

THREE-DIMENSIONAL DIVING BEHAVIORS OF RINGED SEALS (*PHOCA HISPIDA*)

MICHAEL A. SIMPKINS¹

Institute of Marine Science,
University of Alaska Fairbanks,
245 O'Neill Building,
Fairbanks, Alaska 99775, U.S.A.
E-mail: mike.simpkins@noaa.gov

BRENDAN P. KELLY

Juneau Center, SFOS,
University of Alaska Fairbanks,
11120 Glacier Highway,
Juneau, Alaska 99801, U.S.A.

DOUGLAS WARTZOK

Graduate School,
University of Missouri–St. Louis,
8001 Natural Bridge Road,
St. Louis, Missouri 63121-4499, U.S.A.

ABSTRACT

Dives of five freely diving ringed seals were classified into three-dimensional movement types. Horizontally convoluted dives, defined as dives with angular velocity $>15^\circ/\text{sec}$, appeared to be foraging or social dives. Simple dives that did not include convoluted movements (angular velocity $<10^\circ/\text{sec}$) were considered to be exploration dives. Directional dives with nearly linear horizontal travel (horizontal directionality >0.6 , on a scale of 0–1) were presumed to be travel dives. Each three-dimensional dive type was observed with similar frequency in dives with two distinct time-depth profiles: V-shaped profiles in which ascent immediately followed descent, and U-shaped profiles in which >7 sec were spent at depth between descent and ascent. The lack of behavioral differences between dives with distinct time-depth profiles suggested that time-depth profiles are not a reliable means of inferring dive behaviors for ringed seals.

Key words: diving behavior, three-dimensional movement, ringed seal, *Phoca hispida*.

¹ Current address: National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, Washington 98115, U.S.A.

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 (*e.g.*, Kooyman 1968, Hindell *et al.* 1991, LeBoeuf *et al.* 1992, Schreer *et al.* 1998). Functions ascribed to these classes, however, did not consistently correspond to inferences based on analyses of harbor seal feeding events (Lesage *et al.* 1999), ringed seal local search behavior (Simpkins *et al.*, in press), and Weddell seal 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 quantified 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 classified the three-dimensional movements of ringed seals and suggested behavioral functions for dives with distinct movements.

We expected the three-dimensional movements of ringed seals to differ between dives with distinct behavioral functions. We had no basis to define *a priori* relationships between three-dimensional movement variables and specific behaviors, because these variables had never been calculated for marine mammal dives. We were, however, able to categorize dives by "movement types" based on these three-dimensional variables and suggest behavioral functions for dives of each type. Specifically, we examined ringed seal dives for evidence of slow dives (dives with low swim speed and/or acceleration), directional dives (dives with nearly linear horizontal travel), convoluted dives (dives with tortuous, winding paths), simple dives (dives with very simple paths, the opposite of convoluted dives), and stop-and-go dives (dives in which a seal was stationary for much of the dive time).

We expected the recorded movements of ringed seals to include social, foraging, and other behaviors, 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, Furgal *et al.* 1996). During the breeding season, rutting males may defend underwater territories or access to breathing holes used by females (Stirling 1973, 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, Hammill *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 (*e.g.*, Kooyman 1968, Hindell *et al.* 1991, LeBoeuf *et al.* 1992, Schreer *et al.* 1998).

Ringed seal foraging may include tactics inferred for other marine mammals: benthic foraging, pelagic foraging, and sit-and-wait foraging (*e.g.*, Bengtson and Stewart 1992, LeBoeuf *et al.* 1993, Thompson and Fedak 1993, Schreer and Testa 1996, Martin *et al.* 1998). We expected many of these proposed behaviors to involve movements associated with slow, directional, convoluted, simple, or stop-and-go dives. Although we could not independently verify some behaviors based solely on three-dimensional movements, we were able to link dive types to likely behaviors, or suites of behaviors, with more certainty than was possible using time-depth data alone.

METHODS

Data Collection and Processing

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 and Wartzok 1996; Simpkins *et al.*, in press). We captured seals at breathing holes in shore-fast sea ice using nets (Kelly 1996) and tracked their movements under the ice by way of ultrasonic transmitters (Vemco Ltd., Armdale, Nova Scotia, Canada) attached to their hair (Wartzok *et al.* 1992*b*).

We compiled and filtered the data for each seal, removing erroneous locations that would have required swim speeds in excess of 6 m/sec (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 portion of each dive phase was longer than seven seconds.

Division of Dive Paths into Discrete Moves

We divided dives into functional units termed moves. We defined moves as a series of locations that 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 (Fig. 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 m to split 511 randomly chosen dives (10% subsample of all dives) into moves.

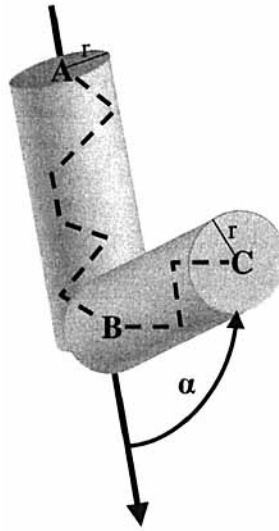


Figure 1. Definition of moves and three-dimensional turning angle between moves for dive analysis. AB is defined as one move, because all points along dotted dive path between A and B are within r (3 m) of line segment AB. BC is defined as a move similarly. Three-dimensional turning angle between AB and BC is α .

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 that 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/min 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/min in this analysis. Seven seals were tracked using transmitters which emitted pulses every 1–1.5 sec (a sufficiently rapid sampling rate). Only five seals had more than 10 dives with 15 or more points/min after data processing (410 dives, Table 1).

Three-dimensional Movement Analyses

We converted three-dimensional move data (start and end points of moves defined by rectangular x , y , z coordinates) to spherical coordinates for analysis

Table 1. Dives analyzed for each seal. Only dives tallied for seals listed below met criteria necessary for inclusion in this detailed analysis. All dives below were to depths greater than 5 m, consisted of at least 10 location data points collected at rate of ≥ 15 points/min (after erroneous locations were removed), and included at least 7 sec of data for each phase of 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

purposes (Fig. 2, modified from Batschelet 1981). For each dive, we calculated angular velocities (horizontal, vertical, and three-dimensional), mean speed, mean acceleration between moves, and horizontal directionality (Appendix 1). We also estimated the proportion of time a seal spent stationary during each dive as the proportion of time spent in slow passages (>7 sec spent within a $3 \times 3 \times 3$ -m volume; Simpkins *et al.*, in press). Although seals may not have been absolutely stationary during these slow passages, any movement during slow passages was unusually slow in comparison to normal swimming behavior of ringed seals (≤ 3 sec spent within 95% of $3 \times 3 \times 3$ -m volumes swum through; Simpkins *et al.*, in press).

We chose these three-dimensional variables, because each variable directly quantified the type of movement expected within one or more of the dive types of interest. Angular velocities measured turning behavior and the resulting complexity of dive paths. Dives with complex paths (convoluted dives) had high angular velocities, whereas dives with simple paths (simple dives) had low angular velocities. Horizontal and vertical angular velocities also served to identify dives with vertically and/or horizontally convoluted paths.

Mean speed and mean acceleration between moves measured the activity of

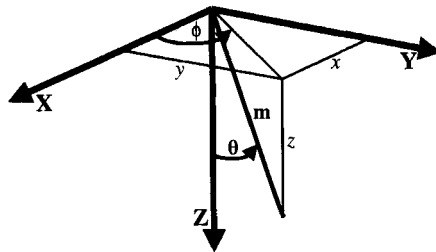


Figure 2. Spherical and rectangular coordinates in three-dimensional space (modified from Batschelet 1981). Rectangular coordinates (x , y , z) shown in italics, and spherical coordinates (m , ϕ , θ) shown in bold. Note that x , y , and z are lengths measured along respective axes (X , Y , Z), and m is a length measured in direction defined by ϕ and θ angles. For our analysis of diving behavior, Z -axis was positive in downward direction as shown.

seals during dives. Dives with low activity (slow dives) had low mean speed and acceleration values. Stop-and-go dives could appear as a subset of slow dives, because slow passages naturally reduced the mean dive speed. We directly identified stop-and-go dives by the proportion of dive time spent in slow passages.

Horizontal directionality measured the distribution of move bearings in the horizontal plane (ϕ), and directional dives had high horizontal directionality values. We calculated horizontal directionality for each dive as the mean vector length of ϕ (Appendix 1), which was a measure related to the standard deviation of ϕ using circular statistics (Batschelet 1981). Horizontal directionality, measured in this fashion, could range from 1, when all horizontal bearings in a sample were identical, to 0, when the bearings were uniformly distributed over 360° .

Empirical Definition of Three-dimensional Dive Types

We defined dive types in terms of three-dimensional movement variables (Appendix 1) based on inspection of dive plots or histograms of each movement variable. We recognized dives with horizontally and/or vertically convoluted dive paths, dives with simple dive paths, and dives involving horizontally directional travel by visual inspection of dive plots. Horizontally convoluted dives showed most turning behavior occurring in the horizontal (X-Y) dimensions (Fig. 3A), and vertically convoluted dives showed repeated vertical excursions at depth (*e.g.*, Hindell *et al.* 1991, Bengtson and Stewart 1992, LeBoeuf *et al.* 1992). Directional dives exhibited nearly linear horizontal movement (Fig. 3B). We visually recognized simple dive plots by the absence of convoluted movement, but we did not require simple dives to involve directional movement (Fig. 3C).

We defined convoluted, directional, and simple dive types by setting limits on either angular velocity or horizontal directionality values. We set these limits conservatively, to ensure that assigned dive types could be corroborated by visual inspection of the dive plot. Some values were inconclusive in defining dive types, therefore, we did not classify dives with those values. For example, we calculated angular velocities between 10° and $15^\circ/\text{sec}$ for dives with highly convoluted movement (convoluted dives), dives without convoluted movement (simple dives), and dives with intermediate movement for which no dive type could be recognized visually. Since angular velocities between 10° and $15^\circ/\text{sec}$ were inconclusive in defining dive types, we did not classify dives with those angular velocities.

We could not recognize slow and stop-and-go dives by visual inspection of dive plots. We quantified these two dive types by mean speed, mean acceleration, and proportion of time spent in slow passages, which did not necessarily affect the appearance of the dive plot. We plotted histograms of mean speed, mean acceleration, and proportion of time spent in slow passages for all dives and looked for evidence of a distinct class of dives with low speed and acceleration (slow dives) or high proportion of time spent in slow passages

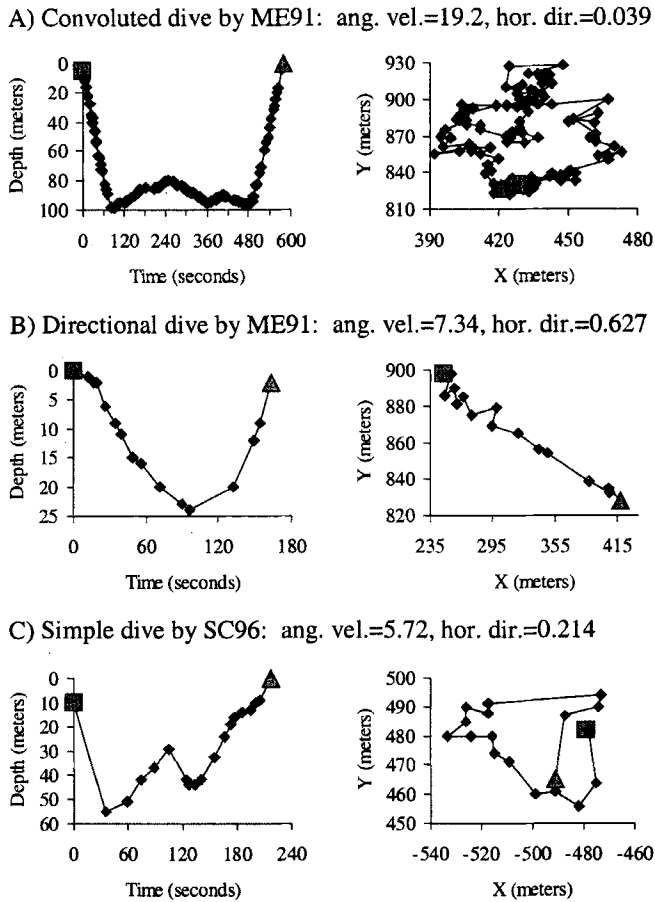


Figure 3. Plots of different dive types. Convoluted (A), directional (B), and simple (C) dives shown with their three-dimensional angular velocity and horizontal directionality values. Line segments represent moves, where each move encompasses a sequence of locations representing movement in one direction. Squares and triangles represent dive start and end, respectively.

(stop-and-go 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 dive type. We did not design dive types to be exclusive, because, in a separate analysis, we found that ringed seals switched between behavioral states within individual dives (Simpkins 2000). Each dive that met a dive type's movement criteria was assigned to that dive type, regardless of whether the dive also qualified under the criteria of another dive type. Thus, dives could be assigned to one or more types. Dives that did

not meet the criteria for any dive type remained unassigned. We described the three-dimensional characteristics of each dive type in terms of the ranges of all movement values calculated for dives of that type. We also compared our classification of dives to previous time-depth profile classifications by comparing the distribution of three-dimensional dive types among dives with two distinct time-depth profiles: V-shaped profiles in which ascent immediately followed descent and U-shaped profiles in which >7 sec were spent at depth between descent and ascent.

RESULTS

Ringed seals exhibited horizontally convoluted, directional, and simple dives, but did not exhibit vertically convoluted, slow, or stop-and-go dives. We grouped data from all seals together, because the number of dives recorded for each seal (after removing incomplete and poorly sampled dives) was insufficient to allow comparisons between individuals (Table 1). Based on our inspection of dive plots and movement variable histograms, we defined convoluted dives as dives with three-dimensional angular velocities $>15^\circ/\text{sec}$, directional dives as dives with horizontal directionalities >0.6 , and simple dives as dives with three-dimensional angular velocities $<10^\circ/\text{sec}$. 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 were horizontally convoluted dives. Consistently low vertical angular velocities for all ringed seal dives suggested that dive paths were convoluted only in the horizontal dimensions and that vertically convoluted movements were not common (95% of all vertical angular velocities $<5^\circ/\text{sec}$).

We found no evidence for a distinct class of slow or stop-and-go dives. During slow dives, we expected seals to move slowly and/or avoid rapid acceleration, but unimodal histograms of mean speed and acceleration indicated no distinct class of low-effort dives (Fig. 4A, B). During stop-and-go 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 (Fig. 4C), indicating that no distinct class of stop-and-go dives was present.

Directional, simple, and convoluted dives involved distinct types of movement based on three-dimensional analysis of ringed seal dives (Table 2). Convoluted dives involved movements with lower horizontal directionality, higher mean speed, higher mean acceleration, and higher angular velocity (horizontal, vertical, and three-dimensional) than directional or simple behavior. Directional and simple dives were similar to each other, but directional dives were shallower and involved movements with higher horizontal directionality than movements in simple dives.

Convoluted dives were the most common type observed for ringed seals, and directional dives were the least common (Table 3). We observed each dive type with similar frequency for V-shaped dives, with only descent and ascent phases, and U-shaped dives with bottom phases (Table 3). Of the 250 dives

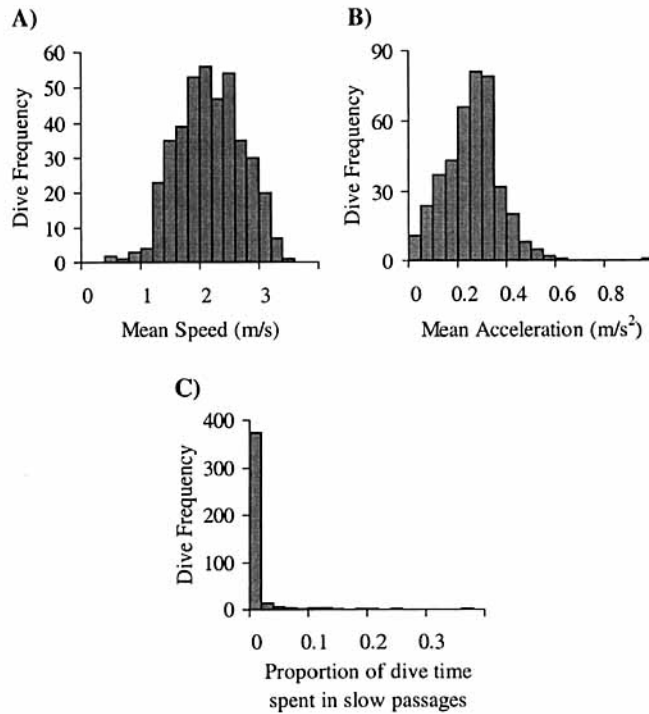


Figure 4. Histograms of mean speed (A), mean acceleration (B), and proportion of dive time spent in slow passages (C). A distinct class of slow dives (low speed or acceleration) was not found in histograms of mean speed (A) and acceleration (B), nor was a distinct class of stop-and-go dives with large proportions of time spent in slow passages found in histogram C.

assigned types, 25 were assigned two types. Most dives with two types were both directional and simple (23 dives: 8 V-shaped, 15 U-shaped). Only two dives were both directional and convoluted (1 V-shaped, 1 U-shaped). No dives were both simple and convoluted, because those dive types were exclusive.

DISCUSSION

The three-dimensional movements of five freely diving ringed seals were analyzed for evidence of convoluted, directional, simple, slow, and stop-and-go dives. Horizontally convoluted, directional, and simple dives were observed, but vertically convoluted, slow, and stop-and-go dives were not observed. Each of these dive types involved distinct types of movement. We suggest that these different types of movement represented distinct behaviors, or suites of behaviors.

Convoluted dives involved higher speed, acceleration, and angular velocities than directional and simple dives (Table 2). These high values indicated that convoluted dives were more energy expensive than other dives. We suggest

Table 2. Three-dimensional movement values by dive type: mean (interquartile range). All movement values differed significantly between dive types (Kruskal-Wallis, $P \leq 0.005$). Non-parametric multiple-comparison tests for unequal sample sizes used to determine significant differences in movement values between each pair of behaviors (Dunn 1964, Zar 1996). Letters indicate significant differences between behaviors with $A < B < C$. For example, horizontal angular velocity did not differ significantly between directional dives (A) and simple dives (A), but convoluted dives (B) showed significantly higher horizontal angular velocities than did directional or simple dives.

Movement variable	Directional dives	Simple dives	Convoluted dives
Horizontal angular velocity	7.94 °/sec A (4.58, 10.84)	8.42 °/sec A (6.68, 10.74)	20.88 °/sec B (18.51, 23.04)
Vertical angular velocity	1.88 °/sec A (0.895, 2.58)	1.95 °/sec A (0.976, 2.58)	2.56 °/sec B (1.39, 3.15)
Three-dimensional angular velocity	8.32 °/sec A (5.85, 10.93)	7.23 °/sec A (6.03, 8.81)	19.02 °/sec B (16.74, 20.92)
Horizontal directionality	0.730 C (0.657, 0.785)	0.393 B (0.132, 0.626)	0.214 A (0.061, 0.346)
Mean speed	1.86 m/sec A (1.49, 2.24)	1.74 m/sec A (1.36, 2.04)	2.49 m/sec B (2.19, 2.81)
Mean acceleration	0.176 m/sec ² A (0.073, 0.233)	0.148 m/sec ² A (0.078, 0.213)	0.329 m/sec ² B (0.265, 0.375)
Maximum depth	16.84 m A (9, 21)	50.43 m B (14, 81)	64.35 m B (17, 115)

that convoluted dives involved local search within prey patches, pursuit of prey, and/or agonistic interactions with other seals (*e.g.*, during territorial defense). Convoluted dives appeared to involve exclusively horizontal turns, suggesting that convoluted movements occurred while a seal was swimming horizontally, as might be expected during benthic foraging. Horizontally convoluted dives, however, occurred at all depths in the water column and were not limited to dives that reached the benthos (interquartile range of horizontally convoluted dive depths = 17–115 m; Table 2). Also, a separate analysis of three-dimensional movements within ringed seal dives indicated that horizon-

Table 3. Frequency of dive types defined by three-dimensional analysis of ringed seal movements. Frequency of defined dive types is contrasted between all dives and two dive types commonly classified using time-depth profiles (V-shaped dives and U-shaped dives). Frequency of dive behaviors determined by three-dimensional analysis does not differ between V-shaped and U-shaped dives deduced by time-depth profiles ($\chi^2 = 0.74$, $P > 0.65$).

Dive type	Count (percent) of all dives	Count (percent) of V-shaped dives	Count (percent) of U-shaped dives
Directional	37 (9%)	12 (12%)	25 (8%)
Simple	81 (20%)	24 (25%)	57 (18%)
Convoluted	157 (38%)	41 (42%)	116 (37%)
Undefined	160 (39%)	29 (30%)	131 (42%)
All dives	410	97	313

tally convoluted movements were not limited to the bottom phase of dives, rather these movements occurred during all phases of dives (Simpkins 2000). During descent and ascent, ringed seals maintained consistent vertical bearings (*i.e.*, descent/ascent angles), but often changed their horizontal bearings. The slow changes in vertical bearing throughout convoluted dives (low vertical angular velocity; Table 2) suggested that these dives did not involve prolonged pursuit of prey (or other seals during social interactions). We would have expected prolonged pursuit to involve rapid changes in both the horizontal and vertical bearing of a seal chasing prey that could flee in any three-dimensional direction. Limited prey pursuit following stalking behavior has recently been observed in Weddell seals (Davis *et al.* 1999).

Directional dives were, by definition, more directional than other dives and were also shallower than convoluted or simple dives (Table 2). We suggest that directional dives represented travel behavior. Shallow directional dives by ringed seals were quite different from the deep travel dives exhibited by elephant and gray seals (*e.g.*, LeBoeuf *et al.* 1988, Hindell *et al.* 1991, Thompson *et al.* 1991). Within the shore-fast sea ice habitat, ringed seal home ranges are restricted, and the seals travel only short distances (<2 km) between their breathing holes (Kelly and Quakenbush 1990). The directional dives we recorded represented ringed seals moving between breathing holes, likely related to breathing hole maintenance or predator avoidance. In contrast, elephant and gray seals travel longer distances, and their deep travel dives may serve as opportunistic foraging dives, during which seals search for and capture prey while traveling (Hindell *et al.* 1991, Thompson *et al.* 1991).

Simple dives included the majority of directional dives (23 of 37), as well as dives which were not directional. We suggest that simple dives represented seals exploring their environment, efficiently searching a large volume during each dive. Simple dive paths allow for unrestricted search, whereas convoluted paths tend to focus search effort to small regions (*e.g.*, local search within prey patches), resulting in inefficient exploration of large regions (Bell 1990). Although directional dives may have represented breathing hole maintenance or predator avoidance, the possibility that directional dives also served an exploratory function could not be discounted. Simple dives may have represented 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 simple 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 2). Simple dives may have represented foraging dives during which prey were not encountered, and convoluted dives may have represented foraging dives during which prey were encountered. In this scenario we would expect foraging dives to involve simple paths until prey were encountered, then the dive paths would become convoluted. In our separate analysis of movements within dives, we found that ringed seals did

switch between directional movement (simple paths) and convoluted movement within dives (Simpkins 2000).

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 refrozen 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 that they actively maintained, we did capture several seals at holes that we had 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 during simple dives or encountered the holes coincidentally.

Vertically convoluted dives, involving 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. 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). The absence of vertically convoluted dives indicated that any pelagic foraging by ringed seals did not involve rapid vertical excursions. The distribution of horizontally convoluted dives throughout the water column, however, suggested that ringed seals might have foraged on pelagic prey using a different strategy, such as stalking prey with minimal pursuit.

We considered slow dives to represent rest behavior, during which a seal minimized its swimming effort. The absence of a distinct class of slow dives suggested that ringed seals did not perform rest dives while in the shore-fast sea ice habitat. Ringed seals in shore-fast sea ice often spend long periods between dives either resting in subnivean lairs or floating at the surface in breathing holes (Kelly and Quakenbush 1990). 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).

We considered stop-and-go dives to represent sit-and-wait predation, with seals remaining stationary in the water column and waiting to ambush approaching prey. The absence of a distinct class of stop-and-go dives suggested that the five ringed seals whose movements we analyzed here did not utilize a sit-and-wait foraging strategy. A separate analysis of dives by all 13 of the seals we tracked indicated that ringed seals did remain stationary in the water column on rare occasions (Simpkins *et al.*, in press). We could not determine

if these rare stationary periods represented sit-and-wait predation or some other behavior.

Although foraging could not be independently verified for individual dives, ringed seals engaged in convoluted movements consistent with local search and prey pursuit during more than $\frac{1}{3}$ of dives (Table 3). If we consider that some simple dives represented unsuccessful search for prey, then the seals may have attempted to forage during more than $\frac{1}{2}$ of all dives. The seals rarely dived 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 have involved convoluted movements indistinguishable from foraging.

The full suite of convoluted, directional, and simple dives was observed with similar frequency for both V-shaped and U-shaped dives (Table 3). The lack of behavioral differences between V-shaped and U-shaped dives, which have very distinct time-depth profiles, suggested 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. Independent verification of behaviors, however, is still required before inferred behaviors can be definitively assigned to three-dimensional dive types.

The definition of dive types using three-dimensional analysis techniques allowed us to distinguish between dives involving different types of movements. 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). Swim speed analysis appears promising as an alternate approach to defining dive types and behaviors (Crocker *et al.* 1994, Crocker *et al.* 1997, Lesage *et al.* 1999).

In addition to the three-dimensional movement variables mentioned here, we also examined the usefulness of meander (angular velocity/speed of movement; Bond 1980) and fractal dimension (calculated using the cluster method; Hastings and Sugihara 1993) as alternative measures of convoluted behavior. Meander was a promising variable because it included angular velocity and speed, both important characteristics of dive behaviors (Table 2). We found correlation between three-dimensional angular velocity and mean speed (Spearman rank correlation = 0.56, $P = 0.0001$), however, which suggested that meander values were likely biased by being the quotient of two correlated variables (Simpkins 2000). Fractal dimensions have been calculated recently in several studies of two-dimensional movement behavior (*e.g.*, Dicke and Bur-

rough 1988, Turchin 1998), as well as one study of three-dimensional movement behavior (Coughlin *et al.* 1992). We found that calculated fractal dimensions appeared to be a result of the volume encompassed by ringed seal dive paths, rather than the complexity of the paths (Simpkins 2000).

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/min 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. When splitting a dive path into "move cylinders" as we did, it is important to choose a radius for the move cylinders that is large enough to incorporate noise in the location data.

Three-dimensional movement data allowed us to describe more fully the diving behavior of ringed seals. We were able to classify dive types quantitatively based on the three-dimensional movements of ringed seals and suggest corresponding behaviors. 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 2000).

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APPENDIX 1

Three-dimensional movement variables calculated for each dive (Batschelet 1981, Bell 1990, Turchin 1998).

$$\text{Horizontal angular velocity} = \sum |\phi_{i+1} - \phi_i| / \sum (\tau_i)$$

$$\text{Vertical angular velocity} = \sum |\theta_{i+1} - \theta_i| / \sum (\tau_i)$$

$$\text{Three-dimensional angular velocity} = \sum (\alpha_i) / \sum (\tau_i)$$

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

$$\text{Mean speed} = \sum (m_i / \tau_i) / n$$

$$\text{Mean acceleration} = \sum \left\{ \left| (m_{i+1} / \tau_{i+1}) - (m_i / \tau_i) \right| / [(\tau_i + \tau_{i+1}) / 2] \right\} / n$$

$$\text{Proportion of time spent in slow passages} = \sum (s_j) / \sum (\tau_i)$$

where:

ϕ_i = counter-clockwise angle from the positive X-axis for move i (Fig. 2)

θ_i = vertical angle up from the positive Z-axis for move i (Fig. 2)

α_i = three-dimensional turning angle between move i and move $i + 1$ (Fig. 1)

τ_i = duration of move i

n = number of moves

m_i = length of move i (Fig. 2)

s_j = duration of slow passage j (note that slow passages are considered moves, so j is a subset of i).