INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

Bell & Howell Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

UMI®

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

THREE-DIMENSIONAL DIVING BEHAVIOR OF RINGED SEALS

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

Michael A. Simpkins, B.S., M.S.

Fairbanks, Alaska

August 2000

UMI Number: 9985513

UMI®

UMI Microform 9985513

Bell & Howell Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

THREE-DIMENSIONAL DIVING BEHAVIOR OF RINGED SEALS

By

Michael A. Simpkins

RECOMMENDED:

Advisory Committee Chair

Program Head

APPROVED:

Dean, School of Fisheries and Ocean Sciences

Dean of the Graduate School

7-21-00

Date

ABSTRACT

The three-dimensional movements of 13 freely diving ringed seals were recorded during the spring of 1990, 1991, 1992, 1996, and 1997 in the Canadian Arctic near Resolute Bay, Nunavut. These data were used to investigate the diving behavior of ringed seals more fully than was possible using previous data, which only recorded the vertical movements of diving animals (time-depth data). During a third of all dives, ringed seals focused much of their effort within a reduced volume, suggesting local search behavior within patches of prey. Local search occurred during descent, ascent, and bottom phases (time spent at depth between the end of descent and the beginning of ascent) of dives, but local search most commonly occurred during bottom phases.

Location data from five seals were detailed enough to allow analysis of three-dimensional movements within individual dives. Behaviors were defined for the dives of these five seals based on the character of movements within the dives. Ringed seal dives included horizontally convoluted, travel, and exploration dives, but vertically convoluted, rest, and sit-and-wait foraging dives were not observed. Horizontally convoluted (presumed foraging), travel, and exploration dive behaviors were defined with similar frequency for V-shaped dives (dives with only descent and ascent phases) and U-shaped dives (dives with descent, bottom, and ascent phases). The lack of behavioral differences between dives with distinct time-depth profiles suggested that time-depth profiles were not a reliable means of classifying behavioral dive types for ringed seals.

The diving behavior of the five seals with detailed data was also analyzed on a move-by-move basis within individual dives. Two distinct movement types, convoluted and directional movements, were distinguished based on horizontal directionality values for sequences of five moves. Most phases of ringed seal dives consisted of repeated switching between convoluted and directional movements, indicating that individual dives and dive phases did not represent single behaviors.

TABLE OF CONTENTS

LIST OF FIGURES

Chapter 2: Three-dimensional analysis of search behavior by ringed seals

Chapter 3: Definition of three-dimensional diving behaviors exhibited by ringed seals

Chapter 4: Three-dimensional movements within individual dives by ringed seals

LIST OF TABLES

Chapter 2: Three-dimensional analysis of search behavior by ringed seals

Chapter 3: Definition of three-dimensional diving behaviors exhibited by ringed seals

Chapter 4: Three-dimensional movements within individual dives by ringed seals

Appendix: Summary of all three-dimensional movement analyses conducted for moves and move sequences within individual ringed seal dives

LIST OF BOXES

Chapter 3: Definition of three-dimensional diving behaviors exhibited by ringed seals

Chapter 4: Three-dimensional movements within individual dives by ringed seals

ACKNOWLEDGMENTS

Funding and support for myself and this project were provided by: U.S. Office of Naval Research; Polar Continental Shelf Project, Canada; Department of Fisheries and Oceans, Canada; and Alaska Sea Grant College Program, West Coast and Polar Regions Undersea Research Center, Institute of Marine Science, and Graduate School, University of Alaska Fairbanks.

This project would not have been possible without the work and cooperation of my colleagues, Doug Wartzok and Brendan Kelly. Doug developed the acoustic tracking system (and kept it running) and Brendan developed our method of capturing the ever-elusive ringed seals. Doug and Brendan also graciously shared their data from 1990, 1991, and 1992 with me, which greatly improved our sample size. I owe a special debt of gratitude to Brendan for introducing me to the stark beauty of the Arctic.

Many friends and colleagues assisted in the field component of this project. I'd like to thank those who helped in the field during my tenure: Steve Amstrup, George Durner, William Stortz, and Peter Waser. Terry Manik helped tremendously by sharing his hunting knowledge and local expertise, in addition to his hard work on all aspects of the field work. Brian Taras helped both in the field and the office, freely sharing his statistical expertise with me and making statistics easy to understand. Zydeco and Jitterbug found all the seals for us and will always be my favorite seal dogs.

Earlier drafts of this dissertation were improved by suggestions from my committee members: Brendan Kelly, Mike Castellini, John Kelley, Ted Cooney, and

Lew Shapiro. The reader should thank Brendan, in particular, because his insight and edits have greatly improved my ability to write concisely and clearly.

My friends and family provided unceasing support throughout all the ups and downs. I'd especially like to thank Grace Abromaitis, Sherri Dressel, Jenn Trask, Fiona Danks, Gay Sheffield, Lauri Jemison, and my family: Edna and Earl Simpkins, Karen Neal, and Jill Kulick. Finally, I thank God for the mysteries He's left for us to discover.

CHAPTER 1: INTRODUCTION

The study of marine mammal diving behavior has been largely restricted to inferences drawn from tracking the vertical movements of animals over time (e.g., Kooyman 1968; Gentry and Kooyman 1986; LeBoeuf *et al.* 1988; Boyd and Croxall 1996; Schreer and Kovacs 1997). Although the vertical movements of diving mammals are important, marine mammals, their prey, and the water they dive through are all capable of moving in three spatial dimensions. Three-dimensional movement data have recently been collected from ringed *(Phoca hispida)* and Weddell *(Leptonychotes weddelli)* seals, but analyses of these data have been largely descriptive (Wartzok *et al.* 1992a; Davis *et al.* 1999; Harcourt *et al.* 2000). Here, I quantitatively describe the three-dimensional movements of a marine mammal for the first time.

The three-dimensional movements of freely-swimming ringed seals were recorded in Resolute Passage, Nunavut, Canada during five pupping and breeding seasons. B. Kelly and D. Wartzok collected these movement data during 1990, 1991, and 1992 (Kelly 1996a; Kelly and Wartzok 1996). I joined the project in 1995, and we collected additional movement data during 1996 and 1997. Here, I draw inferences about the diving behavior of ringed seals based upon my analysis of their three-dimensional movements. I contrast my inferences with those drawn previously from time-depth data.

Ringed seals are ideal study animals, because their horizontal home ranges are small enough to allow the use of a fixed hydrophone array to track ultrasonic transmitters attached to the seals' hair (Wartzok *et al.* 1992b). Ringed seals are small phocids (adults are typically 1.3 – 1.5 meters in length) found throughout the arctic in areas of seasonal sea ice (McLaren 1958; Smith 1987; Kelly 1988). These seals overwinter in areas of pack or shorefast sea ice where they maintain breathing holes through the ice by abrading it with their claws (Smith and Stirling 1975). Ringed seals carve out snow drifts overlying some of their breathing holes to create subnivean lairs which they use to rest, give birth, and nurse their young (Chapskii 1940; McLaren 1958; Smith and Stirling 1975; Smith 1987; Kelly and Quakenbush 1990; Furgal *et al.* 1996). The horizontal home ranges of these seals are limited in size, because the seals must return to a breathing hole or lair to breathe. The breathing holes and lairs used by one seal are generally within 1 to 2 km of each other (Kelly and Quakenbush 1990), a range over which the seals can readily be tracked acoustically (Wartzok *et al.* 1992a).

The acoustic tracking system we used to record the three-dimensional movements of ringed seals was developed by Wartzok *et al.* (1992b). The system relied on a fixed array of four hydrophones to determine the three-dimensional location of each transmission from an ultrasonic transmitter (63-77 kHz, Vemco Ltd., Armdale, Nova Scotia, Canada) attached to the hair of a freely-swimming ringed seal. The horizontal location of the transmitter was calculated based upon the difference in arrival time of the transmitted sound wave at each hydrophone. The vertical location was calculated from the transmitter's pulse rate, which was pressure modulated.

We tracked ringed seals under shorefast sea ice in Resolute Passage, Nunavut, Canada (74° 35' N, 95° 7' W). Resolute Passage lies between Cornwallis Island and Griffith Island in the Canadian Arctic Archipelago and borders upon Barrow Strait, which serves as a connection between the Arctic Ocean and Baffin Bay (Prinsenberg and Bennett 1987). The surface of Resolute Passage freezes each winter, creating nearly continuous ice cover. Resolute Passage is oriented along a northwest-southeast axis, and mean water flow through the passage is to the southeast at < 4 cm/s (Marsden *et al.* 1994b). Water flow in the passage, however, is tidally dominated, and peak along-channel velocities are approximately 20 cm/s (Marsden *et al.* 1994b). Vertical mixing of water under shorefast sea ice in Resolute Passage is limited, but some mixing does occur as a result of internal waves propagating along the shallow pycnocline (Marsden *et al.* 1994a). This vertical mixing may provide nutrients to help perpetuate the spring bloom of ice algae (Cota *et al.* 1987).

Up to 65% of ice-algae production may be exported from the sea ice in Resolute Passage and become available to ringed seals via their prey (Smith *et al.* 1988). The remainder of ice-algae production is recycled within the sea ice and helps to maintain the ice-algae bloom. Ringed seals in and around Resolute Passage prey primarily upon arctic cod and pelagic, benthic, and sympagic (ice-associated) macrozooplankton (Welch *et al.* 1992). Ringed seals are, in turn, preyed upon by polar bears and Inuit hunters (Welch *et al.* 1992). Studies of ringed seal prey distributions under shorefast sea ice near Resolute Passage suggest that ringed seal prey are unevenly distributed in the vertical and horizontal planes and through time (Crawford and Jorgenson 1990; Pike and Welch 1990).

Ringed seals probably engaged in a variety of social, foraging, and other behaviors during the spring breeding and pupping seasons in which we monitored seal movements. During the breeding season, rutting males are believed to defend underwater territories or access to breathing holes used by females (Stirling 1973; Smith and

Hammill 1981; Hammill and Smith 1991; Kelly and Wartzok 1996). During the pupping season, lactating females apparently divide their time between foraging and caring for their pup, including moving their pup from one lair to another to avoid predators (Smith and Stirling 1975; Smith 1987; Hammill *et al.* 1991; Smith *et al.* 1991; Lydersen and Hammill 1993; Kelly and Wartzok 1996). Rutting males and estrous females may also engage in courtship behaviors while diving during the breeding season, in addition to behaviors which are common to all ringed seals such as breathing hole maintenance, predator avoidance, and foraging (Smith 1987).

The functions of marine mammal dives have often been inferred based on the classification of the dives' time-depth profiles (e.g., Kooyman 1968; LeBoeuf *et al.* 1988; Hindell *et al.* 1991; Schreer *et al.* 1998), but these classifications were found to be unreliable when compared to simultaneously collected data on feeding events (Lesage *et al.* 1999) and three-dimensional dive profiles (Harcourt *et al.* 2000). Foraging behavior, in particular, was inferred based on both time-depth profiles and indirect evidence of feeding (e.g., stomach temperature sensors; Wilson *et al.* 1992; Gales and Renouf 1993; Lesage *et al.* 1999). The understanding of foraging behavior based on these inferences was constrained, however, because feeding events were only a subset of foraging behavior. Optimal diving models were also created which related the time a diving animal spent at depth to the time the animal spent at the surface either preparing for, or recovering from, a dive (e.g., Kramer 1988; Houston and Carbone 1992; Mori 1999). Although these models were qualitatively confirmed for a few species (e.g., Boyd *et al.*

1995; Carbone *et al.* 1996), the models did not accurately predict behavior by other species (Kelly 1996a; Jodice and Collopy 1999).

Here, I use three-dimensional movement data collected from ringed seals to evaluate and extend previous inferences drawn from time-depth data. I believe that inferences based on three-dimensional movements are more accurate than those drawn solely from vertical movements, although my inferences are limited to behaviors which involve distinct types of movement. In Chapter 2, I investigate three-dimensional search behavior by ringed seals in order to gain a broader view of foraging behavior than was possible by previous analyses of feeding events. In Chapter 3, I explore methods of defining dive behaviors based on the three-dimensional movements of ringed seals within dives, and I compare my results to previous inferences of dive behaviors based on time-depth profile classification. In Chapter 4, I analyze the three-dimensional movements of ringed seals within dives on a move-by-move basis and test assumptions inherent in previous optimal diving models and classifications of dives by time-depth profiles.

CHAPTER 2: THREE-DIMENSIONAL ANALYSIS OF SEARCH BEHAVIOR BY RINGED SEALS[1]

---

[1] Michael A. Simpkins, Brendan P. Kelly, and Douglas Wartzok; prepared for submission to Animal Behaviour

ABSTRACT

The use of three-dimensional space by 13 freely diving ringed seals was analyzed to distinguish between local search behavior, presumably within prey patches, and travel or exploration behavior between prey patches. The three-dimensional home ranges of ringed seals were subdivided into 3x3x3 meter grid cells. For each dive, the time spent swimming through each grid cell and the frequency of grid cell revisits within the dive were determined. The seals generally spent 1 – 3 seconds in each cell and rarely revisited cells. During 34% of all dives, however, ringed seals focused their effort within a reduced volume, suggesting local search within patches of prey. The disproportionate effort within restricted volumes resulted from seals revisiting cells (18% of dives), reducing speed within cells (9% of dives), or both reducing speed and revisiting cells (7% of dives). Ringed seals searched locally in less than 10% of descents and ascents but did so in 41% of bottom phases (time spent at depth between the end of descent and the beginning of ascent).

INTRODUCTION

Specific aspects of foraging, social, and other behaviors of diving marine mammals are difficult to study using time-depth data, but detailed analyses are possible using three-dimensional movement data (Davis *et al.* 1999; Harcourt *et al.* 2000). Here, we analyze the time spent within each unit of volume traversed by freely-swimming ringed seals for evidence of local search behavior, an important component of foraging behavior which has not been studied previously in marine mammals. The analysis of three-dimensional search behavior occurring within individual dives by ringed seals overcomes three previous limitations to the study of marine mammal foraging behavior.

First, three-dimensional movement data provide a more comprehensive representation of the actual behavior of diving animals than do previously used time-depth data (Figure 2.1). Time-depth data can only provide insight into the vertical component of foraging behavior. Marine mammals, however, forage in an environment where they, their prey, and the water they dive through all move in three spatial dimensions. Foraging behavior in marine mammals has been surmised to occur during the bottom phase (time spent at depth between descent and ascent phases) of flat-bottomed dives (e.g., Kooyman and Gentry 1986; Hindell *et al.* 1991; Lydersen 1991; Thompson *et al.* 1991; LeBoeuf *et al.* 1992; Martin and Smith 1992; Bjørge *et al.* 1995; Werner and Campagna 1995; Westgate *et al.* 1995; Schreer and Testa 1996; Gales and Mattlin 1997). Time-depth profiles of flat-bottomed dives, however, show negligible vertical movement during the bottom phase, so no information is available to describe foraging behavior. Three-dimensional data include both vertical and horizontal movements and inferences of foraging behavior can be sought during any phase of a dive.

Second, the investigation of search behavior broadens the study of foraging behavior beyond the analysis of feeding events. Since foraging behavior by marine mammals can rarely be directly observed, researchers have relied on indirect evidence of feeding to indicate foraging behavior. Feeding events have, for example, been recorded using stomach temperature sensors, which record the ingestion of cold food (Wilson *et al.* 1992; Gales and Renouf 1993; Hedd *et al.* 1995; Hedd *et al.* 1996; Bekkby and Holand 1997; Andrews 1998; Bekkby and Bjørge 1998; Lesage *et al.* 1999), and animal-mounted cameras, which allow visual observation of feeding events (Marshall 1998; Davis *et al.* 1999). It is important to remember, however, that foraging behavior consists of search, pursuit, and handling behaviors. Feeding events are only a subset of handling behavior; animals must search for prey before pursuit or handling can occur.

Third, studying the behavior of animals within individual dives provides more detailed insight into foraging behavior than previous analyses which averaged behavior over entire dives or groups of dives. Data collected by several types of satellite-linked depth recorders (SDR) are binned by 6-hour periods, so diving behavior must be averaged over many dives in analyses involving these data. Furthermore, most analyses of SDR data have been largely descriptive (e.g., Mate 1989; Mate *et al.* 1994; Mate *et al.* 1995; Nordoy *et al.* 1995; Davis *et al.* 1996; Stewart *et al.* 1996), although more quantitative approaches have recently been presented (e.g., Burns *et al.* 1999; Frost *et al.* 1999; Teilmann *et al.* 1999). Since data from time-depth recorders (TDR data) are not binned, analyses of TDR data do not have to average behavior over multiple dives. One approach to synthesizing TDR data, however, has been to group successive dives with similar time-depth profiles into bouts using the hypothesis that all dives within a bout represent the same behavior (Gentry and Kooyman 1986; Feldkamp *et al.* 1989; Kooyman 1989; Goebel *et al.* 1991; Boyd *et al.* 1994; Harcourt *et al.* 1995; Kelly 1996a). More detailed analyses of TDR data (and SDR data which were not binned) have classified dives with distinct time-depth profiles as representing distinct behaviors (Schreer *et al.* 1998). The assumption inherent in these classifications was that individual dives were the basic unit of diving behavior. For example, one could classify a dive as either a foraging dive or a travel dive but not as both a foraging and travel dive. Analysis of three-dimensional movements within individual dives indicated, however, that ringed seals switched between behavioral states within individual dives (Simpkins *et al.* in prep c). Fine-scale studies of foraging behavior, as attempted here, are most appropriately conducted by investigating behavior within individual dives, because examining the behavior of animals by dive or groups of dives may average over multiple behaviors within each dive.

We focused the three-dimensional analysis presented here on search behavior within dives. When prey are distributed in patches, as is common in the marine environment, the search behavior of predators can generally be split between exploratory behavior (ranging behavior *sensu* Bell 1990) when searching for patches of prey, and local search behavior when searching for prey within a patch (Jander 1975). Searching locally involves movements restricted to the interior of a patch, while exploring entails an animal searching widely to increase the likelihood of encountering a patch. Our investigation of the volume traversed, or searched, by ringed seals allows a clear distinction between searching locally and exploring. When exploring, an animal should minimize the time searching each unit of volume, while an animal searching locally should maximize the time searching within the volume of the patch (Bell 1990). We calculated the time spent within each unit of volume transited during a dive and identified local search behavior as portions of a dive in which a seal spent more time within a small volume than was expected based on the average time spent within each unit of volume. We also determined whether an animal restricted its search effort to the volume of a patch by slowing down or by following a more convoluted (self-intersecting) path.

We demonstrate the method using the under-ice movements of freely swimming ringed seals tracked acoustically. We collected three-dimensional diving data from ringed seals over several years during the spring breeding and pupping seasons (Kelly 1996a; Kelly and Wartzok 1996). Although females of phocid species allegedly fast during lactation (Bonner 1984; Costa 1991), females of several phocid species, including ringed seals, forage to varying degrees during lactation (Testa *et al.* 1989; Hammill *et al.* 1991; Lydersen and Kovacs 1993; Boness *et al.* 1994; Lydersen *et al.* 1994; Nilssen *et al.* 1995; Kelly and Wartzok 1996). We believe the seals we tracked were foraging based on weight gains and scat samples from recaptured animals, as well as evidence of foraging in non-tracked seals. Of the four seals we recaptured during our study, three exhibited mass gains over periods ranging from 10 to 31 days, and scat samples from the other were full of amphipod exoskeletons (Kelly and Wartzok 1996; unpublished data). Previous collections of stomach contents and scat samples indicated that seals in our study area fed primarily on arctic cod (*Boreogadus saida*) and pelagic and benthic amphipods during spring (Welch *et al.* 1992; Kelly and Wartzok 1996; unpublished data). These prey are concentrated into several layers under shore-fast ice and are, thus, patchy by depth (Crawford and Jorgenson 1990). We acoustically sampled the prey distribution in the study area to assess the spatial and temporal distribution of ringed seal prey. Based on analysis of three-dimensional behavior within dives (Simpkins *et al.* in prep c), we expected to find local search behavior in dives with and without bottom phases.

METHODS

We recorded the three-dimensional movements of 13 ringed seals during the spring breeding season in 1990, 1991, 1992, 1996, and 1997 in the Canadian Arctic near Resolute Bay, Nunavut (74° 35' N, 95° 7' W; Kelly 1996a; Kelly and Wartzok 1996). We captured seals at breathing holes in shore-fast sea ice using nets (Kelly 1996b) and tracked their movements under the ice by way of ultra-sonic transmitters (Vemco Ltd., Armdale, Nova Scotia, Canada) attached to their hair (Wartzok *et al.* 1992b).

We compiled and filtered the data for each seal, removing erroneous locations which would have required swim speeds in excess of 6 m/s (greater than the maximal speed of harbor seals; Williams and Kooyman 1985). Shallow locations often were inaccurate, primarily as a result of acoustic reflection off of ice keels. We defined dives as seal movements to depths greater than 5 m with at least 10 data points. We interpolated locations for each second of a dive to fill temporal gaps between sequential data points, which were generally on the order of 5 - 9 seconds (interquartile range). We did not extrapolate location data points beyond the recorded segment of each dive. We split dives into phases characterized as: descent (continuous descent from the dive's initiation), ascent (continuous ascent to the dive's conclusion), and bottom (time between the end of descent and beginning of ascent).

We divided each seal's home range into a three-dimensional grid and calculated time spent within each grid cell a seal entered (Figure 2.1B). We made the grid cells as small as possible to provide the highest resolution in three-dimensional behavior. We used cubes with sides of 3 meters for grid cells, because the error in the location data was generally on the order of ± 1 m (maximal error ± 2 m; Wartzok *et al.* 1992a). Each grid cell, then, effectively represented a central location with a volume of uncertainty of ± 1.5 m in each dimension. To simplify the analysis, we assigned each grid cell a reference number for its position within the matrix. These position (reference number) data points represented both a specific three-dimensional grid cell and a second in time, because locations were interpolated by second. For each dive, we tallied sequential data points with the same reference number to determine the time spent swimming through each grid cell.

We used the distribution of all time spent swimming through a grid cell (referred to hereafter as cell time) to differentiate between cell times which represented exploration versus local search. We defined normal swimming behavior, as expected during exploration, as cell times ≤ 3 seconds, because ringed seals spent three seconds or less in 95% of all grid cells swum through (Figure 2.2). We defined slow passages, in which seals slowed down within specific grid cells, as cell times > 7 seconds. Slow passages indicated that a seal was swimming unusually slowly (cumulative probability of cell time > 7 seconds = 0.008, Figure 2.2) and, in some cases, may have been stationary in the water column.

We considered local search to have occurred when slow passages were more common within a dive phase than expected under the assumption that slow passages were randomly and independently distributed throughout dives. For each phase of a dive, a random binomial simulation computed the distribution of expected slow passages (probability of slow passage/grid cell = 0.008, 500 iterations per dive phase). Dive phases which included more slow passages than 95% of the corresponding simulations indicated that seals searched locally during those phases. During this type of local search, seals not only spent more time than expected in certain grid cells (slow passages), but they did so more often than expected by a null model of independent random behavior.

We also determined how often seals revisited the same grid cell and defined the proportion of cells required to be revisited in order to indicate convoluted local search behavior. We calculated the proportions of grid cell revisits (referred to hereafter as revisit proportions) for phases of each dive as: 1 – a/b where a = unique grid cells visited and b = total grid cells visited. Revisit proportions could be affected by the orientation of a dive path with respect to the border between grid cells (Figure 2.3). A dive path could have no revisits if it was centered within grid cells (Figure 2.3A) but have several revisits if it was centered along the border between two grid cells (Figure 2.3B). Most revisits during descent and ascent were probably caused by this "border effect." Revisits during continuous descent or ascent could only result from a seal moving horizontally into another grid cell very briefly and then returning (Figure 2.3B). Brief visits of this sort were likely the result of error in our location data combined with the orientation of the dive path along a grid cell border. Ninety-five percent of descents and ascents had revisit proportions less than 0.1, so we defined local search as having occurred only when the revisit proportion for a dive's phase was greater than 0.1. This type of local search behavior involved convoluted movements, which resulted in the dive path frequently intersecting itself, causing frequent grid cell revisits.

Some recorded dives were incomplete and did not include all phases of the dive. For both the revisit proportion and slow passage analyses above, we used only dives which included at least representative portions of each of the dives' phases (all 3 phases for dives with bottom phases, 2 phases otherwise). We required recorded portions of dive phases to be greater than 7 seconds in duration to allow for identification of possible slow passages. The average duration of phases used in these analyses was 117 seconds (interquartile range = 45 - 150 seconds).

We monitored the prey distribution in the vicinity of tracked seals in 1996 and 1997 using a 200 kHz echosounder (Furuno FE-881 II, Furuno Marine Electronics, Nishinomiya, Japan). We mounted the downward-facing transducer through a hole drilled through the sea ice and recorded echograms from 8 April - 17 May 1996 and 25 April - 27 May 1997. We recorded most echograms with the transducer mounted at our base camp (74° 35' N, 95° 7' W) to monitor changes in prey distribution over time.

In 1996, we conducted a series of experiments to assess the degree of horizontal patchiness in the local prey distribution. On April 26 and 27, we moved the transducer and recorded echograms for 1.5 - 6 hours at each of four sites 0.5 - 2 km from our base camp. From May 6-17, we alternately deployed the transducer for approximately 24 hours each at sites within 100 m of a tracked seal (0.5 – 1.5 km from the base camp) and at the base camp control site. We recorded the presence or absence of individual echoes within 20 meter depth bins for 5 randomly selected minutes during each hour at each of these sites (e.g., for the hour 11:00-11:59 we recorded values for 11:02, 11:15, 11:23, 11:38, and 11:43). We calculated the frequency of occurrence of individual echoes within 20 meter depth bins using these presence/absence data. Frequency of occurrence values provided an objective relative index of potential prey availability at each site using qualitative echograms. We compared frequency of occurrence values between sites which were monitored in sequence and assumed that temporal changes in prey distribution were negligible between sequential recordings.

RESULTS

Ringed seals spent equal time at the majority of three-dimensional grid cells transited, swimming through 95% of grid cells in 1 – 3 seconds (Figure 2.2), and rarely revisited grid cells. Slow passages, in which a seal took more than 7 seconds to swim through a 3x3x3 m grid cell, were rare in terms of all grid cells visited (< 1% of grid cells), but occurred in 43% of dives (1727 dives). In 16% of dives (634 dives), however, slow passages occurred more frequently than expected based on binomial simulations of slow passage frequency. Of all grid cells transited, 5.5% had previously been visited during the same dive. Revisit proportions were low for descent and ascent phases (95% of revisit proportions < 0.1). During bottom phases, however, seals often exhibited revisit proportions greater than the 0.1 necessary to qualify as local search by our definition (Figure 2.4).

Local search behavior occurred in 34% of dives (Table 2.1). During these dives, seals focused their dive time within a few grid cells by either revisiting or slowing down at the cells. Seals searched locally during bottom phases of dives more commonly than during descent and ascent phases (Figure 2.4).

Variability in search behavior was evident between seals. Individual seals searched locally in 9% to 61% of their dives (Table 2.1). Seals most commonly localized their search effort by revisiting grid cells. The degree to which individual seals exhibited slow passages or grid cell revisits varied (Table 2.1). Local search behavior was most commonly found in bottom phases for 12 seals. Another seal, MR97, did not search locally during any bottom phase. Only 23 dives were analyzed from MR97, however, and 4 of these included local search behavior. Most seals searched locally within descent and ascent phases, and eight seals searched locally in more than 10% of their descents or ascents (Table 2.1).

Echograms recorded in 1996 and 1997 indicated that potential prey items (individual echoes) were distributed in patches both horizontally and vertically. Prey were neither continually present (frequency of echo occurrence = 100%) nor continually absent (frequency of echo occurrence = 0%) in any depth bin. Figure 2.5 shows the difference in frequency of echo occurrence between an echogram recorded 850 meters from the base camp on May 6-7, 1996 and an echogram recorded at the base camp on May 7. Vertical differences in frequency of echo occurrence were greater than horizontal differences, with a pattern of low values at midwater bins bracketed by higher values at shallow and deep bins. Horizontal differences in frequency of echo occurrence differed in magnitude by depth. The vertical pattern of frequency of echo occurrence shown in Figure 2.5 was common to all recorded echograms, although the magnitude of frequency of echo occurrence values varied among echograms. Spatial differences in frequency of echo occurrence were more dramatic than changes over time. Temporal changes in frequency of echo occurrence generally were only apparent over the course of several days to weeks. On two separate occasions in 1996, however, the prey distribution changed quickly. Large, dense patches of prey became apparent suddenly in these echograms as a continuous band of maximal echo return which blanketed up to 100 meters of the depth record for 30 minutes to 2 hours.

DISCUSSION

We observed three-dimensional movements consistent with local search behavior during ringed seal dives. Most instances of local search occurred during the bottom phase of dives (Figure 2.4), suggesting that bottom phases commonly represented foraging behavior. Not all bottom phases included local search behavior, however, indicating that bottom phases do not necessarily represent time spent in a prey patch. Studies of optimal foraging by diving animals have been based on time-depth data and the assumption that patch time was equivalent to the duration of the bottom phase (Kramer 1988; Wilson and Wilson 1988; Houston and Carbone 1992; Thompson *et al.*

1993; Boyd *et al.* 1995; Carbone and Houston 1996; Mori 1998a; Mori 1999). It may be, however, that bottom phases include both patch time and travel, or exploring, between patches.

Local search behavior also occurred, to a lesser extent, during descent and ascent phases, especially within dives that lacked a bottom phase. If we assume that all local search behavior reflected foraging within prey patches, and not some non-foraging behavior such as territorial defense, then foraging occurred during all phases of dives with and without bottom phases. Feeding events and, by association, foraging have been recorded during all dive types identified for harbor seals (Lesage *et al.* 1999).

Local search generally involves an increase in turning rate (or angular velocity) and a decrease in velocity (reviewed in Bell 1990). In our analysis, slow passages corresponded to low velocities, and high turning rates created convoluted, self-intersecting dive paths (i.e., grid cell revisits). Ringed seals searched locally during bottom phases primarily by revisiting specific grid cells (e.g., grid cell revisit highlighted in Figure 2.1B), but they searched locally during descent and ascent phases both by revisiting and slowing down at specific locations (Figure 2.4).

Although ringed seals searched locally in one third of all dives (Table 2.1), they allocated equal time to each grid cell and rarely revisited cells during the majority of dives. Seals spent 1 – 3 seconds in 95% of all grid cells (Figure 2.2) and revisited only 5.5% of all grid cells within dives. This continuous movement from one grid cell to the next, coupled with rare grid cell revisits, was consistent with an animal maximizing the net volume (or distance) traversed per unit time, as expected for an animal searching for prey patches, travelling between breathing holes, or exploring its environment. The low frequency of local search behavior by grid cell and dive suggested that ringed seals spent most of their time either searching for prey patches, or engaging in non-foraging behaviors.

Occasionally, seals were stationary for very long periods which may have represented sit-and-wait foraging behavior (243 slow passages ≥ 30 seconds, maximum = 248 seconds). Terrestrial sit-and-wait predators spend their search time in one location, waiting for prey to pass within pursuit distance (Pianka 1966; Schoener 1971; Huey and Pianka 1981; McLaughlin 1989; Bell 1990; Shafir and Roughgarden 1998). Marine predators can use two strategies which are similar to terrestrial sit-and-wait predation. They can drift with the current and allow it to move them to their prey without actively swimming. Alternatively, they can maintain their position in the water column (by swimming) and intercept prey drifting toward them in the current. We call these two strategies drift predation and active ambush respectively. The tidal nature of currents in Resolute Passage made it difficult to distinguish between active ambush and drift predation in ringed seals without simultaneous monitoring of water flow, because stationary animals could be swimming against a current or drifting with no current. It is possible that slow passages represented drift predation, and that the duration of each slow passage was linked to the contemporary current speed. D. Wartzok visually observed one seal drifting under the ice in Resolute Passage while vertical in the water column (i.e., the seal was looking upward while drifting sideways; unpublished data). Grid cell revisits during dives with slow passages, however, indicated that drift was certainly not continuous throughout a dive.

Terrestrial sit-and-wait predators switch from sit-and-wait predation to active search behavior at low prey densities (Jaeger and Barnard 1981; Formanowicz and Bradley 1987; Bell 1990), or when the predator is starved (Akre and Johnson 1979; Inoue and Matsura 1983; Bell 1990). Although sit-and-wait predation minimizes the energetic cost of search, active search increases the rate at which predators encounter prey, which is critical at low prey densities (Norberg 1977; Bell 1990). Sit-and-wait predation may be more profitable at high prey densities, when prey encounter rate is not limiting, because sit-and-wait predation likely minimizes evasive responses by prey, thereby reducing the cost of pursuit (Jaeger and Barnard 1981).

In marine environments, predators can choose between active search, drift predation, and active ambush strategies. We suggest that active search is the optimal strategy in low prey densities, when prey encounter rates for drift predation and active ambush strategies are too low. Since active ambush behavior has a lower search efficiency than active search, we suggest that active ambush behavior is only optimal when prey density is very high, and the energetic cost of maintaining position can be overcome. The relative efficiency of active ambush and drift predation depend on prey behavior. For example, drift predation would be very inefficient at locating planktonic prey, and active ambush would be inefficient at locating sessile benthic prey. Models of optimal foraging strategy which incorporate prey behavior (Thompson *et al.* 1993) and current speeds (Dusenbery 1989) can further elucidate the efficiency of these strategies and provide insight into behavioral choices made by foraging marine mammals.

Echograms recorded in 1996 and 1997 suggested that potential prey were distributed in patches. Availability of potential prey, as estimated by frequency of echo occurrence within echograms, varied most dramatically by depth, consistent with previous findings that small fish and zooplankton were concentrated into vertical layers under shorefast sea ice (Crawford and Jorgenson 1990). Potential prey availability also varied horizontally (e.g., Figure 2.5) and over time. With a single fixed transducer, we were unable to link particular prey patches seen in echograms with the diving behavior of tracked seals. One yearling male seal (TL97) did, however, use the transducer hole as a breathing hole for several hours. He dove vertically under the hole during several dives, and we were able to track portions of his descent and ascent on echograms. Future research into simultaneous tracking of prey and diving predators using echosounders may prove fruitful (e.g., Dolphin 1987).

Our analysis of volume use during individual dives could be modified to study the use of volume during several dives. For example, calculating the total time spent in each location over the course of a foraging bout would allow the identification of three-dimensional foraging sites in the water column. Knowledge of specific foraging sites could be very useful in identifying critical habitat for species which forage at fixed locations, such as endangered Hawaiian monk seals which generally forage along coral reefs (Goodman-Lowe 1998). Our method could also be extended to study interactions between simultaneously tracked animals, which could describe phenomena such as under-water territoriality or intra-specific competition for prey. For example, two seals monitored in our study (HE91 and ME91) appeared to forage in the same horizontal range but separated their effort by depth (Kelly and Wartzok 1996).

Table 2.1: Local search behavior exhibited by ringed seals.

Seal	Sex	Age	Number of dives:		Percent of dives with local search	Percent of dives with local search identified by:			Percent of phases with local search:		
			With bottom phase	Without bottom phase		Slow passages	Revisits	Both	Descent	Bottom	Ascent
EL96	F	9	334	493	15%	9%	5%	1%	3%	12%	8%
FA96	F	2	62	107	29%	15%	11%	3%	8%	24%	15%
HE91	F	7	48	27	57%	11%	25%	21%	19%	60%	15%
HO90	M	7	42	49	34%	6%	26%	2%	14%	31%	14%
JO92	M	5	600	89	52%	11%	24%	17%	4%	54%	4%
LF92	F	6	386	86	54%	8%	26%	20%	7%	56%	10%
ME91	F	7	382	190	47%	11%	32%	5%	9%	50%	12%
MR97	M	8+	12	11	17%	0%	13%	4%	4%	0%	13%
SA91	M	1	13	25	61%	29%	16%	16%	29%	46%	40%
SC96	M	1	167	241	31%	9%	19%	3%	9%	43%	12%
SP90	F	1	53	48	20%	3%	15%	2%	4%	21%	6%
TL97	M	1	168	381	9%	2%	8%	0.2%	4%	9%	3%
TR91	M	7	7	6	23%	23%	0%	0%	15%	29%	8%
Total (all dives)			2274	1753	34%	9%	18%	7%	6%	41%	9%
Average (by seal)					35%	10%	17%	7%	10%	34%	12%

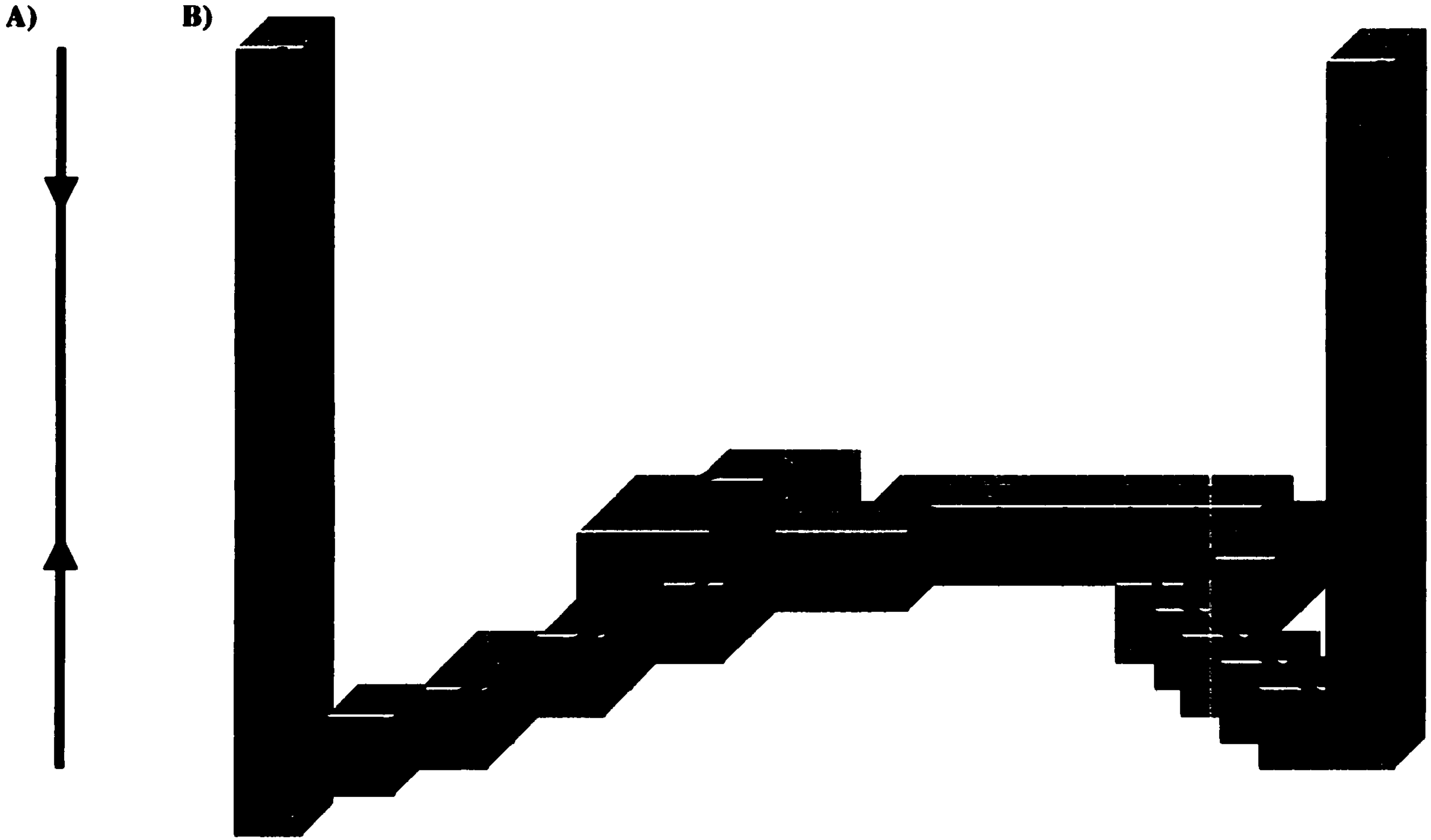


Figure 2.1: Representations of time-depth and three-dimensional dive data. Three spatial representations of one example dive are shown. The lines show the dive path recorded by time-depth (A) and three-dimensional data (B). Notice that time-depth data show only vertical movements up and down the line-segment A. The cubes represent the three-dimensional dive path converted into grid cell format. The dive path is shown on the surface of the grid cells for ease of viewing. A grid cell revisit is highlighted by the dark gray cube in B.

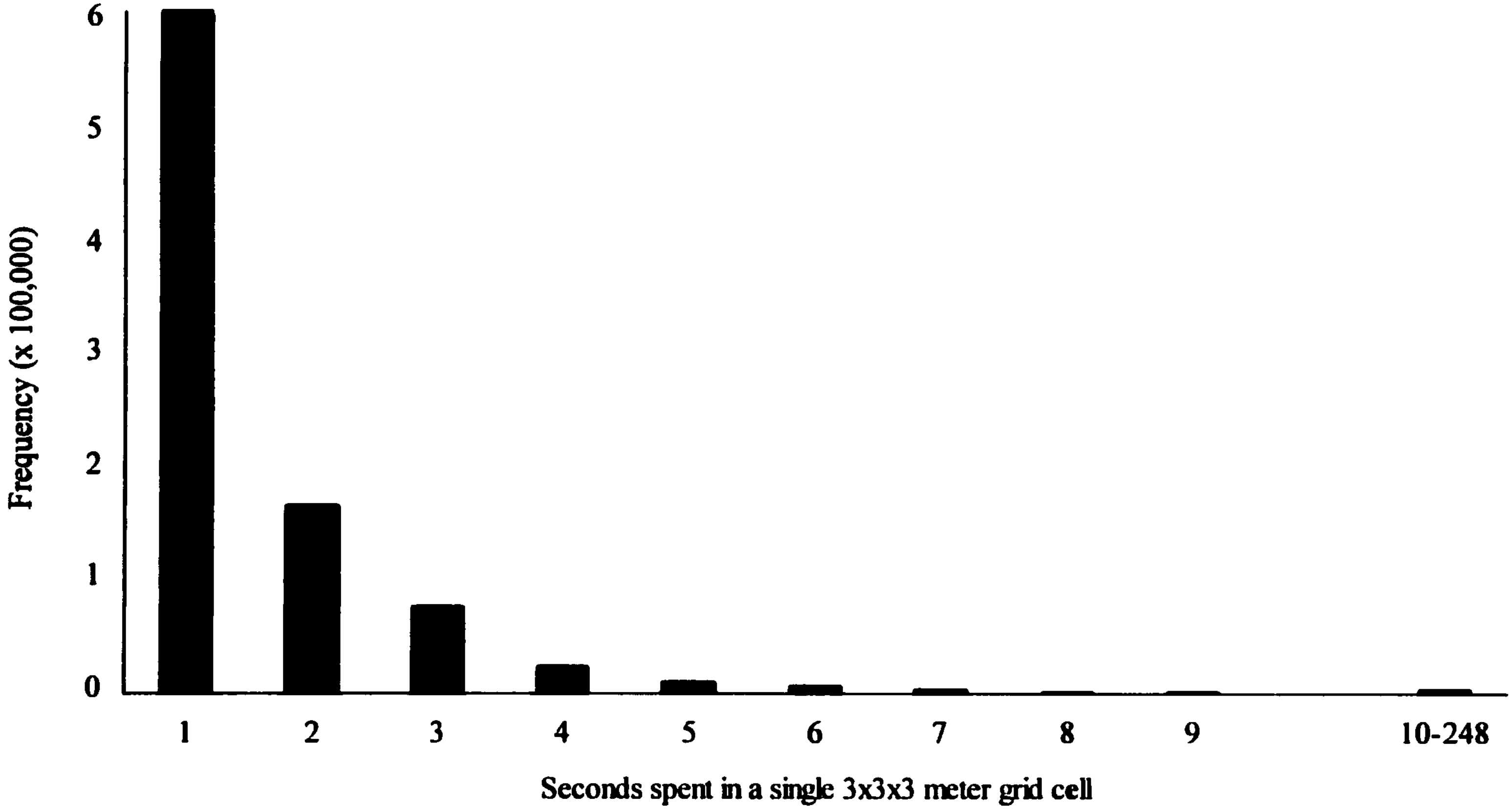


Figure 2.2: Time spent swimming through individual 3x3x3 meter grid cells (cell times). Shown are cell times for every grid cell transited by all seals during all dives (908,756 grid cells). Note that this is the cell time for each grid cell visit, not the cumulative time spent in a grid cell over a series of grid cell revisits.

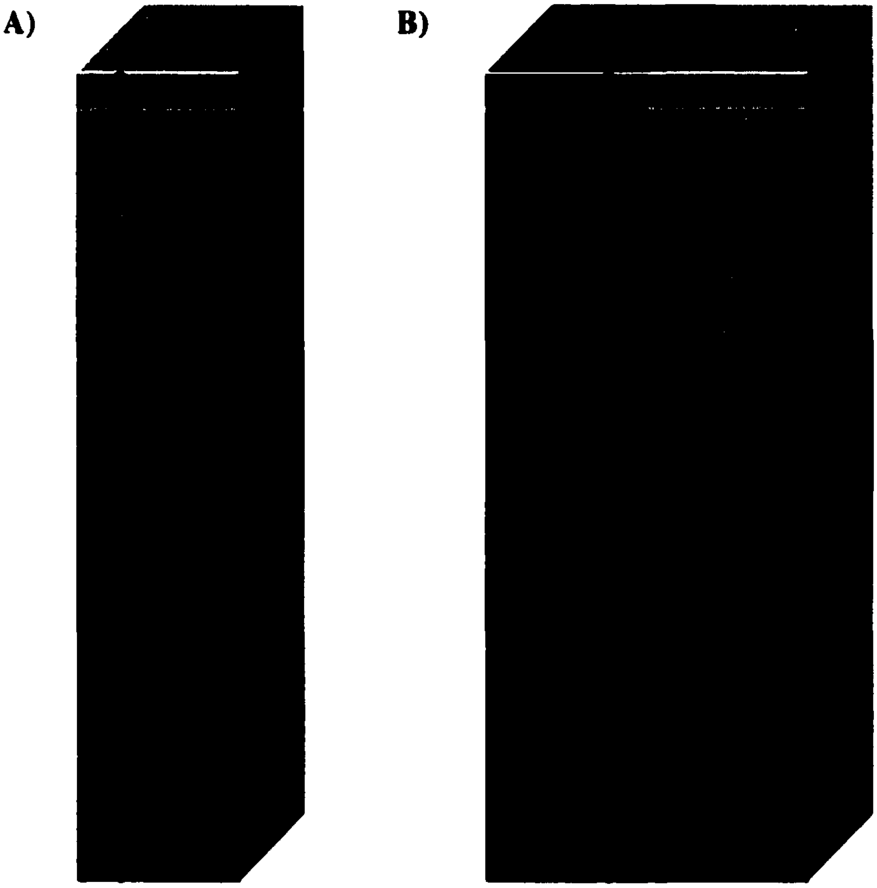


Figure 2.3: Grid cell revisits during descent and ascent due to orientation of path with respect to grid cells. The same path is shown in A and B. Revisits do not occur when the path is centered within the grid cells (A), but do occur when the path is centered along the border between grid cells (B). We eliminated "border effect" revisits (B) from our analysis.

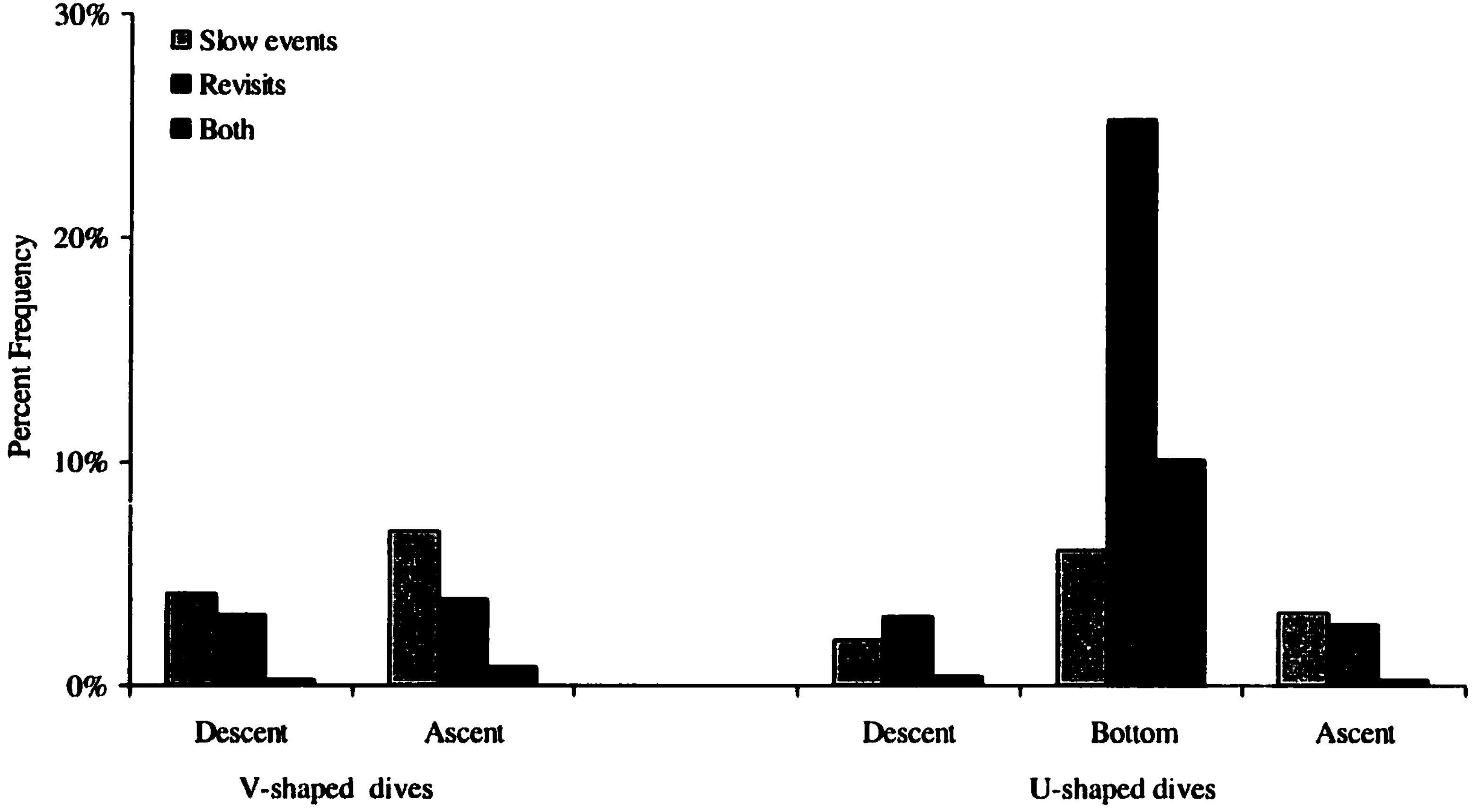


Figure 2.4: Percent of dive phases in which seals searched locally. Local search behavior was identified by slow passages, grid cell revisits, or both.

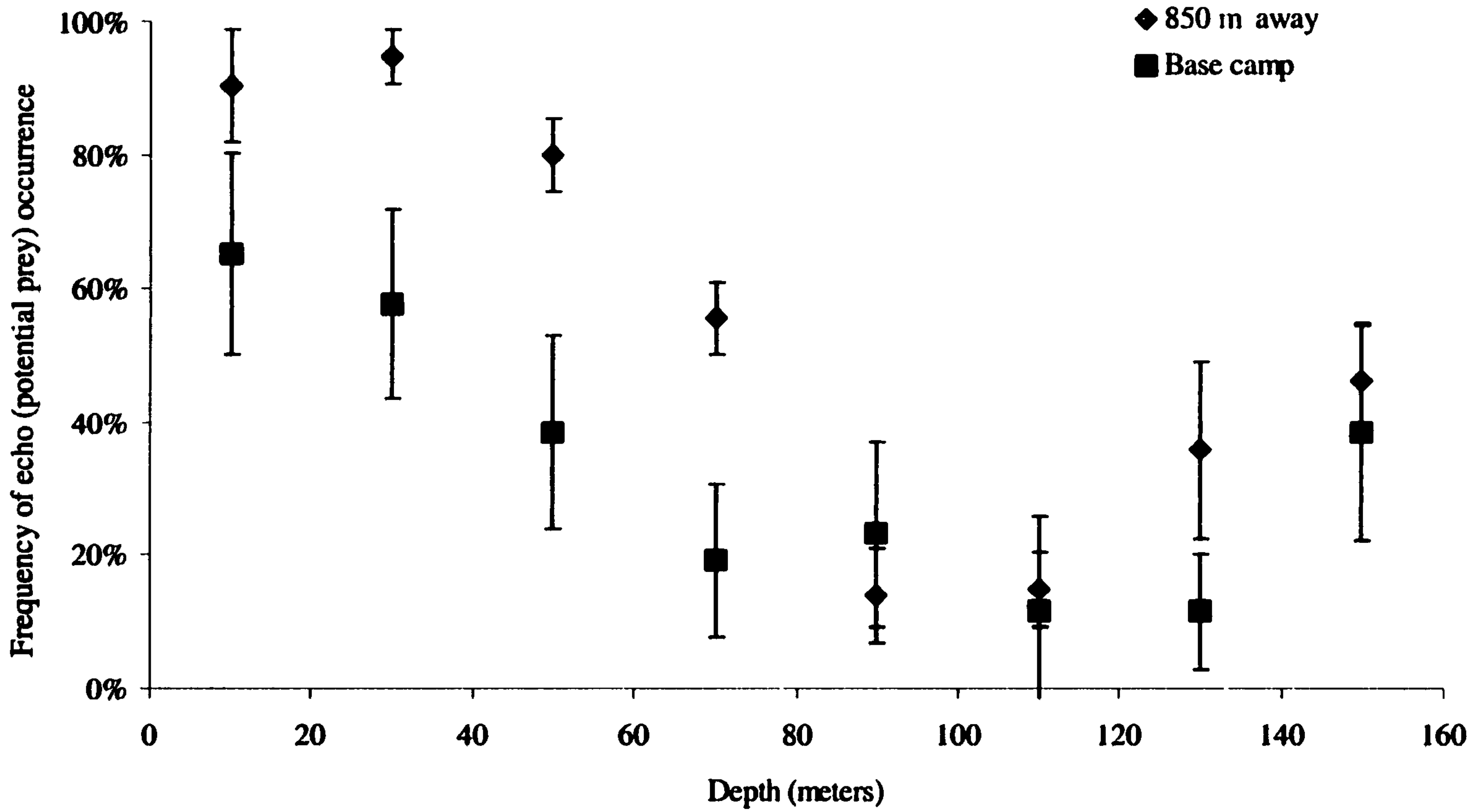


Figure 2.5: Spatial patchiness of prey. Frequency of echo (potential prey) occurrence is shown by 20 meter depth bin for an echogram recorded 850 meters away from our base camp from 13:11 May 6 - 14:24 May 7, 1996, and an echogram recorded at our base camp from 14:55-21:14 May 7, 1996. Values range from 0% (no echoes present in any sampled minute) to 100% (at least one echo present in all sampled minutes). The error bars shown are 95% confidence intervals.

CHAPTER 3: DEFINITION OF THREE-DIMENSIONAL DIVING BEHAVIORS EXHIBITED BY RINGED SEALS[1]

---

[1] Michael A. Simpkins, Brendan P. Kelly, Douglas Wartzok; prepared for submission to Marine Mammal Science

ABSTRACT

Behaviors were defined for ringed seal dives based on the three-dimensional movements of five freely diving seals. Horizontally convoluted dives, defined as dives with angular velocity > 15 °/s, appeared to be foraging dives. Dives that did not include convoluted movements (angular velocity < 10 °/s) were classified as exploration dives. Dives with nearly linear horizontal travel (horizontal directionality > 0.6) were classified as travel dives. Each dive type was observed with similar frequency in V-shaped dives (dives in which ascent immediately followed descent) and U-shaped dives (dives in which time was spent at depth between descent and ascent). The lack of behavioral differences between dives with distinct time-depth profiles suggested that time-depth profiles were not a reliable means of classifying behavioral dive types for ringed seals.

INTRODUCTION

Diving behaviors, which have previously been inferred for marine mammals from time-depth profiles, can be more fully understood by analyzing the movements of diving animals tracked in three dimensions. Previously, the functions of dives were surmised based on classes of time-depth profiles (Table 3.1). Functions ascribed to these classes, however, did not consistently correspond to inferences based on analysis of feeding events (Lesage *et al.* 1999), local search behavior, (Simpkins *et al.* in prep a), and three-dimensional dive profiles (Harcourt *et al.* 2000). The failure to consistently identify specific dive functions may reflect the limitations inherent in classifying three-dimensional diving behavior using one-dimensional (depth) data (Brillinger and Stewart 1997; Harcourt *et al.* 2000). Here, we quantify the three-dimensional diving behavior of freely-swimming ringed seals using techniques modified from previous analyses of two-dimensional movements (Batschelet 1981; Bell 1990; Turchin 1998). We quantitatively classify the three-dimensional movements of ringed seals and suggest behavioral functions for dives with distinct movements.

We expect to find evidence of social, foraging, and other behaviors within the recorded movements of ringed seals, because we monitored the seals' diving behavior during the spring mating and pupping seasons. Maintenance of breathing holes through the ice and avoidance of surface predators (e.g., polar bears and Inuit hunters) likely constitute a significant portion of ringed seal behavior within the shore-fast sea ice environment (Smith and Stirling 1975; Stirling 1977; Smith 1980; Smith and Hammill 1981; Smith *et al.* 1991; Kelly 1996a). During the breeding season, rutting males may defend underwater territories or access to breathing holes used by females (Stirling 1973; Smith and Hammill 1981; Hammill and Smith 1991; Kelly and Wartzok 1996). During the pupping season, lactating females apparently divide their time between foraging and caring for their pup, including moving their pup from one lair to another to avoid predators (Smith and Stirling 1975; Smith 1987; Hammill *et al.* 1991; Smith *et al.* 1991; Lydersen and Hammill 1993; Kelly and Wartzok 1996). Rutting males and estrous females may also engage in courtship behaviors while diving during the breeding season (Smith 1987). In addition, ringed seals likely rest, explore, and travel during dives, behaviors commonly inferred for other marine mammals based on classification of time-depth profiles (Table 3.1). Ringed seal foraging may include strategies inferred for other marine mammals: benthic foraging, pelagic foraging, and sit-and-wait foraging (Table 3.1). We examine the usefulness of three-dimensional movement analyses for quantifying and distinguishing between these proposed behaviors.

We expect three-dimensional movement analyses to readily distinguish between dives involving distinct movement behaviors. For example, we expect to be able to distinguish between travel dives that involve directional movement between two locations and foraging dives that involve convoluted movement during local search or prey pursuit. We do not, however, expect to distinguish between behaviors that involve similar movements. For example, both territorial defense and foraging likely involve convoluted movements as the animal searches for or pursues other seals or prey.

Here, we consider convoluted movement to represent local search or pursuit of prey during active foraging, although some proportion of convoluted movements may be social in nature. We can not independently verify social or foraging interactions based on movement alone. We do, however, have evidence that tracked seals foraged during our study. Of the four seals we recaptured, three exhibited mass gains over periods ranging from 10 to 31 days, and scat samples from the other were full of amphipod exoskeletons (Kelly and Wartzok 1996; unpublished data). Previous collections of stomach contents and scat samples also indicated that seals in our study area foraged during spring (Welch *et al.* 1992; Kelly and Wartzok 1996; unpublished data).

Marine mammal foraging behavior has been inferred from time spent at depth (bottom phase) between descent and ascent phases of dives (e.g., Kooyman 1968; Hindell *et al.* 1991; Thompson *et al.* 1991; LeBoeuf *et al.* 1992; Martin and Smith 1992; Werner and Campagna 1995; Westgate *et al.* 1995; Gales and Mattlin 1997). Time-depth profiles, however, did not indicate whether movements during these bottom phases were consistent with foraging. We directly quantify convoluted behavior by calculating angular velocity, meander, and fractal dimension for each dive and evaluate the usefulness of each method for defining convoluted foraging dives.

Two types of foraging behavior were previously inferred based on recorded or presumed behavior at depth. Pelagic foraging was inferred for dives during which animals performed repeated vertical excursions at depth (e.g., Hindell *et al.* 1991; Bengtson and Stewart 1992; LeBoeuf *et al.* 1992; Schreer and Testa 1996; Bengtson and Stewart 1997). Benthic foraging was often inferred for "flat-bottomed" dives during which much of the dive time was spent at, or near, one depth (e.g., Kooyman 1968; Hindell *et al.* 1991; LeBoeuf *et al.* 1992; Martin and Smith 1992; Werner and Campagna 1995; Westgate *et al.* 1995; Gales and Mattlin 1997). Whether dives of these two types actually were pelagic or benthic was unclear, however, because dive depths were rarely linked to bathymetry at the dive locations. We classify dives as either vertically or horizontally convoluted foraging, based on the primary orientation of presumed foraging movement (vertical for "pelagic foraging" and horizontal for "benthic foraging"). We distinguish between vertically and horizontally convoluted foraging dives based on the vertical and horizontal angular velocities of movement during the dives.

During sit-and-wait foraging an animal spends much of its time in one location, waiting for prey to pass within pursuit distance (Pianka 1966; Schoener 1971). Sit-and-wait foraging has been suggested for flat-bottomed dives, although swim speed data were required to determine if animals moved during the bottom phase (LeBoeuf *et al.* 1993; Thompson and Fedak 1993; Martin *et al.* 1998; Lesage *et al.* 1999). Elsewhere, we found that ringed seals occasionally stopped at one location during a dive (or slowed considerably), and we termed these occasions "slow passages" (> 7 seconds within a 3x3x3 m volume; Simpkins *et al.* in prep a). Here, we define sit-and-wait dives based upon the proportion of dive time spent in slow passages.

Travel behavior (moving from one horizontal location to another) has often been inferred for dives which lack a bottom phase, i.e., dives that have V-shaped time-depth profiles indicating that animals descended to some maximal depth and then immediately began their ascent back to the surface (Bengtson and Stewart 1992; LeBoeuf *et al.* 1992; Thompson and Fedak 1993; Martin *et al.* 1998; Otani *et al.* 1998). Time-depth data, however, lack information on horizontal movement, thus travel behavior can not be confirmed without auxiliary information. We classify travel dives based on the directionality of horizontal movement during dives.

During exploration, an animal efficiently searches a large volume, and exploration has been suggested for dives with a variety of time-depth profiles (Schreer *et al.* 1998). Convoluted paths tend to focus search effort to small regions, resulting in inefficient exploration of large regions (Bell 1990), and we expect exploration dives to have simple paths in contrast to convoluted foraging dives.

Resting animals must minimize their dive effort (i.e., energy expended during a dive) to allow for sleep or the redirection of energy to metabolic processes (Thompson *et al.* 1991; LeBoeuf *et al.* 1992; Crocker *et al.* 1997). Resting was originally inferred for dives during which animals apparently stopped actively swimming and slowly sank (or floated depending on buoyancy) for a portion of the dive (Hindell *et al.* 1991). Subsequently, rest dives were defined by low swim speeds using data from swim speed recorders (LeBoeuf *et al.* 1992; Crocker *et al.* 1994; Crocker *et al.* 1997; Webb *et al.* 1998; Hindell *et al.* 1999). We calculate swim speed as distance moved per unit time and define rest dives based upon a seal's swim speed. We also evaluate the usefulness of mean acceleration between moves as a measure of dive effort and resting behavior, because calculated swim speeds may represent seals drifting with currents rather than actively swimming.

We expect to be able to distinguish between rest, travel, exploration, horizontally convoluted foraging, vertically convoluted foraging, and sit-and-wait foraging dives based on swim speed, acceleration, horizontal directionality, angular velocities, meander, fractal dimension, and/or time spent in slow passages. We have no basis to set *a priori* limits on acceptable values of three-dimensional variables. We can, however, make several predictions. Rest dives should have lower swim speed and/or acceleration than other dives. Travel dives should have higher horizontal directionality than other dives. Exploration and convoluted foraging dives should lie at opposite ends of the convoluted spectrum (low and high respectively) as quantified by angular velocity, meander, or fractal dimension. Vertically and horizontally convoluted foraging dives should have higher vertical and horizontal angular velocities, respectively, than other dives. Sit-and-wait foraging dives should have higher proportions of time spent within slow passages than other dives.

METHODS

Data collection and processing

We used the same database for classifying ringed seal dives as we used elsewhere for definition of movement types within dives (Simpkins *et al.* in prep c). We recorded the three-dimensional movements of 13 ringed seals during the spring breeding season in 1990, 1991, 1992, 1996 and 1997 in the Canadian Arctic near Resolute Bay, Nunavut (74° 35' N, 95° 7' W; Kelly 1996a; Kelly and Wartzok 1996). We captured seals at breathing holes in shore-fast sea ice using nets (Kelly 1996b) and tracked their movements under the ice by way of ultra-sonic transmitters (Vemco Ltd., Armdale, Nova Scotia, Canada) attached to their hair (Wartzok *et al.* 1992b).

We compiled and filtered the data for each seal, removing erroneous locations which would have required swim speeds in excess of 6 m/s (greater than the maximal speed of harbor seals; Williams and Kooyman 1985). Shallow locations often were inaccurate, primarily as a result of acoustic reflection off of ice keels. We defined dives as movements to depths greater than 5 m with at least 10 data points. Some recorded dives were incomplete and did not include all phases of the dive. We included dives in this analysis only if the recorded portions of dive phases were greater than 7 seconds.

Division of dive paths into discrete moves

Analysis of movement paths required the division of each path into discrete, linear segments. Continuous paths could either be divided into time-steps of equal duration (e.g., Kareiva and Shigesada 1983), or divided into moves by combining a series of recorded movements in the same direction into a single move (Turchin *et al.* 1991). We chose to split dives into discrete moves, because we preferred to define path segments using the animals' behavior rather than an arbitrary time step. We defined moves as a series of locations which clustered around a line segment connecting the first and last locations in the move. An iterative procedure grouped sequential locations into moves, if, and only if, the locations were within a radius of three meters from the line segment connecting the first and last locations in the sequence (Figure 3.1; Turchin *et al.* 1991). Thus, each move represented continuous movement in one direction, namely the direction of the line segment. The iterative procedure defined a new move each time an animal changed the direction of its movement enough to move three meters "off course," i.e., away from the move line segment. Using this method, we effectively split dive paths into a series of connected cylinders of radius r (Figure 3.1).

The radius, r, used to define moves (3 m) was the smallest radius for which the number of moves defined was not constrained by the number of data points recorded (Turchin *et al.* 1991). We used r values of 0.5, 1, 2, 3, 4, and 5 meters to split 511 randomly chosen dives (10% subsample of all dives) into moves. At r values less than three meters, the number of moves defined was linearly related to the number of data points, such that each sequential pair or triplet of data points resulted in a new move. These low r values probably defined moves based on noise in the data in addition to behavior, because the error in our location data was ± 1 m (maximal error ± 2 m; Wartzok *et al.* 1992a). In contrast, at r values of three, four, and five meters, moves were not related to the number of data points, suggesting that moves were defined based on behavior, not noise. We chose the smallest radius which compensated for noise in the location data (3 m), because we were interested in characterizing ringed seal movements at the finest scale possible.

We examined our data to determine if sampling rate affected our definition of moves. We found a linear relationship between the number of moves and data points (regardless of r), in dives with fewer than 15 location data points per minute. Dives with fewer than 15 points/minute were undersampled, and more moves would probably have been defined if the dive had been sampled at a higher rate. We used only dives with 15 or more points/minute in this analysis. Eight seals were tracked using transmitters which emitted pulses every 1 – 1.5 seconds (a sufficiently rapid sampling rate). Only five seals had more than ten dives with 15 or more points/minute after data processing (410 dives, Table 3.2).

Quantification of diving behaviors

We converted three-dimensional move data (start and end points of moves defined by rectangular (x, y, z) coordinates) to spherical coordinates for analysis purposes (Figure 3.2, modified from Batschelet 1981). We described each movement along a path in spherical coordinates as a move length (m) in a direction defined by the horizontal angle in the X-Y plane (ϕ, counter-clockwise angle from the positive X-axis) and the vertical angle up from the Z-axis (θ). The Z-axis, in our coordinate system, was positive in the downward direction (Figure 3.2). Note that θ was constrained between 0° (vertical descent) and 180° (vertical ascent), while ϕ could range from 0° to 360° (or −180° to 180°).

For each dive, we calculated angular velocities (horizontal, vertical, and three-dimensional), mean dive speed, horizontal directionality, and proportion of time spent in slow passages (Box 3.1). We quantified convoluted behavior in terms of turning behavior as measured by angular velocities. Based on these measures of convoluted behavior, we distinguished between presumed foraging dives with vertically and/or horizontally convoluted dive paths and exploration dives with simple dive paths.

We quantified sit-and-wait foraging by the proportion of dive time spent in slow passages. Slow passages were periods of time when an animal was stationary in the water column (> 7 seconds within a 3x3x3 meter volume), and we considered slow passages to be moves with no length for analysis purposes. We determined the proportion of dive time spent in slow passages by dividing the total duration of all slow passages during a dive by the total dive time (Box 3.1). Resting was also related to seals slowing down, but we quantified rest dives in terms of mean dive speeds.

We measured travel behavior in terms of horizontal directionality. We calculated horizontal directionality for each dive as the mean vector of ϕ (Box 3.1), which was a measure directly related to the standard deviation of ϕ using circular statistics (Batschelet

1981). Horizontal directionality, measured in this fashion, could range from 1, when all angles in the sample were identical, to 0, when the angles were uniformly distributed over 360°.

In addition to the analyses described above, we calculated mean acceleration between moves for each dive and evaluated it as an alternative to mean speed as a measure of dive effort (Box 3.1). We also calculated meander and fractal dimension for each dive and considered them as alternative measures of convoluted behavior. We calculated meander as three-dimensional angular velocity divided by mean dive speed (Box 3.1). Before using meander to quantify convoluted behavior, we tested for correlation between angular velocity and speed which could bias meander values. We considered correlation between these two variables to be likely, because both angular velocity and speed often increase during foraging behavior and decrease during travel behavior (Bell 1990).

We also evaluated the usefulness of calculating dive fractal dimensions for measuring convoluted behavior. The fractal dimension of a path represents the effective dimension of the path shape (Mandelbrot 1983; Feder 1988; Sugihara and May 1990; Hastings and Sugihara 1993). For example, a straight line path is dimension 1, Brownian motion in a plane is dimension 2, and Brownian motion in three-dimensional space is dimension 3. We expected dive paths to have fractal dimensions between 1 and 3.

We estimated the fractal dimension of dives using the cluster method (Hastings and Sugihara 1993), which is the most appropriate method for a series of points in three-dimensional space like our data. Estimations of fractal dimension using the box method and dividers (or compass) method are more appropriate for data from continuously tracked paths (Hastings and Sugihara 1993), although the dividers method has been most commonly used in the study of movement behavior (following Dicke and Burrough 1988). In general, fractal analysis methods estimate the fractal dimension by calculating the slope of a log/log plot between some measure of a shape and the scale of that measure (Feder 1988; Sugihara and May 1990; Hastings and Sugihara 1993). For example, the cluster method calculates the fractal dimension as the slope of the log/log plot of pairs of points within radius R of each other vs. R (Figure 3.3). To be consistent with the rest of our analyses, we used dive paths consisting of the start and end points of the moves defined earlier. We interpolated locations along move line-segments for each second of dives to remove the effect of move duration on the fractal analysis and to match the maximal precision of our location data. Note that we simplified the dive plots in Figure 3.3 and only showed the start and end points of each move to allow for easier viewing.

In order for calculated fractal dimensions to be valid, they must be constant over a biologically meaningful range of scales. In other words, the fractal dimension must be a scale-independent parameter. Paths which have scale-independent fractal dimensions are termed "self-similar", meaning that the complexity (or effective dimension) of the path is constant between measurement scales. In other words, a self-similar path will appear equally convoluted regardless of the magnification, or scale, at which it is viewed. Here, we tested the assumption of dive path self-similarity by testing for significant curvature in log-log plots (Turchin 1996; Figure 3.3B). We also calculated fractal dimensions for a one order of magnitude range in radius values (5 - 50 meters) and only reported fractal dimensions for cases in which the linear model fit with $r^2 > 0.99$ (Figure 3.3A), following Coughlin *et al.* (1992). We did not use radius values < 5, because the empty space between interpolated points affected the analysis (6 meters maximal distance between sequential points).

Empirical definition of dive behaviors

We defined dive behaviors in terms of three-dimensional movement variables (Box 3.1) based on inspection of dive plots or histograms of each movement variable. We recognized dives with vertically and/or horizontally convoluted dive paths, dives with simple dive paths, and dives involving horizontally directional travel by visual inspection of dive plots. Dives with convoluted paths tended to focus many moves into small regions, consistent with local search and pursuit behaviors during foraging (Figure 3.4A). Horizontally convoluted dives showed most turning behavior occurring in the horizontal (X-Y) dimensions (Figure 3.4A), and vertically convoluted dives showed repeated vertical excursions at depth (e.g., Hindell *et al.* 1991; Bengtson and Stewart 1992; LeBoeuf *et al.* 1992; Schreer and Testa 1996; Bengtson and Stewart 1997). Plots showing nearly linear horizontal movement, with no evidence of convoluted movement, were taken to represent travel (Figure 3.4B). We visually recognized exploration dive plots by the absence of convoluted movement, but we did not require exploration dives to be directional like travel dives (Figure 3.4C).

We defined convoluted, travel, and exploration behaviors by setting limits on either angular velocity or horizontal directionality values. We set these limits conservatively, to ensure that behaviors assigned to any dive could be corroborated by visual inspection of the dive plot. Some values were inconclusive in defining behaviors, therefore, we did not classify dives with those values. For example, we calculated angular velocities between 10 and 15 °/s for dives with highly convoluted movement (presumed foraging dives), dives without convoluted movement (exploration dives), and dives with intermediate movement for which no behavior could be recognized visually. Since angular velocities between 10 and 15 °/s were inconclusive in defining behavior, we did not classify dives with those angular velocities.

We could not recognize rest and sit-and-wait behaviors by visual inspection of dive plots. We quantified these two behaviors by mean dive speed and proportion of time spent in slow passages, which did not necessarily affect the appearance of the dive plot. We plotted histograms of mean dive speed and proportion of dive time spent in slow passages for all dives and looked for evidence of a distinct class of dives with low speed (rest dives) or high proportion of time in slow passages (sit-and-wait dives). Specifically, we inspected each histogram for evidence of a bimodal distribution (i.e., a mixture of distributions; Everitt and Hand 1981; McLachlan and Basford 1988). If we found a bimodal distribution, we determined the point at which the two component distributions intersected and used this value as the limit for distinguishing between the related behaviors.

We calculated all movement variables for each dive and classified dives based on the quantitative definitions of each behavior. Behavioral definitions were not exclusive, and multiple behaviors could be defined for one dive. We described the three-dimensional characteristics of each defined behavior in terms of the ranges of all movement values calculated for the behavior. We also compared our classification of dive behaviors to previous time-depth profile classifications by comparing the distribution of dive behaviors among dives with two distinct time-depth profiles (V-shaped and U-shaped dives).

RESULTS

Ringed seals did exhibit horizontally convoluted, travel, and exploration dives as expected, but did not exhibit vertically convoluted, rest, or sit-and-wait foraging dives. We grouped data from all seals together, because few dives had the very detailed data required for our analysis (Table 3.2). Based on our inspection of dive plots and movement variable histograms, we defined convoluted (presumed foraging) dives as dives with three-dimensional angular velocities > 15 °/s, travel dives as dives with horizontal directionalities > 0.6, and exploration dives as dives with three-dimensional angular velocities < 10 °/s (Table 3.3). Horizontal angular velocity was always high when three-dimensional angular velocity was high (Spearman rank correlation = 0.93, p = 0.0001), hence all convoluted dives fit our definition of horizontally convoluted dives. Although horizontally convoluted dives were consistent with the foraging style previously termed "benthic" (e.g., Kooyman 1968; Hindell *et al.* 1991; LeBoeuf *et al.* 1992; Martin and Smith 1992; Werner and Campagna 1995; Westgate *et al.* 1995; Gales and Mattlin 1997), these dives occurred at all depths in the water column (5 - 169 meters). Previous inferences of pelagic foraging were associated with repeated vertical excursions at depth, i.e., vertically convoluted movements (e.g., Hindell *et al.* 1991; Bengtson and Stewart 1992; LeBoeuf *et al.* 1992; Schreer and Testa 1996; Bengtson and Stewart 1997). Consistently low vertical angular velocities for all ringed seal dives suggested that movements were only convoluted in the horizontal dimensions and that vertically convoluted movements were not common (95% of all vertical angular velocities < 5 °/s).

We found no evidence for a distinct class of rest or sit-and-wait dives. During rest dives, we expected seals to minimize their dive effort by moving slowly and/or avoiding rapid acceleration, but unimodal histograms of mean speed and acceleration indicated no distinct class of low-effort dives (Figures 3.5A and 3.5B). During sit-and-wait dives, we expected seals to spend a large proportion of the dive time in slow passages, but the histogram of proportion of dive time spent in slow passages was also unimodal (Figure 3.5C), indicating that no distinct class of sit-and-wait dives was present.

Travel, exploration, and convoluted dives involved distinct types of movement based on three-dimensional analysis of ringed seal dives (Table 3.4). Convoluted dives involved movements with lower horizontal directionality, higher mean speed, higher mean acceleration, higher angular velocity (horizontal, vertical, and three-dimensional), and higher meander than travel or exploration behavior (Table 3.4). Travel and exploration dives were similar to each other, but travel dives were shallower and involved movements with higher horizontal directionality than movements in exploration dives (Table 3.4).

Convoluted dives were the most common dive observed for ringed seals, and travel dives were the least common (Table 3.5). We observed each dive behavior with similar frequency for dives with only descent and ascent phases and dives with bottom phases (Table 3.5). Often, travel dives were also classified as exploration dives, but convoluted dives were rarely classified as exhibiting any other behavior (Table 3.6).

Two three-dimensional movement variables, meander and fractal dimension proved to be inappropriate for use in quantifying ringed seal diving behaviors. Meander values were likely biased, because meander was the quotient of two variables which were correlated, three-dimensional angular velocity and mean speed (Spearman rank correlation = 0.56, p = 0.0001). We found fractal dimensions to be scale-dependent for ringed seal dives, whereas fractal dimension estimation assumed scale-independence.

Scale-dependent fractal dimensions were indicated by the significant negative curvature found in fractal analysis plots for 332 of 410 dives (e.g., Figure 3.3B). Significant positive curvature was found in fractal analysis plots for only 45 dives. A group of dives with scale-independent fractal dimensions should have an equal number of positively and negatively curved fractal analysis plots (Turchin 1996). The abundance of negatively curved fractal analysis plots for ringed seal dives resulted from each curve approaching an asymptote at the radius R which equaled the greatest distance between a pair of points within the dive analyzed. At the asymptotic radius, all points were within R of each other. Increasing the radius beyond this asymptote resulted in no concomitant increase in pairs of points within radius R of each other, since all pairs had already been included. The plots in Figure 3.3 show the affect of dive size on fractal analysis plot curvature. Note that the larger dive (Figure 3.3A) had no significant curvature in its fractal analysis plot, while the smaller dive (Figure 3.3B) had negative curvature in its fractal analysis plot. In many cases the curvature exhibited in fractal analysis plots was slight, and 266 dives showed a strongly linear relationship ($r^2 > 0.99$) in the log/log plot of points within radius R of each other vs. R (Figure 3.3A). The fractal dimensions calculated from these strongly linear regressions ranged from 0.51 to 1.67. Fractal dimensions less than 1 indicated that the line was fit near the asymptote of curvature (the slope and dimension were 0 at the asymptote).

DISCUSSION

The three-dimensional movements of five freely diving ringed seals were analyzed for evidence of travel, exploration, rest, horizontally convoluted foraging, vertically convoluted foraging, and sit-and-wait foraging. Horizontally convoluted, travel, and exploration dives were observed, but rest, vertically convoluted, and sit-and-wait foraging dives were not observed. Although foraging could not be independently verified for individual dives, ringed seals engaged in convoluted movements consistent with active foraging during more than 1/3 of dives, and we suggest that these dives represented convoluted foraging (Table 3.5). If we consider that some exploration dives represented unsuccessful search for prey, then the seals may have attempted to forage during more than 1/2 of all dives. The seals rarely dove for the sole purpose of traveling from one horizontal location (i.e., breathing hole) to another (< 10% of dives). Some dives, especially those of HO90 (a rutting male), likely included social behaviors such as patrolling territories or agonistic interactions during territorial defense. In our analysis, patrolling could not be distinguished from exploration, and agonistic interactions might involve convoluted movements indistinguishable from convoluted foraging.

Convoluted dives, regardless of their social or foraging functions, were most clearly distinct from all other dives (Table 3.2). Convoluted dives involved higher speed, acceleration, and angular velocities than other dives (Table 3.4). These high values suggested that convoluted dives represented active search, and/or pursuit of prey (or other seals during social interactions), and indicated that these dives were more energetically expensive than other dives. Convoluted dives appeared to exclusively involve horizontal turns, consistent with seals foraging along the benthos. Horizontally convoluted dives, however, occurred at all depths and were not limited to dives that reached the benthos (Table 3.4). Also, our analysis of three-dimensional movements within ringed seal dives indicated that horizontally convoluted movements were not limited to the bottom phase of dives, rather these movements occurred during all phases of dives (Simpkins *et al.* in prep c). The slow changes in vertical bearing throughout convoluted dives (low vertical angular velocity; Table 3.4) suggested that these dives involved stalking of prey without prolonged pursuit. We would have expected prolonged pursuit to involve rapid changes in both the horizontal and vertical bearing of a seal chasing prey which could flee in any three-dimensional direction. Limited prey pursuit following stalking behavior has recently been observed in Weddell seals (Davis *et al.* 1999).

Vertical excursions at depth (i.e., rapid changes in vertical bearing) were not observed in ringed seal dives but have been observed in dives of other pinnipeds (Table 3.1). The vertical excursions have been hypothesized to represent pursuit of individual pelagic prey or plunging through a patch of pelagic prey (e.g., Hindell *et al.* 1991; Bengtson and Stewart 1992; LeBoeuf *et al.* 1992). The vertical movements may also be designed to reduce predator avoidance responses by approaching prey from below and behind where it is most difficult for the prey to detect the predator's approach (Bengtson and Stewart 1992). Ringed seal dives were very constrained in the vertical dimension, as evidenced by the very low vertical angular velocities (Table 3.4). The lack of repeated vertical excursions during dives suggests that ringed seals rarely pursue prey vertically, neither plunging through prey patches nor positioning themselves to reduce prey perception. In addition, the lack of change in vertical bearings throughout ringed seal dives is consistent with the use of burst-and-glide swimming during descent and ascent. Elephant seals, Weddell seals, bottlenose dolphins, and blue whales glide during portions of some dives, once an appropriate speed has been achieved by a burst of initial swimming effort (Webb *et al.* 1998; Skrovan *et al.* 1999; Williams *et al.* 2000). Gliding duration appears to be enhanced by changes in the buoyancy of diving animals with depth (Webb *et al.* 1998; Skrovan *et al.* 1999). The energy saved through burst-and-glide swimming can extend the aerobic dive limit of diving animals (Williams *et al.* 1999; Williams *et al.* 2000). We suggest that ringed seals may utilize burst-and-glide swimming, resulting in fairly constant vertical bearing during descent and ascent, and focus their swimming effort on horizontal movements.

Although a distinct class of dives dedicated to sit-and-wait foraging behavior was not found in the 410 ringed seal dives examined here (Figure 3.5C), some evidence indicates that ringed seals do remain stationary in the water column on rare occasions. Elsewhere, we examined 4027 dives of 13 ringed seals for evidence of slow passages, and found that slow passages occurred more frequently than expected due to chance in 634 dives (16% of dives; Simpkins *et al.* in prep a). We also found that slow passages were occasionally very long, indicating that seals were stationary in the water column (243 slow passages ≥ 30 seconds, maximum = 248 seconds). Stationary seals could have been swimming against a current or drifting with no current.

Travel dives were, by definition (Table 3.3), more directional than other dives and were also shallower than convoluted or exploration dives (Table 3.4). Shallow travel dives by ringed seals were quite different from the deep travel dives observed in some other seal species. Traveling elephant seals apparently dive to the sea floor during each dive as they cross the continental shelf (e.g., LeBoeuf *et al.* 1988; Hindell *et al.* 1991), and some grey seals also dive to the sea floor as they travel between foraging sites (Thompson *et al.* 1991).

During our study, travel dives of ringed seals likely related to breathing hole maintenance. Breathing holes must be regularly maintained by ringed seals or else they will re-freeze, blocking the seals' access to air. Seals should maximize the time they can spend enlarging or opening a hole by maximizing the amount of stored oxygen available to them upon arrival at the hole. Ringed seal travel dives may be constrained to shallow depths in order to minimize the distance traveled between holes, allowing for more time (oxygen) for hole-maintenance.

Exploration dives included the majority of travel dives (Table 3.6), as well as dives which were not directional (Table 3.4). Although travel dives may have been used for breathing hole maintenance, the possibility that travel dives also served an exploratory function could not be discounted. Exploration dives may represent seals searching for novel breathing holes, prey, or other seals (e.g., for breeding or territorial purposes). Exploration for other seals was most likely restricted to shallow exploration dives, because other seals were most easily found at, or near, breathing holes which were limited in number and fixed in space (Kelly and Wartzok 1996). In contrast, exploration for prey may have occurred at any depth, if we assume that the distribution of convoluted dive depths represented the distribution of prey (Table 3.4). Exploration for breathing holes has been studied experimentally in ringed and Weddell seals, and the seals apparently perceived areas with thin snow or ice cover (e.g., breathing holes and re-frozen cracks) as "bright spots" from below the ice (Wartzok *et al.* 1992a). We expect exploration for breathing holes to have occurred at some optimal depth, which was deep enough to allow multiple breathing holes to be seen (ice keels limit the range of sight at shallow depths), yet shallow enough that breathing holes were still "bright" enough to see (i.e., the depth of adequate light transmission). Although the freely-diving ringed seals we tracked generally used a fixed set of breathing holes which they actively maintained, we did capture several seals at holes which we cut through the sea ice, indicating that seals did find and use novel holes. We could not determine, however, whether seals actively searched for novel holes or encountered the holes coincidentally.

Rest dives were not observed in ringed seal dives. Ringed seals often spend long periods between dives either resting in subnivean lairs or floating at the surface in breathing holes (Kelly and Quakenbush 1990; Kelly 1996a). In contrast, elephant seals, for which rest dives were first hypothesized (Hindell *et al.* 1991; LeBoeuf *et al.* 1992), often dive continuously for prolonged periods without spending more than a few minutes at the surface between successive dives (LeBoeuf *et al.* 1988: Hindell *et al.* 1992). Ringed seals may stop swimming briefly during slow passages, but slow passages occur infrequently and sporadically during dives (Simpkins *et al.* in prep a). Sporadic slow passages may represent highly localized search or occasional active ambush or drift predation events, but are not consistent with the prolonged lack of swimming effort expected during rest dives.

The full suite of convoluted (presumed foraging), travel, and exploration dives were observed with similar frequency for both V-shaped and U-shaped dives ($X^2 = 0.74$, $p > 0.65$; Table 3.5). The lack of behavioral differences between V-shaped and U-shaped dives, which have very distinct time-depth profiles, suggests that time-depth profiles are not a reliable means of classifying dive behaviors for ringed seals. Classification of dive behaviors by time-depth profiles has also been found to be unreliable for harbor and Weddell seals (Lesage *et al.* 1999; Harcourt *et al.* 2000). We suggest that time-depth data do not contain enough behavioral information to justify their use in classifying dives by function. Time-depth data lack information on horizontal movement which is essential for inferring behaviors, especially for ringed seals whose movements are most varied in the horizontal dimensions.

The three-dimensional movement variables we calculated proved to be useful in classifying and quantifying diving behavior for ringed seals except for the meander and fractal dimension variables. Meander was a promising variable because it included speed and angular velocity, both important characteristics of dive behaviors (Table 3.4). The correlation between speed and angular velocity (Spearman rank correlation = 0.56, p = 0.0001), however, made the use of meander as a defining variable suspect. If changes in angular velocity values between behaviors were matched by similar changes in speed values, then the ratio of angular velocity to speed (i.e., meander; Box 3.1) would not change between behaviors. Differences in meander between dive behaviors did, however, follow the trends present in speed and angular velocity between behaviors (Table 3.4). Meander values apparently tracked angular velocity values, because angular velocity changed more dramatically between behaviors than did speed.

Fractal dimension was also not useful for quantifying ringed seal diving behaviors. Fractal dimensions have been calculated recently in several studies of two-dimensional movement behavior (Dicke and Burrough 1988; Turchin 1998), as well as one study of three-dimensional movement behavior (Coughlin *et al.* 1992). We found that ringed seal dive paths were not self-similar over the range for which we calculated fractal dimension. Calculated fractal dimensions appeared to be a result of the size of the dive path, rather than the dive's complexity. When fractal dimensions are calculated for scales which are greater than the size of an object or path, the fractal dimensions approach 0. The fractal analysis scale of 5 – 50 meters approached the size of ringed seal dives and resulted in low fractal dimensions, because the fractal analysis log/log plots curved as they approached the asymptote at which fractal dimension was 0 (e.g., Figure 3.3B). Fractal dimension values for ringed seal dives were often less than 1, clearly indicating that fractal analysis was not appropriate for those dives. Fractal analysis may prove useful if used to estimate the fractal dimensions of larger dives. Alternatively, fractal dimension could be estimated over smaller scales (e.g., 1 – 10 meters), which would require more detailed location data than we collected.

The definition of dive behaviors using three-dimensional analysis techniques allowed us to quantitatively distinguish between dives involving different types of movements. In contrast, previous classification of dive types has generally involved multivariate techniques which make the relationship between animal movements and definition of behavior more abstract (Schreer *et al.* 1998).

We suggest that future studies of dive behavior should focus on testing quantifiable hypotheses about diving behavior and developing methods of quantifying relevant behaviors. Here, we have demonstrated several methods of quantifying movement behavior using three-dimensional data. Swim speed analysis appears promising as an alternate approach to quantifying behaviors and testing behavioral hypotheses (Crocker *et al.* 1994; Crocker *et al.* 1997; Lesage *et al.* 1999). At present, swim speed data are more readily obtained than three-dimensional data.

It is our hope that the methods described here will be used and improved upon in other studies of the three-dimensional diving behavior of marine mammals. In this study, we found that a data acquisition rate of greater than 15 locations/minute was necessary to describe the behavior of ringed seals within dives. Animals that move more quickly or follow more complex paths will require a faster data acquisition rate. We recommend dividing dives into distinct moves, which are defined by an animal's movements, rather than subsampling a dive into discrete time-steps. When splitting a dive path into "move cylinders" as we did, it is important to choose a radius for the move cylinders which is large enough to incorporate noise in the location data within the definition of moves. In this study, we found that 3 meters was the best radius for splitting ringed seal dives into moves. This was the smallest radius for which the number of moves defined was not constrained by the number of data points recorded, probably because the maximal error in our data was on the order of ± 2 meters. Reducing the error in the location data would likely allow the move cylinder radius to be reduced as well.

Three-dimensional movement data allowed us to more fully describe the diving behavior of ringed seals. We were able to quantitatively classify dive behaviors based on the three-dimensional movements of ringed seals. The methods described here can be extended to testing behavioral hypotheses when information about environmental or physiological constraints is available. For example, prey distribution data could be used in conjunction with three-dimensional data to test hypotheses about optimal search or pursuit tactics with regard to speed and angular velocity. These methods can also be extended to searching dive paths for evidence of changes in behavioral states within individual dives. We have conducted such an analysis elsewhere and have found evidence of switching between directional and convoluted movements within dives by ringed seals (Simpkins *et al.* in prep c).

Table 3.1: Dive classification studies of marine mammals by species, and behaviors inferred for dive types.

Reference	Species	Inferred dive behaviors						
		Rest	Explore	Travel	Forage	Benthic	Pelagic	Sit & wait
Kooyman (1968)	Weddell seal		X		X			
Schreer and Testa (1996)	Weddell seal		X	X	X	X	X	
Burns *et al.* (1997)	Weddell seal	X	X	X	X	X	X	
Schreer *et al.* (1998)	Weddell seal, S. elephant seal	X	X	X	X			
LeBoeuf *et al.* (1988)	N. elephant seal				X			
LeBoeuf *et al.* (1992)	N. elephant seal	X		X	X	X	X	
LeBoeuf *et al.* (1993)	N. elephant seal			X	X	X	X	X
Asaga *et al.* (1994)	N. elephant seal	X		X	X		X	
Crocker *et al.* (1994)	N. elephant seal	X		X	X	X	X	
LeBoeuf *et al.* (1996)	N. elephant seal	X						
Crocker *et al.* (1997)	N. elephant seal	X		X	X	X	X	
Webb *et al.* (1998)	N. elephant seal	X						
Hindell *et al.* (1991)	S. elephant seal	X		X	X	X	X	
Slip *et al.* (1994)	S. elephant seal	X	X	X	X	X	X	
Jonker and Bester (1994)	S. elephant seal	X	X	X	X		X	
Campagna *et al.* (1995)	S. elephant seal	X		X	X	X	X	
Jonker and Bester (1998)	S. elephant seal	X	X	X	X			
Hindell *et al.* (1999)	S. elephant seal	X						
Bengtson and Stewart (1992)	Crabeater seal		X	X	X		X	
Thompson and Fedak (1993)	Grey seal			X	X	X		X
Lesage *et al.* (1999)	Harbor seal			X	X	X		X
Werner and Campagna (1995)	S. sea lion				X	X		
Hindell and Pemberton (1997)	Austr. fur seal				X			
Martin and Smith (1992)	Beluga				X			
Martin *et al.* (1998)	Beluga	X		X	X	X	X	X
Martin *et al.* (1994)	Narwhal				X			
Otani *et al.* (1998)	Harbor porpoise			X	X			

Table 3.2: Dives analyzed for each seal. Only the dives tallied for the seals listed below met the criteria necessary for inclusion in this detailed analysis. All dives below were to depths greater than 5 meters, consisted of at least 10 location data points collected at a rate of ≥ 15 points/minute (after erroneous locations were removed), and included at least 7 seconds of data for each phase of the dive.

Seal	Age	Sex	Year of capture	Dives
HO90	7	M	1990	14
HE91	7	F	1991	31
ME91	7	F	1991	233
SC96	1	M	1996	119
SP90	1	F	1990	13

Table 3.3: Empirical definitions of ringed seal dive behaviors. Dive behaviors were defined in terms of calculated three-dimensional movement variables (Box 3.1). All convoluted dives were horizontally convoluted dives. No evidence was found for vertically convoluted, rest, or sit-and-wait foraging dives.

Dive behavior	Empirical definition
Convoluted	Three-dimensional angular velocity > 15°/s
Horizontally convoluted	Same as convoluted
Vertically convoluted	NA
Travel	Horizontal directionality > 0.6
Exploration	Three-dimensional angular velocity < 10°/s
Rest	NA
Sit-and-wait foraging	NA

Table 3.4: Three-dimensional movement values by behavior: mean (interquartile range). All movement values differ significantly between behaviors (Kruskal-Wallis, $p \leq 0.005$). Letters indicate significant differences in values between behaviors (a < b < c) using a non-parametric multiple-comparison test for unequal sample sizes (Dunn 1964; Zar 1996).

	Travel	Exploration	Convoluted
Horizontal angular velocity	7.94 a	8.42 a	20.88 b
	(4.58, 10.84)	(6.68, 10.74)	(18.51, 23.04)
Vertical angular velocity	1.88 a	1.95 a	2.56 b
	(0.895, 2.58)	(0.976, 2.58)	(1.39, 3.15)
Three-dimensional angular velocity	8.32 a	7.23 a	19.02 b
	(5.85, 10.93)	(6.03, 8.81)	(16.74, 20.92)
Horizontal directionality	0.730 c	0.393 b	0.214 a
	(0.657, 0.785)	(0.132, 0.626)	(0.061, 0.346)
Meander	4.58 a	4.61 a	7.84 b
	(3.01, 5.70)	(3.26, 5.15)	(6.81, 8.64)
Mean Speed	1.86 a	1.74 a	2.49 b
	(1.49, 2.24)	(1.36, 2.04)	(2.19, 2.81)
Mean Acceleration	0.176 a	0.148 a	0.329 b
	(0.073, 0.233)	(0.078, 0.213)	(0.265, 0.375)
Fractal Dimension	0.98 a	1.09 a	1.25 b
	(0.96, 1.02)	(0.99, 1.20)	(1.15, 1.35)
Maximum Depth	16.84 a	50.43 b	64.35 b
	(9,21)	(14,81)	(17,115)

Table 3.5: Frequency of dive behaviors defined by three-dimensional analysis of ringed seal movements. The frequency of defined dive behaviors is contrasted between all dives and two dive types commonly classified using time-depth profiles (V-shaped dives and U-shaped dives). The frequency of dive behaviors determined by three-dimensional analysis do not differ between V-shaped and U-shaped dives deduced by time-depth profiles ($X^2 = 0.74$, $p > 0.65$).

Diving behavior	Count (percent) of all dives	Count (percent) of V-shaped dives	Count (percent) of U-shaped dives
Travel	37 (9 %)	12 (12 %)	25 (8 %)
Exploration	81 (20 %)	24 (25 %)	57 (18 %)
Convoluted	157 (38 %)	41 (42 %)	116 (37 %)
Undefined	166 (40 %)	30 (31 %)	136 (43 %)
All dives	410 dives	97 V-shaped dives	313 U-shaped dives

Table 3.6: Dives for which two behaviors were defined. The total of dives for which each behavior was defined is contrasted with the numbers of dives for which two behaviors were defined. For example, 37 dives were defined as travel dives, and 23 of those dives were also defined as exploration dives.

	Total	Travel	Exploration	Convoluted
Travel	37	--	23	2
Exploration	81	23	--	0
Convoluted	157	2	0	--

Box 3.1: Three-dimensional movement variables calculated for each dive (Batschelet 1981; Bell 1990; Turchin 1998).

Horizontal angular velocity = $\Sigma\ (\phi_{i+1} - \phi_i)\ /\ \Sigma\ (t_i)$

Vertical angular velocity = $\Sigma\ (\theta_{i+1} - \theta_i)\ /\ \Sigma\ (t_i)$

Three-dimensional angular velocity = $\Sigma\ (\alpha_i)\ /\ \Sigma\ (t_i)$

Horizontal directionality = $\{\ [\ (\Sigma \cos \phi_i)^2 + (\Sigma \sin \phi_i)^2\ ]^{0.5}\ \}\ /\ n$

Meander = three-dimensional angular velocity / mean speed

Mean speed = $\Sigma(m_i)\ /\ \Sigma\ (t_i)$

Mean acceleration = $\Sigma\ \{\text{abs}\ [\ (m_{i+1}/t_{i+1}) - (m_i/t_i)\ ]\ /\ [\ (t_i + t_{i+1})\ /\ 2\ ]\ \}$

Proportion of time spent in slow passages = $\Sigma\ (\ s_j\ )\ /\ \Sigma\ (t_i)$

where: ϕ_i = counter-clockwise angle from the positive X-axis for move i, θ_i = vertical angle up from the positive Z-axis for move i, α_i = three-dimensional turning angle between move i and move i+1, t_i = duration of move i, n = number of moves, m_i = length of move i, abs = absolute value, and s_j = duration of slow passage j (note that slow passages are considered moves, so j is a subset of i).

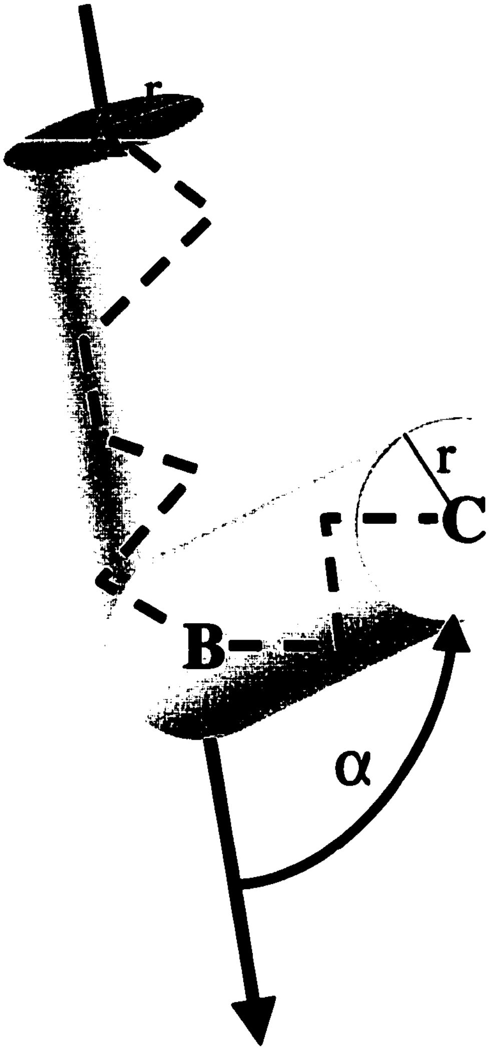


Figure 3.1: Definition of moves and three-dimensional turning angle between moves for dive analysis. AB is defined as one move because all points along the dotted dive path between A and B are within r (3 m) of the line segment AB. BC is defined as a move similarly. The three-dimensional turning angle between AB and BC is α.

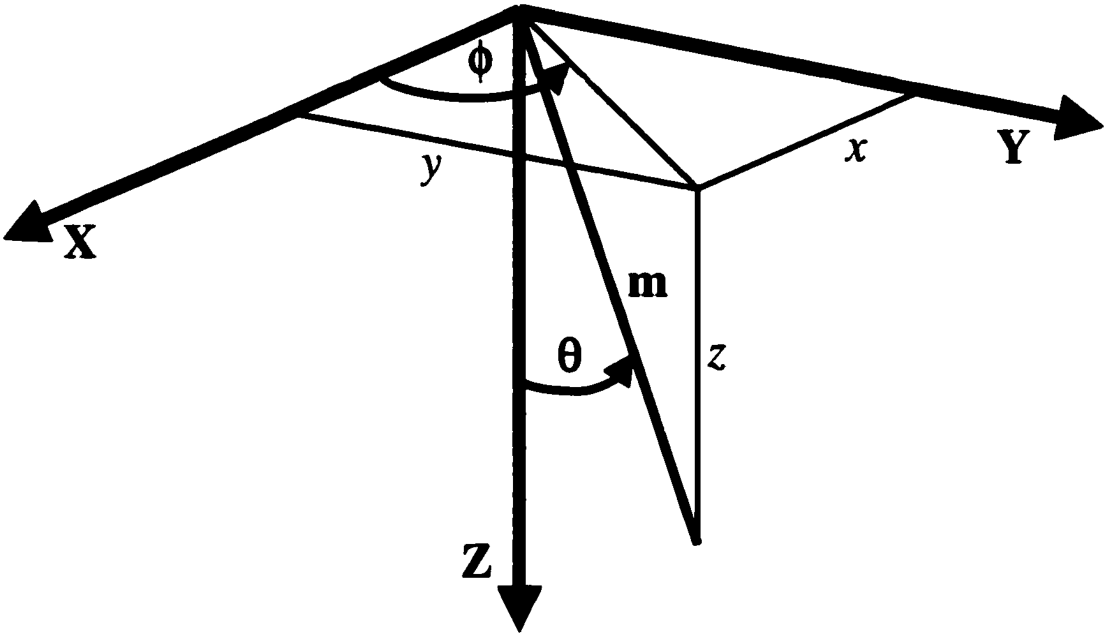
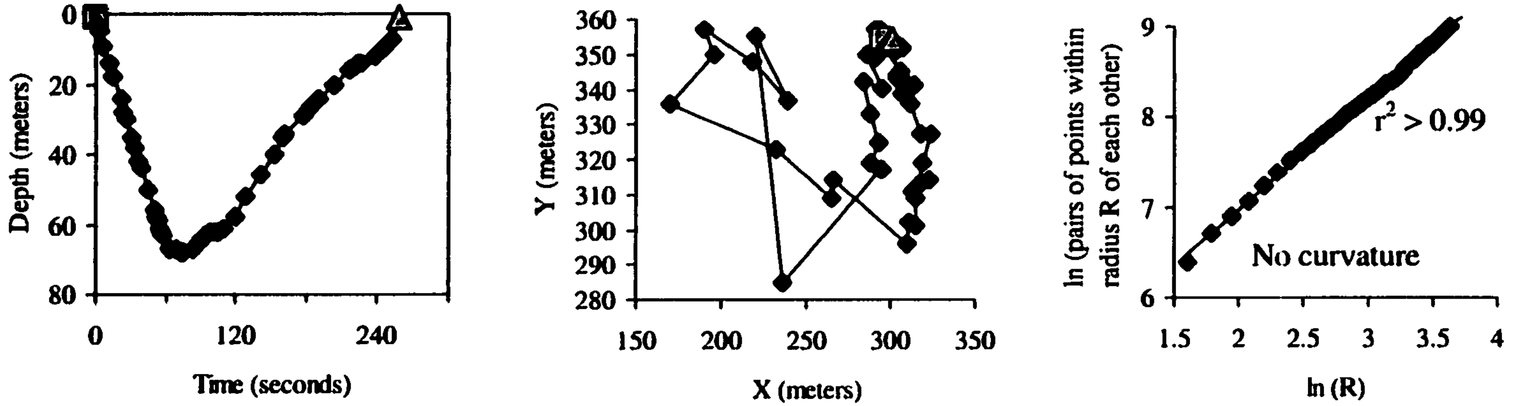


Figure 3.2: Spherical and rectangular coordinates in three-dimensional space.

Rectangular coordinates (x, y, z) are shown in italics, and spherical coordinates (m, ϕ, θ) are shown in bold. Note that x, y, and z are lengths measured along the respective axes (X, Y, Z), and m is a length measured in the direction defined by ϕ and θ angles. For our analysis of diving behavior, the Z-axis was positive in the downward direction as shown.

A) Convoluted dive by HE91: fractal dimension = 1.24



B) Convoluted dive by ME91: fractal dimension = not determined

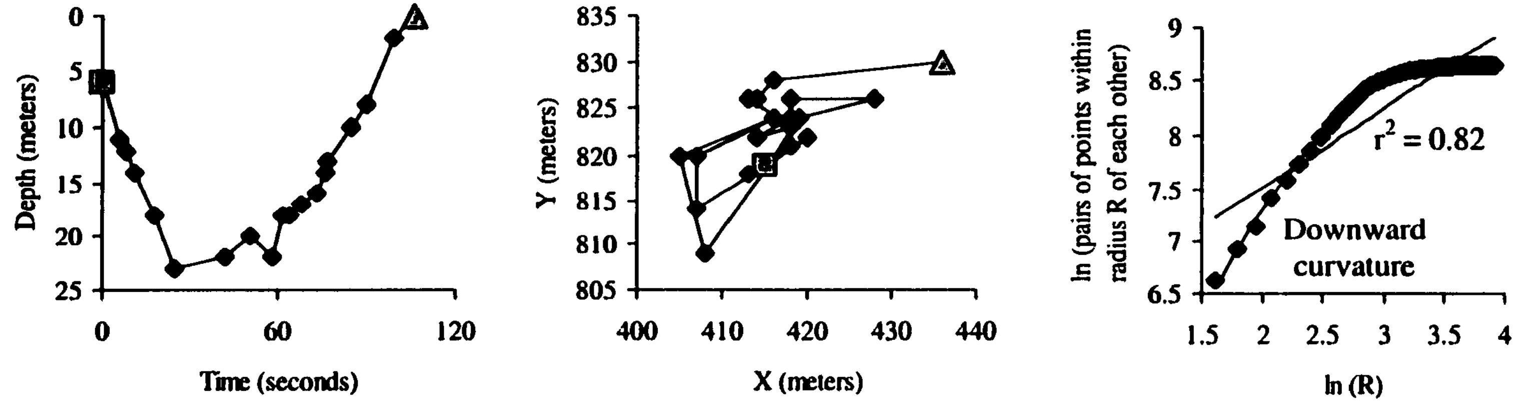
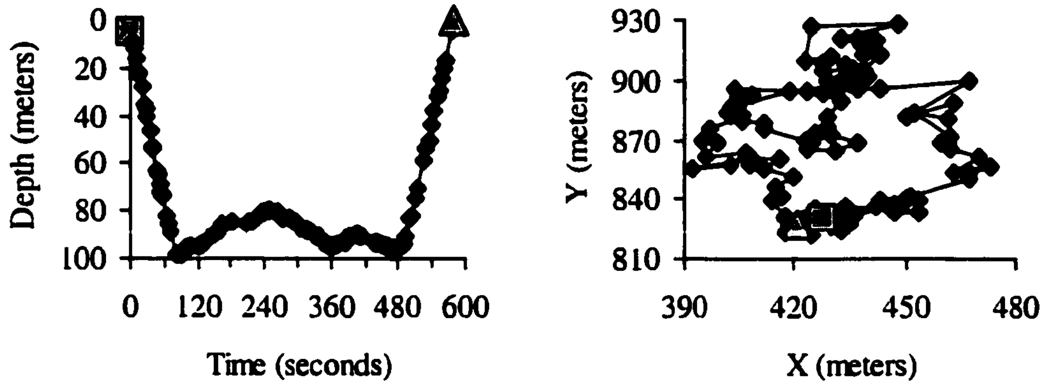
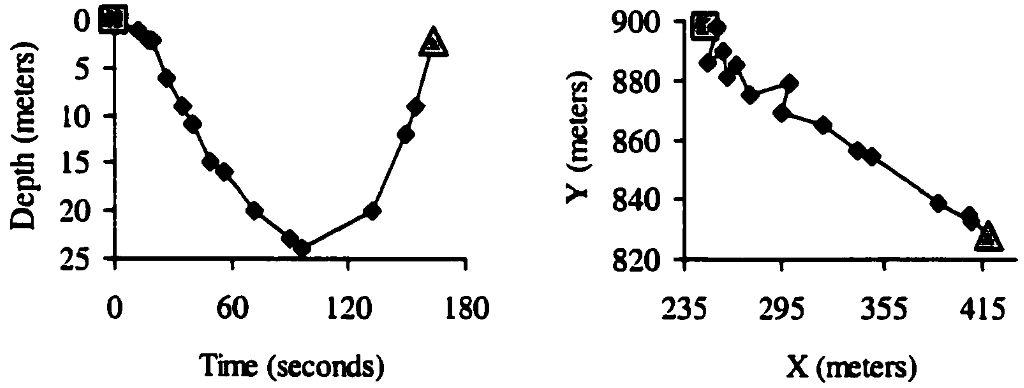


Figure 3.3: Fractal analysis. Time-depth (left) and X-Y plots (middle) are shown with corresponding fractal analysis plots (right). Squares and triangles represent dive start and end, respectively. Dive fractal dimensions were estimated as the linear regression slopes shown on analysis plots. The fractal dimension could not be estimated for B, because the linear regression fit with $r^2 < 0.99$. Also, the analysis plot of B had significant downward curvature (quadratic regression curve shown).

A) Convoluted dive by ME91: ang. vel. = 19.2, hor. dir. = 0.039



B) Travel dive by ME91: ang. vel. = 7.34, hor. dir. = 0.627



C) Exploration dive by SC96: ang. vel. = 5.72, hor. dir. = 0.214

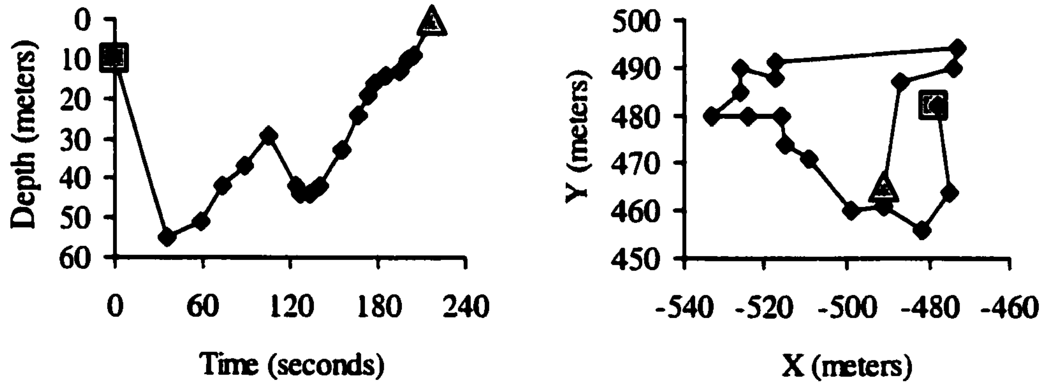


Figure 3.4: Plots of different dive behaviors. Convoluted (A), travel (B), and exploration (C) dives are shown with their three-dimensional angular velocity and horizontal directionality values. Squares and triangles represent dive start and end, respectively.

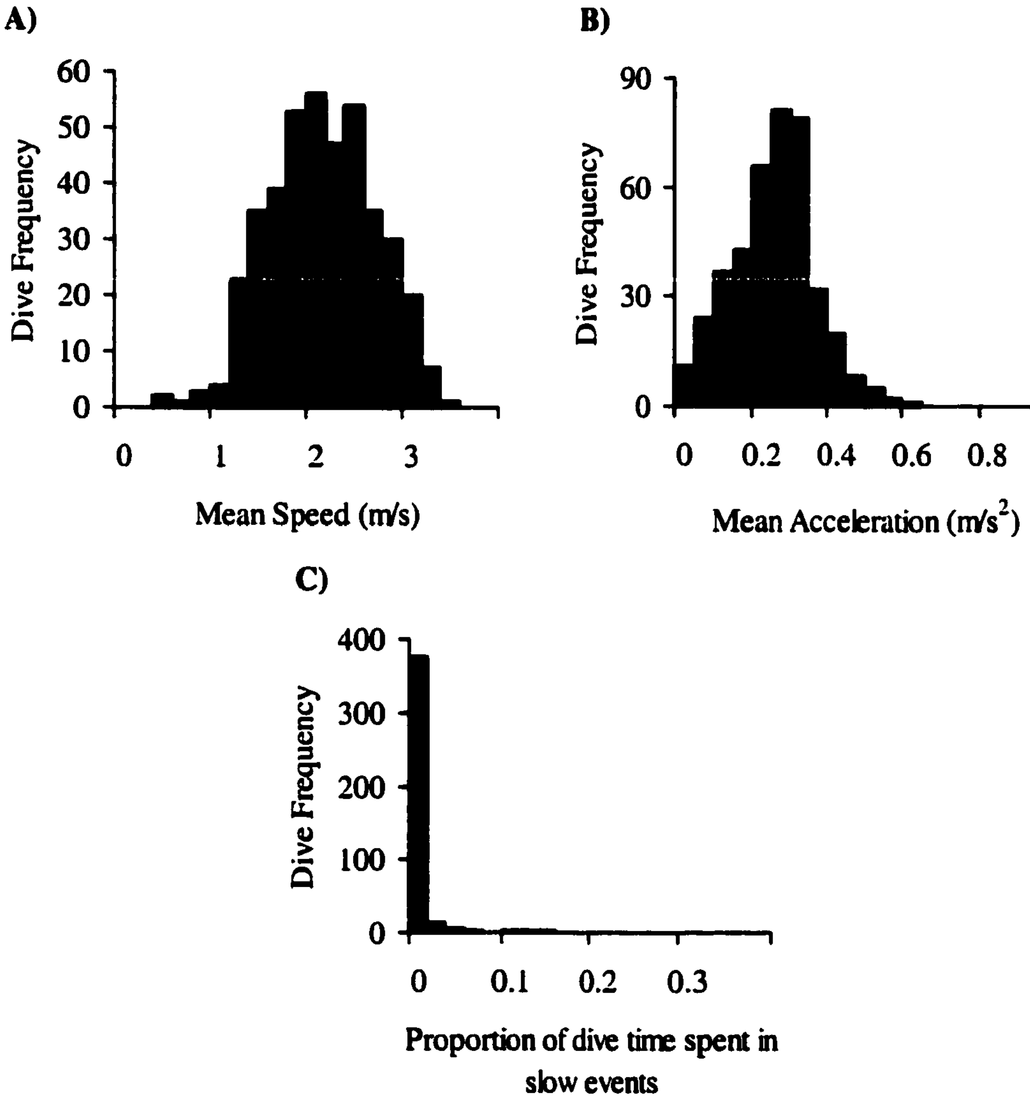


Figure 3.5: Quantification of resting and sit-and-wait behaviors. Resting was expected to involve low dive effort, which we quantified by mean speed and mean acceleration. A distinct class of rest dives (low dive effort = low speed or acceleration) was not found in the histograms of mean speed (A) and acceleration (B). Sit-and-wait behavior was quantified by proportion of time spent in slow passages. A distinct class of dives with large proportions was not found in histogram C.

CHAPTER 4: THREE-DIMENSIONAL MOVEMENTS WITHIN INDIVIDUAL DIVES BY RINGED SEALS[1]

---

[1] Michael A. Simpkins, Brendan P. Kelly, Douglas Wartzok; prepared for submission to Canadian Journal of Zoology

ABSTRACT

The three-dimensional movements within individual dives of five freely swimming ringed seals were analyzed. Dives were divided into a series of moves, each of which represented continuous movement in one direction. Several three-dimensional movement variables were evaluated to distinguish between types of movement within dives. Horizontal directionality proved to be the most useful variable, and convoluted and directional movements were distinguished by fitting a mixture of two normal distributions to the observed horizontal directionality values. Convoluted and directional movements occurred within each phase of most dives indicating that individual dives did not represent single behaviors. Descent and ascent phases were not simply travel behavior, nor were bottom phases equivalent to patch time, as has been assumed in optimal diving models. Most ringed seal dives appeared to consist of a series of patch times separated by travel times. Travel behavior accounted for the majority of dive times.

INTRODUCTION

Diving behavior of marine mammals can be studied at a variety of temporal and spatial scales. Boyd (1996) pointed out that Antarctic fur seals foraged at two scales distinguished by surface intervals between foraging dive bouts. Fine-scale foraging involved dive bouts separated by short surface intervals (< 5 min, 0.18 - 0.27 km maximal distance between dive bouts), while meso-scale foraging involved bouts separated by long surface intervals (>5 min, 1.3 - 1.6 km maximal distance between dive bouts). We suggest that foraging and other behaviors of marine mammals also occur at smaller spatial and temporal scales within individual dives.

Behavior within dives could not be studied until recently, when the movements of diving animals were tracked in three dimensions (Wartzok *et al.* 1992a; Wartzok *et al.* 1992b; Davis *et al.* 1999; Harcourt *et al.* 2000). Previous studies of diving behavior used time-depth recorders (TDRs) which only monitored the depth of an animal over time (e.g., Kooyman 1968; Gentry and Kooyman 1986; LeBoeuf *et al.* 1988; Boyd and Croxall 1996; Schreer and Kovacs 1997). Those data provided a simplified view of actual three-dimensional diving behavior and did not describe animal movements well enough to distinguish between behaviors within dives (Harcourt *et al.* 2000). We have found evidence of local search behavior within descent, ascent, and bottom (time spent at depth between descent and ascent) phases of dives (Simpkins *et al.* in prep a). Here, we analyze the three-dimensional movements of ringed seals and distinguish between convoluted and directional movements. We analyze the distribution of these two types of movement among and within dives and contrast the inferred behavior with current assumptions based on time-depth data.

In previous dive classification studies, unique behaviors were assigned to individual dives based on characteristics of the dives' time-depth profiles (e.g., Kooyman 1968; LeBoeuf *et al.* 1988; Hindell *et al.* 1991; Schreer *et al.* 1998). The resulting dive types were not supported by analysis of feeding events, (Lesage *et al.* 1999), three-dimensional dive profiles (Harcourt *et al.* 2000), and local search behavior (Simpkins *et al.* in prep a). Here, we test the hypothesis that marine mammals can exhibit multiple behaviors during one dive.

Optimal diving models have separated dives into three behavioral units which roughly corresponded to descent, bottom, and ascent phases (Kramer 1988; Wilson and Wilson 1988; Houston and Carbone 1992; Thompson *et al.* 1993; Boyd *et al.* 1995; Carbone and Houston 1996; Mori 1998a; Mori 1999). A diving predator was assumed to travel to a prey patch located at depth (descent phase), forage within that patch for some time (bottom phase), and then travel back to the surface (ascent phase). Here, we test the hypothesis that each dive phase represents a single behavior against the alternative that marine mammals can exhibit multiple behaviors within each phase.

We examine the three-dimensional movements of freely diving ringed seals for evidence of two distinct movement types within individual dives, convoluted movements and directional movements. We focus our three-dimensional analyses on variables related to the fundamental behavioral choices made for each move, e.g., the speed, direction, length, and duration of each move (Turchin *et al.* 1991). The two types of movement should show up as distinct modes in the distributions of these three-dimensional movement variables.

METHODS

Data collection and processing

We used the same database for classifying movements within dives as we used elsewhere for describing diving patterns for ringed seals (Kelly and Wartzok 1996). We recorded the three-dimensional movements of 13 ringed seals during the spring breeding season in 1990, 1991, 1992, 1996 and 1997 in the Canadian Arctic near Resolute Bay, Nunavut (74° 35' N, 95° 7' W; Kelly 1996a; Kelly and Wartzok 1996). We captured seals at breathing holes in shore-fast sea ice using nets (Kelly 1996b) and tracked their movements under the ice by way of ultra-sonic transmitters (Vemco Ltd., Armdale, Nova Scotia, Canada) attached to their hair (Wartzok *et al.* 1992b). We filtered the tracking data to remove erroneous locations which would have required swim speeds in excess of 6 m/s (greater than the maximal speed of harbor seals; Williams and Kooyman 1985). Shallow locations often were inaccurate, primarily as a result of acoustic reflection off ice keels, and we only analyzed dives to depths greater than 5 m with at least 10 data points. Some recorded dives were incomplete and did not include all phases of the dive. We included dives in this analysis only if the recorded portions of dive phases were greater than 7 seconds.

Definition of moves

We divided dives into functional units termed moves. We defined moves as a series of locations which clustered around a line segment connecting the first and last.

locations in the move. An iterative procedure grouped sequential locations into moves, if, and only if, the locations were within a radius (r) of three meters from the line segment connecting the first and last locations in the sequence (Figure 4.1; Turchin *et al.* 1991). Thus, each move represented continuous movement in one direction, namely the direction of the line segment. The iterative procedure defined a new move each time an animal changed the direction of its movement enough to move three meters "off course," i.e., away from the move line segment.

The radius, r, used to define moves (3 m) was the smallest radius for which the number of moves defined was not constrained by the number of data points recorded (Turchin *et al.* 1991). We used r values of 0.5, 1, 2, 3, 4, and 5 meters to split 511 randomly chosen dives (10% subsample of all dives) into moves. At r values less than three meters, the number of moves defined was linearly related to the number of data points, such that each sequential pair or triplet of data points resulted in a new move. These low r values probably defined moves based on noise in the data in addition to behavior, because the error in our location data was ± 1 m (maximal error ± 2 m; Wartzok *et al.* 1992a). In contrast, at r values of three, four, and five meters, moves were not related to the number of data points, suggesting that moves were defined based on behavior, not noise. We chose the smallest radius which compensated for noise in the location data (3 m), because we were interested in characterizing ringed seal movements at the finest scale possible.

We examined our data to determine if sampling rate affected our definition of moves. We found a linear relationship between the number of moves and data points (regardless of r), in dives with fewer than 15 location data points per minute. Dives with fewer than 15 points/minute were undersampled, and more moves would probably have been defined if the dive had been sampled at a higher rate. We used only dives with 15 or more points/minute in this analysis. Eight seals were tracked using transmitters which emitted pulses every 1 – 1.5 seconds (a sufficiently rapid sampling rate). Only five seals had more than ten dives with 15 or more points/minute after data processing (410 dives, Table 4.1).

Three-dimensional analysis of moves

We explored the three-dimensional attributes of ringed seal moves by calculating values related to possible behavioral goals of each move (Box 4.1; Table A.1). For each move, we calculated the move's duration, length, speed, and horizontal and vertical bearings (ϕ and θ, Figure 4.2). For each pair of moves, we also calculated the acceleration, horizontal turning angle, vertical turning angle, and three-dimensional turning angle between the two moves (α, Figure 4.1). For running sequences of five moves (i.e., moves 1-5, 2-6, 3-7, etc.), we calculated mean move length, duration, speed and acceleration, horizontal and vertical directionalities, and horizontal, vertical and three-dimensional angular velocities. We inspected the frequency distribution of each variable for evidence of distinct movement types (i.e., multi-modal distributions). We also inspected time-series plots of these variables for evidence of behaviorally distinct move sequences separated by changes in move values.

We evaluated the effect of move sequence size on the distribution of horizontal directionality. We calculated values for sequences of three, five, eight, and ten moves, and found that the two modes of the resulting horizontal directionality distributions were most clearly separated for sequences of five moves. Including more moves increased the likelihood that at least one of the moves would not be oriented in the same direction as the rest of the moves in the sequence. Thus, the upper mode of the distribution (directional moves) was shifted toward the lower mode (convoluted moves). Including fewer moves tended to result in higher horizontal directionality values, and the lower mode of the distribution was shifted toward the upper mode. Sequences of five moves also represented a reasonable time scale of 15-45 seconds of behavior. Ninety-five percent of analyzed dives contained five or more moves and could be divided into running sequences of five moves.

Definition of movement types

We distinguished convoluted from directional movements by fitting a mixture of two normal distributions to the distribution of horizontal directionality values for each seal using a maximum-likelihood estimation method (Figure 4.3; Venables and Ripley 1997). We determined starting values for the estimations by graphical analysis of the distributions using the Bhattacharya method (Everitt and Hand 1981). We defined convoluted movement as any move sequence that belonged to the lower distribution in the mixture, and directional movement as move sequences which belonged to the upper distribution. For each mixture of distributions, we determined the point of equal probability (i.e., where the two component distributions intersected) and used this value as the limit between the two component distributions (Figure 4.3). Convoluted movement sequences had values less than or equal to the equal probability point, and directional movement sequences had values greater than the equal probability point (e.g., Figure 4.4).

We grouped move sequences into bouts of continuous behavior, during which move sequences were either all directional or all convoluted. In Figure 4.4C, for example, two bouts of directional movement can be identified (black diamonds) surrounding one bout of convoluted movement (gray triangles). We calculated bout duration as the time elapsed between the beginning of the first move sequence in the bout and the end of the last sequence in the bout. For each bout, we also determined the phase, or phases (descent, bottom, and/or ascent), of the dive during which the bout occurred.

Evaluation of movement types

We explored the relative importance of each movement type within dives and phases of dives by comparing the time devoted to each type of movement. We calculated ratios of time spent in convoluted movements to time spent in directional movements during each dive or phase ($\Sigma\, T_C \,/\, \Sigma\, T_D$ where: T_C = duration of convoluted movement bout C, and T_D = duration of directional movement bout D). We calculated ratios for dive phases based upon the time spent within bouts of each type that began and/or ended within the phase. Thus, we included bouts that spanned multiple phases in the ratios calculated for each phase spanned.

We compared $\Sigma\ T_C\ /\ \Sigma\ T_D$ between dives which would have been classified as foraging (U-shaped dives) or non-foraging (V-shaped dives) based on time-depth profiles (e.g., Schreer *et al.* 1998). We grouped U-shaped and V-shaped dives and phases of dives into four categories based on movement type ratios: entirely convoluted movement (ratio = ∞, e.g., 100 s / 0 s), entirely directional movement (ratio = 0), mostly convoluted movement ($1 < \text{ratio} < \infty$), and mostly directional movement ($0 < \text{ratio} < 1$).

RESULTS

Directional and convoluted movement sequences both occurred within ringed seal dives. Directional and convoluted movements were distinguished based on their horizontal directionality values (Table 4.2), but also differed in a variety of other three-dimensional characteristics (Table A.2). Movement types differed most strongly in horizontal and three-dimensional angular velocities. Directional moves, in contrast to convoluted moves, were 2.6°/s (15%) lower in horizontal angular velocity, and 2.0°/s (13%) lower in three-dimensional angular velocity (differences based on parameter estimates from statistical analyses which accounted for temporal autocorrelation in the data and the random effect of seals within the models; Table A.2; Littel *et al.* 1996).

Most dives included several bouts of directional and convoluted movements (Table 4.3). Roughly half of all bouts in a dive were of each type, but directional movement bouts tended to be longer in duration and accounted for the majority of dive time in more than 2/3 of all dives (Figure 4.5). Although U-shaped and V-shaped dives differed in the amount of time allocated to convoluted and directional movements ($X^2 = 40.9$, $p < 0.0001$), most U-shaped and V-shaped dives included bouts of both movement types. In addition, both U-shaped and V-shaped dive types included dives that were all directional and dives that were all convoluted.

Bouts of each type also commonly occurred within each phase of dives, but fewer bouts occurred during descent and ascent phases than occurred during bottom phases (Table 4.3). Although directional movement bouts accounted for the majority of time in more than 2/3 of all phases, convoluted movement bouts occurred during all phases of most dives (Table 4.4).

We chose horizontal directionality values to classify movements based on inspections of histograms and time-series plots of all variables. Only three variables had bimodal distributions: horizontal bearing, horizontal turning angle, and horizontal directionality. Of these three, both horizontal bearing and horizontal turning angle values varied dramatically between sequential moves, and bouts of distinct movement types could not be distinguished in time-series plots of these values. Horizontal directionality values, in contrast, did distinguish between distinct movement types. Low horizontal directionality values were consistently associated with movement that appeared to be convoluted in the three-dimensional dive profiles, and high values were consistently associated with movement that appeared to be directional.

A mixture of distributions fit to the horizontal directionality values for each seal efficiently defined directional and convoluted movements. Visual inspection of three-dimensional dive plots confirmed that the directional and convoluted movements defined for each dive accurately separated the dive into sections of visually distinct behaviors (e.g., Figure 4.4). The means and standard deviations of the distributions fit for each seal were remarkably similar (Table 4.2). Seals did, however, differ in the proportion of their move sequences which were allocated to each distribution, or movement type, although less than half of all move sequences were allocated to the lower distribution (convoluted movement) for every seal (Table 4.2).

DISCUSSION

Ringed seals exhibited two distinct behavioral modes within phases of individual dives. The bimodal nature of horizontal directionality values indicated two distinct types of movement sequences, convoluted sequences and directional sequences. Convoluted sequences had higher horizontal and three-dimensional angular velocities than did directional sequences. The increased turning activity (i.e., high angular velocity) during convoluted sequences was consistent with active local search and/or pursuit behavior within a prey patch (Bell 1990). Alternatively, high angular velocities may have indicated some form of social behavior with a convoluted movement component. Directional sequences, conversely, were consistent with travel behavior, having lower turning activity. Bouts of directional movement could represent travel between breathing holes, exploration, or directional search behavior between prey patches (termed ranging by Bell 1990).

Most dives included bouts of directional and convoluted movements, indicating that a dive did not represent a single behavior when examined at the scale of moves within the dive. Further, most dives involved frequent switching between behaviors, on average including four or more bouts of each movement type within a dive. Switching between directional and convoluted movements may represent seals foraging among several prey patches within one dive. In this scenario, directional movements would represent exploratory behavior between patches, and convoluted movements would represent local search and/or pursuit behavior within patches. Although seals regularly switched between movement types, directional movement behavior still accounted for the majority of time during dives. Assuming that at least some of these dives involved foraging behavior, the predominance of directional movements suggested that seals spent more time traveling or exploring between patches then they spent foraging within patches.

The frequent shifting between movement types within dives suggested that ringed seal dives could not be accurately grouped into simple behavioral categories based on their time-depth profiles as has frequently been done for other species (e.g., Kooyman 1968; LeBoeuf *et al.* 1988; Hindell *et al.* 1991; Schreer *et al.* 1998). U-shaped dives, which have traditionally been classified as foraging dives, included dives with only directional movements, i.e., strictly travel-style movements (Figure 4.5). V-shaped dives, which have been classified as a variety of non-foraging behaviors, included dives with only convoluted movements. More importantly, the majority of both U-shaped and V-shaped dives included both directional and convoluted movements, indicating that ringed seals switched between behaviors within dives of both time-depth profiles.

Other recent studies have also concluded that dive classifications based on time-depth data are misleading. Harcourt et al. (2000) examined three-dimensional dive profiles of Weddell seals and found that time-depth classifications were over-simplistic and, in some cases, misleading. Lesage et al. (1999) compared stomach-temperature data with time-depth classifications and found that harbor seal feeding events were not restricted to one "forage" dive type, rather feeding occurred during all classified dive types. We investigated the search behavior of ringed seals and found that seals performed local search behavior during all phases of both U-shaped and V-shaped dives (Simpkins *et al.* in prep a).

The frequent shifting between movement types within dives also complicates the formulation of optimal diving models (Dunstone and O'Connor 1979; Kramer 1988; Wilson and Wilson 1988; Ydenberg and Clark 1989; Houston and Carbone 1992; Thompson *et al.* 1993; Boyd *et al.* 1995; Carbone and Houston 1996; Mori 1998a; Mori 1998b; Mori 1999). These models generally split the dive cycle into surface time, travel time between the surface and a prey patch at depth, and time spent foraging within the patch. In this scenario, descent and ascent phases were assumed to represent travel time, and bottom phases were assumed to represent patch time. While at the surface, the diver was expected to optimally reload its tissues with oxygen for the next dive and/or recover from the previous dive. Although these models of diving behavior seemed reasonable when only vertical movements were considered (only three possible vertical movement types: down = descent, up = ascent, and no vertical movement = bottom phase), the models are not as reasonable when three-dimensional movements are considered.

Our analysis of three-dimensional movements indicated that seals switched between travel and foraging-style behaviors several times during a dive, not only at the boundaries between descent, bottom, and ascent phases. Descent and ascent phases often included bouts of convoluted movements, indicating that these phases did not simply represent travel time. Although we could not determine if these convoluted movement bouts represented opportunistic foraging or social interactions with other seals, these convoluted movements certainly increased the duration and energetic cost of the presumed travel phases when compared to the direct travel expected by optimal diving models. Directional movements usually accounted for the majority of time spent in bottom phases, suggesting that bottom phases generally included more travel than foraging behavior. Bottom phases probably consisted of foraging among several prey patches, as these phases usually involved repeated switching between travel and foraging-style movements. Thus, bottom phases appeared to be comprised of several short "patch times" separated by longer travel times, which contradicted the optimal diving model assumption that bottom time was equivalent to patch time (Kramer 1988; Wilson and Wilson 1988; Houston and Carbone 1992; Thompson *et al.* 1993; Boyd *et al.* 1995; Carbone and Houston 1996; Kelly 1996a; Mori 1998a; Mori 1999).

Future optimal diving models need to address the possibility of multiple patch encounters during descent, bottom, and ascent phases of dives. If we assume that each convoluted bout represented time spent in one patch, then seals encountered multiple patches not only within bottom phases, but also within descent and ascent phases. If we further assume that the number of convoluted bouts per phase represented the patch encounter rate, then ringed seals encountered more patches during bottom phases than during other phases. Patch encounter rates have previously been modeled on a dive-by-dive basis (Ydenberg and Clark 1989; Mori 1998b), but our results suggest that patch encounter rates should be allowed to vary on a phase-by-phase basis. Modeling of this sort will require detailed information on movement behavior of marine mammals within dives, as is provided by analysis of three-dimensional movement data.

Our method efficiently distinguished between directional and convoluted movements by fitting a mixture of distributions to a behavioral variable that was bimodal, in this case horizontal directionality. Distinguishing between three-dimensional movement types using a horizontal variable was appropriate in this case, because in other analyses of these data we found ringed seal dives to be convoluted only in the horizontal dimensions (Simpkins *et al.* in prep b). Thus, horizontal information was sufficient to distinguish between three-dimensionally convoluted and directional movements.

Previous discriminations between diving behaviors were based on either arbitrary criteria or the output from various clustering algorithms (e.g., Schreer *et al.* 1998). The maximum-likelihood technique we used to fit distributions allowed for robust discrimination between movement types. Our use of a behavioral variable as the basis for discrimination provided a clear link between actual movements and the definition of movement types. In contrast, clustering algorithms transform behavioral variables into abstract indices which are often difficult to interpret (e.g., Schreer *et al.* 1998). Our method of defining behaviors can be easily generalized for use with any behavioral variable with a bimodal, or multimodal, empirical distribution.

The similarity of the mixtures of distributions fit for each seal suggested that the two movement types (directional and convoluted) represented the same behaviors (or suite of behaviors) for all seals. Directional movement for each seal was defined by a broad distribution of directionality values centered at 0.45-0.55, and convoluted movement was defined by a narrow distribution of directionality values centered at 0.2-0.25. For all seals, less than half of the horizontal directionality values belonged to the convoluted movement distribution (Table 4.2), consistent with our finding that directional movements accounted for the majority of time during dives. Seals varied, however, from allocating less than 20% to almost 50% of their movements to convoluted behavior. If we assume that convoluted movements represent foraging behavior, then the variation in the proportion of convoluted movement between seals indicates that seals varied in their foraging efficiency and/or desire to forage (e.g., hunger vs. need to nurse pup, defend territory, breed, etc.). Alternatively, convoluted movements may be involved in a suite of both foraging and social behaviors, and variation in convoluted movement between seals may represent differing allocation of dive time among these and other behaviors. For example, HO90 was a rutting male whose convoluted movements (49% of his movements) often may have represented interactions with other seals as he guarded an under-ice territory (Kelly and Wartzok 1996).

Table 4.1: Ringed seal dives analyzed for within-dive movements. Included in the analysis were dives to depths greater than 5 meters, with at least 10 location data points collected at a rate of ≥ 15 points/minute (after erroneous locations were removed), and with at least 7 seconds of data for each phase of the dive.

Seal	Age	Sex	Year of capture	Dives
HO90	7 yr.	M	1990	14
HE91	7 yr.	F	1991	31
ME91	7 yr.	F	1991	233
SC96	1 yr.	M	1996	119
SP90	1 yr.	F	1990	13

Table 4.2: Mixture of normal distributions fit for horizontal directionality for each seal. Parameter estimates for mixtures of distributions fit for each seal are shown (proportion of mixture in the lower distribution and the mean and standard deviation (SD) of horizontal directionality for each distribution). In addition, the point of equal probability for the lower and upper distributions is given. Horizontal directionality values are distances within the trigonometric unit circle, and thus range between 0 and 1 (Batschelet 1981; Bell 1990).

Seal	Proportion of mixture in lower distribution	Lower distribution (convoluted movement) Mean	SD	Upper distribution (directional movement) Mean	SD	Equal point
HO90	0.488	0.239	0.070	0.567	0.137	0.367
HE91	0.182	0.207	0.018	0.442	0.194	0.238
ME91	0.316	0.243	0.058	0.452	0.177	0.310
SC96	0.286	0.217	0.038	0.449	0.185	0.275
SP90	0.321	0.218	0.052	0.560	0.211	0.304

Table 4.3: Mean frequency (± standard deviation) of directional and convoluted movements by dive and dive phase. Each movement bout consisted of a series of movement sequences which were either all convoluted or all directional.

	Convoluted bouts	Directional bouts
Dive	4.1 ± 4.1	4.4 ± 3.8
Descent phase	1.3 ± 1.3	1.6 ± 1.1
Bottom phase	3.3 ± 3.1	3.7 ± 2.9
Ascent phase	1.3 ± 1.4	1.6 ± 1.2

Table 4.4: Allocation of convoluted movement bouts among dive phases. The number of dives which included convoluted movement bouts within each dive phase, and each combination of dive phases, is shown. Dive phases which included at least one convoluted bout (labeled convoluted) are distinguished from those which included only directional bouts (labeled all directional). Note that the first eight rows indicate values for U-shaped dives which had a bottom phase, and the last four rows indicate values for V-shaped dives which did not have a bottom phase.

Dives	Descent phase	Bottom phase	Ascent phase
48	All directional	All directional	All directional
4	**Convoluted**	All directional	All directional
6	All directional	**Convoluted**	All directional
3	All directional	All directional	**Convoluted**
38	**Convoluted**	**Convoluted**	All directional
33	All directional	**Convoluted**	**Convoluted**
5	**Convoluted**	All directional	**Convoluted**
174	**Convoluted**	**Convoluted**	**Convoluted**
31	All directional	No bottom phase	All directional
6	**Convoluted**	No bottom phase	All directional
1	All directional	No bottom phase	**Convoluted**
41	**Convoluted**	No bottom phase	**Convoluted**

Box 4.1: Variables calculated for three-dimensional movements within ringed seal dives (Batschelet 1981; Bell 1990; Turchin 1998). Horizontal directionality was used to classify movements.

Calculated for each move

Move duration = t_i
Move length = m_i (Figure 4.2)
Speed = m_i / t_i
Horizontal bearing = ϕ_i = bearing to the right of the Y-axis for move i (Figure 4.2)
Vertical bearing = θ_i = bearing up from the Z-axis for move i (Figure 4.2)

Calculated for each pair of moves

Acceleration = $[(m_{i+1}/t_{i+1}) - (m_i/t_i)] / [(t_i + t_{i+1}) / 2]$
Horizontal turning angle = $|\phi_{i+1} - \phi_i|$
Vertical turning angle = $|\theta_{i+1} - \theta_i|$
Three-dimensional turning angle = α_i = magnitude of three-dimensional turning angle between move i and move i+1 (Figure 4.1)

Calculated for running sequences of five moves

(n = 5 moves, i = moves 1-5, 2-6, 3-7, etc.)

Mean move length = $\Sigma(m_i) / n$
Mean move duration = $\Sigma (t_i) / n$
Mean speed = $\Sigma(m_i) / \Sigma (t_i)$
Mean acceleration = $\Sigma \{ [(m_{i+1}/t_{i+1}) - (m_i/t_i)] / [(t_i + t_{i+1}) / 2] \}$
Horizontal directionality = mean vector [ϕ] = $\{ [(\Sigma \cos \phi_i)^2 + (\Sigma \sin \phi_i)^2]^{0.5} \} / n$
Vertical directionality = mean vector [θ] = $\{ [(\Sigma \cos \theta_i)^2 + (\Sigma \sin \theta_i)^2]^{0.5} \} / n$
Horizontal angular velocity = $\Sigma (\phi_{i+1} - \phi_i) / \Sigma (t_i)$
Vertical angular velocity = $\Sigma (\theta_{i+1} - \theta_i) / \Sigma (t_i)$
Three-dimensional angular velocity = $\Sigma (\alpha_i) / \Sigma (t_i)$

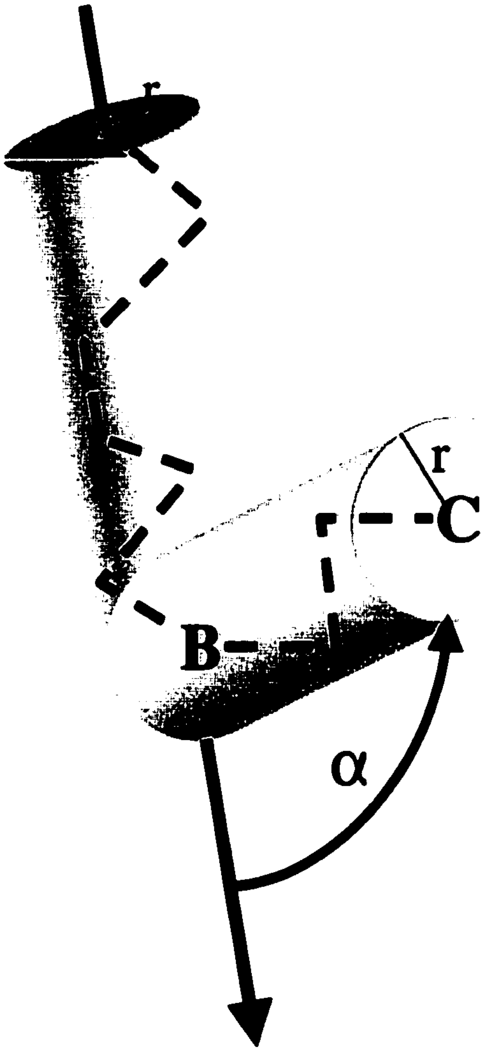


Figure 4.1: Definition of moves and three-dimensional turning angle between moves for movement analysis. AB is defined as one move because all points along the dotted dive path between A and B are within r (3 m) of the line segment AB. BC is defined as a move similarly. The three-dimensional turning angle between AB and BC is α.

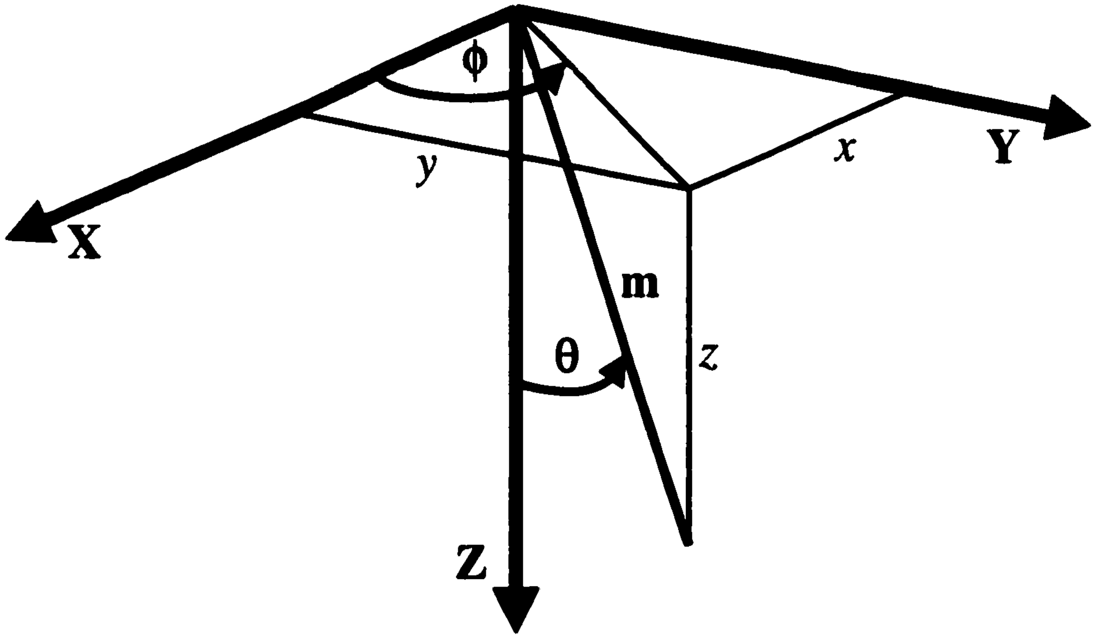


Figure 4.2: Spherical and rectangular coordinates used in three-dimensional movement analysis (modified from Batschelet 1981). Rectangular coordinates (x, y, z) are shown in italics, and spherical coordinates (m, ϕ, θ) are shown in bold. Note that x, y, and z are lengths measured along the respective axes (X, Y, Z), and m is a length measured in the direction defined by ϕ and θ angles. For our analysis of diving behavior, the Z-axis is positive in the downward direction as shown.

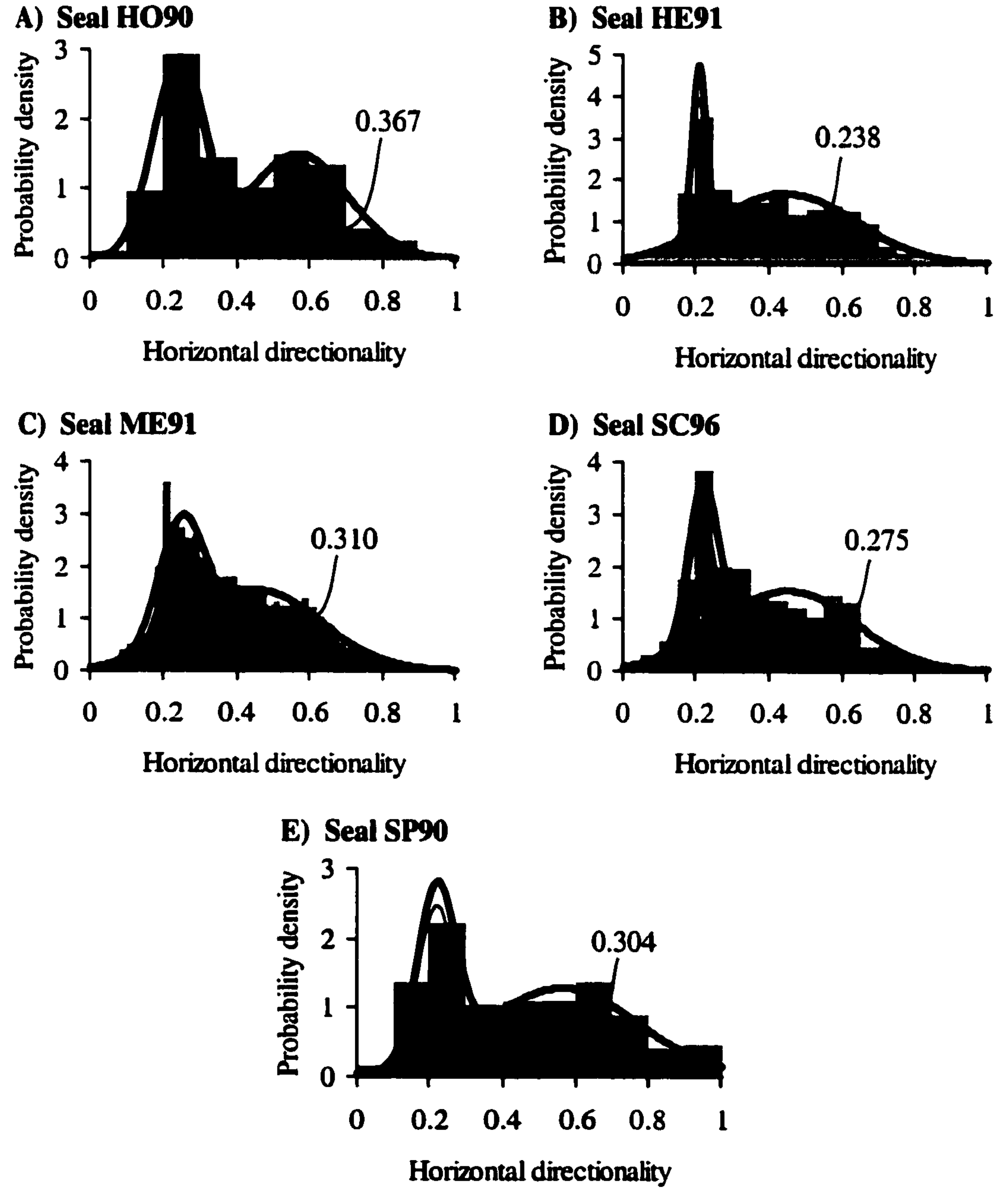


Figure 4.3: Mixtures of distributions fit for horizontal directionality. Probability density histograms of horizontal directionality values are shown for each seal (A-E) along with the probability density functions for the mixtures of distributions fit by maximum-likelihood estimation (bold curves; Venables and Ripley 1997). The thin-line curves represent the two component distributions of the fit mixture, and the point of equal probability (i.e., intersection) is indicated with an arrow and its associated value. The scale of the y-axis varies between plots for ease of viewing.

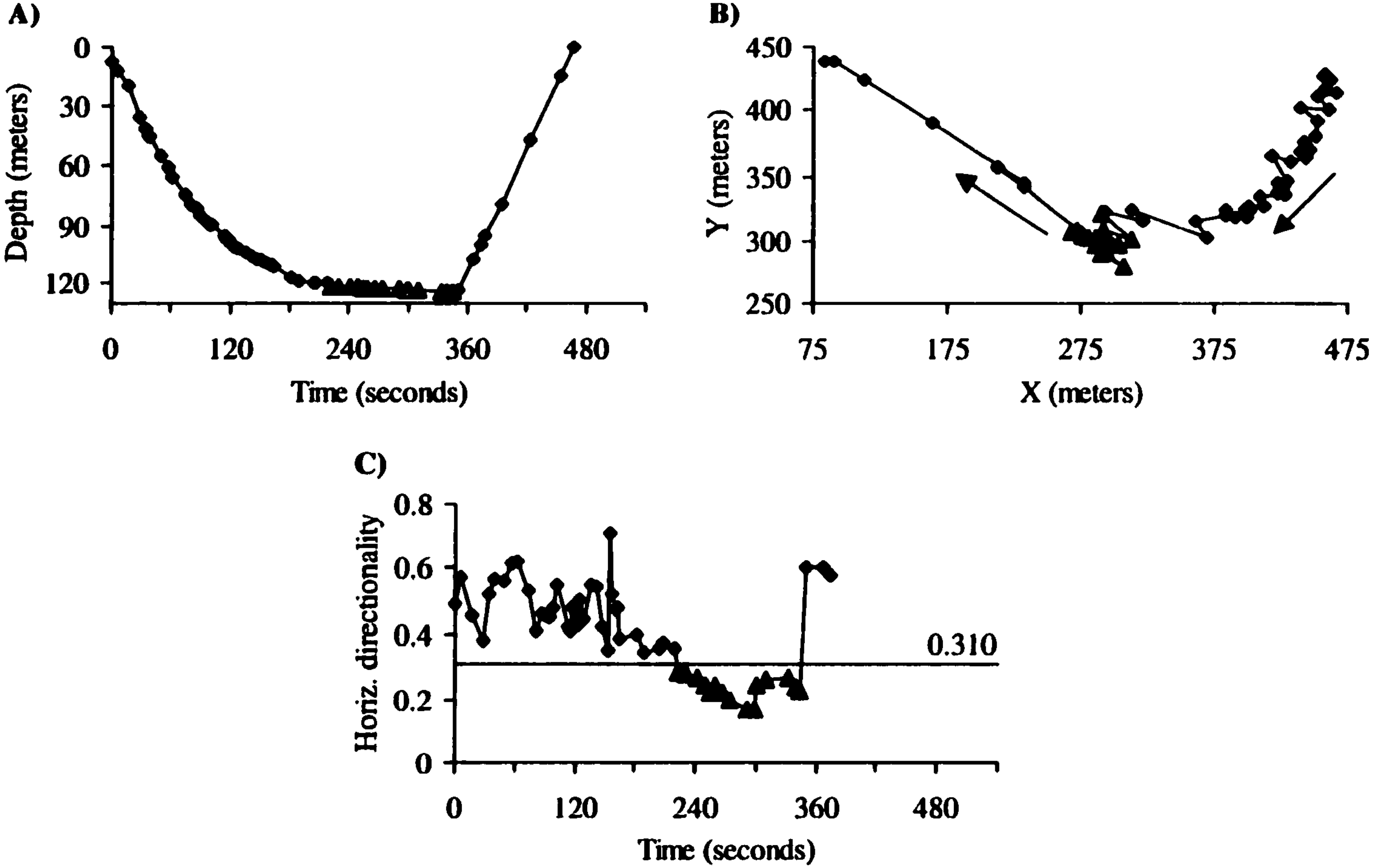


Figure 4.4: Definition of move sequence types. Time-depth (A) and X-Y (B) plots are shown for a dive by seal ME91 (arrows denote direction of travel). The horizontal directionality for each move sequence in the dive (C) is used to assign move sequences to behavioral types. The equal probability point (0.310) is shown by a horizontal line in C. Move sequences with horizontal directionality values below this line are convoluted sequences (gray triangles), and those above the line are directional (black diamonds). All moves are shown in A and B, but only the start points of move sequences are shown in C.

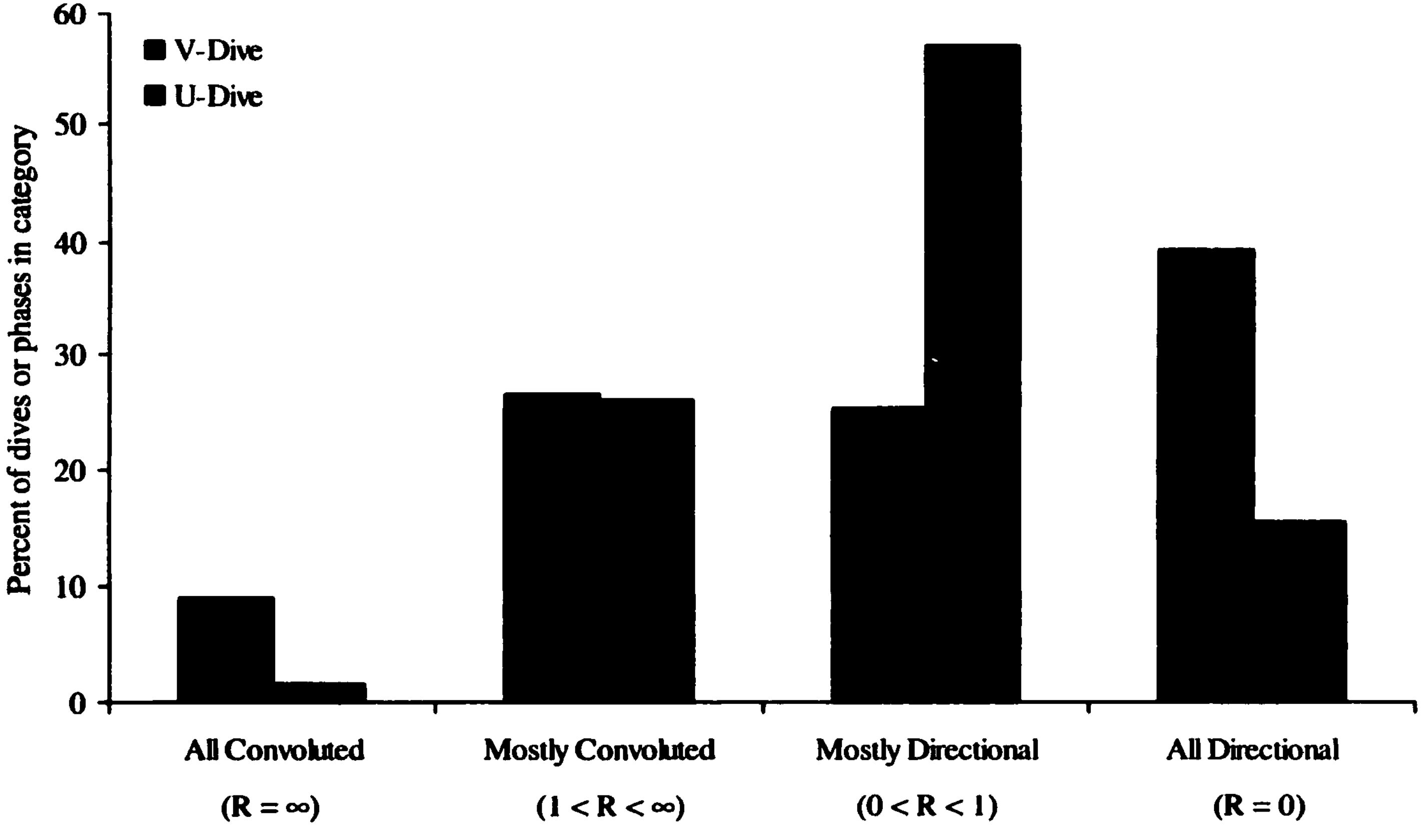


Figure 4.5: Frequencies of directional and convoluted movements in V-shaped and U-shaped dives. Dives are shown grouped into four categories based on the ratio (R) of total convoluted movement bout duration to total directional movement bout duration.

CHAPTER 5: SUMMARY

Ringed seals appeared to frequently change their behavior within individual dives, presumably in response to encounters with prey or other seals during a dive. Seals often switched between directional and convoluted movements within dives, consistent with directional travel or exploratory behavior interrupted by convoluted movements in response to an encounter. Convoluted movements may have represented a seal pursuing prey or another seal, or a seal searching locally to find more prey or other seals. Travel and exploration dives apparently did not involve encounters, because these dives showed no evidence of convoluted movements. Convoluted dives, however, included multiple bouts of convoluted movement and, presumably, reflected multiple encounters with prey or other seals. These convoluted dives likely represented a variety of dive behaviors, including travel and exploration behaviors interrupted by opportunistic foraging or social encounters.

The movements during convoluted dives were always much more convoluted horizontally than vertically, pointing out a weakness in time-depth data which ignore the horizontal component of movements. I found no evidence of behavioral differences between dives with very distinct time-depth profiles (V-shaped and U-shaped dives), suggesting that time-depth profiles were not a reliable means of classifying dive behaviors for ringed seals. I also found that ringed seals performed similar types of movement during descent, bottom, and ascent phases, suggesting that these dive phases were not behaviorally distinct as previously assumed based upon time-depth profiles.

I focused my analyses on dives with the most detailed data, because I was interested in studying ringed seal movement behavior on the finest scale possible. As a result, many dives were eliminated from consideration in my analyses and continuous series (i.e., bouts) of dives were rare within the final datasets. Future studies may either collect more detailed dive data or focus on larger scale behavior. Such studies could analyze differences in three-dimensional movement behavior between dives within different bouts. For example, three-dimensional behavior could be contrasted between dives within presumed foraging bouts and those outside of such bouts (Gentry and Kooyman 1986; Boyd *et al.* 1994; Kelly 1996a).

Ringed seal behaviors that were not studied here may be quantified in the future using different data collection methods. For example, poor acoustic location data near the undersurface of the ice made quantification of shallow movement behavior impossible in this study. Ringed seals, however, do prey upon ice-associated zooplankton (Welch *et al.* 1992) and presumably forage along the undersurface of sea ice for these zooplankton and arctic cod which are occasionally found near the ice undersurface (Crawford and Jorgenson 1990). Much of ringed seal social behavior may also occur near the surface (especially around breathing holes; Kelly and Wartzok 1996). The use of a non-acoustic tracking system (e.g., Davis *et al.* 1999) may allow the important shallow component of ringed seal behavior to be assessed. In addition, modification of our tracking system to allow simultaneous tracking of multiple seals would allow the identification of social interactions, which in this study were indistinguishable from other behaviors such as foraging or exploration.

Combining three-dimensional movement data with simultaneous current data would clarify how much of ringed seal movements are controlled by currents. Currents in Resolute Passage are tidally dominated and range as high as 20 cm/s in either direction along the passage (Marsden *et al.* 1994b). Without simultaneous current measurements, I could not determine whether a moving seal was swimming with, against, or across a current. I also could not determine if a stationary seal was maintaining its position against a current or simply drifting during slack tide.

Correlating three-dimensional diving behavior with prey distribution data would enable a more comprehensive study of foraging behavior than was possible here. Although the vertical distribution of prey was monitored acoustically using a fixed transducer, the resulting echograms could not be directly linked to the diving behavior of specific seals. Also, echoes appearing on the echograms could not be assigned to particular prey species, although attempts were made to relate echoes to prey species using vertical net tows and fixed underwater video camera surveys. Large, inter-disciplinary research projects have begun to address the problem of relating prey distribution to diving behavior, although these projects are currently limited to the use of time-depth data (Croll *et al.* 1998).

By analyzing the three-dimensional movements of ringed seals, I was able to gain new insight into the diving behavior of these animals and to dispute previous assumptions and inferences drawn from time-depth data. I encourage others to use, and improve upon, the methods presented here in future analyses of the three-dimensional diving behavior of other species. These methods should prove useful in testing a variety of behavioral hypotheses, and future increases in the availability of three-dimensional movement data from other marine mammals should dramatically improve our understanding of marine mammal diving behavior.

APPENDIX: SUMMARY OF ALL THREE-DIMENSIONAL MOVEMENT ANALYSES CONDUCTED FOR MOVES AND MOVE SEQUENCES WITHIN INDIVIDUAL RINGED SEAL DIVES

Table A.1: Three-dimensional variables for moves and move sequences. The values summarized are for five seals combined (> 15,700 moves, 410 dives). All variables had unimodal distributions, except for the three bold variables, which had bimodal distributions.

Move Variable	Mean (interquartile range)	Move sequence variable (5 moves per sequence)	Mean (interquartile range)
Move Length (m)	14.2 (5.7, 16.0)	Mean Move Length (m)	13.9 (8.3, 15.8)
Move Duration (s)	7.3 (3.0, 9.0)	Mean Move Duration (s)	7.3 (4.8, 8.6)
Speed (m/s)	2.23 (1.15, 3.15)	Mean Speed (m/s)	1.99 (1.35, 2.54)
Acceleration (m/s^2)	0.27 (0.04, 0.37)	Mean Acceleration (m/s^2)	0.29 (0.14, 0.39)
Horizontal bearing, ϕ (°)	**87.6 (0.0, 180.0)**	**Horizontal directionality**	**0.39 (0.24, 0.52)**
Vertical bearing, θ (°)	89.3 (80.3, 102.2)	Vertical directionality	0.96 (0.95, 1.00)
Horizontal turning angle (ϕ°)	**108.0 (57.5, 158.2)**	Horizontal angular velocity (ϕ°/s)	19.6 (11.7, 25.2)
Vertical turning angle (θ°)	15.3 (1.5, 20.0)	Vertical angular velocity (θ°/s)	2.7 (6.8, 3.5)
Turning angle (α°)	98.9 (58.2, 142.1)	Angular velocity (α°/s)	18.0 (10.9, 23.1)

Table A.2: Differences between three-dimensional variables for each move sequence type. Parameter estimates are shown for mixed model analyses (Littel *et al.* 1996) of three-dimensional variables by move sequence type for five seals (13,884 move sequences, 390 dives). Fixed effect parameter estimates (± standard error of estimate) are given for convoluted and directional move sequences (bold indicates a significant difference between the two move sequence types, $p < 0.0001$). Covariance parameters are given for the random effect of individual seals within the model and for repeated measures analysis (variance explained by temporal autocorrelation, range of temporal autocorrelation, and residual variance).

Three-dimensional variable	Convoluted sequences	Directional sequences	Seal random effect	Temporal Autocor.	Range (seconds)	Residual
Mean Move Length (m)	16.96 ± 1.34	16.83 ± 1.34	5.25	247.2	250.8	1.0
Mean Move Duration (s)	**8.71 ± 0.22**	**8.97 ± 0.22**	0.06	25.2	143.8	0.6
Mean Speed (m/s)	**1.99 ± 0.13**	**1.90 ± 0.13**	0.08	0.78	110.1	0.02
Mean Acceleration (m/s^2)	**0.26 ± 0.02**	**0.24 ± 0.02**	0.001	0.030	43.2	0.002
Horizontal directionality	**0.27 ± 0.01**	**0.49 ± 0.01**	0.0006	0.012	74.0	0.005
Vertical directionality	**0.94 ± 0.01**	**0.94 ± 0.01**	0.0002	0.006	72.4	0.0002
Horizontal angular velocity (ϕ°/s)	**17.15 ± 0.76**	**14.60 ± 0.75**	2.15	95.69	46.5	10.64
Vertical angular velocity (θ°/s)	2.43 ± 0.15	2.41 ± 0.15	0.05	8.84	65.9	0.42
Three-dimensional angular velocity (α°/s)	**15.50 ± 0.79**	**13.50 ± 0.79**	2.51	76.79	44.6	8.29

LITERATURE CITED

Akre, B. and D. Johnson (1979). Switching and sigmoid functional response curves by damselfly naiads with alternative prey available. Journal of Animal Ecology **48**: 703-720.

Andrews, R. (1998). Remotely releasable instruments for monitoring the foraging behaviour of pinnipeds. Marine Ecology Progress Series **175**: 289-294.

Asaga, T., Y. Naito, B. LeBoeuf and H. Sakurai (1994). Functional analysis of dive types of female northern elephant seals. *in* Elephant seals: population ecology, behavior, and physiology. B. LeBoeuf and R. Laws. Berkeley, University of California Press: 310-327.

Batschelet, E. (1981). Circular statistics in biology. San Francisco, Academic Press.

Bekkby, T. and A. Bjørge (1998). Variation in stomach temperature as indicator of meal size in harbor seals, *Phoca vitulina*. Marine Mammal Science **14**: 627-637.

Bekkby, T. and B. Holand (1997). A temperature-sensitive acoustic transmitter for remote monitoring of stomach temperature in aquatic endotherms. Sarsia **82**: 77-80.

Bell, W. (1990). Searching behaviour: The behavioural ecology of finding resources. New York, Chapman and Hall.

Bengtson, J. and B. Stewart (1992). Diving and haulout behavior of crabeater seals in the Weddell Sea, Antarctica, during March 1986. Polar Biology **12**: 635-644.

Bengtson, J. and B. Stewart (1997). Diving patterns of a Ross seal (*Ommatophoca rossii*) near the eastern coast of the Antarctic Peninsula. Polar Biology **18**: 214-218.

Bjørge, A., D. Thompson, P. Hammond, M. Fedak, E. Bryant, H. Aarefjord, R. Roen and M. Olsen (1995). Habitat use and diving behaviour of harbour seals in a coastal archipelago in Norway. *in* Whales, seals, fish and man. A. Blix, L. Walløe and Ø. Ulltang. Amsterdam, Elsevier Science B.V.: 211-223.

Boness, D., W. Bowen and O. Oftedal (1994). Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal. Behavioral Ecology and Sociobiology **34**: 95-104.

Bonner, W. (1984). Lactation strategies in pinnipeds: problems for a marine mammalian group. *in* Physiological strategies in lactation. M. Peaker, R. Vernon and C. Knight. London, Academic Press. **51**: 253-272.

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

Boyd, I., J. Arnbom, T. Barton and J. Croxall (1994). Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. Journal of Animal Ecology **63**: 703-713.

Boyd, I. and J. Croxall (1996). Dive durations in pinnipeds and seabirds. Canadian Journal of Zoology **74**: 1696-1705.

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

Brillinger, D. and B. Stewart (1997). Elephant seal movements: dive types and their sequences. *in* Modelling Longitudinal and Spatially Correlated Data: Methods, Applications, and Future Directions. T. Gregoire, D. Brillinger, P. Diggle, E. Russek-Cohen, W. Warren and R. Wolfinger. New York, Springer. **122**.

Burns, J., M. Castellini and J. Testa (1999). Movements and diving behavior of weaned Weddell seal (*Leptonychotes weddellii*) pups. Polar Biology **21**: 23-36.

Burns, J., J. Schreer and M. Castellini (1997). Physiological effects on individual dive patterns and foraging strategies in yearling Weddell seals. Canadian Journal of Zoology **75**: 1796-1810.

Campagna, C., B. LeBoeuf, S. Blackwell, D. Crocker and F. Quintata (1995). Diving behaviour and foraging location of female southern elephant seals from Patagonia. Journal of Zoology, London **236**: 55-71.

Carbone, C., J. DeLeeuw and A. Houston (1996). Adjustments in diving time budgets of tufted duck and pochard: is there evidence for a mix of metabolic pathways? Animal Behaviour **51**: 1257-1268.

Carbone, C. and A. Houston (1996). The optimal allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. Animal Behaviour **51**: 1247-1255.

Chapskii, K. (1940). The ringed seal of western seas of the Soviet Arctic (the morphological characteristic, biology and hunting production). Trudy Arkticheskogo Nauchno-Issledovatel'skogo Instituta Glavnovo Upravleniya Severnogo Morskogo Puti Pri SNK SSSR **145**: 1-72. (Translated from Russian by Fisheries Research Board of Canada, Translation Series No. 1665 (1971).)

Costa, D. (1991). Reproductive and foraging energetics of pinnipeds: implications for life history patters. *in* The behaviour of pinnipeds. D. Renouf. New York, Chapman and Hall: 300-344.

Cota, G., S. Prinsenberg, E. Bennett, J. Loder, M. Lewis, J. Anning, N. Watson and L. Harris (1987). Nutrient fluxes during extended blooms of Arctic ice algae. Journal of Geophysical Research **92**: 1951-1962.

Coughlin, D., J. Strickler and B. Sanderson (1992). Swimming and search behaviour in clownfish, *Amphiprion perideraion*, larvae. Animal Behaviour **44**: 427-440.

Crawford, R. and J. Jorgenson (1990). Density distribution of fish in the presence of whales at the Admiralty Inlet landfast ice edge. Arctic **43**(3): 215-222.

Crocker, D., B. LeBoeuf and D. Costa (1997). Drift diving in female northern elephant seals: implications for food processing. Canadian Journal of Zoology **75**: 27-39.

Crocker, D., B. LeBoeuf, Y. Naito, T. Asaga and D. Costa (1994). Swim speed and dive function in a female northern elephant seal. *in* Elephant seals: population ecology, behavior, and physiology. B. LeBoeuf and R. Laws. Berkeley, University of California Press: 328-339.

Croll, D., B. Tershy, R. Hewitt, D. Demer, P. Fiedler, S. Smith, W. Armstrong, J. Popp, T. Kiekhefer, V. Lopez, J. Urban and D. Gendron (1998). An integrated approach to the foraging ecology of marine birds and mammals. Deep-Sea Research 2 **45**: 1353-1371.

Davis, R., L. Fuiman, T. Williams, S. Collier, W. Hagey, S. Kanatous, S. Kohin and M. Horning (1999). Hunting behavior of a marine mammal beneath the Antarctic fast-ice. Science **283**: 993-996.

Davis, R., G. Worthy, B. Würsig and S. Lynn (1996). Diving behavior and at-sea movements of an Atlantic spotted dolphin in the Gulf of Mexico. Marine Mammal Science **12**: 569-581.

Dicke, M. and P. Burrough (1988). Using fractal dimensions for characterizing tortuosity of animal trails. Physiological Entomology **13**: 393-398.

Dolphin, W. (1987). Ventilation and dive patterns of humpback whales, *Megaptera novaeangliae*, on their Alaskan feeding grounds. Canadian Journal of Zoology **65**: 83-90.

Dunn, O. (1964). Multiple contrasts using rank sums. Technometrics **6**: 241-252.

Dunstone, N. and R. O'Connor (1979). Optimal foraging in an amphibious mammal. I. The aqualung effect. Animal Behaviour **27**: 1182-1194.

Dusenbery, D. (1989). Optimal search direction for an animal flying or swimming in a wind or current. Journal of Chemical Ecology **15**: 2511-2519.

Everitt, B. and D. Hand (1981). Finite Mixture Distributions. New York, Chapman and Hall.

Feder, J. (1988). Fractals. New York, Plenum Press.

Feldkamp, S., R. DeLong and G. Antonelis (1989). Diving patterns of California sea lions, *Zalophus californianus*. Canadian Journal of Zoology **67**: 872-883.

Formanowicz, D. and P. Bradley (1987). Fluctuations in prey density: effects on the foraging tactics of scolopendrid centipedes. Animal Behaviour **35**: 453-461.

Frost, K., M. Simpkins and L. Lowry (1999). Diving behavior of non-pup harbor seals in Prince William Sound, Alaska, 1993-1996. *in* Monitoring, habitat use, and trophic interactions of harbor seals in Prince William Sound, Alaska. Annual Report to the *Exxon Valdez* Oil Spill Trustee Council. Restoration Study 99064. Fairbanks, AK, Alaska Department of Fish and Game, Division of Wildlife Conservation: 126-145.

Furgal, C., S. Innes and K. Kovacs (1996). Characteristics of ringed seal, *Phoca hispida*, subnivean structures and breeding habitat and their effects on predation. Canadian Journal of Zoology **74**: 858-874.

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

Gales, R. and D. Renouf (1993). Detecting and measuring food and water intake in captive seals using temperature telemetry. Journal of Wildlife Management **57**: 514-519.

Gentry, R. and G. Kooyman, Eds. (1986). Fur seals: Maternal strategies on land and at sea. Princeton, Princeton University Press.

Goebel, M., J. Bengtson, R. DeLong, R. Gentry and T. Loughlin (1991). Diving patterns and foraging locations of female northern fur seals. Fishery Bulletin **89**: 171-179.

Goodman-Lowe, G. (1998). Diet of the Hawaiian monk seal (*Monachus schauinslandi*) from the Northwestern Hawaiian islands during 1991 to 1994. Marine Biology **132**: 535-546.

Hammill, M., C. Lydersen, M. Ryg and T. Smith (1991). Lactation in the ringed seal (*Phoca hispida*). Canadian Journal of Fisheries and Aquatic Sciences **48**: 2471-2476.

Hammill, M. and T. Smith (1991). The role of predation in the ecology of the ringed seal in Barrow Strait, Northwest Territories, Canada. Marine Mammal Science **7**: 123-135.

Harcourt, R., M. Hindell, D. Bell and J. Waas (2000). Three-dimensional dive profiles of free-ranging Weddell seals. Polar Biology **23**: 479-487.

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

Hastings, H. and G. Sugihara (1993). Fractals: a user's guide for the natural sciences. New York, Oxford University Press.

Hedd, A., R. Gales and D. Renouf (1995). Use of temperature telemetry to monitor ingestion by a harbour seal mother and her pup throughout lactation. Polar Biology **15**: 155-160.

Hedd, A., R. Gales and D. Renouf (1996). Can stomach temperature telemetry be used to quantify prey consumption by seals? A re-examination. Polar Biology **16**: 261-270.

Hindell, M., B. McConnell, M. Fedak, D. Slip, H. Burton, P. Reijnders and C. McMahon (1999). Environmental and physiological determinants of successful foraging by naive southern elephant seal pups during their first trip to sea. Canadian Journal of Zoology **77**: 1807-1821.

Hindell, M. and D. Pemberton (1997). Successful use of a translocation program to investigate diving behavior in a male Australian fur seal, *Arctocephalus pusillus doriferus*. Marine Mammal Science **13**: 219-228.

Hindell, M., D. Slip and H. Burton (1991). The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia: Phocidae). Australian Journal of Zoology **39**: 595-619.

Hindell, M., D. Slip, H. Burton and M. Bryden (1992). Physiological implications of continuous, prolonged, and deep dives of the southern elephant seal (*Mirounga leonina*). Canadian Journal of Zoology **70**: 370-379.

Houston, A. and C. Carbone (1992). The optimal allocation of time during the dive cycle. Behavioral Ecology **3**: 255-265.

Huey, R. and E. Pianka (1981). Ecological consequences of foraging mode. Ecology **62**: 991-999.

Inoue, T. and T. Matsura (1983). Foraging strategy of a mantid, *Paratenodera angustipennis* S.: mechanisms of switching tactics between ambush and active search. Oecologia **56**: 264-271.

Jaeger, R. and D. Barnard (1981). Foraging tactics of a terrestrial salamander: choice of diet in structurally simple environments. American Naturalist **117**: 639-665.

Jander, R. (1975). Ecological aspects of spatial orientation. Annual Reviews in Systematics and Ecology: 171-188.

Jodice, P. and M. Collopy (1999). Diving and foraging patterns of Marbled Murrelets (*Brachyramphus marmoratus*): testing predictions from optimal-breathing models. Canadian Journal of Zoology **77**: 1409-1418.

Jonker, F. and M. Bester (1994). The diving behaviour of adult southern elephant seal, *Mirounga leonina*, cows from Marion Island. South African Journal of Antarctic Research **24**: 75-93.

Jonker, F. and M. Bester (1998). Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. Antarctic Science **10**: 21-30.

Kareiva, P. and N. Shigesada (1983). Analyzing insect movement as a correlated random walk. Oecologia **56**: 234-238.

Kelly, B. (1988). Ringed seal. *in* Selected marine mammals of Alaska: species accounts with research and management recommendations. J. W. Lentfer. Washington, D.C., Marine Mammal Commission: 57-75.

Kelly, B. (1996a). Behavior of ringed seals diving under shore-fast sea ice. Ph.D. dissertation, Purdue University, West Lafayette, IN.

Kelly, B. (1996b). Live capture of ringed seals in ice-covered waters. Journal of Wildlife Management **60**: 678-684.

Kelly, B. and L. Quakenbush (1990). Spatiotemporal use of lairs by ringed seals (*Phoca hispida*). Canadian Journal of Zoology **68**: 2503-2512.

Kelly, B. and D. Wartzok (1996). Ringed seal diving behavior in the breeding season. Canadian Journal of Zoology **74**: 1547-1555.

Kooyman, G. (1968). An analysis of some behavioral and physiological characteristics related to diving in the Weddell seal. *in* Biology of the Antarctic Seas. G. Llano and W. Schmitt. Washington, D.C., American Geophysical Union. **3**: 27-261.

Kooyman, G. (1989). Diverse divers: physiology and behaviour. Berlin, Springer-Verlag.

Kooyman, G. and R. Gentry (1986). Diving behaviour of South African fur seals. *in* Fur seals: maternal strategies on land and at sea. R. Gentry and G. Kooyman. Princeton, Princeton University Press: 142-152.

Kramer, D. (1988). The behavioral ecology of air breathing by aquatic mammals. Canadian Journal of Zoology **66**: 89-94.

LeBoeuf, B., D. Costa, A. Huntley and S. Feldkamp (1988). Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. Canadian Journal of Zoology **66**: 446-458.

LeBoeuf, B., D. Crocker, S. Blackwell, P. Morris and P. Thorson (1993). Sex differences in diving and foraging behaviour of northern elephant seals. Symposia of the Zoological Society of London **66**: 149-178.

LeBoeuf, B., P. Morris, S. Blackwell, D. Crocker and D. Costa (1996). Diving behavior of juvenile northern elephant seals. Canadian Journal of Zoology **74**: 1632-1644.

LeBoeuf, B., Y. Naito, T. Asaga, D. Crocker and D. Costa (1992). Swim speed in a female northern elephant seal: metabolic and foraging implications. Canadian Journal of Zoology **70**: 786-795.

Lesage, V., M. Hammill and K. Kovacs (1999). Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. Canadian Journal of Zoology **77**: 74-87.

Littel, R., G. Milliken, W. Stroup and R. Wolfinger (1996). SAS System for Mixed Models. Cary, NC, SAS Institute Inc.

Lydersen, C. (1991). Monitoring ringed seal (*Phoca hispida*) activity by means of acoustic telemetry. Canadian Journal of Zoology **69**: 1178-1182.

Lydersen, C. and M. Hammill (1993). Diving in ringed seal (*Phoca hispida*) pups during the nursing period. Canadian Journal of Zoology **71**: 991-996.

Lydersen, C., M. Hammill and K. Kovacs (1994). Activity of lactating ice-breeding grey seals, *Halichoerus grypus*, from the Gulf of St. Lawrence, Canada. Animal Behaviour **48**: 1417-1425.

Lydersen, C. and K. Kovacs (1993). Diving behaviour of lactating harp seal, *Phoca groenlandica*, females from the gulf of St. Lawrence, Canada. Animal Behaviour **46**: 1213-1221.

Mandelbrot, B. (1983). The fractal geometry of nature. San Francisco, W.H. Freeman.

Marsden, R., R. Ingram and L. Legendre (1994a). Currents under land-fast ice in the Canadian Arctic Archipelago Part 2: vertical mixing. Journal of Marine Research **52**: 1037-1049.

Marsden, R., R. Paquet and R. Ingram (1994b). Currents under land-fast ice in the Canadian Arctic Archipelago Part 1: vertical velocities. Journal of Marine Research **52**: 1017-1036.

Marshall, G. (1998). CRITTERCAM: An animal-borne imaging and data logging system. Marine Technology Society Journal **32**: 11-17.

Martin, A., M. Kingsley and M. Ramsay (1994). Diving behaviour of narwhals (*Monodon monoceros*) on their summer grounds. Canadian Journal of Zoology **72**: 118-125.

Martin, A. and T. Smith (1992). Deep diving in wild, free-ranging beluga whales, *Delphinapterus leucas*. Canadian Journal of Fisheries and Aquatic Sciences **49**: 462-466.

Martin, A., T. Smith and O. Cox (1998). Dive form and function in belugas *Delphinapterus leucas* of the eastern Canadian High Arctic. Polar Biology **20**: 218-228.

Mate, B. (1989). Watching habits and habitats from earth satellites. Oceanus **32**: 14-18.

Mate, B., K. Rossbach, S. Nieukirk, R. Wells, A. Irvine, M. Scott and A. Read (1995). Satellite-monitored movements and dive behavior of a bottlenose dolphin (*Tursiops truncatus*) in Tampa Bay, Florida. Marine Mammal Science **11**: 452-463.

Mate, B., K. Stafford, R. Nawojchik and J. Dunn (1994). Movements and diving behavior of a satellite-monitored Atlantic white-sided dolphin (*Lagenorhynchus acutus*) in the Gulf of Maine. Marine Mammal Science **10**: 116-121.

McLachlan, G. and K. Basford (1988). Mixture Models: Inference and Applications to Clustering. New York, Marcel Dekker, Inc.

McLaren, I. (1958). The biology of the ringed seal (*Phoca hispida* Schreber) in the Eastern Canadian Arctic. Fisheries Research Board of Canada Bulletin **118**.

McLaughlin, R. (1989). Search modes of birds and lizards: evidence for alternative movement patterns. American Naturalist **133**: 654-670.

Mori, Y. (1998a). Optimal choice of foraging depth in divers. Journal of Zoology, London **245**: 279-283.

Mori, Y. (1998b). The optimal patch use in divers: optimal time budget and the number of dive cycles during bout. Journal of Theoretical Biology **190**: 187-199.

Mori, Y. (1999). The optimal allocation of time and respiratory metabolism over the dive cycle. Behavioral Ecology **10**: 155-160.

Nilssen, K., T. Haug, V. Potelov, V. Stasenkov and Y. Timoshenko (1995). Food habits of harp seals (*Phoca groenlandica*) during lactation and moult in March-May in the southern Barents Sea and White Sea. ICES Journal of Marine Science **52**: 33-41.

Norberg, R. A. (1977). An ecological theory on foraging time and energetics and choice of optimal food-searching method. Journal of Animal Ecology **46**: 511-529.

Nordoy, E., L. Folkow and A. Blix (1995). Distribution and diving behaviour of crabeater seals (*Lobodon carcinophagus*) off Queen Maud Land. Polar Biology **15**: 261-268.

Otani, S., Y. Naito, A. Kawamura, M. Kawasaki, S. Nishiwaki and A. Kato (1998). Diving behavior and performance of harbor porpoises, ***Phocoena phocoena***, in Funka Bay, Hokkaido, Japan. Marine Mammal Science **14**: 209-220.

Pianka, E. (1966). Convexity, desert lizards, and spatial heterogeneity. Ecology **47**: 1055-1059.

Pike, D. and H. Welch (1990). Spatial and temporal distribution of sub-ice macrofauna in the Barrow Strait area, Northwest Territories. Canadian Journal of Fisheries and Aquatic Sciences **47**: 81-91.

Prinsenberg, S. and E. Bennett (1987). Mixing and transports in Barrow Strait, the central part of the Northwest Passage. Continental Shelf Research **7**: 913-935.

Schoener, T. (1971). Theory of feeding strategies. Annual Reviews in Ecology and Systematics **2**: 369-404.

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

Schreer, J., R. O'Hara Hines and K. Kovacs (1998). Classification of dive profiles: a comparison of statistical clustering techniques and unsupervised neural networks. Journal of Agricultural, Biological, and Environmental Statistics **3**: 383-404.

Schreer, J. and J. Testa (1996). Classification of Weddell seal behavior. Marine Mammal Science **12**: 227-250.

Shafir, S. and J. Roughgarden (1998). Testing predictions of foraging theory for a sit-and-wait forager, ***Anolis gingivinus***. Behavioral Ecology **9**: 74-84.

Simpkins, M., B. Kelly and D. Wartzok (in prep a). Analysis of three-dimensional search behavior by ringed seals. Animal Behaviour.

Simpkins, M., B. Kelly and D. Wartzok (in prep b). Definition of three-dimensional diving behaviors exhibited by ringed seals. Marine Mammal Science.

Simpkins, M., B. Kelly and D. Wartzok (in prep c). Three-dimensional movements within individual dives by ringed seals. Canadian Journal of Zoology.

Skrovan, R., T. Williams, P. Berry, P. Moore and R. Davis (1999). The diving physiology of bottlenose dolphins (*Tursiops truncatus*). II. Biomechanics and changes in buoyancy with depth. Journal of Experimental Biology **202**: 2749-2761.

Slip, D., M. Hindell and H. Burton (1994). Diving behavior of southern elephant seals from Macquarie Island: an overview. *in* Elephant seals: population ecology, behavior, and physiology. B. LeBoeuf and R. Laws. Berkeley, University of California Press: 253-270.

Smith, R., J. Anning, P. Clement and G. Cota (1988). Abundance and production of ice algae in Resolute Passage, Canadian Arctic. Marine Ecology Progress Series **48**: 251-263.

Smith, T. (1980). Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. Canadian Journal of Zoology **58**: 2201-2209.

Smith, T. (1987). The ringed seal, ***Phoca hispida***, of the Canadian Western Arctic. Canadian Bulletin of Fisheries and Aquatic Sciences **216**.

Smith, T. and M. Hammill (1981). Ecology of the ringed seal, ***Phoca hispida***, in its fast ice breeding habitat. Canadian Journal of Zoology **59**: 966-981.

Smith, T., M. Hammill and G. Taugbøl (1991). A review of the developmental, behavioural, and physiological adaptations of the ringed seal, *Phoca hispida*, to life in the Arctic winter. Arctic **44**: 124-131.

Smith, T. and I. Stirling (1975). The breeding habitat of the ringed seal (*Phoca hispida*). The birth lair and associated structures. Canadian Journal of Zoology **53**: 1297-1305.

Stewart, B., E. Petrov, E. Baranov, A. Timonin and M. Ivanov (1996). Seasonal movements and dive patterns of juvenile Baikal seals, *Phoca sibirica*. Marine Mammal Science **12**: 528-542.

Stirling, I. (1973). Vocalization in the ringed seal (*Phoca hispida*). Journal of the Fisheries Research Board of Canada **30**: 1592-1594.

Stirling, I. (1977). Adaptations of Weddell and ringed seals to exploit the polar fast ice habitat in the absence or presence of surface predators. *in* Adaptations Within Antarctic Ecosystems: Proceedings of the Third SCAR Symposium of Antarctic Biology. G. Llano. Washington, D.C., Smithsonian Institution: 741-748.

Sugihara, G. and R. May (1990). Applications of fractals in ecology. Trends in Ecology and Evolution **5**(3): 79-86.

Teilmann, J., E. Born and M. Acquarone (1999). Behaviour of ringed seals tagged with satellite transmitters in the North Water polynya during fast-ice formation. Canadian Journal of Zoology **77**: 1934-1946.

Testa, J., S. Hill and D. Siniff (1989). Diving behavior and maternal investment in Weddell seals (*Leptonychotes weddellii*). Marine Mammal Science **5**: 399-405.

Thompson, D. and M. Fedak (1993). Cardiac responses of grey seals during diving at sea. Journal of Experimental Biology **174**: 139-164.

Thompson, D., P. Hammond, K. Nicholas and M. Fedak (1991). Movements, diving and foraging behaviour of grey seals (*Halichoerus grypus*). Journal of Zoology, London **224**: 223-232.

Thompson, D., A. Hiby and M. Fedak (1993). How fast should I swim? Behavioural implications of diving physiology. Symposia of the Zoological Society of London **66**: 349-368.

Turchin, P. (1996). Fractal analyses of animal movement: a critique. Ecology **77**(7): 2086-2090.

Turchin, P. (1998). Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sunderland, MA, Sinauer Associates, Inc.

Turchin, P., F. Odendaal and M. Rausher (1991). Quantifying insect movement in the field. Environmental Entomology **20**(4): 955-963.

Venables, W. and B. Ripley (1997). Modern Applied Statistics with S-Plus. New York, Springer-Verlag.

Wartzok, D., R. Elsner, H. Stone, B. Kelly and R. Davis (1992a). Under-ice movements and the sensory basis of hole finding by ringed and Weddell seals. Canadian Journal of Zoology **70**: 1712-1722.

Wartzok, D., S. Sayegh, H. Stone, J. Barchak and W. Barnes (1992b). Acoustic tracking system for monitoring under-ice movements of polar seals. Journal of the Acoustical Society of America **92**: 682-687.

Webb, P., D. Crocker, S. Blackwell, D. Costa and B. LeBoeuf (1998). Effects of buoyancy on the diving behavior of northern elephant seals. Journal of Experimental Biology **201**: 2349-2358.

Welch, H., M. Bergmann, T. Siferd, K. Martin, M. Curtis, R. Crawford, R. Conover and H. Hop (1992). Energy flow through the marine ecosystem of the Lancaster Sound region, arctic Canada. Arctic **45**: 343-357.

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

Westgate, A., A. Read, P. Bergrenn, H. Koopman and D. Gaskin (1995). Diving behaviour of harbour porpoises, *Phocoena phocoena*. Canadian Journal of Fisheries and Aquatic Sciences **52**: 1064-1073.

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

Williams, T., J. Haun and W. Friedl (1999). The diving physiology of bottlenose dolphins (*Tursiops truncatus*). I. Balancing the demands of exercise for energy conservation at depth. Journal of Experimental Biology **202**: 2739-2748.

Williams, T. and G. Kooyman (1985). Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. Physiological Zoology **58**: 576-589.

Wilson, R., J. Cooper and J. Plötz (1992). Can we determine when marine endotherms feed? A case study with seabirds. Journal of Experimental Biology **167**: 267-275.

Wilson, R. and M. Wilson (1988). Foraging behaviour in four sympatric cormorants. Journal of Animal Ecology **57**: 943-955.

Ydenberg, R. and C. Clark (1989). Aerobiosis and anaerobiosis during diving by western grebes: an optimal foraging approach. Journal of Theoretical Biology **139**: 437-449.

Zar, J. (1996). Biostatistical Analysis. Upper Saddle River, NJ, Prentice Hall.