicator of dive metabolism, and the modeling methods evaluated by comparison.

For pups, the physiological ADL was the lowest of the three estimates. One possible explanation for the longer behavioral ADL is that pups diving in the isolated hole had elevated MRs due to stresses associated with handling, or with being at a non-familiar site over deep water. Higher MRs would have lowered the physiological ADL for pups in the experimental setting relative to those diving in the wild. However, as the behavioral ADL of pups diving in the isolated hole was not significantly different from pups of the same age diving in the wild, it is more likely that the use of 95% as a cut-off point for determining the behavioral ADL is not applicable to young, rapidly developing animals, perhaps for ecological reasons.

In McMurdo Sound, all age classes of Weddell seals are thought to forage on similar prey species which occur predominantly at depths greater than 200 m (Burns and Testa 1997, Castellini et al. 1992a, Eastman 1985, Hubold and Ekau 1985). Travel time on a foraging dive to 350 m is approximately 6 min, which is probably longer than the physiological ADL of newly weaned pups. In the absence of shallow water prey, younger animals such as pups, or even yearlings, may be required to dive longer than their physiological ADL in order to maximize foraging efficiency (Fedak and Thompson 1993, Houston and Carbone 1992, Ydenberg and Clark 1989). As adult Weddell seals have physiological ADL of approximately 20 min (Kooyman et al. 1980), most foraging dives probably occur within the ADL, and 95% has been shown to be an appropriate delimiter for aerobic and anaerobic dives (Kooyman et al. 1983, 1980).

For pups, the ADL calculated from MR and TBO$_2$ stores was the highest of the three estimates (see Table 3.4). Inaccuracies in the calculated ADL probably result from difficulties in estimating both the TBO$_2$ stores and the DMR for young pups, two measures which vary with age and body composition. The modeled pup TBO$_2$ stores were derived from estimates of the separate component stores in Weddell seals of as close to the same age as the pups in this study as possible (see Table 3.1). However, mass specific TBO$_2$ stores are known to be lower relative to adult values, in northern elephant seal pups and yearling Weddell seals (Thorson and Le Boeuf 1994, Ponganis et al. 1993), and it is likely that our estimates of pup stores were high. It is also probable that the using the RMR to approximate the DMR of pups resulted in an underestimation of the DMR. Although DMRs are similar to RMRs in immature and adult Weddell seals (Castellini
et al. 1992b), pups do not appear to be as capable swimmers or divers (Burns and Testa 1997, Kooyman 1968, pers. obs.), and clearly do not have the physiological control of the older animals. In combination, the high TBO$_2$ stores and low DMRs produced calculated ADL estimates for pups that were too long and that decreased with age.

There were also differences between the physiological, behavioral, and calculated ADL estimates in yearling and adult Weddell seals. However, in contrast to the pups, the calculated ADL and physiological ADL were similar, and the behavioral ADL was the longest. The similarity between the calculated and physiological ADL is not surprising, as the DMR and many components of the TBO$_2$ stores were directly measured (Ponganis et al. 1993, Kooyman et al. 1983). However, the high behavioral ADLs relative to calculated values, especially in yearlings, suggests that even for older animals 95% may not always be an appropriate cut-off point. Long behavioral ADLs' (relative to calculated estimates of the ADL) have previously been noted in pregnant northern and southern elephant seals (Mirounga leonina) (Slip et al. 1994, Hindell et al. 1992, Le Boeuf et al. 1989, Le Boeuf et al. 1988) a period when adult physiology, MR, TBO$_2$ stores, and dive behavior are likely to be rapidly changing.

Overall, results suggest that differences between the ADL estimates are driven primarily by variations in activity patterns and/or TBO$_2$ stores and DMR that are themselves a result of age and/or physiological status. The long behavioral ADLs of both pups and yearlings suggest differences in dive patterns which may reflect foraging efficiency constraints, while the long calculated ADLs in rapidly developing pups reflect the difficulty of accurately estimating TBO$_2$ stores and DMR. As similar problems have been noted in other species (Slip et al. 1994, Hindell et al. 1992, Lydersen et al. 1992, Feldkamp et al. 1989, Le Boeuf et al. 1989, Le Boeuf et al. 1988), it is clear that care needs to be taken when the modeling methods are used to estimate the ADL or to interpret dive behavior.

**Diving Metabolic Rate Development**

When the DMR of Weddell seal pups was calculated based on estimates of pup TBO$_2$ stores and the ADL determined from post-dive lactate levels and behavioral data, the estimated values of 24 to 50 ml O$_2$/kg$^{0.75}$ min were only 2 to 4 times the BMR estimated using Kleiber's (1961) equation, and 1 to 2 times the resting value reported for young Weddell seal pups by Eisner et al. (1977). While these DMRs are higher relative to the RMR, than the DMRs measured for yearlings and adults (Ponganis et al. 1993, Castellini et al. 1992b), they indicate that even very young Weddell seal pups have a high level of physiological control. The decline in the estimated
DMR with age, from pre-weaned pup through yearlings to adults, probably reflects ongoing changes in physiological control, TBO$_2$ stores, and BMR associated with increases in age and body mass.

Unfortunately, it is impossible to compare the DMRs estimated for pups in this study to those of other species, for the DMR of pups in the wild has never been directly measured. The only approximation that exists is for ringed seal pups, but that estimate of 60 ml O$_2$/kg$^{0.75}$min, or 5.88 x BMR, was based on partitioning doubly-labeled water measurements of field metabolic rate according to the simultaneously measured time activity budget, and is highly speculative (Lydersen and Hammill 1993a). However, laboratory based estimates of diving metabolic rates for fasting northern elephant seal pups are only slightly lower, and show a similar decline with increasing age (Thorson and Le Boeuf 1994). The bracketing of our DMR estimates by the only others available for comparison, suggests that using the ADL and TBO$_2$ stores to estimate DMR can produce reasonable results.

CONCLUSIONS

This study has demonstrated that it is possible to estimate the ADL in young, developing pups from post-dive lactate levels. The isolated dive hole protocol was used successfully with pups as young as 5 weeks, and in all cases, pups dove naturally during the experiment and were soon returned to the colony. The blood samples and dive information collected make it clear that young pups are rapidly developing their diving skills and their physiological regulatory abilities, and this is reflected in the increase in the ADL with age. However, it is also evident that, regardless of the method used, the ADL of Weddell seal pups is still considerably shorter, and the DMR higher, than that of yearlings or adults. The comparison of the ADL determined from the post-dive lactate data to those estimated by modeling techniques reveals that, while the ADL estimates differed most in the youngest pups, they were not equivalent in yearling and adult Weddell seals either. Results suggest that the differences in the duration of the ADL and in the factors which influence it, are due to age- and/or condition- related variation in dive physiology and ecology. The demonstration that the three methods currently used to estimate the ADL of marine mammals are not interchangeable, emphasizes the need to carefully consider the modeling technique used when producing or interpreting ADL estimates for other species.
ACKNOWLEDGMENTS

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Table 3.1: Values used in the calculation of total body oxygen (TBO$_2$) stores for pup and yearling Weddell seals. Age categories are pup (P), yearling (Y), and adult (A).

<table>
<thead>
<tr>
<th>Oxygen Stores</th>
<th>Age</th>
<th>Content</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>In Muscle</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Body Mass</td>
<td>Y</td>
<td>30% muscle</td>
<td>Fujise et al. 1985</td>
</tr>
<tr>
<td>Mb Content</td>
<td>Y</td>
<td>4.4 g/100 g muscle</td>
<td>Ponganis et al. 1993</td>
</tr>
<tr>
<td>O$_2$ Content</td>
<td>A</td>
<td>1.34 ml O$_2$/g Mb</td>
<td>Kooymann and Sinnett 1982</td>
</tr>
<tr>
<td>TOTAL</td>
<td></td>
<td>17.1 ml O$_2$/kg</td>
<td></td>
</tr>
<tr>
<td><strong>In Lung</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diving Lung Volume</td>
<td>A</td>
<td>27.3 ml/kg</td>
<td>Kooymann et al. 1971</td>
</tr>
<tr>
<td>O$_2$ content</td>
<td>A</td>
<td>15%</td>
<td>Kooymann et al. 1971</td>
</tr>
<tr>
<td>TOTAL</td>
<td></td>
<td>4.1 ml O$_2$/kg</td>
<td></td>
</tr>
<tr>
<td><strong>In Blood</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plasma Volume</td>
<td>Y</td>
<td>7.8%</td>
<td>Ponganis et al. 1993</td>
</tr>
<tr>
<td>High HCT</td>
<td>P</td>
<td>58</td>
<td>This study</td>
</tr>
<tr>
<td>Blood Volume</td>
<td>P</td>
<td>18.5%</td>
<td>This study</td>
</tr>
<tr>
<td>Hb Content</td>
<td>Y</td>
<td>17.1 g Hb/100 ml blood</td>
<td>Ponganis et al. 1993</td>
</tr>
<tr>
<td>O$_2$ Content</td>
<td>A</td>
<td>1.34 ml O$_2$/g Hb</td>
<td>Kooymann and Sinnet 1982</td>
</tr>
<tr>
<td>Blood Distribution</td>
<td>A</td>
<td>33% Arterial, 66%</td>
<td>Kooymann 1975</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Venous</td>
<td></td>
</tr>
<tr>
<td>Arterial Saturation</td>
<td>A</td>
<td>95 to 20% Saturation</td>
<td>Kooymann 1975, Lenfant et al. 1970</td>
</tr>
<tr>
<td>Veinous Saturation</td>
<td>A</td>
<td>Arterial Content - 5%</td>
<td>Kooymann 1975</td>
</tr>
<tr>
<td>TOTAL</td>
<td></td>
<td>33.2 ml O$_2$/kg</td>
<td></td>
</tr>
<tr>
<td><strong>Total TBO$_2$ Stores</strong></td>
<td></td>
<td>55 ml O$_2$/kg</td>
<td></td>
</tr>
</tbody>
</table>

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Table 3.2: The age, sex, mass, sampling, and summary dive data for the four Weddell seal pups used in the isolated hole dive experiment in McMurdo Sound, Antarctica. Mean ± standard deviation and (maximum) values are shown for dive depth and duration.

<table>
<thead>
<tr>
<th>Pup</th>
<th>Age (days)</th>
<th>Sex</th>
<th>Mass (kg)</th>
<th># of blood samples</th>
<th># of dives</th>
<th>Mean Dive Depth (m)</th>
<th>Mean Dive Duration (min)</th>
</tr>
</thead>
<tbody>
<tr>
<td>21R</td>
<td>37</td>
<td>F</td>
<td>106</td>
<td>none</td>
<td>111</td>
<td>11 ± 10 (60)</td>
<td>1.8 ± 1.0 (4.3)</td>
</tr>
<tr>
<td>75R</td>
<td>41</td>
<td>F</td>
<td>137</td>
<td>25</td>
<td>95</td>
<td>14 ± 15 (24)</td>
<td>2.2 ± 1.3 (5.7)</td>
</tr>
<tr>
<td>24R</td>
<td>46</td>
<td>M</td>
<td>124</td>
<td>50</td>
<td>124</td>
<td>35 ± 33 (123)</td>
<td>2.3 ± 1.7 (7.4)</td>
</tr>
<tr>
<td>22R</td>
<td>50</td>
<td>F</td>
<td>107</td>
<td>55</td>
<td>126</td>
<td>14 ± 15 (74)</td>
<td>2.5 ± 2.3 (11.0)</td>
</tr>
</tbody>
</table>

Table 3.3: The ADL (min) determined from post dive lactate levels using the classical and statistical methods. The ADL estimated statistically is the midpoint between the two best-fit linear regression lines used (Yeager and Ultsch 1989). Values for yearlings from Kooyman et al. (1983) and for adults from Kooyman et al. (1980).

<table>
<thead>
<tr>
<th>Seal</th>
<th>Mass (kg)</th>
<th>Classic Lactate ADL</th>
<th>Statistical ADL lactate vs. dive duration</th>
<th>Statistical ADL lactate vs. log(dive duration)</th>
<th>Statistical ADL log(lactate) vs. log(dive duration)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P75R</td>
<td>137</td>
<td>4</td>
<td>4.6</td>
<td>4.6</td>
<td>3.5</td>
</tr>
<tr>
<td>P24R</td>
<td>124</td>
<td>4.2</td>
<td>4.1</td>
<td>4.1</td>
<td>3.1</td>
</tr>
<tr>
<td>P22R</td>
<td>107</td>
<td>5</td>
<td>6.4</td>
<td>6.4</td>
<td>5.2</td>
</tr>
<tr>
<td>Yearlings</td>
<td>135</td>
<td>10</td>
<td>10.2</td>
<td>10.2</td>
<td>6.2</td>
</tr>
<tr>
<td>Adults</td>
<td>355 ± 59</td>
<td>22</td>
<td>25.7</td>
<td>25.7</td>
<td>19.8</td>
</tr>
</tbody>
</table>
Table 3.4: A comparison of the ADLs (min) determined for the Weddell seal pups in the isolated hole experiment. ADLs determined from post dive lactate levels (classic method and statistical regression analysis of lactate vs. dive duration), behavioral dive data, and calculations using TBO$_2$ stores and MR. All values are mean ± standard deviation. Data for yearlings and adults are from this study, *Kooyman et al. (1980), †Kooyman et al. (1983), and ‡Ponganis et al. (1993).

<table>
<thead>
<tr>
<th>Seal</th>
<th>Mass (kg)</th>
<th>Classic Lactate ADL</th>
<th>Mean Statistical Lactate ADL</th>
<th>Behavioral ADL</th>
<th>Calculated ADL</th>
</tr>
</thead>
<tbody>
<tr>
<td>P75R</td>
<td>137</td>
<td>4</td>
<td>4.3 ± 0.7</td>
<td>4.1</td>
<td>7.5</td>
</tr>
<tr>
<td>P24R</td>
<td>124</td>
<td>4.2</td>
<td>3.8 ± 0.6</td>
<td>5.2</td>
<td>7.3</td>
</tr>
<tr>
<td>P22R</td>
<td>107</td>
<td>5</td>
<td>6.0 ± 0.7</td>
<td>7.3</td>
<td>7</td>
</tr>
<tr>
<td>Yearlings</td>
<td>132 ± 23</td>
<td>10†</td>
<td>8.9 ± 2.3</td>
<td>14.8 ± 3.4</td>
<td>9.3 ± 0.4</td>
</tr>
<tr>
<td>Adults</td>
<td>355 ± 59*</td>
<td>22*</td>
<td>23.7 ± 3.4*</td>
<td>26*</td>
<td>18.0 ± 1.0‡</td>
</tr>
</tbody>
</table>

Table 3.5: DMRs (ml O$_2$/kg$^{0.75}$ min) estimated from TBO$_2$ stores and the ADL determined from post dive lactate levels, behavioral dive data, and balance equations. For comparison, the DMR and RMR measured by respirometry by Elsner et al. 1977 (pups), Ponganis et al. 1993 (yearlings), and Castellini et al. 1992b (adults), are shown in the last column.

<table>
<thead>
<tr>
<th>Seal</th>
<th>Mass (kg)</th>
<th>TBO$_2$ stores (ml O$_2$)</th>
<th>Classic Lactate DMR</th>
<th>Statistical Lactate DMR</th>
<th>Behavioral DMR</th>
<th>DMR (♂) or RMR (♀) measured by Respirometry</th>
</tr>
</thead>
<tbody>
<tr>
<td>P75R</td>
<td>137</td>
<td>7535</td>
<td>47</td>
<td>45 ± 7</td>
<td>40</td>
<td>25 (♂)</td>
</tr>
<tr>
<td>P24R</td>
<td>124</td>
<td>6820</td>
<td>44</td>
<td>50 ± 8</td>
<td>35</td>
<td>25 (♂)</td>
</tr>
<tr>
<td>P22R</td>
<td>107</td>
<td>5885</td>
<td>35</td>
<td>30 ± 4</td>
<td>24</td>
<td>25 (♂)</td>
</tr>
<tr>
<td>Yearlings</td>
<td>132 ± 23</td>
<td>7260</td>
<td>19</td>
<td>22 ± 7</td>
<td>13</td>
<td>14 to 25 (♂)</td>
</tr>
<tr>
<td>Adults</td>
<td>355 ± 59*</td>
<td>30609</td>
<td>17</td>
<td>16 ± 2</td>
<td>14</td>
<td>15 to 22 (♂)</td>
</tr>
</tbody>
</table>

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Figure 3.1: Post-dive plasma lactate concentrations for three Weddell seal pups in the isolated hole dive experiment in McMurdo Sound, Antarctica.
Figure 3.2: Post-dive hematocrit levels following dives made by the three Weddell seal pups in the isolated hole dive experiment in McMurdo Sound, Antarctica.
Figure 3.3: Changes in plasma lactate (a) and glucose (b) concentration, and hematocrit (c), during recovery at the surface following several dives longer than the measured aerobic dive limit. Dives were made by pup 22R.

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Figure 3.4: The ADL determined from post dive plasma lactate levels in pup 22R using classical and statistical methods.  
(a) The ADL determined by the classical method. The solid line is the highest resting plasma lactate value.  
(b) Statistical ADL, plasma lactate vs. dive duration;  
(c) Statistical ADL, plasma lactate vs. log(dive duration);  
and (d) Statistical ADL, log(plasma lactate) vs. log(dive duration). On all plots the dashed line indicates the ADL.  
The solid lines on (b), (c), and (d) are the best fit linear regression lines. The statistical ADL was taken as the midpoint between the two lines.
Figure 3.5: The effect of age (a) and mass (b) on the behavioral ADL of pups and yearlings. (a) The increase in the behavioral ADL with age determined from 38 free ranging pups, the 3 experimental pups, and 15 yearlings Weddell seals diving in McMurdo Sound. Mean and standard deviation shown for free ranging data; (b) The relationship between the behavioral ADL and mass in yearlings and the three experimental pups.
LITERATURE CITED


Chapter 4: Dive data from satellite tags and time depth recorders: a comparison in Weddell seal pups

ABSTRACT

The diving behavior of juvenile Weddell seals was monitored simultaneously with time depth recorders (TDRs) and satellite-linked time depth recorders (SLTDRs). Recovered TDRs provided a complete record of the depth and duration of all dives made during the entire deployment. Data collected by SLTDR tags was compressed into the number of dives in each of six depth or duration bins, and relayed via the Argos system. The dive information from the two tags were compared in order to determine data compression, processing, and transmission gaps influenced the types and quantity of data received.

Approximately half of the dive data collected by TDRs was also received from the SLTDR tags. However, the number of dives in each depth and duration bin was an accurate representation of the actual dive behavior, and the chance of receiving SLTDR data was not dependent on when the diving occurred, when the data was transmitted, or the subsequent dive activity of the pups. As a result, SLTDR tags were judged to provide data qualitatively similar to that provided by TDRs.

The accuracy of seal locations provided by Service Argos was assessed in comparison to GPS locations. LC0 positions had an average error of 11 km, and LC1 positions had an error of 5 km. These errors are significantly greater than predicted by Service Argos or found in other studies.

INTRODUCTION

The study of marine mammal diving behavior has benefited greatly from the development of time depth recorders (TDRs) and satellite-linked time depth recorders (SLTDRs). Both of these computerized devices can collect and store in memory, behavioral and environmental data such as dive depth, duration, swim speed, and water temperature (Costa 1993, Hill 1993a,b). The two main differences between TDRs and SLTDRs are the way in which data are processed and retrieved. To obtain data stored in TDR memory, the tag itself must be retrieved from the animal on which it was deployed (Hill 1993b), while SLTDRs never need to be recovered because they transmit the collected data to overhead satellites (the Argos system). Service Argos then forwards these data to the scientist (Service Argos 1996, Hill 1993a). There are advantages and disadvantages to each system, but in general TDRs are deployed on marine mammals when there is a good chance that the tagged animal can be recaptured, and SLTDRs are used when the probability of recapture is low (Costa 1993). As a result, species (or season) specific information on dive behavior tends to come from only one type of tag. Dive data collected by these two tags have never been directly compared for animals diving in the wild.

The comparison of dive data from the two types of tags is of interest due to the different ways in which each tag processes the data it collects. TDRs record data (depth, temperature, light levels, swim speed, etc.) at preset time intervals and all subsequent data processing is performed by the researcher after the tag is recovered and the data downloaded (Hill 1993b). The amount of data collected (and recovered) is determined solely by the computer memory in the tag (although in older versions of mechanical TDRs, data storage was limited by film capacity) (Kooyman 1965,1968, Kooyman et al. 1983). SLTDRs collect, process, and compress data prior to transmission to the satellite. The specific nature of the data transmitted depends on the manufacturer and model of tag, but all designs summarize the data to compensate for a transmission bottleneck (Frost et al. 1995, Martin et al. 1994, Merrick et al. 1994, Testa 1994, Hill 1993a, Martin and Smith 1992). The bottleneck exists for three reasons: Service Argos constrains message length so that satellites are not overwhelmed with data; reception time is limited by the overhead pass schedule of the satellite; and animal behavior impacts transmission success because data can only be received by Argos if the antenna is out of the water long enough for a complete message to be transmitted (Service Argos 1996, Priede and French 1991, Hamis et al 1990, Fancy et al. 1988). Even though SLTDRs are designed to maximize data throughput by repeatedly transmitting short data messages, received data sets are often incomplete due to gaps created by the pass schedule of the satellite and the activity of the
tagged animal. How data compression, processing, and gaps influence the types and quantity of data received has rarely been analyzed for animals diving in the wild, in part because there has never previously been sufficient data available for comparison (Stewart et al. 1989).

This paper compares dive data collected from TDRs (Wildlife Computers mark 5 or 6) and SLTDRs (Wildlife Computers version 3.x) deployed simultaneously on young Weddell seal (Leptonychotes weddellii) pups in McMurdo Sound, Antarctica. In addition, the accuracy of animal positions estimated by Argos is assessed by comparing to locations determined for the tagged seal pups using a Global Positioning System (GPS) receiver. This is the first time that data recovered from SLTDRs deployed on marine mammals has been verified by direct comparison to data collected by any other method. As such, it offers insight on how best to interpret data obtained from this widely used method of collecting behavioral data from marine mammals.

METHODS

Animal Handling

In the austral summer of 1993-1994, 11 Weddell seal pups (five females, six males) were outfitted with both SLTDRs and TDRs. Pup age at the time the SLTDR was first attached ranged from six to 13 weeks. The SLTDRs were attached to the fur with epoxy glue (Devcon 5-minute marine epoxy), and were designed to be carried by the animal for the next nine months. TDRs were attached to a mounting bracket and carried for a few days every other week (Burns and Testa 1997). Most pups carried TDRs more than once after being fitted with a SLTDR. In addition to these animals, 15 other Weddell seal pups were outfitted only with SLTDR tags between January 1993 and December 1994. The information from the SLTDR tags deployed on these seal pups was only used in the determination of SLTDR location accuracy.

Dive Data

The SLTDR tags deployed on all Weddell seal pups transmitted the number of dives in each of six depth and duration ‘bins’ for each of four, six-hour periods of the day. The minimum depth for a dive was 12m, and depth bins were set as follows: 12-80 m, 81-160 m, 161-240 m, 241-320 m, 321-400 m, and greater than 400 m. Five duration bins each had a range of four minutes, and the sixth bin recorded all dives of longer than 20 minutes. Time of day was divided into four periods: 21:00-02:59, 03:00-08:59, 09:00-14:59, and 15:00-20:59. The SLTDRs were set to transmit all data in the memory buffer whenever the animal was at the surface, unless the tag temperature was below -20° C, or the local time was between 11:00-13:00, because few satellite
over passes were scheduled between these hours. The summarized depth and duration data for each of the previous four periods was stored in a buffer for 24 hours, during which time all data were transmitted as often as possible. When the SLTDR finished collecting data for the current period, the oldest period in the buffer was discarded, and the recently collected data added. Therefore, collected data had 24 hours to be transmitted before being lost. The SLTDR status, on ice (land) or at sea, was also included in each transmission, and seal position was determined by the Argos system provided that message reception met criteria set by Service Argos (1996).

Dive data were also recovered from the TDRs deployed on the pups that were outfitted with both SLTDRs and TDRs. Unlike the SLTDRs, the TDRs did not process or compress any dive data. To recover the dive data, TDRs were retrieved and the memory decoded with programs provided by Wildlife Computers (Zoc.exe and Da.exe). This allowed the depth and duration of all dives to be determined. The TDR data were transformed into SLTDR data format by assigning the depth and duration of each dive to the appropriate bin, and summing the number of dives in each bin for each period of the day. The transformed TDR data was then matched to the SLTDR data by individual, date and period. The difference between the two data sets in the total number of dives, and the number of dives in each depth and duration bin was determined. Paired t-tests were run to determine if the mean difference varied significantly from zero. These data sets were considered similar if \( p > 0.05 \). In addition, paired t-tests and ANOVA were used to determine if the difference in the total number of dives was effected by seal age, tag status (on ice or at sea), period of day, or individual seal.

The mean depth and duration of dives in each bin were determined from the TDR data for each period and seal age, and then compared to the midpoint depth and duration value for each bin. Because the SLTDRs separated dive depth and duration records, the analysis of differences between the SLTDR and TDR records were performed independently on the two types of records. T-tests were used to determine if the mean value was significantly different from the bin midpoint. In addition, differences in the mean depth or duration of dives within each bin as a result of changes in animal age or period of day were tested for using linear regression (age) and ANOVA techniques. Significance was assumed if \( p < 0.05 \).

**Data Reception**

In order to determine if biases were associated with when SLTDR data were received by the Argos system, we used a series of chi-squared tests to model the probability of receiving data given the time of dive activity, the amount of subsequent dive activity, and the location of the
animal (on ice or at sea). Chi-square tests for heterogeneity were first used to compare the period when data were collected with whether it was received, and then to compare the collection and reception periods. Chi-squared tests were also used to determine if dive activity in the subsequent four periods, those when the SLTDR would be attempting to transmit the data, affected the chance that the SLTDR data were received. To do this, the number of dives in each of the subsequent four periods was determined from the TDR records, and the number of periods in which no diving occurred tallied (0, 1, 2, 3, or 4). Then two sets of chi-square tests were run: the first determined if the presence of one or more periods without dives increased the probability of Argos reception, and a second determined if one or more periods of low dive frequency (n < 6 dives/period) increased the probability of Argos reception. Finally, the effect of transmitter location (on ice or at sea) on the number of messages received in each period was tested using chi-square analysis. In all cases heterogeneity was assumed if p < 0.05.

Location Accuracy

During the austral summers of 1992, 1993 and 1994, all SLTDR tagged seals (n = 26) were repeatedly located during visual surveys, and when found, their position determined using a hand-held GPS unit (Magellan Systems NavPro 5000), with a horizontal accuracy (95%) of 100 m (Magellan Systems, product support literature). Argos positions were compared to GPS positions that were determined within 24 hours of the Argos position fix. Only those Argos positions that were possible, given the topography, animal age, and sighting history were used. We did not use alternative methods of discriminating between 'good' and 'bad' locations, such as the Keating error index (Keating 1994), or iterative processes that eliminated locations based on animal speed (Frost et al. 1995, Frost and Lowry 1994) because we were interested in specific locations. The diagonal distances between the Argos and GPS positions were determined, as were the differences between the two latitudes and longitudes.

Two-sample t-tests were used to determine if position error differed by location class (LC: an index of location quality reported by Argos, Service Argos 1996) and if the latitudinal error was greater than the longitudinal error. Significance was assessed at p < 0.05. LC1 positions meet the minimum standards of Service Argos for position determination, and have an predicted accuracy of 1 km. Locations with class codes of two or three are calculated only if more than five messages are received by the satellite during a pass, meet strict Service Argos quality standards, and have a predicted accuracy of less than 500 m. LC codes of less than one do not meet quality control standards set by Service Argos, require special processing before tag position can be estimates, and were grouped into the LC0 class for analysis.
RESULTS

Tagging Success
Both SLTDRs and TDRs were carried by 11 pups during the summer of 1993-94. Because many pups carried TDRs more than once, there were 20 instances when both types of tags were carried simultaneously. However, complete failure of SLTDR tags on two pups (both females) reduced the total to 16 periods of duplicate coverage (Table 4.1), resulting in 222 cases of duplicate depth records and 230 cases of duplicate duration records from nine individuals aged between five and 13 weeks. During this same period there were 203 cases when depth records, and 190 cases where duration records were not received by the Argos system (48%, and 45% respectively).

Dive Data
There were no significant differences between the SLTDR and TDR records in the mean number of dives in each depth bin, or for the total number of dives when all depth bins were combined. However, there were significantly more dives total in the duration record from SLTDRs as compared to the TDR record. This difference was due to a larger number of dives in the first duration bin from the SLTDR record, even though differences in the number of dives as determined by the TDRs and SLTDRs in duration bins two through six were not significant (Table 4.2). While the mean difference in the number of dives determined by the two methods was always less than four dives, the absolute difference in counts varied by as much as 70 dives (Table 4.2). Seal age, collection period, reception period, individual animal, and tag status (ice/sea) did not affect the mean difference in the counts.

The mean dive depth and duration for each bin as determined from the original TDR records was significantly different from the midpoint value for almost all bins (t-test, \( p < 0.05 \)), but in no case was the difference large (Table 4.3). Age or period had no significant effect on the mean depth or duration determined for any bin.

Data Reception
Argos data were received for roughly half of the periods for which there should have been both SLTDR and TDR coverage (52% of depth records, and 55% of duration records received). The chance of receiving Argos data for a period was independent of the period in which diving occurred \( (\chi^2 = 3.29, p = 0.35, \text{Table 4.4}) \), and was also independent of the amount of diving activity which occurred in the 24 hour period after the dive data were collected \( (\chi^2 = 4.36, \text{Table 4.4}) \).
This was true if dive activity in the subsequent four periods was coded high (dives in all four subsequent periods) or low (no dives in at least one of the subsequent periods) ($\chi^2 = 1.0, p = 0.32$). Increasing the low dive cutoff from zero dives/period to 5 dives/period did not change the outcome ($\chi^2 = 0.21, p = 0.65$). While the probability of receiving information from SLTDRs on ice vs. at sea could not be tested because status information was only available if the SLTDR data were received, 78% of the received data came from animals on land, despite the fact that diving occurred in 79% of all periods. At sea transmissions occurred most frequently during periods 2 and 3 (afternoon and evening), while on land transmissions occurred more often during periods 0 and 1 (night and morning, $\chi^2 = 43.42, p < 0.00$).

Although the chance of receiving dive data was independent of when the data were collected, the period in which the data were first received by the Argos system was highly dependent on the period in which the data were collected ($\chi^2 = 21.83, p = 0.01$). In general, the probability of receiving dive data (given that it was received) was higher than expected in the period immediately following the period in which diving occurred, and slightly lower than expected in the period 24 hours after collection. The least number of dives were first received in the afternoon period, probably because transmissions were only attempted in four of the six hours.

**Location Accuracy**

Over three years, 56 positions were determined by Argos and GPS methods within 24 hours of each other. Eighteen different seals were located between one and 15 times by both methods. All duplicate sightings occurred between 29 November and 2 February. There were an average of $1.8 \pm 0.1$ days between Argos position fixes and an average of $2.1 \pm 0.1$ locations/day on those days that locations were received. All the Argos position fixes came from tags on ice and were of location class (LC) 0 or 1, no quality 2 or 3 positions were received. The straight line, latitudinal and longitudinal distances between the Argos and GPS locations were significantly larger for LC0 positions (8.8, 5.5, and 11.3 km respectively), than for LC1 positions (4.1, 2.4 and 5.0 km) (Table 4.6). Within each location class, the error in latitude was slightly greater than the error in longitude, but the differences were not significant (LC0 $p = 0.06$, LC1 $p = 0.11$).
mean dive depth and duration within each bin did not differ by time of day or seal age; 3) the chance of receiving dive data was independent of when diving occurred; and 4) the chance of receiving data was not affected by subsequent dive behavior.

In general, the mean difference between the number of dives within each depth and duration bin was not significantly different from zero, and the few times that the difference was significant can be attributed to the manner in which SLTDRs and TDRs determined dive start and end points. The SLTDRs started timing dives when the depth reading from the pressure transducer was greater than the minimum dive depth (12 m) and the tag was wet, and stopped timing dives when the pressure transducer read less than 12 m or the tag was dry. The TDRs assigned dive start and stop points when the pressure transducer read depths greater (or less than) the resolution of the TDR (2-3 m) (Hill 1993a,b). Dives less than the minimum depth were only secondarily removed from the TDR record. As a result of these procedural differences, the largest discrepancies in dive numbers should be seen in the shortest and shallowest bins, as was the case. The significant difference between the total number of dives recorded by TDR and SLTDR based on dive duration was due entirely to the difference in the number of dives of less than four minutes long. These methodological differences also explain why the magnitude of the difference decreased as dive depth and duration increased (see Table 4.2).

Before extrapolating this study's findings, it is important to note that in this study the minimum depth for a dive to be considered was fairly large (12 m), the sampling frequency high (10 s), and the dives made by the seals relatively long and deep (mean depth 94 ± 0.9 m, mean duration 5.20 ± 0.03 min). Together, these factors reduce the magnitude of the error introduced by the different methods used. It is likely that differences between the number of dives determined by SLTDR and TDR will change based on tag settings and animal behavior. Larger differences would be expected for species that make many dives close to the depth resolution of the TDR or the minimum depth setting of the SLTDR, because the difference in calculated dive start and stop times would probably be exaggerated. This will also be the case if dives are short and/or the sampling interval long.

Similarly, although we found no change with seal age or period in the mean dive depth or duration for each of the bins, this may not hold for all species or in all seasons. For the seals in this study, neither age nor time of day were expected to have a significant effect on mean dive depth or duration because the age range was small (five to 13 weeks), and the light levels in the study area were relatively constant during the study (Burns and Testa 1997, Castellini et al.)

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1992). In studies where the age range is greater, or in places and seasons where diurnal rhythms are expected to be more influential, the mean depth and duration of dives would be expected to differ (Merrick et al. 1994, Testa 1994, Thorson and LeBoeuf 1994, Thompson et al. 1989). In these cases, the choice of bin ranges will significantly impact how and if these changes are detected. Even in this study, the midpoint of the bin range was different from the mean depth and duration for dives within the bin, as determined from TDR records.

The amount of dive data that we received from the SLTDR was much lower than expected given the number of satellite passes and the behavior of the seals. McMurdo Sound, Antarctica, has one of the highest levels of Argos coverage: 28 satellite passes and greater than six hours of coverage a day versus seven passes and fewer than two hours in the equatorial regions (Service Argos 1996, Harris et al. 1990). Given that the tags were set to transmit 22 of 24 hours a day and the young pups in this study spent a considerable amount of time resting on the ice, we were surprised to receive data only half of the time. This proportion of coverage is much less than that found for adult Weddell seals, and many other species of marine mammals, even in areas where satellite coverage is less complete (Frost et al. 1995, Merrick et al. 1994, Testa 1994, McConnell et al. 1992, Stewart et al. 1989). It is possible that signals were blocked by close proximity between animals or deformed by the nearness of the transmitters to the ice, but at this time we have no definitive explanation for why signal reception on pups was so poor.

Despite problems with data reception, perhaps the most encouraging results of this study were that the chance of receiving dive data from the SLTDR tags was not affected by when the dive activity occurred (period of day) or the amount of dive activity in the subsequent 24 hour period. If increased dive activity had reduced the chance of receiving SLTDR data, not only would the SLTDR record be biased, but determining the direction of bias would have been difficult. This is because the pattern of variation in dive activity would determine if data from only periods with low or high dive frequencies were received. As there was no bias in when and if data were received, the dive data received was judged to be an accurate representation of all the diving activity that occurred.

The finding that the period in which dive data were first received was not independent of when the data were collected is more likely a reflection of the relatively high transmission frequency rather than an indication of bias. Because SLTDRs send out the oldest data first, 'new' data can only be received after six other messages (one depth and one duration message from each of the older three periods) are sent (Hill 1993a). Thus, receiving a greater than expected proportion
of 'new' data in the first possible period after the diving occurred indicates that the tag was dry long enough to transmit all the data. Not surprisingly, we received most messages received from dry tags (78%). However, given the observed pattern of message reception, it is hard to explain why it was rare to receive data from four periods in a row (44 of 379 possible times, 12%).

The comparison of seal locations reported by Argos with those determined by GPS revealed that the position errors associated with Argos locations were much greater than those predicted (Service Argos 1996). Service Argos predicts that 68% of all LC1 fixes fall within 1.0 km of the true location, but in this study the mean diagonal error was 5 km and 68% of LC1 positions were within 5.4 km of the GPS location. Although Service Argos does not estimate errors for LC0 locations, in this study LC0 locations had a mean error of 11 km and 68% were inside 20.25 km. Not only were the errors found in this trial some of the largest reported for field trials of this system (McConnell et al. 1992, Bom and Knutsen 1992, Stewart 1990, Stewart et al. 1989), they also differ from other studies in the direction of the error. While many previous studies have found longitudinal error to be significantly greater than latitudinal error (see Harris et al. 1990), we found the opposite, perhaps because of the high latitude at which this study was conducted.

It is possible that the magnitude of the position errors calculated here were compounded by the error associated with the GPS fixes and the 24 hour time window. However, it is unlikely that these factors were significant contributors to the overall error. The GPS system is extremely accurate (95% of reported locations are within 100 m of the true location; Magellan Systems product support literature, Tomkiewicz 1996), and seal pups during the study tended to show a high degree of site fidelity with few long distance movements (Bums and Testa 1997). More likely, the magnitude of the error was due to some of the same factors which reduced transmission frequency: low angle of satellite passes, temperature induced fluctuations in transmission frequency, and attenuation of the SLTDR signal due to the proximity of the transmitter to the ice and seal. Location accuracy also could have been negatively affected by the low number of messages received (1-2 per day) and the long time between messages (1-2 day gaps) (McConnell et al. 1992, Harris et al. 1990, Stewart et al. 1989).

Together these findings suggest that marine mammal positions determined by Argos need to be carefully screened for accuracy, and even then, interpreted carefully. This is especially true when correlations are being made between animal locations and oceanographic or terrestrial habitat data (Frost et al. 1995, Costa 1993, McConnell et al. 1992, Stewart et al. 1989). From this study it does not appear that Argos positions are accurate enough to permit discrimination between
foraging or haulout areas that are within 5-10 km of each other, at least in the polar regions. However, even the 10 km error associated with LCO locations is better than that predicted for locations determined by geolocation with light levels (Hill 1995, Delong et al. 1992). Certainly, a significant amount of information on animal habitat choice and migration patterns can be gathered using the locations provided by Argos.

Overall, the results of this study suggest that the dive data collected by TDRs and SLTDRs can be directly compared, provided that consideration is given to how the two types of tags were programmed, the overhead pass schedule of the satellites, and the behavior of the animals under study.

ACKNOWLEDGMENTS

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Table 4.1: The dates and ages of those seals that carried both SLTDRs and TDRs during the 1993-94 austral summer. The SLTDRs on seals 10691 and 10768 failed upon deployment.

<table>
<thead>
<tr>
<th>Seal ID</th>
<th>Overlap Dates</th>
<th>Seal Age (weeks)</th>
</tr>
</thead>
<tbody>
<tr>
<td>10691</td>
<td>12/28-1/2, 1/5-1/7</td>
<td>9, 10</td>
</tr>
<tr>
<td>10768</td>
<td>12/26-12/29, 1/2-1/7</td>
<td>8, 9</td>
</tr>
<tr>
<td>10475</td>
<td>12/14-12/17, 12/30- 1/3</td>
<td>8, 10-11</td>
</tr>
<tr>
<td>10531</td>
<td>12/12-12/29, 12/30-1/5</td>
<td>7-8, 10</td>
</tr>
<tr>
<td>10549</td>
<td>12/5-12/9, 12/19-12/28</td>
<td>6, 8-9</td>
</tr>
<tr>
<td>10717</td>
<td>12/6-12/9</td>
<td>5</td>
</tr>
<tr>
<td>10533</td>
<td>12/26-12/29, 1/22-1/24</td>
<td>9, 13</td>
</tr>
<tr>
<td>10481</td>
<td>11/30-12/3</td>
<td>6</td>
</tr>
<tr>
<td>10718</td>
<td>12/13-12/17, 12/28-12/30</td>
<td>7, 9</td>
</tr>
<tr>
<td>10869</td>
<td>12/14-12/17, 12/28 -1/2</td>
<td>5, 7</td>
</tr>
<tr>
<td>10767</td>
<td>12/14-12/27, 1/15-2/4</td>
<td>6-7, 10-13</td>
</tr>
</tbody>
</table>

Table 4.2: The difference in the number of dives as recorded by TDRs vs. SLTDRs. The mean ± SE and range of the difference is determined for each bin (80 m or 4 min increments) and for the total number of dives. Significant differences (* p < 0.05) were only present in the first duration bin, and in the total number of dives for duration records.

<table>
<thead>
<tr>
<th>Bin</th>
<th>Depth Histograms</th>
<th>Range</th>
<th>Duration Histograms</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean Difference</td>
<td></td>
<td>Mean Difference</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>-1.30 ± 0.76</td>
<td>-58 to 59</td>
<td>-3.69 ± 0.69*</td>
<td>-61 to 36</td>
</tr>
<tr>
<td>2</td>
<td>0.32 ± 0.38</td>
<td>-20 to 34</td>
<td>0.45 ± 0.45</td>
<td>-25 to 28</td>
</tr>
<tr>
<td>3</td>
<td>-0.16 ± 0.49</td>
<td>-13 to 18</td>
<td>0.55 ± 0.49</td>
<td>-21 to 19</td>
</tr>
<tr>
<td>4</td>
<td>-0.08 ± 0.24</td>
<td>-13 to 6</td>
<td>0.03 ± 0.07</td>
<td>-5 to 3</td>
</tr>
<tr>
<td>5</td>
<td>-0.29 ± 0.29</td>
<td>-18 to 5</td>
<td>0.01 ± 0.01</td>
<td>0 to 1</td>
</tr>
<tr>
<td>6</td>
<td>-0.07 ± 0.12</td>
<td>-10 to 2</td>
<td>0.32 ± 0.06</td>
<td>0 to 2</td>
</tr>
<tr>
<td>Total</td>
<td>-0.77 ± 0.87</td>
<td>-50 to 70</td>
<td>-2.28 ± 0.89*</td>
<td>-64 to 55</td>
</tr>
</tbody>
</table>

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Table 4.3: The mean and standard error of dive depth and duration for dives within each bin, as determined from TDRs deployed on pups that also carried SLTDRs. The bin midpoint is the midpoint of the bin range. Significance (*) between the mean depth or duration and the bin midpoint was assumed at \( p < 0.05 \)

<table>
<thead>
<tr>
<th>Bin</th>
<th>Mean Depth ± SE</th>
<th>Bin Midpoint</th>
<th>N</th>
<th>Mean Duration ± SE</th>
<th>Bin Midpoint</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>30.4 ± 0.3*</td>
<td>34</td>
<td>4801</td>
<td>1.95 ± 0.02*</td>
<td>2.00</td>
<td>3336</td>
</tr>
<tr>
<td>2</td>
<td>122.3 ± 0.4*</td>
<td>120</td>
<td>2640</td>
<td>6.20 ± 0.02*</td>
<td>6.00</td>
<td>4087</td>
</tr>
<tr>
<td>3</td>
<td>196.0 ± 0.7*</td>
<td>200</td>
<td>977</td>
<td>9.33 ± 0.03*</td>
<td>10.00</td>
<td>1514</td>
</tr>
<tr>
<td>4</td>
<td>272.6 ± 1.2*</td>
<td>280</td>
<td>304</td>
<td>13.30 ± 0.13*</td>
<td>14.00</td>
<td>57</td>
</tr>
<tr>
<td>5</td>
<td>363.4 ± 1.5*</td>
<td>360</td>
<td>209</td>
<td>18.30 ± 0.79</td>
<td>18.00</td>
<td>4</td>
</tr>
<tr>
<td>6</td>
<td>418.2 ± 2.1</td>
<td>400+</td>
<td>68</td>
<td>21.17</td>
<td>20.00+</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 4.4: The relationship between when dives occurred, determined from the TDR record, and whether the dive information was received by Argos. Data are the number of records in each category, and the (expected number) given independence. The overall \( \chi^2 = 3.29, p = 0.35 \).

<table>
<thead>
<tr>
<th>Period of Diving</th>
<th>21:00-02:59</th>
<th>03:00-08:59</th>
<th>09:00-14:59</th>
<th>15:00-20:59</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Data Received</td>
<td>64 (51.6)</td>
<td>53 (51.6)</td>
<td>50 (49.7)</td>
<td>55 (50.2)</td>
<td>222</td>
</tr>
<tr>
<td>No Data Received</td>
<td>44 (56.4)</td>
<td>55 (56.4)</td>
<td>54 (54.3)</td>
<td>50 (54.3)</td>
<td>203</td>
</tr>
<tr>
<td>Total</td>
<td>108</td>
<td>104</td>
<td>105</td>
<td>108</td>
<td>425</td>
</tr>
</tbody>
</table>

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Table 4.5: The relationship between whether dive data were received by Argos, and the number of the subsequent four periods in which there was no diving activity, as determined from the TDR record. Data are the number of records in each category, and the (expected number) given independence. The overall $\chi^2 = 4.36$, $p = 0.36$. Only records with complete information for the subsequent 24 hours were used.

<table>
<thead>
<tr>
<th># of Subsequent Periods Without Dives</th>
<th>0</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Data Received</td>
<td>68 (72.6)</td>
<td>78 (77.3)</td>
<td>36 (31.8)</td>
<td>5 (4.2)</td>
<td>0 (1.1)</td>
<td>187</td>
</tr>
<tr>
<td>No Data Received</td>
<td>69 (64.4)</td>
<td>68 (68.7)</td>
<td>24 (28.2)</td>
<td>3 (3.8)</td>
<td>2 (0.9)</td>
<td>166</td>
</tr>
<tr>
<td>Total</td>
<td>137</td>
<td>146</td>
<td>60</td>
<td>8</td>
<td>2</td>
<td>353</td>
</tr>
</tbody>
</table>

Table 4.6: Mean distances (km) between Argos positions of location class 0 and 1, and GPS positions. The straight-line and longitudinal distance error for LC 0 was significantly larger than that for LC 1 ($p = 0.05$, $p = 0.04$), but there was no significant difference within location classes between the latitudinal error ($p = 0.07$).

<table>
<thead>
<tr>
<th>Location Class</th>
<th>N</th>
<th>Straight-line (km)</th>
<th>Latitudinal (km)</th>
<th>Longitudinal (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>39</td>
<td>11.35 ± 1.67</td>
<td>8.76 ± 1.59</td>
<td>5.54 ± 0.91</td>
</tr>
<tr>
<td>1</td>
<td>17</td>
<td>5.03 ± 1.17</td>
<td>4.06 ± 1.12</td>
<td>2.45 ± 0.56</td>
</tr>
</tbody>
</table>
LITERATURE CITED


Chapter 5: Movements and diving behavior of weaned Weddell seal pups

ABSTRACT

The diving behavior and movement patterns of 26 weaned Weddell seal (Leptonychotes weddellii) pups from in Erebus Bay, Antarctica, were tracked using satellite linked time depth recorders between 1993 and 1995. Tags transmitted data for up to 5½ months, and for all seals between eight and 27 weeks old, the proportion of dives in each of six depth and duration bins, the total number of dives, and the maximal dive depth was monitored. Regression analyses were used to determine if seal age or time of day had any effect on diving behavior. In addition, seal locations within the Ross Sea were tracked, and differences in diving behavior and movement patterns were analyzed by month and region.

Seal age had little effect on the proportion of dives in any depth or duration category, dive frequency, or maximum dive depth. The maximum dive depth recorded in this study was 678 m for a 12 week old juvenile, and maximum dive duration never exceeded 16 min. However, most parameters measured differed by time of day, and deeper and longer dives were more frequent in the afternoon period. There were no obvious differences by region, and dive patterns suggested that juvenile Weddell seals were foraging on similar prey items throughout the Ross Sea.

Most juvenile Weddell seals left their natal area by the end of February, and traveled north along the Antarctic continent coastline. While several individuals returned to McMurdo Sound by the end of April, others did not, and at least one traveled in excess of 700 km to the north. This study suggests that juveniles are capable of using the pack ice habitat, but prefer to remain closer to the coastline than do adults. Differential migration patterns and timing in juveniles may reflect strategies to avoid intraspecific foraging competition with adults.

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INTRODUCTION

Most field based studies of young marine mammals have concentrated on the lactation and post-weaning period when the animals are relatively easy to find and observe (for review: Riedman 1990, Gentry and Kooyman 1986). Far fewer studies have focused on juvenile behavior after the animals have left the natal colonies (Bums et al. in press., Burns and Testa 1997, Homing and Trillmich 1997, Burns and Castellini 1996, Le Boeuf et al. 1996, Thorson and Le Boeuf 1994, Lydersen and Hammill 1993). In part, this has been due to the difficulties associated with finding, tracking, and monitoring animals that often remain at sea for long periods of time and travel over large areas. However, recent recognition that juvenile survivorship in marine mammals is a critical factor in determining population size has focused attention on those aspects of juvenile behavior and physiology that may effect survivorship (Hastings 1996, Hindell 1991, Merrick et al. 1987, Eberhardt and Siniff 1977). At the same time, technical advances have reduced the size, weight, and cost of telemetry tags, while increasing their reliability and power output (Service Argos 1996, Merrick et al. 1994, Costa 1993, Priede and French 1991, Harris et al. 1990). This has made it possible to remotely monitor the behavior and movements of many young animals as never before possible. As a result, there has been an great increase in the number of studies on juveniles, and in the types and breadth of information collected.

In McMurdo Sound, Antarctica, studies of juvenile and adult Weddell seals (Leptonychotes weddellii) have revealed that juvenile diving behavior is affected by a combination of factors including (but not necessarily limited to) age, body size and condition, time of day, and season (Burns et al. subm., Burns and Testa 1997, Burns and Castellini 1996, Castellini et al. 1992, Kooyman 1968). Young Weddell seal pups begin to dive and swim several weeks prior to weaning, and during the period between birth and weaning at six weeks of age their diving skills and ability are determined mainly by their age (Burns and Testa 1997, Burns and Castellini 1996, Bryden et al. 1984, Kooyman 1968). This may be because young pups are unable to control heart rate, respiration, and metabolism to the same degree as older pups, yearlings, or adults. However, by the time pups make the transition to independent foraging, they have matured physiologically, and their behavioral patterns appear to be determined more by body size and condition than by age (Burns et al. subm., Burns and Castellini 1996, Le Boeuf et al. 1996, Castellini et al. 1994, Kooyman et al. 1980, 1983, Eisner et al. 1977, Kooyman and Campbell 1972). At this point, untangling the different roles that age, physiology, and size play in determining pup behavior becomes more complex. Not only do age and size influence behavior, but so do other factors such as time of day and season (Burns et al. subm., Burns and Testa...
In addition, soon after weaning, Weddell seal pups leave Erebus Bay and disperse from McMurdo Sound (Testa 1987, Stirling 1969, Kooyman 1968). They are often never seen again; fewer than 25% of the pups born in Erebus Bay recruit into the breeding adult population (Hastings 1996, Testa 1987).

In the face of high juvenile mortality and emigration rates, the stable population of Weddell seals in Erebus Bay is sustained by high adult survivorship and immigration rates (Hastings 1996, Testa 1987, Testa and Siniff 1987). However, despite extensive studies on the Weddell seal population in Erebus Bay, and surveys of other colonies within the Ross Sea, neither the origins of the immigrants, nor the destination of the emigrants is currently known (Hastings 1996, Testa 1987, Stirling 1969). In addition, while the annual movements and dispersal patterns of resident females has been documented (Testa 1994), the routes followed by dispersing pups or returning juveniles have not been studied. However, it has been hypothesized that after juveniles leave the breeding colonies they utilize pack ice and the Antarctic coastline as a refuge from competition and predation (Stirling 1969, Smith 1965).

Given the extensive information available on the behavior and physiology of juvenile Weddell seals during the summer months, the absence of data on pup behavior during their first, critical, winter is especially noticeable. Very little data regarding juvenile behavior or movement patterns after the end of their natal summer has been collected. What little information that does exist suggests that, as is the case in other pinnipeds, juvenile diving behavior continues to develop throughout the winter as pups grow and mature (Burns et al. subm., Burns and Testa 1997, Homing and Trillmich 1997, Le Boeuf et al. 1996, Thorson and Le Boeuf 1994). In addition, data collected from adults during the fall and winter suggests that pup behavior may be substantially different from that seen in the summer due to changes in ice conditions and light levels (Testa 1994, Castellini et al. 1992, Kooyman 1975). In order to determine those factors which influence juvenile Weddell seal behavior, and to identify emigration and dispersal routes, we tagged young pups with satellite-linked time depth recorders (SLTDRs) designed to collect and transmit information on both diving behavior and animal location for up to one year. From the data collected we hoped to determine: 1) how pup dive behavior changed throughout the winter; 2) which factors (age, season, time of day, location) influenced dive behavior after weaning; and 3) where pups went during their winter migration and dispersal.
METHODS

Animal Handling

Over the austral summers of 1992, 1993, and 1994, in McMurdo Sound, Antarctica, 26 weaned Weddell seal pups (11 females, 15 males) were outfitted with 0.5 watt SLTDRs (Wildlife Computers, Mark 3.x). The SLTDRs were attached to the fur with epoxy glue (Burns and Testa 1997), and were designed to be carried by the animal for the next nine months. Pup age at the time the SLTDRs were attached ranged from five to 15 weeks (Table 5.1). In 1992, tags were mounted dorsally with the antenna pointing towards the tail, while in 1993 and 1994 tags were mounted above the shoulders with the antenna pointed forward (1993) or skyward (1994).

Dive Data

The SLTDR tags deployed transmitted the number of dives in each of 6 depth and duration 'bins' for each of four, six hour periods of the day. Depth bins were set as follows: 12-80 m, 81-160 m, 161-240 m, 241-320 m, 321-400 m, and greater than 400 m. Five duration bins each had a range of 4 minutes, and the sixth recorded all dives longer than 20 min. Periods were set as 21:00-02:59 (night), 03:00-08:59 (morning), 09:00-14:59 (afternoon), and 15:00-20:59 (evening) local time (GMT + 12 h). In 1992, tags were set to transmit the complete memory every other hour, provided the tag was above water and the temperature was above -20° C. In 1993 and 1994, the transmission window was expanded to include all hours except those between 11:00-13:00 when there was no overhead satellite coverage. The summarized depth and duration data for each of the previous four periods was stored in a buffer for 24 hours, during which time all the data was transmitted as often as possible, provided transmission criteria were met. When the SLTDR finished collecting data for the current period, the oldest period in the buffer was discarded, and the most recent data added. Therefore, collected data had 24 hrs to be transmitted before being lost. The SLTDR status, on ice (land) or at sea, was also included in each transmission. Seal positions were determined by the Argos system provided that message reception met criteria set by Service Argos (Service Argos 1996, Hill 1993). The depth of the deepest dive in the previous 24 hrs was reported in separate status messages sent by the tags. These messages were received infrequently, and did not include the actual date, time, or duration of the deepest dive.

Transmitted data received by Service Argos were retrieved and analyzed by programs supplied by Wildlife Computers (SatPak 3.0). The number of dives in each depth and duration bin, the total number of dives, the date and period of data collection and transmission, and the status (on
ice or at sea) of the tag were determined for each record. The age of the seal (in weeks) was secondarily added into the data file, and dive parameters were calculated for each seal at each age and period. For each period, the mean dive frequency was determined as the average total number of dives for each seal at each age. Mean dive depth and duration could not be determined because the data reported were categorical (number of dives in each of six depth and duration bins). Instead, the proportion of dives in each bin was determined for each record, provided that the total number of dives was greater than zero. In those cases where the total number of dives was zero, the proportion of dives in all bins was also set to zero. The mean proportion of dives in each bin was then determined for each individual seal at each age and period. The mean maximum dive depth was determined from the status messages of each seal at each age.

The effects of seal age and/or period on dive behavior (proportion of dives, mean frequency, and maximum depth) were tested using parametric statistics, provided that the data were normally distributed and there were more than 10 data points in any given period and bin. Data normality was assessed using rankit plots and the Wilk-Shapiro (W-S) statistic (normality accepted if W-S > 0.90), and outliers were visually identified and removed (Zar 1984). All proportional data were arcsin transformed.

Linear regression was used to model the effect of age on the dive parameters of interest for each period separately, so that four regression equations were produced. The mean value for each individual seal at each age, and not the pooled mean value for all seals at each age, was used. Regression equations were reported providing that seal age accounted for more than 10% of the overall variation in dive behavior within any given period. In these cases, differences among periods in the effect of age were tested for by comparing the slopes and intercepts of the resultant regression equations using standard techniques (Zar 1984). If the neither the slope nor intercept differed significantly between periods ($p < 0.05$) then the periods were pooled, and a new regression equation computed. When seal age had no effect on dive behavior, one-way ANOVA methods were used to test for differences among periods in the mean dive parameters.

The total amount of time spent diving (depth > 12 m) was roughly estimated for each seal by multiplying the mean number of dives in each duration bin by the duration midpoint of the bin. 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 subm.). However, 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. The effect of age and time of day on the total time underwater was determined in the same manner as described above.

Location Data

Seal positions were calculated by the Argos system based on the Doppler shift in transmitted signals, provided that a sufficient number of signals were received during the satellite overpass. When an insufficient number of signals were received, dive data, but no location data, were received. The accuracy of the locations calculated by Argos varied with the number of signals received during a satellite overpass, and was reflected in the location quality codes (called the location class or LC). However, other factors such as long time intervals between messages, low angle of satellite overpasses, temperature induced fluctuations in transmission frequency, and attenuation of the SLTDR signal due to the proximity of the transmitter to the ice and seal, can also affect the position accuracy (Service Argos 1996, Fancy et al. 1988). For these reasons, the location data was screened for outliers before animal locations and movement rates were calculated.

To remove inaccurate locations, we used a three step process (Frost et al. 1995, Frost and Lowry 1994, Keating 1994). First, all positions with a LC < -5 were discarded. These locations were calculated by Argos using fewer than two signals, and were generally unreliable. Secondly the Keating error index (KEI) value was calculated for each record, and all records with a KEI > 20 and a LC < 1 were omitted. The KEI identifies erroneous locations by taking into account the time and distance between sequential positions and assuming that any single, relatively large distance movement followed shortly thereafter by a return to the original position, is an error (Keating 1994). The records were then screened for improbable locations given the time and distance between sequential positions, and the maximum swimming speed of the seals. Following the removal of records that required improbable swim speeds, the KEI was recalculated, and all records with a KEI > 20 were omitted. Before any locations marked for deletion were permanently removed from the dataset, they were carefully rechecked to verify their outlier status. Only those positions that remained were used to track Weddell seal movements. However because locations were only mapped after this process was performed, and locations with class codes < 2 had an estimated error of > 5 km (Bums and Castellini, subm.), it was possible to have "good" locations that placed seals on land.

Once a database of all reasonable locations was compiled, daily positions were estimated for each seal by averaging all positions received during each day. Daily movement rates were then
determined by calculating the distance between two subsequent locations, and dividing by the number of days between the position fixes. Average daily movement rates for each month, and within each of five regions of the Ross Sea (Erebus Bay, West McMurdo Sound, North McMurdo Sound, Antarctic Continental Coastline, Ross Sea) were also calculated.

Finally, seal locations were used to identify dispersal routes, and to determine the impact of location (region) on dive behavior. However, because seal locations were determined separately from dive behavior, and because there were far fewer days with good positions than days with dive records, not all dive records could be associated with known animal positions. In order to assign a position to all dive records, animals were assumed to remain within a region until they were located outside that region. Because these regions are large with respect to the average daily movement rate, it is unlikely that this methodology introduced significant error.

RESULTS

Animal Handling
Among the 26 pups outfitted with SLTDRs during the course of this study, there was a high tag failure rate, and no tag transmitted for longer than 5 ½ months. Three tags failed immediately upon deployment for unknown reasons, and during the 1994 and 1995 seasons 10 tags were retrieved within six weeks of deployment with missing or broken antennas (Table 5.1). Only one tag transmitted after May of the following year.

Dive Data
For analysis of dive behavior and locations, seal age was limited to the period between eight and 27 weeks old. In this period, a total of 1459 depth, 1481 duration, and 204 maximum dive depth records were received. There were dives in all six depth bins (to 400+ m), but no dives in duration bins five or six indicating a maximum dive duration of no greater than 16 minutes. The maximum dive depth, as determined from the status messages, was 678 m for a 12 week old pup. The maximum dive duration was not reported.

Approximately half of all dives made by pups were to depths less than 80 m, and a quarter of dives were to depths between 80 and 160 m. The proportion of dives deeper than 160 m increased in the afternoon period, but remained a fairly small fraction for all but the oldest animals (Figure 5.1). One third of all pup dives had a duration of less than 4 min, and half were between 4 and 8 min. In the afternoon period, the proportion of dives between 8 and 12 min long
increased with age to more than 40%; in the remaining periods, long dives accounted for fewer than 20% of the total dives made (Figure 5.2).

For the most part, age and time of day had little effect on the proportion of dives in each depth bin (Table 5.2). Age had no effect on the proportion of dives in bins with a maximum depth of less than 240 m (bins 1-3) or deeper than 400 m (bin 6) in any period of the day. The proportion of dives in depth bins 4 and 5 (241-320 and 321-400 m) increased with age, but only in the afternoon and evening periods. However, in no case did age account for more than 36% of the variation in the proportion of dives. Time of day did influence dive behavior, but the effect varied by period and depth. The proportion of dives in all depth bins except bin 2 (81-160 m) differed by period, but while some periods could be pooled, the grouping patterns differed by bin (1-way ANOVA, and post hoc comparison of means, \( p < 0.05 \)).

In contrast to the observed changes in the proportion of dives within each depth bin, the maximum depth of dives made by individual seals between the age of eight and 27 weeks did not increase significantly as seals aged (max. depth = 198.5 + 6.4*Seal Age, \( n = 204, r^2 = 0.06 \); overall mean 295.9 ± 8.7 (SE) m). This result did not significantly differ from that using mean maximum dive depth for individual seals at each age. The effect of time of day on maximum dive depth could not be determined because it was not reported by the satellite tag.

The influence of age and period of day on dive duration was more prevalent than in the analysis of dive depth (Table 5.3). Although age never accounted for more than 16% of the variation in dive duration, its effects were evident in duration bins 1, 3, and 4 (0-4, 8-12, and 12-16 min, respectively). The proportion of short dives (bin 1, 0-4 min) decreased with age in the afternoon period, but remained constant with age in all other periods. In contrast, the proportion of dives longer than 8 minutes increased with age in the afternoon period, but was constant or decreased with age in the remaining periods. And while there was no effect of age on the proportion of dives in bin 2 (4-8 min duration dives), there were more dives in the evening period than in the other three periods (which were combined: 1-way ANOVA and post-hoc comparison of means, \( p > 0.05 \)).

Both age and time of day had a significant impact on mean dive frequency (total # of dives/period). However, while there was no effect of age on the number of dives in the afternoon period (09:00-14:59), dive frequency increased significantly with age in the morning, evening, and night periods. These three periods were combined because their slopes and intercepts were
not significantly different from each other (t-tests, \( p > 0.05 \)), and the resultant regression equation explained 15% of the variation in dive frequency. In these three periods, dive frequency increased from 22.3 ± 16.7 (SE) dives per period for eight week old seals, to 46.6 ± 16.8 dives per period for 27 week old seals (Figure 5.3). In contrast, seals of all ages made an average of 24.4 ± 1.1 dives (per period) in the afternoon (n = 121). In combination, these data indicate that, for seals in this study, overall dive frequency increased from approximately 91 to 164 dives per day. However, note that both the differences among periods and the increase in total dive frequency occurred predominantly after pups were older than four months.

There was no effect of age on the total time spent underwater in the morning, afternoon, or night periods. In the evening, the amount of time spent underwater increased with pup age (time underwater = 19.6 + 8.0 * Seal Age, \( p < 0.001 \), \( r^2 = 0.32 \); Figure 5.4). Overall, the mean time spent underwater in the evening period (152.38 ± 7.21 min) was similar to that in the morning and night periods. Seals spent the less time underwater during the afternoon period (126.79 ± 6.85 vs. 158.16 ± 6.21 min, 1-way ANOVA).

**Location Data**

Of the 1071 original locations received, 559 (52.2 %) were discarded in the screening process. Of the remaining locations, 54.9% were location class (LC) 0 or lower, 41.8% were LC1, and 2.9% LC2 (Table 5.4). Overall, 67.8% of the locations received from tags on ice were of LC1 or better, but only 30.5% of locations received from tags at sea were of similar quality. When tag status could not be determined, approximately half the locations were of LC1 or better (Table 5.5).

The majority of pups stayed within the greater Erebus Bay Region during the months of November, December, and January (Figure 5.5). As all 1994 tags failed by the end of January, all positions calculated for seals in 1994-1995 were within this region. Satellite records exist for 10 seals in February (three from 1993, and seven from 1992). Of these seals, four (10145, 10297, 10524, 10533) remained in Erebus Bay during February, while the remaining animals began to move out of Erebus Bay and towards the coastline of the Antarctic Continent. Four animals traveled northwest up the coast towards Granite Harbor and Cape Ross, while two (10092 and 10253) traveled southwest out of Erebus Bay towards the Dailey Islands and Cape Chocolate (Figure 5.6).
In March of 1993 and 1994, transmissions were received from seven seals, of which only two remained for the entire month within Erebus Bay (10524 and 10533). All other seals moved north along the coastline. Seal 10253 traveled the furthest, and by the end of March was to the southeast of Coulman Island (a distance of over 400 km). After a trip north to Franklin Island and Cape Crozier, seal 10140 returned to Erebus Bay in March (Figure 5.7). By the middle of April, three of the seals which had traveled north out of Erebus Bay (10140, 10082, and 10297) returned. However, two other seals did not return: 10253 continued to move north along the Antarctic coast and by the end of April was just south of Cape Hallet (a distance of over 700 km from Erebus Bay), while 10092 remained between the Fry and Drygalski Glaciers (Figure 5.8). In May, all animals remained within 15 km of their location at the end of April. However, this finding is based on only 15 positions from four animals, so should be cautiously interpreted.

Transmissions were received from only one animal (10082) after the end of May, and the reported locations suggested that 10082 remained in the North McMurdo Sound region from the end of April until resighted in the same region during an October aerial survey. Also in October, seal 10092's radio transmitter was heard during an aerial survey near Cape Hallet, but neither the animal nor tag could be visually located. The last estimated location in late May placed 10092 just south of the Drygalski Glacier, over 400 km to the south of Cape Hallet.

Average rates of travel (km/day) differed by month, with January having the lowest rate of travel (5.7 ± 0.8 km/day) and March the greatest (18.5 ± 1.9 km/day) (Table 5.6). All movement rates were based on the average daily positions and do not necessarily indicate that the seals were moving in a directed fashion. When compared by region, movement rates within Erebus Bay were clearly lower than those outside the region (Table 5.6).

The mean proportion of dives in each depth and duration range differed significantly by region but not all regions were different from each other (Figure 5.9; 1-way ANOVA p< 0.05, post-hoc comparison of means). Seals in Erebus Bay made the most short and shallow dives, while mid-depth and duration dives predominated in the McMurdo Sound regions. Dive behavior in the Ross Sea and along the Antarctic coast were similar. The effect of seal age on dive behavior within each region was not examined because the range of seal ages in most regions was large, and age never accounted for more than a third of the variation in dive behavior when all regions were combined. The effect of time of day was not modeled because there was no reason to assume differences from the overall pattern.

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DISCUSSION

Diving Behavior

This study clearly demonstrates that the rapid increase in dive ability observed in pups during the period around weaning slows soon after independent foraging is achieved. In contrast to studies on younger pups in which age accounted for between half and three quarters of the variation in dive behavior throughout the day (Burns and Testa 1997), the effect of age on the diving ability of Weddell seals between the ages of two and seven months was only reflected in changes in the proportion of deep and long dives in the afternoon and evening periods, and in mean dive frequency during all but the afternoon period. The absence of age effects on dives shorter than 8 minutes and shallower than 160 m was not unexpected given that these dives are well within the diving capability of newly weaned Weddell seal pups (Burns and Testa 1997). It was surprising, however, that a strong correlation between age and deeper and longer dives was absent. It appears that while rapid changes in the diving ability of young pups are driven by the maturation of physiological control mechanisms (Burns and Testa 1997, Burns and Castellini 1996), in weaned pups slower changes in mass, body condition, and physiology cause more gradual increases in dive ability (Burns et al. in press., Rea 1995). Similar shifts in the importance of age and mass have also been seen in the diving patterns of juvenile northern elephant seals and Galapagos fur seals (Homing and Trillmich 1997, Le Boeuf et al. 1996, Thorson and Le Boeuf 1994).

In contrast to dive depth and duration, mean dive frequency was generally positively correlated with age. Combining data on dive depth and duration also suggests that all Weddell seals are attempting to maximize dive time, but that the manner in which this is done changes with age and time of day. In those periods where dive frequency increased with age, the mean proportion of dives in each depth and duration bin remained fairly constant, whereas in the afternoon period the proportion of deep and long dives increased with age but dive frequency remained constant. Overall, as animals aged, they made more dives, and made proportionally more deep and long dives. However, as the proportion of deep and long dives increased in the afternoon, seals appeared unable to also increase dive frequency, suggesting that dive frequency may have been constrained by physiological or behavioral limits on the total time Weddell seal pups could spend diving. The average amount of time pups spent beneath 12 m never exceeded three out of six available hours, and in the afternoon period when the proportion of long dives increased, the total time underwater averaged less than 2.5 hours.
These estimates of time underwater are necessarily rough, and do not include the time seals spent in the water near the surface. Nevertheless, they do suggest that the deep and long dives made by pups are physiologically more expensive than shorter dives, and that as the proportion of these dives increases, the time animals must spend at the surface in recovery increases. Given that the aerobic dive limit of a six week old Weddell seal pup is approximately six minutes, and that of a yearling less than 10 minutes, it is likely that the long and deep dives made by pups during the afternoon period include anaerobic dives that require increased surface recovery periods (Burns and Castellini 1996, Castellini 1991, Kooyman et al. 1980). As such recovery periods would effectively reduce the total time spent underwater, and presumably the time available for foraging, pups may be adjusting the frequency, depth, and duration of dives in response to both their physiological limitations and their need to make deep and long dives in order to obtain prey. Such tradeoffs between dive frequency, depth, and duration have been frequently hypothesized but not often observed in the field (Fedak and Thompson 1993, Houston and Carbone 1992, Ydenberg and Clark 1989, Fedak et al. 1988).

The effect of time of day, and shift in the importance of deep and long afternoon dives, resembles the pattern seen in adult female Weddell seals and other Antarctic pinnipeds that forage on vertically migrating species (Wilson et al. 1993, Bengtson and Stewart 1992, Boyd and Croxall 1992, Castellini et al. 1992, Croxall et al. 1985). It also supports the hypothesis that foraging Weddell seal juveniles must make deep and long dives in the afternoon in order to obtain prey, but are able to concentrate their efforts in shallower waters during the rest of the day. However, directly relating dive behavior with prey abundance or light levels during the different periods is complicated by the extreme changes in daylight patterns which occur in the region, and the absence of information on the ecology of Weddell seal prey items within the Ross Sea or underneath sea ice (Wilson et al. 1993, Castellini et al. 1992, Kooyman 1975).

Weddell seals forage on a wide variety of prey species, including fish, squid, octopods, and large crustaceans (Castellini et al. 1992, Green and Burton 1987, Plötz 1986, Testa et al. 1985, Dearborn 1965). In the ice-free Antarctic waters outside of McMurdo Sound, the majority of these species occur midwater, make diurnal vertical migrations, or are separated in size by depth (White and Piatkowski 1993, Rodhouse 1990, Kellermann 1986, Eastman 1985, Hubold 1984). While the Weddell seal diet varies by region, in the McMurdo Sound area the principal prey for adults throughout the year appears to be the Antarctic silverfish (*Pleuragramma antarcticum* Boulanger), a small (<15cm) fish most often found between the depths of 100 and 350 m. As approximately a third of the dives made by seals in this study fell within this depth range, and...
scats collected within Erebus Bay contained predominantly fish bones and small squid beaks, it is likely that newly weaned Weddell seals are also foraging on *Pleuragramma* and other midwater prey items. This conclusion is also supported by visual observation of foraging pups (Thomas and DeMaster 1983, Kooyman 1968), and contradicts earlier ideas that weaned pups ate primarily small crustaceans and krill (Bertram 1940, Lindsey 1937). Bottom dives, which suggest foraging on benthic prey were not often prevalent in adult or juvenile dive records (Burns et al. in press, Schreer and Testa 1996, Testa 1994). Thus, while both the diet and dive information suggest that Weddell seal adults, juveniles, and pups forage on similar prey, and that the prey species show some degree of vertical migration throughout the year, there is no direct evidence for such behavior.

**Movement Patterns**

In addition to information on juvenile Weddell seal dive patterns, the SLTDRs provided a large amount of data on the movement patterns of pups from the late summer through the early winter. From this study it appears that pups are also capable of using the pack ice habitat, but may do so to a lesser extent than adults (Testa 1994, Stirling 1969). Like adults, all pups remained associated with the fast ice of Erebus Bay during the months of November, December and January. However, soon after weaning, pups began to move away from their natal colony, and by February many of the pups had left Erebus Bay and moved into McMurdo Sound. As adult females did not move from Erebus Bay until March or April, this early movement of pups from Erebus Bay suggests an attempt by pups to improve foraging success by avoiding competition with the more capable adults (Testa 1994, Castellini et al. 1992). Alternatively, adults may remain in the area to complete their molt on the more stable fast ice, while pups move away in order to avoid the regions of low prey abundance around the breeding and molting areas (Castellini et al. 1992, Testa et al. 1985). Changes in the pattern of ice breakup and pack ice availability between 1990-1991, when the adult study was conducted, and 1992-1994 may also have contributed to the observed behavioral differences.

While pup movements as they left Erebus Bay were similar to those observed in SLTDR tagged adult females, pups tended to remain closer to the Antarctic coastline than adults (Testa 1994). This apparent reliance on coastal fast ice during the migration from Erebus Bay may serve two purposes: young seals would be able to continue foraging within shallower coastal areas while at the same time using the fast ice as a refuge against killer whale predation (Smith 1965). It is interesting to note that several pups returned to North McMurdo Sound in mid-April, after killer whales and many Weddell seal adults are thought to have left the area (Testa 1994, Mikhalev et
In contrast, some pups used habitat similar to that selected by adults. Three pups remained within Erebus Bay until March/April (when their tags ceased transmitting), while two others were found primarily within the pack ice habitat of the open Ross Sea. Therefore, it was hard to determine if the absence of juveniles within Erebus Bay during the breeding season was a result of competitive exclusion during periods of high population density, or an indication that juvenile Weddell seals favored different habitats than adults, as has been shown in young elephant and harbor seals (Hastings 1996, Le Boeuf et al. 1996, Thompson 1989).

While not all pups traveled away from Erebus Bay, the long distances traversed by many of the pups revealed that Weddell seal pups were capable of migrating far from their natal colony. At least one pup moved more than 700 km to the north of Erebus Bay, and several pups moved past the small Weddell seal colonies at Terra Nova Bay, Wood Bay, Coulman Island, and the Nordenskjold Glacier (Stirling 1969). While two pups last located within Erebus Bay have been seen as sub-adults, none of the pups that 'permanently' left Erebus Bay have been resighted. However, juvenile resighting probabilities are low, and we do not know if these pups have died, recruited into other colonies, or just not yet returned to McMurdo Sound (Hastings 1996). In any case, there exists a large potential for migration and genetic exchange between Weddell seal colonies all along the Western coast of the Ross Sea.

In addition to tracking migration patterns, it was also possible to examine dive behavior and average daily movement rates within different regions of the Ross Sea. Overall, the dive behavior in the five regions was remarkably similar and supported the hypothesis that seals throughout the Ross Sea were foraging on similar prey items, as was the case for adult Weddell seals throughout the winter. Similarity of diet probably reflects the uniformity of the prey base in McMurdo Sound where *Pleuragramma* makes up > 90% of the biomass (Testa 1994, Castellini et al. 1992, Eastman 1985, Everson 1985, Laws 1985). The few observed differences in diving behaviour among regions could generally be attributed to seal age, and were not clearly related to variation in bathymetry or sea ice conditions. While the shallow inner Erebus Bay region where young pups were concentrated in December and January had the highest proportion of shallow and short dives, this probably reflected its use as a natal area, rather than its bathymetry (Testa 1994). With the exception of the deeper Ross Sea, the maximum sea-floor depth of all regions was similar.

In contrast, differences in seal movement rates between areas were helpful in better understanding overall travel and migration patterns. As expected from the sedentary nature of
young pups during the summer, Erebus Bay had the lowest movement rates of all the regions, while high movement rates outside of Erebus Bay in February and March reflected the migration of seals from the natal area. Low movement rates in late April and May suggested that pups were once again remaining in fairly localized areas, but because all tags stopped working in May, it was impossible to determine if this was a temporary or permanent behavioral change. Overall, the low average daily movement rates in this study probably reflect the continuous availability of sea ice for haul out (Testa 1994, 1987, Castellini et al. 1992, McConnell et al. 1992, Stirling 1969).

Clearly, the SLTDRs used in this study provided a significant amount of data on the diving behavior and movement patterns of Weddell seal pups that would have been impossible to collect otherwise. However, the SLTDRs did not work as well as expected: the transmission frequency was low, and both the proportion of improbable location fixes and the tag failure rate was high. Despite high transmission rates and frequent satellite overpasses, only 50% of the expected SLTDR data was received. In contrast, studies of SLTDR tagged adult Steller sea lions, Weddell, harbor, and grey seals received almost complete coverage (Burns et al. subm., Frost et al. 1995, Merrick et al. 1994, Testa 1994, McConnell et al. 1992, Stewart et al. 1989).

Another problem experienced in this study was that almost half of the locations provided by Service Argos were secondarily discarded due to low location quality, high KEI's, or long distances from previous locations. In combination with the low uplink frequency, this reduced the number of positions per seal per day to fewer than one. The high proportion of low quality fixes was not unique to this study, and was probably a result of animal movement and dive patterns. Good data coverage and high quality fixes are only possible if multiple messages are received during a satellite overpass, and are much more likely to occur if an animal is hauled out (Service Argos 1996, Priede and French 1991). Because these young animals spent a considerable time at sea, and did not show the strong bout diving patterns of many other phocid seals (Boyd and Croxall 1992, Castellini et al. 1992, Feldkamp et al. 1989, pers. obs.), the transmission window was disproportionately reduced, and therefore the majority of received locations were of poor quality.

The other major problem we experienced in this study was that the SLTDR tags deployed on pups remained functional for a much shorter period than expected. While the cause of the failures during the 1992 season could not be determined, the high tag failure rates in 1993 and 1994 were due almost exclusively to antenna breakage. Of 11 tag failures in which the cause was known, three were due to technical problems, and eight due to antenna breakage. Antenna
failure has been observed in other species, but never to this extent (Stewart et al. 1989, Hills, Merrick, Blix, and Frost pers. comm.). At this point, we have no definitive explanation for the high antenna failure rate. However, based on examination of broken tags and antennas, we know that it was not due to abrasion or mastication, and suspect that antenna oscillation during swimming caused rapid metal fatigue.

Despite problems with the tags, it is important to reiterate that the SLTDRs did provide a significant amount of data that could not have been collected in any other fashion. Data collected formed the basis for the two main conclusions of this study: that the diving behavior of weaned Weddell seal pups was not strongly correlated with animal age, and that young Weddell seals were capable of long distance movements similar to those made by adults. Overall, post-weaning increases in dive capacity appeared to be gradual, and were probably a result of the slow increase in mass that accompanied age, rather than any dramatic changes in physiological processes related to diving. This is not to say that pups were physiologically mature soon after weaning, only that gradual physiological development post-weaning was probably masked by larger changes in mass and composition. Despite diving limitations imposed by age and size, this study suggested that Weddell seal pups older than two months could dive deep enough to compete in the same areas and for the same prey items as adults. However, pups may not have been able to remain at these depths for long enough to make such dives energetically efficient. Both the timing and the routes followed suggested that juvenile dispersal was a mechanism to avoid intraspecific competition with the larger, more capable adult divers.

ACKNOWLEDGMENTS

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was carried out under permit # 801 of the Marine Mammal Protection Act. Experimental protocols were approved by the UAF Institutional Animal Care and Use Committee.
Table 5.1: Satellite tag deployment history. SLTDRs with identification numbers 92-x were version 3.04, while tags 93-x were version 3.1. The age of the seal (in weeks) at the time of deployment is indicated in parenthesis below the ID number. Dates indicate the range of transmission dates, rather than when tags were deployed and recovered. Unless otherwise noted tag failure was due to a lost or broken antenna.

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<th>SLTDR</th>
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\textsuperscript{*} Tag failed upon deployment due to technical error.
\textsuperscript{f} Tag retrieved after failure detected. Unless noted, the failure was caused by a broken antenna.
\textsuperscript{\#} Tag retrieved in the subsequent season.
Table 5.2: The effect of age and period on the mean proportion (± SE) of dives in the different depth bins. Letters indicate that the mean proportion of dives in the separate periods were not significantly different (1-way ANOVA, post-hoc comparison of means, \( p > 0.05 \)) or that the slope and intercept of regression equations for the periods were similar (t-test, \( p > 0.05 \)).

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<th>Depth Bin</th>
<th>Night (21:00-02:59)</th>
<th>Morning (03:00-08:59)</th>
<th>Afternoon (09:00-14:59)</th>
<th>Evening (15:00-20:59)</th>
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<td>( n=132 )</td>
<td>( n=135 )</td>
<td>( n=121 )</td>
<td>( n=119 )</td>
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<td>1: 12 - 80 m</td>
<td>66.83 ± 0.08</td>
<td>50.56 ± 0.04</td>
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<td>2: 81 - 160 m</td>
<td>22.15 ± 0.01</td>
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<td>3: 161 - 240 m</td>
<td>3.95 ± 0.03</td>
<td>10.20 ± 0.02</td>
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<td>4: 241 - 320 m</td>
<td>0.47 ± 0.01</td>
<td>2.12 ± 0.02</td>
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<td>+ AGE(^2)</td>
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<td>5: 320 - 400 m</td>
<td>0.11 ± 0.01</td>
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<td>6: 400+ m</td>
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</tbody>
</table>

1: \( Y = -0.21 + 0.027 \times \text{Age}, \ r^2 = 0.36 \ Y = \arcsin(\text{mean proportion}) \)
2: \( Y = -0.10 + 0.018 \times \text{Age}, \ r^2 = 0.25 \ Y = \arcsin(\text{mean proportion}) \)
3: \( Y = -0.12 + 0.013 \times \text{Age}, \ r^2 = 0.17 \ Y = \arcsin(\text{mean proportion}) \)

Table 5.3: The effect of age and period on the mean proportion (± SE) of dives in the different duration bins. The letters indicate that the mean proportion of dives in the separate periods were not significantly different (1-way ANOVA, post-hoc comparison of means, \( p > 0.05 \)).

<table>
<thead>
<tr>
<th>Duration Bin</th>
<th>Night (21:00-02:59)</th>
<th>Morning (03:00-08:59)</th>
<th>Afternoon (09:00-14:59)</th>
<th>Evening (15:00-20:59)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( n=129 )</td>
<td>( n=130 )</td>
<td>( n=130 )</td>
<td>( n=124 )</td>
</tr>
<tr>
<td>1: 0 - 4 min</td>
<td>46.07 ± 0.06</td>
<td>34.36 ± 0.04</td>
<td>- AGE(^1)</td>
<td>34.36 ± 0.04</td>
</tr>
<tr>
<td>2: 4 - 8 min</td>
<td>44.21 ± 0.02</td>
<td>44.21 ± 0.02</td>
<td>44.21 ± 0.02</td>
<td>54.09 ± 0.08</td>
</tr>
<tr>
<td>3: 8 - 12 min</td>
<td>- AGE(^2)</td>
<td>8.59 ± 0.02</td>
<td>+ AGE(^3)</td>
<td>8.59 ± 0.02</td>
</tr>
<tr>
<td>4: 12 - 16 min</td>
<td>0.05 ± 0.00</td>
<td>0.05 ± 0.00</td>
<td>+ AGE(^4)</td>
<td>0.05 ± 0.00</td>
</tr>
</tbody>
</table>

1: \( Y = 1.01 - 0.022 \times \text{Age}, \ r^2 = 0.12 \ Y = \arcsin(\text{mean proportion}) \)
2: \( Y = 0.43 - 0.013 \times \text{Age}, \ r^2 = 0.11 \ Y = \arcsin(\text{mean proportion}) \)
3: \( Y = 0.02 + 0.022 \times \text{Age}, \ r^2 = 0.16 \ Y = \arcsin(\text{mean proportion}) \)
4: \( Y = -0.06 + 0.006 \times \text{Age}, \ r^2 = 0.10 \ Y = \arcsin(\text{mean proportion}) \)

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Table 5.4: The type and quality of locations received from SLTDR tags. The total number of tag locations, the number of locations remaining after the screening process, and the number (and proportion) of positions in each location class.

<table>
<thead>
<tr>
<th>Year</th>
<th>Total # of locations</th>
<th># of Good Locations</th>
<th>LC0</th>
<th>LC1</th>
<th>LC2</th>
<th>LC3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>(51.5%)</td>
<td>(50.7%)</td>
<td>(46.2%)</td>
<td>(2.8%)</td>
</tr>
<tr>
<td>1992</td>
<td>555</td>
<td>286</td>
<td>145</td>
<td>132</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(36.3%)</td>
<td>(44.4%)</td>
<td>(55.6%)</td>
<td></td>
</tr>
<tr>
<td>1993</td>
<td>342</td>
<td>124</td>
<td>55</td>
<td>69</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(58.6%)</td>
<td>(79.4%)</td>
<td>(12.7%)</td>
<td>(6.9%)</td>
</tr>
<tr>
<td>1994</td>
<td>174</td>
<td>102</td>
<td>81</td>
<td>13</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(47.8%)</td>
<td>(54.9%)</td>
<td>(41.8%)</td>
<td>(2.9%)</td>
</tr>
<tr>
<td>TOTAL</td>
<td>1071</td>
<td>512</td>
<td>281</td>
<td>214</td>
<td>15</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 5.5: The number (and proportion) of locations received in each class for tags on ice, at sea, or with no known status.

<table>
<thead>
<tr>
<th>Year</th>
<th>Tag Status</th>
<th>Total # of good locations</th>
<th>LC0</th>
<th>LC1</th>
<th>LC2</th>
<th>LC3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>All</td>
<td>134</td>
<td>43</td>
<td>83</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>on ice</td>
<td>(32.1%)</td>
<td>(61.9%)</td>
<td>(5.2%)</td>
<td>(0.7%)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>at sea</td>
<td>262</td>
<td>182</td>
<td>74</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(69.5%)</td>
<td>(28.2%)</td>
<td>(2.3%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>not known</td>
<td>115</td>
<td>56</td>
<td>57</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(48.7%)</td>
<td>(49.6%)</td>
<td>(1.7%)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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Table 5.6: Average movement rates (km/day ± SE) calculated for seals in different months and in different regions of the Ross Sea. NSD indicates that, although seals were located in that region during the month, there were not sufficient data to determine average movement rates (n< 5).

<table>
<thead>
<tr>
<th></th>
<th><em>Erebus Bay</em></th>
<th><em>W. McMurdo Sound</em></th>
<th><em>N. McMurdo Sound</em></th>
<th><em>Antarctic Coast</em></th>
<th><em>Central Ross Sea</em></th>
<th><em>Overall</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Dec.</td>
<td>6.0 ± 0.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>6.0 ± 0.6</td>
</tr>
<tr>
<td>Jan.</td>
<td>5.7 ± 0.8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>5.7 ± 0.8</td>
</tr>
<tr>
<td>Feb.</td>
<td>5.0 ± 0.8</td>
<td>14.6 ± 3.1</td>
<td>NSD</td>
<td>17.1 ± 4.0</td>
<td>15.6 ± 10.0</td>
<td>10.2 ± 1.4</td>
</tr>
<tr>
<td>March</td>
<td>5.8 ± 2.0</td>
<td>NSD</td>
<td>19.1 ± 8.9</td>
<td>21.0 ± 3.6</td>
<td>23.9 ± 2.7</td>
<td>18.5 ± 1.9</td>
</tr>
<tr>
<td>April</td>
<td>NSD</td>
<td>NSD</td>
<td>NSD</td>
<td>11.4 ± 4.3</td>
<td>14.7 ± 3.3</td>
<td>13.0 ± 2.1</td>
</tr>
<tr>
<td>May</td>
<td>-</td>
<td>-</td>
<td>NSD</td>
<td>NSD</td>
<td>9.2 ± 3.3</td>
<td>8.0 ± 2.4</td>
</tr>
<tr>
<td>All</td>
<td>5.9 ± 0.4</td>
<td>14.3 ± 2.7</td>
<td>10.8 ± 3.2</td>
<td>17.1 ± 2.3</td>
<td>19.2 ± 2.0</td>
<td>10.6 ± 0.7</td>
</tr>
</tbody>
</table>

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Figure 5.1: The mean proportion of dives within each of the six depth bins for each of the four periods of the day.
Figure 5.2: The mean proportion of dives within each of the four duration bins for each of the four periods of the day.
Figure 5.3: The mean number of dives (± SE) in each period of the day for seals between the ages of eight and 27 weeks. The mean dive frequency increased significantly with age in the combined evening, night, and morning periods (15:00-8:59; dive frequency = 12 + 1.3 * Seal Age, $r^2 = 0.15$) but did not change with age in the afternoon period.
Figure 5.4: The mean total time (±SE) spent underwater in the evening period for seals between the ages of eight and 27 weeks.

Time UW = 8.0 * Seal Age + 19.6, $r^2 = 0.32$
Figure 5.5: Average daily locations in November, December, and January for pups tagged in 1992, 1993, and 1994. The five regions within the Ross Sea used for grouping animal locations, dive behavior, and movement rates are also shown.

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Figure 5.6: Average daily locations in February for pups tagged in 1992 and 1993
Figure 5.7: Average daily locations in March for pups tagged in 1992 and 1993
Figure 5.8: Average daily locations in April and May for pups tagged in 1992.
★ North of Moubray Bay indicates where transmitter from seal 10092 was found.
Figure 5.9: The mean proportion of dives in each depth and duration bin within each of the five regions. * indicate significant differences in the mean proportion between areas ($p < 0.05$).
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Chapter 6: Physiological effects on dive patterns and foraging strategies in yearling Weddell seals (Leptonychotes weddelli)\textsuperscript{5}

ABSTRACT

Fifteen yearling Weddell seals (Leptonychotes weddelli) were captured, measured, weighed, bled, equipped with time depth recorders (TDR), and released to determine if diving behavior was related to physical condition. Upon recovery of the TDRs, 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 was 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 suggested that large yearlings foraged primarily on small, shallow-water prey items, while small yearlings concentrated on energy-dense, deep-water prey. However, the interpretation of diving behavior, foraging locations, and diet that resulted from separating individuals and dive types was very different from that based on average diving behavior. This argues against ignoring variation among individuals and using only average diving behavior when describing marine mammal dive patterns.

INTRODUCTION

Since the development of time-depth recorders, the free-ranging diving behavior of many marine mammal species has been examined. The majority of these studies has focused on average and maximal dive ability (Lydersen and Kovacs 1993, Castellini et al. 1992, Riedman 1990, Kooyman 1989, Le Boeuf et al. 1989, 1988, Gentry and Kooyman 1986, Croxall et al. 1985). Variation in the diving behavior among individuals within a species has been addressed far less often, and the focus often has 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 were attributed to the factor which varied, and variation among individuals within these “homogeneous” groups was not explored. Behavioral differences among individuals of similar age and under similar conditions have been discussed only recently (Testa 1994, McConnell et al. 1992, Hindell et al. 1991, Goebel et al. 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 there have been attempts to link variation in diving behavior to physiological differences. This technique has been successfully employed to explain differences in diving capacity between species, and within species among individuals of different age, condition, or sex (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 age and condition, have rarely been linked to observed differences in diving behavior. As a result, it has been difficult to assess the role that physiology plays in determining the “normal” diving behavior of individuals, and the significance of variation among similar individuals.

Weddell seals (Leptonychotes weddelli) in McMurdo Sound offer the opportunity to test hypotheses about the role that physiology plays in individual variation in diving behavior. Weddell seals have been studied extensively, and their diving behavior and physiology is 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 have potential effects on
diving patterns (Burns and Testa 1997, Burns and Castellini 1996, Ponganis et al. 1993, Kooyman et al. 1983, Kooyman et al. 1980). Furthermore, many studies of diving behavior have led to the development of techniques to classify dives, and permit reasonable inferences about the purpose of different dive types (Schreer and Testa 1996, Testa 1994, Bengtson and Stewart 1992, Le Boeuf et al. 1992, Hindell 1991, Kooyman 1968). As a result of this knowledge, it may be possible to attribute differences in average dive characteristics to differences in certain types of dives. In addition, these differences might be able to be related 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 (± 3 weeks) and apparently healthy and foraging. In addition, yearlings were instrumented in the same area (± 5 km) and during the same time of year. Still, there remained significant variation between individuals in all measures of diving behavior and physiology.

The goals of this study were 1) to quantify the diving behavior of yearling Weddell seals, 2) to assess the differences in diving behavior among individuals, and 3) to relate observed differences in 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°45'S, 166°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 ± 0.1 kg). Seals were manually restrained while morphometric measurements were taken, a blood sample drawn, and a time depth recorder (TDR, Wildlife Computers, Woodinville, WA, USA, Mark 5 or 6) attached to the mid-dorsal pelage with Devcon™ 5 minute epoxy adhesive. Seals were released as soon as the epoxy hardened. Three to 10 days later, the seals were recaptured, and the TDRs retrieved.

In addition to mass, the axial girth (AG: girth just behind the fore-flippers) and total length (TL: tip of nose to tip of tail) of each seal was measured (accuracy ± 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 + 4.28x10^5(AG^2 * 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, pers. comm).

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 one hour. Hematocrit (Hct) was determined in duplicate using a battery-operated field micro-hematocrit centrifuge (Compur M1100, samples spun at 5400 x g for 3.5 min). Hemoglobin (Hb) content 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 was 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 which exceeded 30 s and 12 m were considered for further analysis in this report (Schreer and Testa 1996, 1995, 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 such that the maximum depth was one and the remaining depths scaled less than one. 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 all dives to be compared regardless of their maximum depth or duration, and permitted the comparison of dive shapes.
A k-means clustering algorithm (Proc FASTCLUS, SAS Institute 1990) was used to assess the number of dive types and to 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 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 also used for determining a suitable number of dive types following Schreer et al. 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 only created 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 1-way ANOVA. Post-hoc comparison of means were made using the Tukey 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) was calculated. This was done for all dives combined, and for dives separated by type. In addition, the dive depth and duration that was exceeded by only 5% of dives was calculated (as Burns and Castellini, 1996). This measure of maximal 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 16:00 to 15:59, 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 from seal-days for which there was complete TDR coverage only. 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

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comparisons using the Tukey (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) in order 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 was
regressed against individual mass, RMI, sex, Hct, Hb, plasma glucose, lactate, specific gravity,
and ketone body concentration. As in the pooled data, 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 arcsin transformed (p' =
\sqrt{\text{arcsin}(p+0.01)}). Correlation analysis was used also 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), then 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, and 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 hours in length, and a cosine function was fitted to the data. Depth and duration were judged to have a significant diel fluctuation if both the first order trigonometric polynomial coefficients (cos \(\omega t\) and sin \(\omega t\)) were significant (\(p < 0.05\)), and if 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 6.1). There also were significant differences among individual seals in the number of dives per day, and average dive depth and duration, as determined by 1-way ANOVA (\(p < 0.001\) in all cases). Yearling Weddell seal dives averaged 120.3 ± 67.1 m and 8.83 ± 1.49 min, and yearlings dove 57 ± 23 (SD) times per day. However, mean dive depths 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 (Figure 6.1). Yet the groups determined from mean depth were not the same as the groups determined from mean duration (12 overlapping groups which contained 3 to 7 individuals each) or average dive frequency (3 overlapping groups).

The individual differences in diving behavior did not appear to be determined by the location of TDR deployment. Figure 6.2 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 haul-out location between TDR deployment and retrieval (furthest movement 33.6 km), and rarely remained within the study area (approximately 160 km²) for more than a week. In addition, all but two 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. There were no significant differences in the mean dive depth of animals tagged in waters < 100 m vs. those tagged in water 100-200 m deep. However, all animals (n = 3) tagged over water > 200 m
were deep divers (ANOVA, $p < 0.05$, Tukey HSD post-hoc comparison of means). 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.

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*Mass + 343), 33% of the variation in mean dive duration (Mean Duration = 0.04*Mass + 3.83) and 49% of the variation in mean dive frequency (Mean Frequency = -0.66*Mass + 146). As mass increased, depth and dive frequency tended to decrease, and dive duration tended to increase (Figure 6.3). Measures of body size (mass, RMI) were also the only variables which 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 maximal dive duration (Maximum Duration = 0.12*Mass - 1.79), but only 22% of the variation in maximal dive depth (Maximum Depth = -2.49*Mass + 558.85). Blood chemistry parameters showed little individual variation and were not correlated with dive parameters (HCT 58.9 ± 2.0%, Hb 25.60 ± 1.15 gm%, Lactate 6.4 ± 0.9 mM, Glucose 7.1 ± 0.3 mM, ketone bodies 0.179 ± 0.088 mM, specific gravity 1.022 ± 0.002 g/ml).

The 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 (Figure 6.4). However, the 95% confidence interval was large (5 am ± 6 hours), 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 am, 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 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 (Figure 6.4), these trends were not significant (periodic regression analysis, $p > 0.05$). However, when the dive patterns of each seal were analyzed separately, six 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 10420 was due to time of day). In these yearlings, the deepest and longest dives occurred mid-day, and the diel pattern was more evident in depth than in duration.

**Dive Types**

The results for cluster analyses performed on all the data and the sub-samples indicated that four clusters (dive shapes) were an appropriate number for this data set. These shapes were Slow Ascent, Slow Descent, U, and Square (Figure 6.5). 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: dives less than 60 m (Shallow U), dives between 60 and 230 m (Mid-Depth U), and dives deeper than 230 m (Deep U). Square dives were divided into two groups: dives shallower than 30 m (Shallow Square) and dives deeper than 30 m (Deep Square).

Table 6.2 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. The results of 1-way ANOVA indicated that not all dive types differed in mean depth, duration, frequency, or proportion (Table 6.2). Shallow U and Shallow Square dives only differed 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, Deep U, and Deep Square, had similar mean dive durations. Similarity between dive types in mean dive depth, duration, or frequency was possible because dive types were based initially on shape and not measures of 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 (22:45 ± 1:00 hr), all other types occurred most frequently in the early morning, with overlap in their 95% confidence intervals between the hours of 2 and 6 am (Table 6.3). 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 more often were distributed non-uniformly (Table 6.3). 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 in seal 10112, while seal 9836 showed diel variation in all types. For the other 13 seals, the proportion of dive types which 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 (Figure 6.6). However, when the yearlings were treated separately, some seals 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 duration.

There was significant variation among individuals in mean dive depth, duration, frequency, and proportion within and between dive types (1-way ANOVA by type, \( p < 0.05 \) in all cases) (Figure 6.7). Mean dive duration differed by individual for all dive types, while mean dive depth, frequency, and proportion differed by individual for all types except Shallow U. Variation among individuals could only be explained partially by differences in seal size. In all instances, stepwise regression procedures demonstrated that mass or RMI were the only measured variables which influenced diving behavior. However, while mass or RMI were often significant, they explained more than half of the variation in diving behavior for only some dive types and measures (Table 6.4). 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 proportion of Square and U-shaped dives. As the proportion of Deep Square dives increased, the proportion of Deep U dives decreased, the mean dive depth and frequency declined, and the mean dive duration increased (\( p < 0.05 \)) (Table 6.5). 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 (Figure 6.8).
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 individuals 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 amount of 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, and the pattern observed in the 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 6.4, $r^2$ ranged between 0.19 to 0.72), few 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 have shown 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 could account for up to 72% of the behavioral variation suggests that the diving behavior of yearling Weddell seals was 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. 1983, Kooyman et al. 1980). 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

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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 the total time spent diving (1.18 to 15.27 hours/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 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 of 8.5 to 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 in order 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 to 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, both in 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 which occur throughout the day.

**Slow Descent** dives were also short, shallow dives that occurred most often in the early morning hours. The Slow Descent dives made by yearlings appeared 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 suggested that these dives were 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, together with the Shallow U and Shallow Square dives, these 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 were thought to represent processing dives or unsuccessful foraging dives where the seal slowly ascended 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, suggested that Slow Ascent dives were similarly associated with foraging behavior.

**Mid-Depth and Deep** L-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 in 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. 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 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 yearling Deep Square dives occurred at depths of less than 100 m, and there was little diel variation in depth, duration, or frequency, 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 which made many U-shaped dives made few Square dives, and seals which made predominantly Deep Square dives made very few 'foraging' dives of other types (see Figure 6.8, Table 6.5).

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 adult 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, fairly shallow, and their depth and duration changed little throughout the day. On average, 26.2 ± 14.5% (combined %) of the dives made by yearlings were classified as Shallow U, Shallow Square, and Slow Descent dives. The remaining dive activity (73.8 ± 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 the course of 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 (Bums 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 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 to represent 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, Ploetz 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
that 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 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 which 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 where both diet and mean dive depth were known to differ. In general, deeper diving
individuals foraged on more energy-dense prey or expended less energy while foraging (Goebel

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 non-breeding animals concentrate their diving and
foraging activity in deep water, and have suggested that the near shore 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 suggested that both deep and shallow diving yearlings faced similar duration constraints. Individual yearlings from both groups exceeded their calculated ADL 16 to 79% of the time, much more frequently than did free-diving adult Weddell seals (5 to 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 not any shorter than pelagic dives suggests that the dives had a low energy return rate, long search and handling times. Pelagic foraging yearlings probably exploited a more energy-dense prey resource, but as their time at depth was limited due to 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 can not 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 homogenous 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 could be explained by differences in body size, a significant amount of variation remained 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 when comparing the diving behavior of different sex and age groups. Finally, this study suggests that all yearlings, whether they are foraging in deep or shallow water, are required to push their physiological limits in order to forage effectively.

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Table 6.1: Capture history, morphological, and physiological data for the 15 Weddell seal yearlings which carried TDRs in McMurdo Sound, Antarctica.

<table>
<thead>
<tr>
<th>ID #</th>
<th>Sex</th>
<th>Dates</th>
<th>Mass (kg)</th>
<th>Length (cm)</th>
<th>Girth (cm)</th>
<th>RMI</th>
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<td>9791</td>
<td>M</td>
<td>Oct. 14-20, 1992</td>
<td>119.2</td>
<td>155</td>
<td>124</td>
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<tr>
<td>9836</td>
<td>M</td>
<td>Nov. 2-9, 1992</td>
<td>141.7</td>
<td>152</td>
<td>133</td>
<td>4.69</td>
</tr>
<tr>
<td>10095</td>
<td>M</td>
<td>Oct. 15-20, 1992</td>
<td>145</td>
<td>172</td>
<td>128</td>
<td>2.46</td>
</tr>
<tr>
<td>10112</td>
<td>F</td>
<td>Oct. 20-25, 1992</td>
<td>155.5</td>
<td>184</td>
<td>130</td>
<td>0.48</td>
</tr>
<tr>
<td>10149</td>
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<td>124</td>
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<tr>
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Table 6.2: Mean ± SE dive depth (m), duration (min), frequency (dives/day), and proportion (% of total dives) for each of the seven dive types made by Weddell seal yearlings in McMurdo Sound, Antarctica. Dive types with the same group code had mean values that did not significantly differ (Tukey HSD post-hoc comparison of means, \( p < 0.05 \)). Groups were determined using one value for each yearling.

<table>
<thead>
<tr>
<th></th>
<th>Shallow U</th>
<th>Shallow Square</th>
<th>Slow Ascent</th>
<th>Slow Descent</th>
<th>Mid-Depth U</th>
<th>Deep Square</th>
<th>Deep U</th>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td>25 ± 0.9</td>
<td>14.5 ± 0.4</td>
<td>132.4 ± 3.1*</td>
<td>45.6 ± 1.8*</td>
<td>150 ± 1.5*</td>
<td>62.4 ± 0.4*</td>
<td>304.3 ± 0.4*</td>
</tr>
<tr>
<td><strong>Maximum</strong></td>
<td>60</td>
<td>30</td>
<td>384</td>
<td>326</td>
<td>231</td>
<td>405</td>
<td>480</td>
</tr>
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<td>a</td>
<td>c, d</td>
<td>a, b</td>
<td>d</td>
<td>b, c</td>
<td>e</td>
</tr>
<tr>
<td><strong>Duration</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><strong>Mean</strong></td>
<td>2.5 ± 0.2*</td>
<td>2.3 ± 0.1*</td>
<td>8.9 ± 0.2*</td>
<td>4.5 ± 0.2*</td>
<td>9.4 ± 0.1*</td>
<td>9.7 ± 0.1*</td>
<td>10.0 ± 0.1*</td>
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<td><strong>Maximum</strong></td>
<td>19.9</td>
<td>12.5</td>
<td>30.7</td>
<td>27.8</td>
<td>29.9</td>
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<td><strong>Group</strong></td>
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<td>b</td>
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<td>b</td>
<td>b</td>
<td>b</td>
</tr>
<tr>
<td><strong>Frequency</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td>3 ± 0.3</td>
<td>2.4 ± 0.3</td>
<td>7.5 ± 1*</td>
<td>7.3 ± 0.7*</td>
<td>12 ± 1.8*</td>
<td>12.9 ± 1.7*</td>
<td>14.7 ± 2.6*</td>
</tr>
<tr>
<td><strong>Maximum</strong></td>
<td>12</td>
<td>12</td>
<td>39</td>
<td>22</td>
<td>55</td>
<td>55</td>
<td>73</td>
</tr>
<tr>
<td><strong>Group</strong></td>
<td>a</td>
<td>a</td>
<td>a</td>
<td>a, b</td>
<td>b, c</td>
<td>b, c</td>
<td>c</td>
</tr>
<tr>
<td><strong>Proportion</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td>6 ± 1</td>
<td>5.7 ± 0.6</td>
<td>11.5 ± 1.4*</td>
<td>13.9 ± 1.6</td>
<td>17 ± 2</td>
<td>26.9 ± 3.3*</td>
<td>19 ± 3.2*</td>
</tr>
<tr>
<td><strong>Maximum</strong></td>
<td>18.2</td>
<td>21.8</td>
<td>46.9</td>
<td>54.6</td>
<td>60</td>
<td>85.7</td>
<td>84.2</td>
</tr>
<tr>
<td><strong>Group</strong></td>
<td>a</td>
<td>a</td>
<td>a, b</td>
<td>a, b</td>
<td>b</td>
<td>c</td>
<td>b, c</td>
</tr>
</tbody>
</table>

* indicates significant variation between individual means \( (p<0.05) \).
Table 6.3: Diel Variation in dive frequency by type. The mean time ± 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.

<table>
<thead>
<tr>
<th>Dive Type</th>
<th>Number of Dives</th>
<th>Mean Time</th>
<th>Yearlings with Diel Cycle</th>
<th>Time of Peak Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slow Ascent</td>
<td>510</td>
<td>22:40 ± 5:34 ‡</td>
<td>8/11 (73%)</td>
<td>20:06 - 3:44</td>
</tr>
<tr>
<td>Slow Descent</td>
<td>547</td>
<td>4:18 ± 6:30 ‡</td>
<td>5/12 (42%)</td>
<td>22:15 - 3:32</td>
</tr>
<tr>
<td>Shallow U</td>
<td>203</td>
<td>5:43 ± 7:50 †</td>
<td>1/9 (11%)</td>
<td>5:58</td>
</tr>
<tr>
<td>Mid-Depth U</td>
<td>806</td>
<td>23:12 ± 8:29 *</td>
<td>7/11 (64%)</td>
<td>19:23 - 4:45</td>
</tr>
<tr>
<td>Deep U</td>
<td>1003</td>
<td>5:48 ± 6:23 ‡</td>
<td>6/7 (66%)</td>
<td>0:17 - 5:00</td>
</tr>
<tr>
<td>Shallow Square</td>
<td>213</td>
<td>5:18 ± 7:24 *</td>
<td>3/10 (30%)</td>
<td>1:43 - 5:17</td>
</tr>
<tr>
<td>Deep Square</td>
<td>902</td>
<td>2:30 ± 10:10</td>
<td>8/12 (66%)</td>
<td>19:03 - 3:29</td>
</tr>
</tbody>
</table>

* Non-uniform at p<0.05, † non-uniform at p<0.01, ‡ non-uniform at p<0.001.
Table 6.4: Morphometric factors that significantly influenced dive parameters for yearling Weddell seals in McMurdo Sound, Antarctica. Regression analysis was 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>
<thead>
<tr>
<th>Type</th>
<th>Mean Depth (m)</th>
<th>Maximal Depth (m)</th>
<th>Mean Duration (min)</th>
<th>Maximal Duration (min)</th>
<th>Frequency (dives/day)</th>
<th>Proportion (% dives by type)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slow Ascent</td>
<td>-1.19 Mass, ( r^2 = 0.27 )</td>
<td>+0.09 Mass, ( r^2 = 0.43 )</td>
<td>+0.18 Mass, ( r^2 = 0.5 )</td>
<td>-0.16 Mass, ( r^2 = 0.32 )</td>
<td>-0.3 Mass, ( r^2 = 0.3 )</td>
<td></td>
</tr>
<tr>
<td>Slow Descent</td>
<td>+0.04 Mass, ( r^2 = 0.19 )</td>
<td>-0.25 RMI, ( r^2 = 0.52 )</td>
<td>-0.6 RMI, ( r^2 = 0.46 )</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shallow U</td>
<td>+0.21 Mass, ( r^2 = 0.48 )</td>
<td>+0.11 Mass, ( r^2 = 0.36 )</td>
<td>+0.18 Mass, ( r^2 = 0.45 )</td>
<td>-0.04 RMI, ( r^2 = 0.31 )</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mid-Depth U</td>
<td>-0.81 Mass, ( r^2 = 0.53 ), +1.2 RMI</td>
<td>+0.13 Mass, ( r^2 = 0.34 )</td>
<td>+0.15 Mass, ( r^2 = 0.38 )</td>
<td>-0.16 Mass, ( r^2 = 0.25 )</td>
<td>-0.3 Mass, ( r^2 = 0.19 )</td>
<td></td>
</tr>
<tr>
<td>Deep U</td>
<td>+2.4 RMI, ( r^2 = 0.31 )</td>
<td>+0.12 Mass, ( r^2 = 0.4 )</td>
<td>+0.16 Mass, ( r^2 = 0.41 )</td>
<td>-0.64 Mass, ( r^2 = 0.31 )</td>
<td>-0.7 Mass, ( r^2 = 0.31 )</td>
<td></td>
</tr>
<tr>
<td>Shallow Square</td>
<td>+0.09 RMI, ( r^2 = 0.21 )</td>
<td>+0.19 RMI, ( r^2 = 0.27 )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deep Square</td>
<td>+0.7 Mass, ( r^2 = 0.25 )</td>
<td>+0.15 Mass, ( r^2 = 0.5 )</td>
<td>+0.36 Mass, ( r^2 = 0.5 )</td>
<td>+0.8 Mass, ( r^2 = 0.52 )</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 6.5: The correlation coefficients between mass (kg), mean dive depth (m), duration (min), and frequency (# dives/day) for all dive types combined, and the mean daily proportion of dives of each type made by yearling Weddell seals. — indicates that there was no significant correlation (p > 0.05).

<table>
<thead>
<tr>
<th></th>
<th>Mass Depth</th>
<th>Mean Duration</th>
<th>Mean Frequency</th>
<th>% Slow Ascent</th>
<th>% Slow Descent</th>
<th>% Shallow U</th>
<th>% Mid-Depth U</th>
<th>% Deep U</th>
<th>% Shallow Square</th>
<th>% Deep Square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Depth</td>
<td>-0.67</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean Duration</td>
<td>0.70</td>
<td>-0.72</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean Frequency</td>
<td>-0.68</td>
<td>0.70</td>
<td>-0.67</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Slow Ascent</td>
<td>-0.55</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Slow Descent</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Shallow U</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.70</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Mid-Depth U</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.61</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Deep U</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-0.58</td>
</tr>
<tr>
<td>% Shallow Square</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.64</td>
</tr>
<tr>
<td>% Deep Square</td>
<td>0.72</td>
<td>-0.84</td>
<td>0.87</td>
<td>-0.65</td>
<td>-0.56</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.87</td>
</tr>
</tbody>
</table>
Figure 6.1: The relationship between mean (± SE) dive depth and duration. Dashed circles indicate the different overlapping groups in which the mean depth (A) or duration (B) did not significantly differ ($p < 0.05$ Tukey HSD).
Figure 6.2: Yearling location at either TDR deployment of recovery. Dark circles indicate deep divers (mean depth > 100 m) and open circles indicate shallow divers (mean depth < 100 m). Ocean depth (m) is indicated by the dashed bathymetric 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 which were tagged in close proximity to each other.
Figure 6.3: The relationship between mass and mean (± 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.
Figure 6.4: Diel variation in the total number of dives (A), mean dive depth (B), and duration (C) for all yearlings combined.
Figure 6.5: The shape of the four main dive types determined by cluster analysis.
Figure 6.6: Diel variation in the mean dive depth and duration for each of the seven dive types, all yearlings combined.
Figure 6.7: Mean dive depth (A), duration (B), and proportion (C) of total dives per day for each dive type and yearling. Dive types are: 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 number.
Figure 6.8: The mean daily proportion of total Deep Square and Deep U dives for all yearlings.
LITERATURE CITED


Chapter 7: The diet of Weddell seals in McMurdo Sound Antarctica as determined from scat collections and stable isotope analysis.

ABSTRACT

The diet of adult and juvenile Weddell seals (Leptonychotes weddellii) in McMurdo Sound, Antarctica, was determined from both scat and stable isotope analyses, to ascertain if foraging behavior varied with age, season, or diving pattern. Scats were collected over five years and recovered hard parts identified. Stable carbon and nitrogen isotope values were determined for seal blood samples and potential prey items and used to identify primary prey species and assess trophic interactions. Pleuragramma antarcticum remains were recovered from between 70 and 100% of the scats, and provided little evidence for interannual or age specific variation in foraging behavior. However stable isotope and dive data analyses indicated that while most seals foraged predominantly on pelagic fish and squid, some juveniles concentrated on shallow benthic Trematomus spp. Combining these three methods permitted strong conclusions about diet and foraging behavior.

INTRODUCTION

The diet of Weddell seals (*Leptonychotes weddellii*) in Antarctica has been well studied, and is generally thought to consist mainly of nototheniid fishes, cephalopods, prawns, and other small invertebrates (Castellini et al. 1992, Plötz et al. 1991, Green and Burton 1987, Plötz 1986, Testa et al. 1985, Clarke and MacLeod 1982, Dearborn 1965, Bertram 1940, Lindsey 1937). Differences in diet due to location, season, and age of seal have been documented in Weddell seal populations outside of McMurdo Sound, as well as in many other marine mammal species (Slip 1995, Boyd et al. 1994, Green and Burton 1993, 1987, Haug et al. 1991, Plötz et al. 1991, Croxall et al. 1988, Laws 1984, Sergeant 1973, Bertram 1940, Lindsey 1937). In general, the prey species consumed by marine mammals that are not specialist foragers varies seasonally, with foraging location, or with animal age. Within McMurdo Sound, little is known about dietary variation among individuals or by season, but given the large shifts in population structure and environmental conditions that occur through the year, such variation is likely to exist (Castellini et al. 1992, Testa et al. 1991, 1985). Other factors that may affect foraging behavior are sea ice extent, air temperature, El Niño- Southern Oscillation index, and fluctuations in prey abundance (Testa et al. 1991, Croxall et al. 1988, Bengtson and Laws 1985, Laws 1984).

Most studies on the foraging behavior of Weddell seals and other marine mammals have determined diet from scats, vomitus, or stomach contents (for review, Croxall 1993). These techniques rely on the identification of the remains of prey item hard parts, and are associated with unavoidable errors due to the nature of the collection methods. All of these samples are single "snapshots" of the most recent diet and, therefore, may not be representative of the overall diet. In addition, recovered prey parts are often too far digested to permit identification, and the contribution of soft bodied prey to the diet can be significantly underestimated. Technical and logistical difficulties associated with collecting a sufficiently large and representative sample can also constrain the interpretation of the data (Tollit et al. 1997, Croxall 1993, Gales and Cheal 1992, Harvey 1989, Murie and Lavigne 1986, 1985, daSilva and Neilson 1985, Pitcher 1980). To avoid some of these difficulties, researchers have made inferences about marine mammal diets based on diving patterns and the presumed foraging location and behavior of potential prey items. However, this method also suffers from errors and biases because the actual purpose of dives is not known. Furthermore, as marine mammals may forage selectively, without observations of prey capture it is difficult to determine if dives to certain depths or regions actually represent foraging activity (Burns et al. press, Schreer and Testa 1996, Testa 1994, Bengtson and Stewart 1992, Le Boeuf et al. 1992, Hindell et al. 1991, Kooyman 1968).
Analysis of stable isotope ratios in animal tissues has recently emerged as a powerful technique for determining the trophic level at which foraging occurs, and the importance of different prey items in the diet (Hobson et al. 1997, Hobson and Welch 1992, Rau et al. 1991, Wada et al. 1991, Owens 1987, Wada et al. 1987). Tropho-dynamic research using stable isotopes generally focuses on carbon and nitrogen, since the isotopic ratio of these elements varies in relation to the diet, trophic level, and foraging location (Hobson and Welch 1992, Owens 1987). The carbon and nitrogen isotope values (δ\text{13}C and δ\text{15}N) differ between organisms and their diets because of selective retention and excretion of the heavy and light isotope. Fractionation occurs because the lighter isotope has a lower activation energy for bond breakage, reacts more often, and is therefore more likely to be excreted. As a result, organisms tend to retain the heavier isotope, become enriched, and have a higher δ value than their diet (Owens 1987). Because this is a long term process, stable isotope ratios in tissue reflect the diet over the past weeks to months (Hobson et al. 1997, Tieszen et al. 1983, Hirons et al. subm.).

Generally, there is an enrichment of approximately 3.0‰ in nitrogen and 0.8‰ in carbon per trophic level (Wada et al. 1991, Owens 1987, Fry and Sherr 1984, Minagawa and Wada 1984, DeNiro and Epstein 1981, 1978). Differences in nitrogen isotope ratios are frequently used to predict trophic level, and in cases where the isotopic ratios of different prey items are known, actual diet (Wada et al. 1991, Minagawa and Wada 1984, Schrenninger and DeNiro 1984, DeNiro and Epstein 1981). However, because carbon isotope ratios differ more between terrestrial vs. marine, inshore vs. offshore, and pelagic vs. benthic food webs than by trophic level, carbon has more often been used to assess foraging location (France 1995, Schell et al. 1989, Fry and Sherr 1984, Schrenninger and DeNiro 1984, DeNiro and Epstein 1978). The interpretation of δ\text{13}C values may also be complicated by a strong correlation between δ\text{13}C and tissue C:N ratio, which varies inversely with lipid content (Hobson and Welch 1992, Rau et al. 1992, 1991, Tieszen et al. 1983, McConnaughey and McRoy 1979). While differences in δ\text{15}N and δ\text{13}C among organisms and tissues can arise from a variety of factors, when all are taken into consideration, stable isotope methods have proven to be powerful tools for understanding animal diet. This is especially true when stable isotope techniques have been combined with the more traditional dietary analysis methods (Hobson et al. 1997).

By using a combination of scat and stable isotope analysis in this study, our aim is to determine if the diet of Weddell seals in McMurdo Sound varies with age, sex, season, or diving pattern. Weddell seals in McMurdo Sound provide a unique opportunity to test the relationship between

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the diet as determined by scat and stable isotope analysis and as indicated from foraging and diving behavior. This is possible because the prey base within McMurdo Sound has been well studied. One family, the Nototheniids, dominates the ecosystem, with one species, *Pleuragramma antarcticum*, making up more than 90% of the fish biomass (Eastman 1985, Everson 1985). In addition, scat and tissue collection is relatively simple, and the diving behavior of adults and juveniles has been previously documented (Burns et al. in press, Burns and Testa 1997, Schreer and Testa 1996, Testa 1994, Castellini et al. 1992, Macdonald et al. 1987, Eastman 1985, Everson 1985, Testa et al. 1985). It should therefore be possible to construct, and then compare, the diet of adults and juveniles using the different available methods.

**METHODS**

**Scat Collection and Analysis**

All identifiable seal scats within a 0.25 km² area at Cape Evans, Ross Island, Antarctica (77.63°S, 166.40°E) were collected once yearly between 1989 and 1993. Collected scats were placed into individually labeled Whirl-pak® bags, and kept frozen until cleaning and analysis. In addition to these samples, scats were opportunistically collected from individuals of known age within the Erebus Bay region between 1992 and 1994.

Hard part remains were separated from the scats by two methods. Samples collected in 1989, 1990, and 1992 were processed using a series of progressive sieves (4.0, 2.0, and 0.8 mm), while samples collected in 1991, 1993, and 1994 were processed using an elutriator system which separated fecal material from hard parts using a running water/density gradient (Croxall 1993, Murie and Lavigne 1985). All hard parts recovered from the scats were sorted under a dissecting microscope. The following parts were separated and identified: teleost sagittal otoliths, cephalopod beaks, fish bones, eye lenses, crustacean fragments, and other invertebrate remains. Vertebrae of the Antarctic silverfish, *Pleuragramma antarcticum*, were separately identified and recorded based on the unique and large central lumen and the general fragility of the bones (Castellini et al. 1992, Macdonald et al. 1987, Eastman and DeVries 1982). All sagittal otoliths and cephalopod beaks were keyed to the lowest taxon possible, unless too badly eroded, and sagittal otoliths were measured to the nearest 0.1 mm (Hecht 1987, Fischer and Hureau 1985, Okutani and Clarke 1985, Clarke 1980). Several scats contained small, badly eroded cephalopod beaks that could not be identified in house; these were sent to the National Marine Mammal Laboratory in Seattle, WA and to Pacific Identifications in Vancouver, B.C. The beaks
were determined to have come from a small *Brachioteuthiid* squid, tentatively identified as *B. picta* (William Walker, pers. comm.). In addition, all identifiable invertebrate fragments found in the 1989 scat samples were classified to the family level.

The percent frequency of occurrence of prey items in Weddell seal scats was determined for each year and seal age class individually. For *P. antarcticum*, fish length was estimated using regression equations that related otolith diameter to fish length (Hubold and Tomo 1989, Hecht 1987, Kock et al. 1985). All *Trematomus* spp. otoliths were treated as if they had come from *T. bernacchii*, and the fish lengths were estimated using equations from Hecht (1987). Fish mass was not estimated because different equations in the literature produced values that differed by more than 100% (Radtke et al. 1993, Hubold and Tomo 1989, Hecht 1987, Kock et al. 1986). Before calculating fish lengths, otolith diameters were first corrected to account for erosion in the digestive process using the factor of 1.275 determined for small fishes by Harvey (1989) (see also Tollit et al. 1997, Murie and Lavigne 1986, daSilva and Neilson 1985). Comparison between years in the mean size of *P. antarcticum* eaten was performed using one-way ANOVA techniques with significance assumed at \( p < 0.05 \). Tukey HSD post-hoc comparison of means were used to identify groups (overall \( p < 0.05 \)). We did not estimate the size of squid eaten by Weddell seals because, for most species, few beaks were retrieved. The size of *B. picta* eaten by seals could not be accurately estimated because the rostral length of the beak was < 2 mm and beaks were extremely eroded.

**Stable Isotope analyses**

Blood samples were collected between 1992 and 1994 from known aged pups (\( n = 16 \)), yearlings (\( n = 14 \)) and adults (6 males, 6 females). The blood collection and handling techniques have been described by Rea (1995), and plasma samples were kept frozen at -80°C until analyzed. Four species of notothenid fishes, *P. antarcticum, Dissostichus mawsoni, Pagotthenia borchgrevinki*, and *T. loennbergii*, as well as the eelpout, *Rhigophilia dearborni*, were collected opportunistically in the field and stored frozen until analysis. Stable isotope values for *T. bernacchii* determined by Wada et al. (1987) were also used in the analyses of foraging behavior.

The C:N ratio and the \( \delta^{15}N \) and \( \delta^{13}C \) stable isotope ratios in Weddell seal blood plasma and selected prey items were analyzed as follows. Plasma samples (1 ml) and prey muscle samples (1 gm) were dried at 60°C, ground for homogeneity, and prepared for mass spectrometry (Schell and Hirons 1997, Schell et al. 1989). All carbon and nitrogen isotope ratios were determined in...
duplicate with a Europa™ 20/20 continuous flow mass spectrometer. Stable isotope ratios are expressed in del (δ) notation according to the following equation:

$$\delta X (\%) = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000$$

where X is $^{13}$C or $^{15}$N and R is the ratio of $^{13}$C/$^{12}$C or $^{15}$N/$^{14}$N in the standard or sample. The standard for carbon was Pee Dee Belemnite and atmospheric N$_2$ was the standard for nitrogen (DeNiro and Epstein 1981, 1978). Analytical error for both carbon and nitrogen was ± 0.1‰, and samples were reanalyzed if the difference between duplicates was greater than 0.5‰. The total amount of carbon and nitrogen in the samples was determined by the mass spectrometer, and the ratio of total carbon to total nitrogen calculated. Analytical error in the C:N ratio was ± 0.10.

The $\delta^{15}$N, $\delta^{13}$C, and C:N ratios were compared among seals of different age, sex, year, and foraging behavior using one-way ANOVA techniques. Significance was assumed at $p < 0.05$. The effect of collection year and sex on these ratios was tested within each age class (adult, yearling, or pup) and, if there was no significant difference in the $\delta^{15}$N, $\delta^{13}$C, or C:N ratio between years or sexes, groups were pooled. The effects of age and foraging behavior were subsequently tested. Yearlings were subdivided into three categories: shallow divers (mean dive depth < 100 m, $n = 4$), deep divers (mean dive depth > 100 m, $n = 6$), and yearlings with no dive records (NDR yearlings, mean dive depth unknown). These categories were based on dive records that had previously been analyzed (Burns et al. in press). The $\delta^{15}$N, $\delta^{13}$C, and C:N ratios were then compared between adults, pups, deep, shallow and NDR yearlings. Seal groups were pooled if there were no significant differences in any measured ratio. Finally, linear regression techniques were used to test for the effect of the C:N ratio on the $\delta^{13}$C value determined for all seals. The regression was judged significant if $p < 0.05$ and the residuals were normally distributed.

Due to the small sample sizes for individual fish species, we did not test for differences in the $\delta^{15}$N and $\delta^{13}$C stable isotope ratios. However, as the C:N ratio differed among species, linear regression techniques were used to test for the effect of the C:N ratio on the $\delta^{13}$C values. As with the plasma samples, the regression was judged significant if $p < 0.05$ and the residuals were normally distributed.

To better understand the foraging behavior of Weddell seals in McMurdo Sound, the isotopic values determined for the different groups of seals were compared to those of the prey items collected. As stable isotope ratios in blood plasma have been shown to be similar to those of other marine mammal tissues (with the exception of blubber and keratin), we assumed the blood
values to be representative of the animal as a whole (Tieszen et al. 1983, DeNiro and Epstein 1981, 1978, A. Hirons pers. comm.). In constructing the food web, predators were assumed to be approximately 3% enriched in $\delta^{15}N$ over their prey. The $\delta^{13}C$ value was assumed to remain relatively constant across trophic levels, provided that habitats and C:N ratios were similar (Rau et al. 1992).

RESULTS

Scat Analysis

Between 1989 and 1993, 189 scats were collected from the sampling site at Cape Evans. Eight scats were collected between 1992 and 1994 from known age animals (1 adult, 5 yearlings, 2 pups). Tables 7.1 and 7.2 show the number and types of prey hard parts identified from scats. The most common prey item, as determined by both numbers and frequency of occurrence was *P. antarcticum*. Other fishes identified from recovered otoliths were *T. bernacchii* and other *Trematomus* species. Identifiable remains from these fishes were found in only a few scats (2.7%), and did not appear to make up a significant proportion of the diet. However, as *P. antarcticum* bones were found in 88.4% of the scats and otoliths in only 10.6% of the scats, it is possible that the *Trematomus* species were underrepresented in this Weddell seal diet sample because no other hard parts from these fishes were uniquely identifiable. Eleven percent of the recovered otoliths could not be identified due to breakage or severe erosion.

Forty-seven cephalopod beaks were recovered from the scats collected at Cape Evans from seals of unknown age, and another 765 from scats collected from four juveniles (1 pup and 3 yearlings). All identified beaks came from squid: three from an unidentified *Histiotethuid* species, two from *Gonatus antarcticus*, two from *Kondakovia longimana*, and one from an unidentified *Mastigoteuthid* species. The bulk of the beaks, 804, were badly eroded lower beaks of the small *Brachioteuthid* squid tentatively identified as *B. picta*.

While a wide variety of invertebrates were identified from the scats collected in 1989 (Table 7.3), the vast majority of these items were benthic invertebrates of less than 5 mm in size. Because of their small size, and the fact that these items form the bulk of the fish diet in McMurdo Sound, these items were thought to have been ingested secondarily. More than half of the scats collected in 1989 contained parasites, the majority of which were nematodes.
The mean size of the sagittal otoliths recovered from the scat samples, and the estimated length of the *P. antarcticum* and *Trematomus* species consumed are shown in Table 7.4. There was significant inter-annual variation in the estimated mean length of *P. antarcticum* eaten (Figure 7.1) as otoliths collected in 1989 and 1990 were significantly larger than those collected from 1991 to 1994 (1 way ANOVA $p=0.000$, Tukey HSD post-hoc comparison of means, $p < 0.05$). While the number of fish otoliths per scat collected (mean of $0.9 \pm 3.3$ (SD) otoliths/scat) did not differ among years ($p = 0.49$), the fewest otoliths were recovered in 1992, and 1992 had the lowest proportion of scats with remains from *P. antarcticum* and other fishes.

An examination of the percent frequency of occurrence of prey items from scats of known age animals to that of the whole sampled population (the Cape Evans scat collection) suggested that juveniles may have eaten more invertebrates and benthic fishes. Similarly, the mean *P. antarcticum* otolith diameter and estimated fish length was smallest in the youngest animals (Table 7.2). However, these samples were too unbalanced to permit any statistical tests, and the conclusions are necessarily tentative.

**Stable Isotope Analysis**

The stable isotope ratios determined from the Weddell seal plasma samples are shown in Figure 7.2. There were no significant differences in the $\delta^{15}N$, $\delta^{13}C$, and C:N ratios by collection year or sex within any group ($p < 0.05$ in all cases), so samples from males and females from all years were pooled for among group comparisons. While there were no significant differences in the $\delta^{15}N$ ratio among adults and any group of yearlings, nursing pups did have a slightly elevated $\delta^{15}N$ value when compared to adult females (mean difference of 0.8%). The mean $\delta^{15}N$, $\delta^{13}C$, and C:N ratios for all groups of seals are given in Table 7.5.

While the C:N ratio of seal blood was significantly correlated with its $\delta^{13}C$ value ($\delta^{13}C = -1.61 \times \text{C:N ratio} -19.06$, $n = 42$, $p < 0.001$, $r^2 = 0.53$, Figure 7.3a), there were no significant differences in the C:N ratio among adults and foraging yearlings. However pups did have a slightly higher C:N value than all other seals (Table 7.5). Despite the similarity in $\delta^{15}N$ and C:N ratio, adults and all yearlings were not pooled because there were significant differences in their $\delta^{13}C$ values.

Shallow diving yearlings had significantly enriched $\delta^{13}C$ values relative to those of adults, deep diving and NDR yearlings (Table 7.5).

The stable isotope and C:N ratios of Weddell seal prey items are shown in Table 7.6. There were clear differences in the isotopic ratios between prey items, with the large Antarctic cod,
Dissostichus mawsoni, the most nitrogen enriched and carbon depleted. The C:N ratios also differed by prey, with the most δ13C depleted species having the highest C:N ratio (δ13C = -0.81*C:N ratio - 22.73, n = 15, p < 0.001, r² = 0.79, Figure 7.3b). Figure 7.4 combines the stable isotope information from predator and prey. Note that when the mean δ13C values for P. antarcticum and D. mawsoni were adjusted to reflect a C:N ratio of 3.75 (the mean for foraging seals) using the regression equation above, their δ13C value, -25.8‰, was similar to those of all seals except shallow diving yearlings.

DISCUSSION

There was general agreement between the diet determined for Weddell seals by scat analysis and the diet and trophic level estimated from stable isotope analyses. In addition, the diet estimated by both techniques agreed with observed diving behavior and with previous studies on the diet of Weddell seals in McMurdo Sound (Castellini et al. 1992, Green and Burton 1987, Testa et al. 1985, Dearborn 1965). While each technique had associated biases and uncertainties, by combining these methods it was possible to more completely characterize the diet of Weddell seals than would otherwise have been possible.

The scats collected at Cape Evans over five years indicated that there was remarkably little variation in the diet of Weddell seals. In all years, P. antarcticum was the primary constituent of the diet, and remains were found in 70 to 100% of the collected scats. Otoliths from other nototheniids were rare, as were cephalopod remains. However, given the absence of P. antarcticum otoliths from many of the scats in which vertebrae were found, and the extremely eroded condition of many of the otoliths and all of the small B. picta beaks, it is possible that both small fishes and squids were eaten more commonly than indicated by recovered remains. Crustacean and mollusc parts were found in approximately a quarter of the scats collected each year, but it is likely that the majority of the amphipods, mysid shrimps, molluscs, and polychaetes came from the stomachs of ingested fishes, as all nototheniids in McMurdo Sound are known to forage on these items (Everson 1985, Eastman 1985, Dearborn 1965, Bertram 1940). Euphausiids and prawns, which were more common than fishes in the stomachs of seals collected in Davis Sound (Green and Burton 1987) have never been identified as important food items for seals in McMurdo Sound, probably due to their absence in large numbers from this ecosystem (Everson 1985, Eastman 1985).
The mean size of *P. antarcticum* otoliths recovered from the collected scats, 1.4 mm, was at the low end of the size range reported in other studies from throughout Antarctica (1.4 to 1.8 mm) (Castellini et al. 1992, Green and Burton 1987, Plötz 1986). However, the majority of otoliths recovered in these other studies came from stomach samples, and were probably less eroded than those we recovered from scats (Croxall 1993). Fish standard length calculated using the corrected otolith diameters indicated that, as in other areas of Antarctica, the mean size class of *P. antarcticum* eaten was 141 mm (Castellini et al. 1992, Green and Burton 1987, Plötz 1986). While there was some variation in the size of fish eaten, differences between years were small. However, if the calculated fish sizes are correct, these small differences may be significant. *P. antarcticum* reaches maturity at approximately 140 mm and the mean length of of fish ingested in 1989 and 1990 indicated that most fish eaten were mature. However, otoliths collected between 1991 and 1993 suggested that more immature fish were taken (see Figure 7.1). We do not know if this shift is indicative of changes in the ecosystem, circulation patterns, fish growth rates and availability, or if it is an artifact from the calculations of fish size. In any case, as *P. antarcticum* larger than approximately 120 mm are generally found at depths greater than 200 m, it was not surprising that the mean depth of foraging dives for adults and most yearlings was greater than 200 m (Burns et al. in press, Schreer and Testa 1996, Testa 1994, Castellini et al. 1992, Radtke et al. 1993, Hubold and Tomo 1989, Kellermann 1986, Eastman 1985, Hubold 1985, 1984).

While we did not estimate the size of squid eaten, *B. picta*, the most common species identified, is not thought to reach sizes in excess of 15 cm (mantle length) (Fischer and Hureau 1985, W. Walker pers. comm.). In Antarctic waters, *B. picta* has been caught in trawls from the surface to the bottom (> 1000 m), but is thought to occur predominantly below 200 m during the day (Rodhouse and Piatkowski 1995, Rodhouse 1990, 1989, Filipppova 1972). Commonly caught in research nets, *B. picta* has been seen in the diet of Southern Elephant seals (*Mirounga leonina*), Weddell seals, and sperm whales (*Physeter catodon*), and its absence in the diet of other Antarctic predators has been remarked upon (Rodhouse and Piatkowski 1995, Slip 1995, Green and Burton 1993, Rodhouse et al. 1992, Rodhouse 1990, Clarke and MacLeod 1982). While cephalopod beaks have generally been thought to be indigestible (Harvey 1989, Clarke and MacLeod 1982), heavily eroded beaks of the market squid, *Loligo opalescens*, have been found in the stomachs of Emperor penguins (*Aptenodytes forsteri*, Pütz 1995), and “a fine gravel composed entirely of fragmented (squid) beaks” was found in Weddell seal stomachs by Bertram (1940). Seals may retain squid beaks for long periods of time (Gales et al. 1993, Pitcher 1980) and, if the beak fragments retrieved in this study are any indication, then perhaps the absence of...
B. picta from the estimated diet of many marine animals is due to erosion of these small beaks during the digestive process.

Inferences about seasonal variation in the diet of seals in McMurdo Sound rely on the assumption that scats collected from Cape Evans were deposited throughout the year, as has been supported by animal tracking and observational studies (Testa 1994; Burns et al. Subm.). If this assumption is valid, then there was little evidence for seasonal or annual variation in the diet. The contents of all collected scats were similar, and very few 'unusual' scats were found. While comparable to other studies in McMurdo Sound, this differs from observed seasonal variation in the diet of Weddell seals from the Weddell Sea which foraged mainly on *P. antarcticum* in the summer but concentrated on other species in the spring (Castellini et al. 1992, Plötz et al. 1991, Green and Burton 1987, Plötz 1986). It may be that seasonal variation is more common in lower Antarctic latitudes or in areas where the prey base is more diverse. In McMurdo Sound, *P. antarcticum* makes up more than 90% of the fish biomass, so it is not surprising that it is the major prey of the local Weddell seal population (Eastman 1985, Everson 1985).

Variation in the diet due to age was difficult to test because of the limited number of scats collected from known age animals. However, it appeared that younger animals may have been foraging on smaller fishes or more cephalopods than the population as a whole. Ontogenetic shifts in diet have been observed in some phocid species, and are generally apparent when juveniles are unable to efficiently capture the prey consumed by adults due to physiological constraints on dive depth and duration (Slip 1995, Haug et al. 1991, Lydersen et al. 1991, Sergeant 1973). Studies on the diving behavior of juvenile Weddell seals have suggested that young animals are capable of reaching the depths selected by foraging adults, but that dive durations are limited by smaller body size and immature physiological processes (Burns et al. in press, Burns and Testa 1997, Burns and Castellini 1996, Kooyman et al. 1983). To avoid direct competition with adults, juvenile Weddell seals may forage in different locations, but as yet, studies have been unable to determine if they concentrate their foraging on different prey (Burns et al. In press, Burns and Testa 1997).

The diet of Weddell seals estimated based on the examination of the stable isotope ratios in seal blood and fish tissues was remarkably similar to that determined from scat samples. While there was a wide range in the $\delta^{15}N$ values among individuals, there were no significant differences due to animal age, sex, year of sample collection, or diving behavior. This similarity indicated that all
seals in this study had been foraging at a similar trophic level during the previous eight weeks. The slight enrichment in δ¹⁵N between nursing pups and adult females was expected as pups were effectively 'foraging' on their mothers (Hobson et al. 1997). When the mean δ¹⁵N values for seals were compared to those of the potential prey items, it appeared that foraging Weddell seals of all ages were feeding primarily on *P. antarcticum*, *P. borchgrevinki*, and/or *Trematomus* species. As expected for a single trophic level increase there was approximately a 2.5% enrichment in δ¹⁵N between seals and these prey items, (Hobson et al. 1997, Rau et al. 1992, Wada et al. 1991, Owens 1987). *D. mawsoni* and *R. dearborni* had δ¹⁵N values similar to those of the seals, and therefore could not have contributed significantly to the seal's diet.

Unfortunately, we did not have specimens or reported isotopic ratios for any cephalopods found in the diet, or for the five other *Trematomus* species known to occur within McMurdo Sound (Macdonald et al. 1987). Therefore, using only the δ¹⁵N values, it was impossible to determine the relative importance of some of the prey items that appeared in scat samples, or to distinguish which of several small nototheniids were most important in the diet. This difficulty results from the dietary and trophic level overlap (and therefore similar δ¹⁵N values), of most nototheniids in McMurdo Sound (Eastman 1985, Everson 1985).

In contrast to the nitrogen data, there was significant variation in the δ¹³C and C:N values between the five fish species, fishes and seals, and seals with dissimilar diving patterns. These differences were helpful in determining the relative importance of individual prey species and foraging locations to Weddell seals feeding in McMurdo Sound. Because nototheniid fishes use lipid as a means for controlling buoyancy, the lipid content (and therefore δ¹³C and C:N ratios) of different species is strongly correlated with their lifestyle, and this is reflected in their C:N ratios and δ¹³C values (Hobson and Welch 1992, Rau et al. 1992, 1991, Reinhardt and Van Vleet 1986, Eastman 1985, Clarke et al. 1984, Tieszen et al. 1983, McConnaughey and McRoy 1979). The high lipid content of the more active, pelagic fishes such as *P. antarcticum* and *D. mawsoni* was reflected in their high C:N ratio and low δ¹³C values. The cryopelagic lifestyle of *P. borchgrevinki* is indicated by their intermediate lipid levels, C:N, and δ¹³C values. The more benthic and sedentary *Trematomus* species had the lowest lipid levels of all the nototheniids and also the lowest C:N and δ¹³C values measured in this study (Friedrich and Hagen 1994, Macdonald et al. 1987, Clarke et al. 1984). In addition, as benthic habitats are carbon enriched relative to the pelagic system due to the different dynamics surrounding carbon uptake by benthic and pelagic algae (France 1995, Fry and Sherr 1984), the high δ¹⁵C values seen in the
Trematomus species probably resulted both from their lower lipid content and their benthic habitat.

Unlike the fishes, there were differences in the seals' $\delta^{13}C$ values that were not clearly related to differences in their C:N ratios. All foraging seals had approximately the same C:N ratios, but the $\delta^{13}C$ values of shallow diving yearlings were significantly enriched in comparison to adults, and other yearlings. This suggested that shallow diving yearlings were foraging on different prey, or in different locations, than other seals. Because all animals were captured in the same area, differences in foraging location probably resulted from shallow diving yearlings concentrating their foraging in the more $\delta^{13}C$ enriched benthic community, as was also indicated by their diving behavior (Burns et al. in press, France 1995). As shallow diving yearlings were larger and made longer dives (on average) than the deep diving yearlings, differences in foraging behavior probably did not reflect physiological limitations, but instead were a result of behavioral preferences (Burns et al. In press, Burns and Castellini 1996, Kooyman et al. 1983).

When the $\delta^{13}C$ values for both deep and shallow diving yearlings were compared to those of the prey items sampled, it was possible to estimate the prey types selected. The $\delta^{13}C$ values of many nototheniids were comparable to those of adults and most yearling seals (once the fish's $\delta^{13}C$ values were normalized to the seal's C:N ratio). Only T. bernacchii, a benthic scavenger with a relatively low lipid content (Friedrich and Hagen 1994, Clarke et al. 1984) was carbon enriched relative to other fishes, and its $\delta^{13}C$ value approached that of the shallow diving yearlings. When combined with the nitrogen isotope data, these findings strongly suggested that most adults and juveniles were foraging primarily in the pelagic ecosystem on P. antarcticum and perhaps P. borchgrevinki, and concentrating less on benthic species. In contrast, while the nitrogen data indicated that shallow diving yearlings were foraging at the same trophic level as other seals, their enriched $\delta^{13}C$ values suggested they were foraging more frequently in the benthic ecosystem on species such as T. bernacchii. Fecal samples collected from three deep divers and one shallow diver seem to confirm this hypothesis. Scats from the deep diving yearlings contained several P. antarcticum otoliths, many vertebrae, and 83 B. picta beaks, but that from the shallow diver did not have any P. antarcticum otoliths, and few vertebrae.

When the food web constructed in this study is compared to that proposed by Rau et al. (1992) for vertebrates in the Weddell sea, it is clear that Weddell seals in McMurdo Sound occupy a higher trophic level than other Antarctic pinnipeds. The average Weddell seal $\delta^{15}N$ value, 13.3 ±
0.1%, places Weddell seals at the trophic level of an obligate fish or squid predator, a niche apparently not occupied by Ross (Ommatophoca rossi), crabeater (Lobodon carcinophagus), leopard (Hydrurga leptonyx), or fur (Arctocephalus gazella) seals in the Weddell sea (Rau et al. 1992). Because fish in both areas have similar $\delta^{15}N$ values, the lower $\delta^{15}N$ values (highest value 9.4%) for pinnipeds in the Weddell sea probably reflects the larger role that Euphausiids ($\delta^{15}N < 5\%$) play in their diet (Rau et al. 1992, 1991, Lowry et al. 1988, Green and Williams 1986, Laws 1984). From this work, it appears that Weddell seals occupy a higher trophic level than all other phocids within the Antarctic ecosystem, at least in regions such as the Ross Sea where they concentrate their foraging primarily on nototheniid fish and cephalopods.

In conclusion, by combining scat collections with stable isotope analysis and diving behavior records, this study was able to more completely characterize the diet of Weddell seals in McMurdo Sound than would have been possible using any one of these methods singly. In the instance of deep and shallow divers, dietary differences suggested by diving behavior were unable to be verified by scat analysis, but were clearly identified by the analysis of predator and prey isotope ratios. Within the deep divers, the dietary specialization on P. antarcticum, as indicated by the scat samples, could not have been determined from the isotope data alone because both P. antarcticum and P. bernacchii had similar $\delta^{15}N$ values. And finally, all three methods were needed to conclusively determine that Weddell seal adults and most yearlings were foraging primarily in the pelagic ecosystem on P. antarcticum, while the shallow diving yearlings were foraging mainly on the benthic Trematomus species. Unfortunately, because isotopic values were not available for the squid species identified in scats, the contribution of cephalopods to the diet of benthic or pelagic foraging seals could not be determined in this study. Similarly, small sample sizes prevented definitive conclusions about age related variation in the diet of Weddell seals in McMurdo Sound. However now that these techniques have been proven effective in determining small scale dietary differences, it would be a relatively simple matter to collect sufficient samples from predator and prey to quantify age and seasonal dietary shifts. Clearly, these three methods complement each other, and in combination are a powerful tool for better understanding the foraging behavior of marine mammals.

ACKNOWLEDGMENTS

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1989 samples, and Amy Hirons and Norma Haubenstock for performing the stable isotope analysis. Andrew Trites generously let us use the elutriator system at the Vancouver Aquarium. Help with field collection of scats and tissues came from T. Zenteno-Savin, L. Rea, B. Fadely, J. Fadely, and many others. The research was carried out under permit # 801 of the Marine Mammal Protection Act. Experimental protocols for the studies were approved by the UAF Institutional Animal Care and Use Committee, and comply with the "Principles of animal care" publication No. 86-23 revised 1985 of the National Institute of Health, and the current laws of the United States of America.
Table 7.1: Squid, fish, and invertebrate prey items identified in Weddell seal scat samples collected yearly from Cape Evans, McMurdo Sound, Antarctica. The 1989 collection was the first, and likely includes scats from more than one year. The age of the seals that deposited the scat were not known.

<table>
<thead>
<tr>
<th>Year</th>
<th>total # scats</th>
<th># beaks</th>
<th># otoliths</th>
<th>P.a. bones</th>
<th>Fish Parts</th>
<th>Crustacean parts</th>
<th>Mollusc parts</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>75 G.a. 1 (1)</td>
<td>P.a. 62 (16)</td>
<td>75</td>
<td>74</td>
<td>70</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M.sp. 2 1 (1)</td>
<td>T.sp. 7 1 (1)</td>
<td>100%</td>
<td>98.7%</td>
<td>93.3%</td>
<td>37.3%</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Unid. 6 (2)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1990</td>
<td>23 G.a. 1 (1)</td>
<td>P.a. 23 (1)</td>
<td>18</td>
<td>18</td>
<td>2</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>T.sp. 1 (1)</td>
<td>78.3%</td>
<td>78.3%</td>
<td>8.7%</td>
<td>21.7%</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>T.b. 1 (1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1991</td>
<td>30 B.sp. 9 (3)</td>
<td>P.a. 43 (4)</td>
<td>26</td>
<td>21</td>
<td>3</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>H.sp. 1 (1)</td>
<td>Unid. 6 (4)</td>
<td>86.7%</td>
<td>70%</td>
<td>20%</td>
<td>20%</td>
<td></td>
</tr>
<tr>
<td>1992</td>
<td>30 B.sp. 6 (4)</td>
<td>P.a. 2 (2)</td>
<td>21</td>
<td>20</td>
<td>6</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>K.I. 2 (1)</td>
<td>T.sp. 1 (1)</td>
<td>70%</td>
<td>66.7%</td>
<td>20%</td>
<td>20%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Unid. 1 (1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1993</td>
<td>31 B.sp. 24 (3)</td>
<td>P.a. 24 (7)</td>
<td>27</td>
<td>23</td>
<td>2</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>H.sp. 2 (2)</td>
<td>T.sp. 2 (2)</td>
<td>87.1%</td>
<td>74.2%</td>
<td>6.5%</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Unid. 7 (6)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>189 B.sp. 39 (10)</td>
<td>P.a. 154 (30)</td>
<td>167</td>
<td>156</td>
<td>83</td>
<td>41</td>
<td></td>
</tr>
<tr>
<td></td>
<td>H.sp. 3 (3)</td>
<td>T.sp. 5 (5)</td>
<td>88.4%</td>
<td>82.5%</td>
<td>43.9%</td>
<td>21.7%</td>
<td></td>
</tr>
<tr>
<td></td>
<td>G.a. 2 (2)</td>
<td>T.b. 1 (1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>K.I. 2 (1)</td>
<td>Unid. 20 (13)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>M.sp. 1 (1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 Gonatus antarcticus, 2 Mastigoteuthis spp., 3 Brachiotethus picta (?), badly eroded, 4 Histiotethid spp., 5 Kondakovia longimanus, 6 Pleuragramma antarcticum, 7 Trematomus spp., 8 Unidentified otoliths, usually due to excessive erosion, 9 T. bernacchi, 10 Pleuragramma antarcticum vertebrae, 11 not including cephalopods

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Table 7.2: The proportion of scats collected from known and unknown age individuals in McMurdo Sound Antarctica which contained *B. picta* beaks or fish otoliths. Mean otolith size (uncorrected) and *P. antarcticum* (*P. a.*) standard length are indicated for each age group. Fish size was calculated following Hubold and Tomo (1989), and corrected otolith diameters (1.275*OD, Harvey 1989) were used.

<table>
<thead>
<tr>
<th>Age</th>
<th># scats</th>
<th># B. picta beaks (% scats)</th>
<th># Trematomus spp. otoliths (% scats)</th>
<th>% scats with P. a. otoliths (% scats)</th>
<th># P. a. with P. a. vertebrae (% scats)</th>
<th>Mean P. a. OD ± SD</th>
<th>Mean fish length ± SD (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td>1</td>
<td>0</td>
<td>100%</td>
<td>2</td>
<td>2.6 ± 0.1</td>
<td>249.8 ± 13.1</td>
<td></td>
</tr>
<tr>
<td>Yearlings</td>
<td>5</td>
<td>87</td>
<td>1</td>
<td>80%</td>
<td>12</td>
<td>1.0 ± 0.1</td>
<td>99.9 ± 13.2</td>
</tr>
<tr>
<td></td>
<td>(60%)</td>
<td>(20%)</td>
<td></td>
<td>(40%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pups</td>
<td>2</td>
<td>678</td>
<td>1</td>
<td>50%</td>
<td>2</td>
<td>0.9 ± 0.0</td>
<td>89.5</td>
</tr>
<tr>
<td></td>
<td>(50%)</td>
<td>(50%)</td>
<td></td>
<td>(50%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unknown</td>
<td>189</td>
<td>39</td>
<td>6</td>
<td>88%</td>
<td>154</td>
<td>1.5 ± 0.4</td>
<td>143.2 ± 40.8</td>
</tr>
<tr>
<td></td>
<td>(21%)</td>
<td>(3%)</td>
<td></td>
<td>(16%)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 7.3: Invertebrates identified from 75 Weddell seal scat samples collected at Cape Evans, Ross Island, Antarctica, in October 1989.

<table>
<thead>
<tr>
<th>Group</th>
<th>Order</th>
<th># Scats</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crustaceans</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Isopods¹</td>
<td></td>
<td>23</td>
</tr>
<tr>
<td>Amphipods²</td>
<td></td>
<td>37</td>
</tr>
<tr>
<td>Calanoid Copepods</td>
<td></td>
<td>12</td>
</tr>
<tr>
<td>Shrimps³</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td>Fragments</td>
<td></td>
<td>68</td>
</tr>
<tr>
<td>Parasites</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nematodes</td>
<td></td>
<td>48</td>
</tr>
<tr>
<td>Acanthocephalans</td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>Cestodes</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>Benthic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hydazoans</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>Invertebrates</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Molluscs</td>
<td></td>
<td>10</td>
</tr>
<tr>
<td>Gastropods</td>
<td></td>
<td>21</td>
</tr>
<tr>
<td>Balanomorpha valves</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Polychaete setae/palaea⁴</td>
<td></td>
<td>8</td>
</tr>
</tbody>
</table>

¹ Gnathidae, Flabelliferae, Idoteidae, Arcturidae
² Hyperidae, Leucothoidae;³ Euphausiidae, Pleocyemata
⁴ Pectinariidae or Flabelligeridae

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Table 7.4: Diameter of sagittal otoliths (OD) recovered from Weddell seal scats collected from 1989-1994 in McMurdo Sound, Antarctica, and the estimated length of fish consumed. Corrected otolith diameters (1.275*OD, Harvey 1989) were used in the estimation of fish lengths.

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Uncorrected OD mean ± SD (range)</th>
<th>Corrected OD mean ± SD (range)</th>
<th>Mean fish standard length (mm) ± SD</th>
<th>Range (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. antarcticum</em></td>
<td>168</td>
<td>1.4 ± 0.5 mm (0.5 - 2.7)</td>
<td>1.8 ± 0.6 (0.6 - 3.4)</td>
<td>140.7 ± 42.7</td>
<td>50.7 - 259.1</td>
</tr>
<tr>
<td><em>Trematomus species</em></td>
<td>6</td>
<td>3.3 ± 1.2 (1.9 - 5.2)</td>
<td>4.2 ± 1.5 (2.4 - 6.6)</td>
<td>233.4 ± 78.9</td>
<td>127.3 - 341.0</td>
</tr>
<tr>
<td><em>T. bernacchii</em></td>
<td>1</td>
<td>2.1</td>
<td>2.7</td>
<td>140.4</td>
<td></td>
</tr>
</tbody>
</table>

1 Standard length, following Hubold and Tomo 1989, 2 Total length, following Hecht 1987

Table 7.5: The δ¹³C, δ¹⁵N, and C:N ratios (mean ± SE) in the plasma of Weddell seals of known age. Diving patterns for deep and shallow diving yearlings were determined from time depth recorder records (Bums et al. in press).

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>δ¹³C</th>
<th>δ¹⁵N</th>
<th>C:N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td>12</td>
<td>-25.5 ± 0.1</td>
<td>13.1 ± 0.2</td>
<td>3.82 ± 0.08</td>
</tr>
<tr>
<td>Deep Diving Yearlings</td>
<td>6</td>
<td>-25.4 ± 0.2</td>
<td>12.6 ± 0.2</td>
<td>3.87 ± 0.05</td>
</tr>
<tr>
<td>NDR Yearlings</td>
<td>4</td>
<td>-25.1 ± 0.2</td>
<td>12.9 ± 0.1</td>
<td>3.65 ± 0.11</td>
</tr>
<tr>
<td>Shallow Diving Yearlings</td>
<td>4</td>
<td>-23.5 ± 0.1*</td>
<td>13.3 ± 0.1</td>
<td>3.68 ± 0.12</td>
</tr>
<tr>
<td>Pups</td>
<td>16</td>
<td>-26.0 ± 0.2</td>
<td>13.8 ± 0.1†</td>
<td>4.12 ± 0.16*</td>
</tr>
</tbody>
</table>

*Significantly different from all other groups (p < 0.05)
† Significantly different from adult females (n = 6, p < 0.05) and deep diving yearlings

Table 7.6: The δ¹³C, δ¹⁵N, and C:N ratios of fish collected in McMurdo Sound, Antarctica.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>δ¹³C</th>
<th>δ¹⁵N</th>
<th>C:N</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dissostichus mawsoni</em></td>
<td>5</td>
<td>-28.9 ± 0.6</td>
<td>13.5 ± 0.2</td>
<td>7.17 ± 1.19</td>
</tr>
<tr>
<td><em>Pleuragramma antarcticum</em></td>
<td>4</td>
<td>-28.3 ± 0.4</td>
<td>10.9 ± 9.2</td>
<td>6.37 ± 0.58</td>
</tr>
<tr>
<td><em>Pagothenia borchgrevinki</em></td>
<td>3</td>
<td>-25.5 ± 0.5</td>
<td>11.0 ± 0.2</td>
<td>3.73 ± 0.39</td>
</tr>
<tr>
<td><em>Trematomus loennbergii</em></td>
<td>2</td>
<td>-25.7 ± 1.2</td>
<td>11.9 ± 1.5</td>
<td>3.89 ± 0.40</td>
</tr>
<tr>
<td><em>Trematomus bernacchii</em></td>
<td>1</td>
<td>-23.4</td>
<td>10.4</td>
<td>---</td>
</tr>
<tr>
<td><em>Rhigophilia dearbomi</em></td>
<td>1</td>
<td>-23.6</td>
<td>13.2</td>
<td>3.31</td>
</tr>
</tbody>
</table>

1 Values from Wada et al. 1989

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Figure 7.1: Mean (± SD) standard length of *P. antarcticum* identified from otoliths (n) recovered from Weddell seal scats collected between 1989 and 1994 in McMurdo Sound, Antarctica. Fish length estimated following Hubold and Tomo (1989).
Figure 7.2: The $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios in Weddell seal blood plasma. Dive patterns for yearlings determined from TDR records (Bums et al. in press). NDR Yearlings are those for which there were no dive records.
Figure 7.3: The relationship between $\delta^{13}$C and tissue C:N ratio for all seals (A) and fish (B) sampled.

$\delta^{13}$C = -1.61$^\circ$C:N -19.06, $r^2 = 0.53$

$\delta^{13}$C = -0.81$^\circ$C:N -22.73, $r^2 = 0.79$
Figure 7.4: The $\delta^{13}$C and $\delta^{15}$N stable isotope values for Weddell seals and fishes in McMurdo Sound. Arrows to second data points for *P. antarcticum* and *D. mawsoni* indicate the $\delta^{13}$C values corrected to account for their higher C:N ratios.
LITERATURE CITED


Chapter 8: The ontogeny of Weddell seal diving behavior and physiology: ecological implications of phocid developmental patterns; Conclusions.

Since 1992 when this study began, there has been a significant increase in the number and breadth of studies on the development of diving behavior and physiology in a wide variety of juvenile marine mammals (Homing and Trillmich 1997, Gazo 1996, LeBoeuf et al. 1996, Stewart et al. 1996, Corpe et al. 1995, Merrick and Loughlin 1995, Castellini et al. 1994, Lydersen et al. 1994, Thorson and LeBoeuf 1994, Lydersen and Hammill 1993a,b). From this research on a wide variety of species has emerged a general consensus: that pup diving behavior and ability increases rapidly during the period surrounding the onset of independent foraging, that during this period of initial development age is the primary determinant, and that soon after the onset of independent foraging, mass and body condition begin to play a more prominent role. The research presented in this thesis supports and extends these general findings by providing extensive records on both the diving behavior and physiology of pre- and post-weaned Weddell seal pups, comparative data from one-year-old seals, and information on the foraging habits of different age classes.

In the first two chapters of this thesis, data indicated that the diving behavior of Weddell seal pups developed rapidly in the period from birth to soon after weaning, and that this behavioral development was accompanied by, and was closely linked to, ontogenetic shifts in the ability to regulate physiological processes related to diving such as heart rate, vasoconstriction and metabolic control. In the period surrounding weaning, rapid changes in diving physiology and metabolic rate occurred and permitted young Weddell seals to shift their diving behavior from short and shallow dives, to longer and deeper ones. As a result, Weddell seal pups were able to begin foraging successfully within a few weeks of weaning. In combination, these findings explained why age, rather than mass, was the primary determinant of diving behavior in young pups.

In contrast, once pups were weaned and foraging successfully, changes in the diving behavior were no longer strongly correlated with age. For seals between two and four months of age, there was little relationship between age and any measure of dive ability, and it was only once pups were older than four months that significant increases in dive depth or duration were observed. These post-weaning increases in dive capacity were gradual, and probably the result of slow changes in mass and body composition, rather than any dramatic shifts in physiological
processes related to diving. This is not to say that pups were physiologically mature soon after weaning. Rather, that gradual physiological development post-weaning was probably masked by larger changes in mass and composition. As a result, after the weaning period, dive ability was better predicted by mass than any measure of physiological status.

Despite diving limitations imposed by age and size, the study of the diving behavior and movement patterns suggested that Weddell seal pups older than two months could dive deep enough to compete in the same areas and for the same prey items as adults. However, pups may not have been able to remain at these depths for long enough to make such dives energetically efficient. In fact, weaned pups were observed to disperse away from their natal colonies several weeks before adults left the area, and both the timing and the routes followed, suggested that juvenile dispersal was a mechanism to avoid intraspecific competition with the larger, more capable adult divers.

The diving behavior of yearling Weddell seals was reported throughout this thesis to demonstrate the changes in diving ability that must take place during the first year in order for pups to survive. However, when the diving ability of yearling Weddell seals was closely examined it became clear that the foraging behavior of yearlings was still constrained by physiological limitations imposed by their smaller body size, and that yearling Weddell seals were not as capable divers as adults. As with older pups, it appeared that mass was the primary determinant of mean dive duration in yearling seals. However, mass was not a good predictor of dive depth, and individual variation in diving behavior could not be adequately explained by physiological or condition indexes. In addition, the interpretation of yearling dive behavior, foraging locations, and diet that resulted from separating individuals and dive types was very different from that based on the average dive behavior, which suggested that average dive behavior is an inadequate metric for comparing behavior or understanding foraging strategies.

Through most of this thesis, I made inferences about the foraging behavior of young Weddell seals based on observed diving patterns. In combination with previously published diet studies, the diving behavior observed generally suggested that weanlings, yearlings, and adult Weddell seals were all foraging on similar prey items in McMurdo Sound, and that these prey were mainly mid-water and benthic species. These conclusions were confirmed by the analyses of Weddell seal tissues, scat, and prey items, which revealed that Pleuragramma antarcticum was the primary prey item for all seals within the Erebus Bay Region. While there were some suggestions from scat samples that younger seals ate smaller fishes and more squid than adults, this could
not be confirmed due to low sample sizes. However, as these prey items predominantly occur below several hundred meters (Eastman 1985, Hubold and Ekau 1985, Hubold 1984), these findings also support the hypothesis that the foraging efficiency of younger seals is reduced relative to that of adults due to physiological constraints on maximum aerobic dive durations, and this limitation may partially account for the higher juvenile mortality rates.

Overall, the findings of these studies suggest that in young pups there is a close link between the ontogeny of diving behavior, physiology, and the age at which independent foraging is achieved. Additionally, they suggest that these processes are jointly regulated, and reflect both evolutionary history and environmental influences (Smith et al. 1991). In Weddell seals, pups are born on a relatively stable substrate, and food is easily accessible to all age classes. As a result, lactation is relatively long, and there is little reason for a post-weaning fast (Testa et al. 1989). Pup diving behavior develops rapidly during the lactation period, and pups are ready to begin foraging soon after weaning. In contrast, northern elephant seal pups (Mirounga angustirostris), which are born on offshore beaches far from their foraging grounds, do not begin to develop diving skills or the ability to regulate physiological processes related to diving until near the end of the fasting period, eight weeks post-weaning (LeBoeuf et al. 1996, Castellini et al. 1994, Thorson and LeBoeuf 1994). At the other extreme, bearded seal pups (Erignathus barbatus) which are born on an unstable substrate (pack ice) are able to swim and dive at birth, and probably possess greater control over the physiological processes related to diving than Weddell seal pups of similar age. It has been suggested that bearded seal pups may even begin to supplement their milk diet with solid prey prior to weaning at 18 days of age (Lydersen et al. 1994). While these three species show different patterns of behavioral and physiological development, in all cases, the pups are capable divers by the time they need to forage independently. Similar patterns have also been observed in the ontogeny of otariid diving behavior and physiology, but are much less clear due to the protracted weaning period (Homing and Trillmich 1997, Merrick and Louglin 1995, Homing pers. comm).

In older juveniles, the primary determinants of diving behavior appeared to be related to individual physiological characteristics, foraging, and behavioral preferences. This was true in Weddell seals as well as other species (Homing and Trillmich 1997, Corpe et al. 1995, Thorson and LeBoeuf 1994, Homing pers. comm). In older Weddell seal pups and yearlings mass, and not age, accounted for approximately half of the variation in diving behavior, with larger animals able to make longer aerobic dives. Similar interaction between individual diving and foraging behaviors and age, size, and condition has also been observed in juvenile elephant seals, harbor
seals (*Phoca vitulina*), and Galapagos fur seals (*Zalophus californianus wollebaeki*), as well as in pregnant elephant seals (Le Boeuf et al. 1996, Slip et al. 1994, Thorson and Le Boeuf 1994, Hindell et al. 1992, Homing pers. comm). In all these cases, gradual shifts in mass and body condition were related to slow changes in diving capacity and behavioral patterns. However, in contrast to the link between dive duration and animal size, in Weddell seal juveniles neither mass, nor any other measured physiological variable, was a good predictor of dive depth. These findings suggest that physiological limitations on diving behavior are best reflected in dive duration, and that, within realistic boundaries, differences in dive depth probably reflect individual foraging preferences.

In combination, these findings indicate that the diving behavior of juvenile marine mammals is most limited before weaning (or independent foraging) by ontogenetic constraints on the ability to regulate physiological processes related to diving, and after weaning by mass and composition constraints on maximal dive duration. The relationship between mass and the aerobic dive limit in post-weaned juveniles is mediated by the effect that mass and body composition have on total oxygen stores and diving metabolic rate, which in turn affects how long animals can remain submerged, the maximal depth that can be reached, and the optimal foraging dive depth, duration and frequency. As a result, juveniles may experience reductions in foraging efficiency when compared to adults, especially if prey items are relatively deep, or the search time long. Recent evidence of differential migration and foraging strategies in both adults and juveniles has suggested that smaller individuals may concentrate foraging effort in different locations, or on different prey items to overcome such disadvantages (Le Boeuf et al. 1996, Slip 1995, Stewart and DeLong 1995, Hindell et al. 1992).

As the successful transition from weanling to subadult is dependent on the ability of marine mammals to develop adequate diving and foraging skills within the limited time between weaning and the depletion of body reserves, understanding the ontogeny of juvenile diving physiology, behavior, and foraging patterns is essential to better understanding those factors which influence juvenile survivorship. In the case of Weddell seal pups and juveniles it appears that physiological and behavioral limitations on diving and foraging are partially compensated for by resource partitioning in post-weaned pups. Juveniles appear to forage in different regions, and perhaps on different species or size classes of prey than adults, and thus avoid direct competition with adults while they gain the necessary body size and experience. However, it is clear from this research that we need a better understanding of the dispersal routes followed, the
prey items selected, and the physiological factors which influence diving and foraging success throughout the first year before we are able to directly relate behavior to juvenile survivorship.
LITERATURE CITED


