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# CLASSIFICATION OF WEDDELL SEAL DIVING BEHAVIOR

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## ABSTRACT

Most studies of pinniped diving behavior have manually grouped dives according to similarities in the depth, duration, and appearance of the dive profile. Dives of 15 adult female Weddell seals (*Leptonychotes weddellii*) were recorded with time-depth recorders and 39,119 dives were classified manually and statistically (principal components analysis, discriminant function analysis, cluster analysis, and shape-fitting algorithms). Four dive types, common to all classification methods, and a fifth dive type, common to two of the methods, represented most of the observed diving behavior. However, a few variations of these dive types, specifically a flat-bottomed dive determined manually, may have also represented important behavior. Using a combination of these methods, all dives were classified into six dive types. Inspection of dive variables (mean maximum depth, mean duration, and frequency) over time for each dive type, as well as comparisons to previous studies of pinniped diving behavior, indicated different behaviors that the dive types may represent. Hypothesized functions for the dive types were pelagic foraging, benthic foraging, exploration, and traveling. The results indicate that there are strong similarities in diving behavior across various phocid species, that statistical analyses of diving behavior are useful in the analysis of a large data set, and that these analyses reduced human subjective bias in interpreting diving behavior.

Key words: classification, diving behavior, *Leptonychotes weddellii*, multivariate statistical tests, satellite-linked time-depth recorder, time-depth recorder, Weddell seal.

The Weddell seal (*Leptonychotes weddellii*) inhabits the coastal waters surrounding the Antarctic Continent. Each spring Weddell seals return to traditional colonies within the land-fast ice to breed and give birth. The summer behavior of Weddell seals is well documented (*e.g.*, Kooyman 1968, 1975, 1981; Stirling

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1971; Kooyman *et al.* 1983; Testa and Siniff 1987; Testa *et al.* 1989; Siniff 1991). However, little is known of their winter behavior (approximately eight months of the year) and information on their overwinter diving behavior is scarce (Castellini *et al.* 1992, Testa 1994). Recent development of microprocessor-controlled time-depth recorders (TDRs) and satellite-linked time-depth recorders (SLTDRs) has allowed more detailed study of the diving behavior of Weddell seals and other marine mammals.

As recorded by TDRs and SLTDRs, maximum depths and durations provided the primary basis for original classifications of marine mammal diving behavior. These criteria for classifying diving behavior have been widely applied in studying the diving ecology of marine mammals (*e.g.,* Kooyman 1968, DeLong and Stewart 1991, Goebel *et al.* 1991, Castellini *et al.* 1992). Weddell seal dives were originally classified into three patterns: (1) dives less then 100 m in depth and 5 min in duration, (2) dives less than 200 m in depth and greater than 20 min in duration, and (3) dives with maximum depths greater than 200 m and durations usually between 8 and 15 minutes (Kooyman 1968).

A few recent studies (Le Boeuf *et al.* 1988, 1992; Hindell *et al.* 1991; Bengtson and Stewart 1992) have attempted to take these analyses a step further by classifying diving behavior by not only maximum depth and duration, but also by the shape of the dive profile (depth *vs.* time). Hindell *et al.* (1991) made an attempt at statistical classification of southern elephant seal (*Mirounga leonina*) diving behavior by plotting the first two principal components of a multivariate principal components analysis and looking for clumping. This method only indicated two groups, and manual comparisons of dive profiles were used to further separate the dive profiles into six types.

The objectives of this study were to (1) test the use of multivariate statistical analyses as a more objective method of classifying marine mammal diving behavior, using Weddell seals as a model; (2) compare multivariate statistical analyses to commonly used manual methods; and (3) test the utility of the various classification methods by describing some of the diving behavior, specifically suggesting possible functions of the dive types determined for Weddell seals.

## Methods

TDRs (Mark I, Wildlife Computers, Woodinville, WA, U.S.A.) were attached to eight lactating females in 1986 at Hutton Cliffs, McMurdo Sound, Antarctica (Testa *et al.* 1989). SLTDRs (Wildlife Computers) weighing 1 kg each were attached with epoxy adhesive to the hair on the lower back of 11 adult females in early 1990 and 13 adult females in early 1991 at various sites in McMurdo Sound, Antarctica (Matsuki and Testa 1991, Schreer and Testa 1992). Once the devices were removed or lost, complete regeneration of the pelage on the lower back was seen for all (n=20) seals observed after their annual molt. The archived data of depth and time were used, depending on recovery of the TDR or SLTDR (*i.e.*, all depth records within a dive were used, not just the maximum depth and duration transmitted to the satellite by the

SLTDRs). The TDRs were set to sample at 20-sec intervals or less in 1986, and the SLTDRs were set to sample at 60-sec intervals in 1990 and 1991. Due to some animals not being recaptured, only 11 dive records recorded from seven animals in 1986 (many animals had TDRs attached more than once), three dive records from 1990, and five dive records from 1991, for a total of 15 animals, were used in the analyses. Dives with a maximum depth of less than 50 m and a duration of less than 10 min (20,275 dives of the total 59,394 dives recorded) were excluded because the sampling rate of the SLTDRs (every 60 sec) provided insufficient representation of these shorter dives and their exclusion created a unimodal distribution over these two variables. Also, these short, shallow dives most likely represent a variety of behaviors including exploration, resting, and social functions (Kooyman 1968) making them even more difficult to classify. This resulted in a total of 39,119 dives (968 dives from 1986, 4,823 dives from 1990, and 33,328 dives from 1991) that were used for the analyses.

A number of different methods were performed to classify Weddell seal diving behavior: (1) manual comparisons of dive profiles; (2) manual comparison of dive profiles in combination with discriminant function analysis; (3) multivariate statistical techniques: principal components analysis, discriminant function analysis, and cluster analysis; and (4) comparison of dive profiles to simple geometric shapes.

*Dive Classification*

*Manual comparison of dive profiles*—Approximately 5,000 dive profiles (13% of the entire data set) from 15 seals were viewed using Wildlife Computers DIVE ANALYSIS (DA) program and classified into dive types. Maximum depth, duration, bottom time (the time interval between the first and last depths equal to or greater than 70% of the dive's maximum depth), wiggle count (the number of ascent-to-descent occurrences that occur during bottom time that differ by more than 6 m), average descent rate (the rate of travel between the start of the dive and the beginning of bottom time), and average ascent rate (the rate of travel between the end point of bottom time and the end point of the dive) were used to aid in the classification (Wildlife Computers DIVE ANALYSIS Manual). Other variables calculated by DA were average wiggle distance (the average difference in depth between the two inflections of a wiggle), maximum descent rate, and maximum ascent rate. Dive profiles were classified into dive types such that all dives within a group were similar in appearance and had similar values for the variables mentioned above.

*Manual comparison of dive profiles in combination with discriminant function analysis* (MDFA)—A total of 564 dive profiles classified using the manual methods mentioned in the previous section were used as a training set. Discriminant function analysis (two nearest neighbors) with cross-validation was then performed on the dive variables generated by DIVE ANALYSIS. Discriminant function analysis, with two nearest neighbors, classifies observations based on information from the two closest observations in the multidimensional space (dimensions = number of variables). Cross-validation error rates represent the percentage of observations misclassified using discriminant functions created while excluding the observation being classified (DISCRIM Procedure, SAS Institute Inc. 1990). All error rates discussed hereafter are cross-validation error rates. These error rates provide a realistic idea of how well a new data set would be classified by the discriminant functions. The error rates indicate whether the manually determined dive types were valid for the data. A high error rate for a particular group indicates that the group is not valid because a large proportion of the dives manually classified into that group were placed (misclassified) into other groups by the discriminant function analysis. The error rates do not directly determine which groups are appropriate for the observed behavior, but whether or not the observations in a given group were classified correctly given the variables used to create the discriminant functions. Groups with high error rates were merged into the groups most often selected by discriminant function analysis when they were misclassified. Once adequate dive types were created (*i.e.,* low error rates), discriminant functions were calculated using the variables from the classified data set (training set) and the whole unclassified Weddell seal data set was subsequently classified using these discriminant functions.

*Statistical techniques* (ST)—Multivariate statistical techniques for classifying diving behavior are described in Schreer and Testa (1995), and a similar approach for diving bouts in antarctic fur seals is described in Boyd *et al.* (1994). Briefly, several different types of multivariate techniques used in grouping observations were tested to see which would be the most appropriate for classifying Weddell seal dives: principal components analysis, discriminant function analysis, and cluster analysis.

*Comparison of dive profiles to geometric shapes* (GEO)—Standardized dive profiles (maximum depth equal to one, and other depths scaled less than one) were compared to five simple geometric shapes with the equation

$$S_{gn} = \Sigma(d_g \cdot d_n)/\mathrm{sqrt}(\Sigma d_g^2 \cdot \Sigma d_n^2) \qquad (1)$$

where $d_g$ equals the depth of the geometric shape at time $t_n$, and $d_n$ equals the depth of the dive profile at time $t_n$ (Johnson and Wichern 1992). $S_{gn}$ equals the similarity of a dive profile to a shape or cos $(\theta)$ between the vectors representing the geometric shape and the shape of the dive profile. Each dive was compared to a geometric shape that had a maximum depth equal to one and a duration equal to that of the dive profile. A dive was thereby classified according to its similarity to a respective geometric shape. This was achieved by selecting the maximum value of $S_{gn}$ for the five geometric shapes (Fig. 1), where a value of 1 indicated a perfect fit. The five original geometric shapes are shown in Fig. 1A and, after some practical modifications, in Fig. 1B. Some of the original simple shapes needed to be modified because they represented impossible behavior. For example, for a truly square dive to occur, the seal would need to dive from the surface to the maximum depth of the dive in zero seconds. Obviously, this is impossible and, therefore, descent and ascent phases of the appropriate shapes (square, skewed right, and skewed left shapes) were replaced with periods taking 25% of the dive duration between maximum depth and

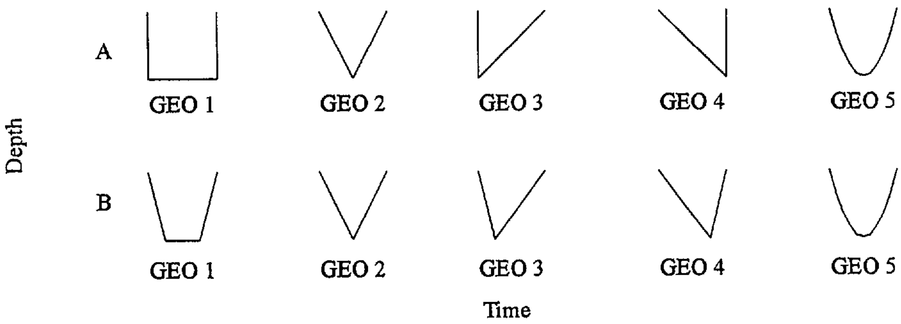


*Figure 1.* Geometric shapes used in the geometric shape classification method. (A) Initial geometric shapes. (B) Modified geometric shapes after substituting average descent and ascent periods lasting 25% of the dive duration for unrealistic infinite rates.

surface. Inspection of dive profiles indicated that a bottom phase lasting for 50% of the dive duration was common for square dives, and descent periods three times longer than ascent periods were commonly observed for skewed left dives (the converse was also observed for skewed right dives). The square shape in this method is now a trapezoid, but it will still be referred to as "square" to remain consistent with the other methods and because trapezoid-shaped dives throughout the literature are referred to as square, suggesting only a "square-like" shape and not an exact match with a square.

The parabolic geometric shape (GEO5) was subsequently eliminated from the analysis because the other statistical analyses did not indicate such a group and this dive type was very rare amongst dives manually observed. The final comparison to geometric shapes was conducted with four shapes and allowed more direct comparisons with the other methods.

Dives from each classification method were pooled into square, triangular, skewed left, and skewed right dive types (rectangular dives, discussed below, were not used by the GEO method and the dives indicated as this type by ST and MDFA were merged into square dives) and cross-tabulated to determine overlap across methods (for example, the number of dives that were classified as square by MDFA that were also classified as square by ST and vice versa). A second cross-tabulation was conducted on just MDFA- and ST-determined dive types, allowing rectangular dives (MDFA5 and ST5a, below) to be compared. Dives from each method were pooled into square, triangular, skewed left, skewed right, and rectangular dive types. *Chi*-square statistics were used for all comparisons to test for measures of association.

### *Behavior*

In order to describe the diving behavior and suggest possible functions of the dive types, the classification results from the above methods were combined so as to allow a more manageable and comprehensible interpretation of the behavior. A total of 1,399 dives (3.6% of the total 39,119 dives) was initially analyzed and classified into six dive types. All dives that were indicated as the same dive type by two or three of the methods were placed into that dive type.

The remaining dive profiles were manually inspected and placed into suitable types. Discriminant functions were calculated using 10 equally spaced mean depths for each dive (see Schreer and Testa 1995), maximum depth, duration, and the dive category (six nearest neighbors in DISCRIM Procedure, SAS Institute Inc. 1990). All 39,119 dives were subsequently classified using these discriminant functions.

Mean maximum dive depth, mean duration, and frequency were plotted against date and time, enabling the detection of diel and seasonal patterns within the six dive types and over all dives. Hourly means and frequencies were calculated over a 24-h period for pooled dates during the austral spring and fall (variable light periods) to detect diel trends. Daily means and frequencies were calculated over 365 d for pooled years to detect seasonal trends. Two sample *t*-tests were performed on the diel patterns to detect significant differences between day and night diving behavior. The power of these tests was exaggerated by the large, pooled data set, but relative differences could still be observed. Visual inspection of the dive variables (mean maximum depth, mean duration, and frequency) over time was performed to look for general trends. Utilizing these patterns and comparing the dive types to previous studies of pinniped diving behavior indicated different behaviors the dive types may represent.

Finally, utilizing location data, dives were further analyzed relative to region to test the validity of some of the proposed functions for the six dive types. Determination of locations was described in Testa (1994). Briefly, SLDTRs with a transmission power of 1 W were linked with orbiting Tiros-NOAA satellites every three days. These transmissions were used by Service Argos to calculate the position of the transmitter (Fancy *et al.* 1988). Only locations with spatial resolution with a standard deviation less than 1.5 km (Argos location code ≥ 1) were used in the analyses. The study area was divided into five regions (Fig. 2): 0, coastal region north of Ross Island but south of 77.25°S; 1, Erebus Bay east of 166.6°E; 2, west of area 1 to the middle of McMurdo Sound at 166°E; 3, central and western McMurdo Sound (west of 166°E); 4, all locations north of 77.25°S (Testa 1994). Merging archived depth data and satellite-determined locations, dives occurring one day before and after the day of a known location were placed into the corresponding region. This allowed 24,299 (62%) of the dives to be analyzed relative to location.

## Results

Approximately 5,000 of the 39,119 dives were classified into nine groups by purely manual inspection of dive profiles. The full set of dives were classified into seven groups by manual inspection aided by discriminant function analysis (MDFA), six groups by a two-stage cluster analysis (ST), and four groups by comparison to simple shapes (GEO). There was considerable variation in mean depth and duration across dive types (Table 1), ranging from 60 ± 56 m to 339 ± 107 m and 8.3 ± 3.8 min to 31.0 ± 5.7 min. Means across all dives were 212 ± 117 m and 15.4 ± 6.2 min with maximums of 726 m and 78 min.

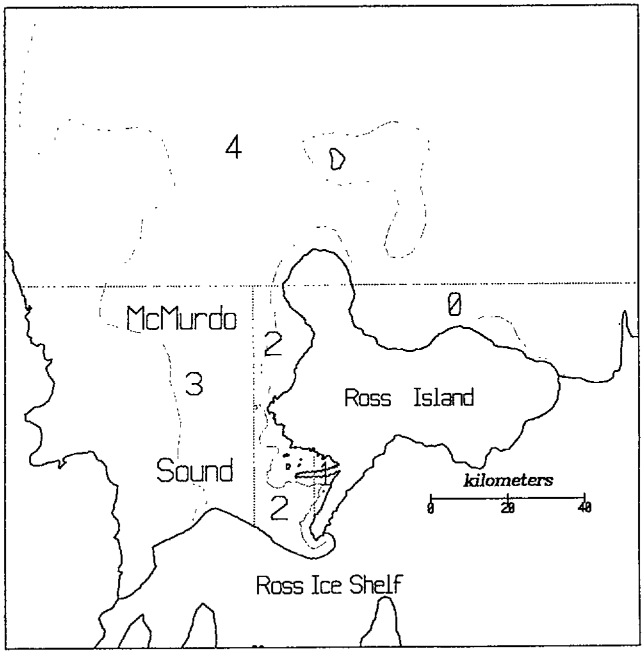


*Figure. 2.* Map of the western Ross Sea, Antarctica, showing the five regions used to classify seal locations. The regions are described in the text.

*Table 1.* Mean maximum depths and durations for all dive types.

| Dive type | Number | Mean depth (m) ± SD | Mean duration (min) ± SD |
|---|---|---|---|
| MDFA 1 | 22,891 | 227 ± 102 | 16.7 ± 4.9 |
| MDFA 2 | 4,884 | 339 ± 107 | 14.2 ± 3.6 |
| MDFA 3 | 2,188 | 138 ± 73 | 15.8 ± 6.4 |
| MDFA 4 | 1,473 | 120 ± 66 | 10.6 ± 5.0 |
| MDFA 5 | 1,737 | 60 ± 56 | 16.5 ± 5.9 |
| MDFA 6 | 1,031 | 273 ± 100 | 31.0 ± 5.7 |
| MDFA 7 | 4,915 | 118 ± 50 | 8.3 ± 3.8 |
| ST 1 | 14,610 | 258 ± 108 | 16.7 ± 5.6 |
| ST 2 | 8,107 | 241 ± 131 | 14.6 ± 6.4 |
| ST 3 | 5,408 | 167 ± 89 | 17.7 ± 5.9 |
| ST 4 | 4,549 | 153 ± 100 | 13.4 ± 6.6 |
| ST 5a | 2,742 | 80 ± 51 | 17.6 ± 6.3 |
| ST 5b | 3,703 | 198 ± 69 | 17.7 ± 5.2 |
| GEO 1 | 23,477 | 212 ± 109 | 17.1 ± 5.6 |
| GEO 2 | 7,578 | 255 ± 141 | 14.0 ± 6.2 |
| GEO 3 | 5,410 | 193 ± 102 | 17.1 ± 6.5 |
| GEO 4 | 2,654 | 139 ± 92 | 12.9 ± 6.6 |
| Overall | 39,119 | 212 ± 117 | 15.4 ± 6.2 |

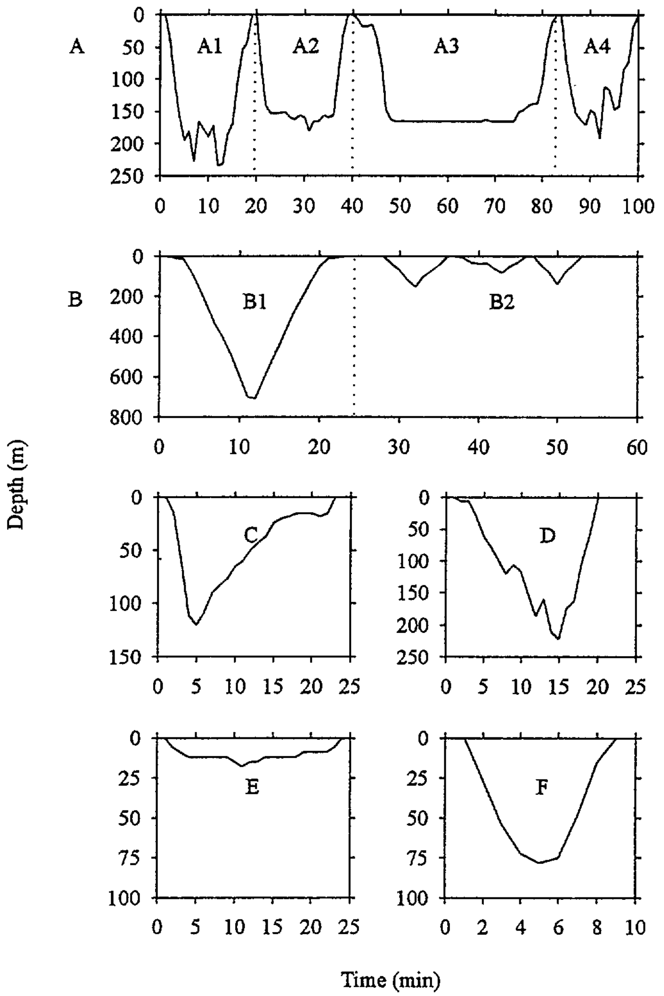


*Figure 3.* Examples of Weddell seal dive profiles. Dive profiles are plotted from time-depth recorder data recorded every 60 sec. Four dive types common to all methods are: (A) square, (B) triangular, (C) skewed right, and (D) skewed left. Rectangular shaped dives (E) were indicated by manual/discriminant function analysis and cluster analysis. Parabolic shaped dives (F) were observed manually but were thought to be variations of square and triangular dives. Time-depth recorder data collected from 15 adult female Weddell seals in McMurdo Sound, Antarctica, during 1986, 1990, and 1991.

## *Dive Classification*

*Manual comparison of dive profiles*—The shape of the dive profiles (depth *vs.* time) was used initially for manually separating the dives, and maximum depth, duration, bottom time, wiggle count, and ascent and descent rates were used to further separate the dives. Dives observed were classified into nine different dive types (Fig. 3). The main shapes were square dives (A), triangular dives (B), skewed right dives (C), skewed left dives (D), rectangular dives with shallow depth and long duration (E), and parabolic dives (F). Dives types A1 and A2 (Fig. 3) were not separated by this analysis and were indicated as one dive type (*i.e.,* the cluster analysis method determined A2 to be a separate dive type). The square dives were further divided into three groups: (1) rigidly square dives with large numbers of wiggles (A1 and A2); (2) loosely square dives (A4); and (3) square dives with long durations, long bottom times, and few wiggles (A3). Triangular dives were further divided into less than 200 m (B2) and greater than 200 m (B1). All of these additional divisions were indicated by patterns observed during manual inspection of the dive profiles.

*Manual comparison of dive profiles in combination with discriminant function analysis* (MDFA)—Discriminant function analysis was performed on 564 dives classified using the manual classification method (nine dive types with types A1 and A2 representing one type) (Fig. 3). Initially, the variables produced directly from DIVE ANALYSIS (maximum depth, duration, bottom time, wiggle count, average wiggle distance, average descent and ascent rate, and maximum descent and ascent rate) were used to create the discriminant functions. This produced a total error rate (mean of error rates for all dive types) of 48% with most of the error occurring when dives from dive type A4 (70%), type D (68%), and type F (61%) were classified.

Total error rate was reduced by manipulating the variables produced by DIVE ANALYSIS to better represent the dive types manually proposed. Two different relative bottom times were used instead of bottom time. Relative bottom time 1 was bottom time divided by dive duration and relative bottom time 2 was bottom time divided by maximum depth. These relative bottom times proved more useful in classifying dives, because dives with the same bottom time may have very different shapes (*e.g.*, long, deep dives with small proportions of bottom time [triangular] *vs.* shallow, short dives with high proportions of bottom time [square]). By using the new relative bottom times we were better able to distinguish dives by shape. Average descent and ascent rates were replaced by the quotients of average descent rate divided by average ascent rate, and average ascent rate divided by average descent rate, respectively. These new variables were useful in detecting skewed dives. Average wiggle distance, maximum descent and ascent rates did not improve the resolving power of the discriminant functions and were excluded. The final set of variables used to create the discriminant functions were maximum depth, duration, wiggle count, relative bottom time 1, relative bottom time 2, average descent rate divided by average ascent rate, and average ascent rate divided by average descent rate.

Discriminant function analysis performed on the new variables produced a total error rate of 42%, with dive types A4 (68%) and F (65%) accounting for much of the error. These two dive types were excluded and the dives within these groups were placed into the next most appropriate group (*e.g.*, most of the type A4 dives were reclassified into the dive type encompassing A1 and A2). Discriminant function analysis with seven dive types produced a total error rate of 14%. This value was much more acceptable and all other dive types seemed to be sufficiently different from one another. Dive types A1/A2 and

A3 were similar in appearance and might have been combined, but the error rates for these dive types were very low (9% and 0%, respectively).

Inspection of the variables (maximum depth, duration, relative bottom time 1, relative bottom time 2, average ascent rate divided by average descent rate, and average descent rate divided by average ascent rate) associated with the misclassified dives (dives indicated as one type by manual inspection and classified as a different type by discriminant function analysis) suggested more specific criteria for classifying the dives (*e.g.*, instead of separating triangular dives; B in Fig. 3) by a maximum depth of approximately 200 m, these dives were now separated by a maximum depth of 180 m and a duration of 10 min). All dives were reclassified with the more rigorous manual classification method. Discriminant function analysis performed on the reclassified dives (seven dive types aided by variable information from misclassified dives) produced a total error rate of 6%. Dive type E accounted for much of the error (23% of the dives manually classified as this type were misclassified by discriminant function analysis), but removing the group increased the total error rate to 7%, so it was left as a dive type. The classification method using seven dive types was used to create discriminant functions that classified the entire Weddell seal data set. Using this procedure, 39,119 dives were classified into seven dive types (Table 2). Comparing Table 2 to Fig. 3 indicates dive type MDFA1 = A1, A2, and A4; MDFA2 = B1; MDFA3 = C; MDFA4 = D; MDFA5 = E; MDFA6 = A3; and MDFA7 = B2. Mean maximum depths and durations for these dive types are shown in Table 1.

*Statistical techniques* (ST)—Cluster analysis aided by discriminant function analysis was found to be the most useful in determining the number of dive types and classifying the recorded dives. This was the only technique able to categorize the data, as well as determine an appropriate number of dive types for the data set using $R^2$ values, pseudo $F$-statistics, and cross-validation error rates (Schreer and Testa 1995). Five dive types were determined for the data by the first cluster analysis performed on 10 mean depths for each dive (dive types 1–5, Table 2). Type ST 5 dives were further classified into two groups, the first group having very long durations relative to maximum depth and the second group having short durations relative to maximum depth. Statistically classifying diving behavior resulted in six dive types (Table 2). Comparing Table 2 to Fig. 3 indicates dive type ST1 = A1, A3, and A4; ST2 = B1 and B2; ST3 = C; ST4 = D; ST5a = E and A3; and ST5b = A2 and A3. Mean maximum depths and durations for these dive types are shown in Table 1.

*Comparison of dive profiles to geometric shapes* (GEO)—A total of 39,119 dives was originally classified into five geometric shapes (Fig. 1) resulting in 47% type GEO 1 dives, 13% type GEO 2, 14% type GEO 3, 7% type GEO 4, and 20% type GEO 5 dives. After excluding parabolic-shaped dives (GEO 5), the dives were classified into four shapes (Table 2). Comparing Table 2 to Fig. 3 indicates dive type GEO1 = A, GEO2 = B, GEO3 = C, and GEO4 = D. Mean maximum depths and durations for these dive types are shown in Table 1.

Results of all the two-way cross-tabulation tables are too lengthy to present

*Table 2.* Frequency distribution of dive types within each method and over common dive types. Rectangular (long duration) dives were pooled with square dives for the comparison of four common dive types.

| Manual comparison + Discriminant function analysis | | Cluster analysis | | Geometric shapes | |
|---|---|---|---|---|---|
| Dive type | Percent dive type | Dive type | Percent dive type | Dive type | Percent dive type |
| MDFA1 | 58% | ST1 | 37% | GEO1 | 60% |
| MDFA2 | 12% | ST2 | 21% | GEO2 | 19% |
| MDFA3 | 6% | ST3 | 14% | GEO3 | 14% |
| MDFA4 | 4% | ST4 | 12% | GEO4 | 7% |
| MDFA5 | 4% | ST5a | 7% | | |
| MDFA6 | 3% | ST5b | 9% | | |
| MDFA7 | 13% | | | | |
| Dive types common across methods | | | | | |
| Square | 61% | | 46% | | 60% |
| Triangle | 25% | | 21% | | 19% |
| Skewed right | 6% | | 14% | | 14% |
| Skewed left | 4% | | 12% | | 7% |
| Rectangular | 4% | | 7% | | |

here, but some key cells will be mentioned. Cross-tabulation of the four dive types indicated that the strongest overlap between classification methods occurred within square dives (72% to 93%). Triangular dives had less overlap (51% to 72%), and depending on the direction of the tabulation (row to column or column to row), the skewed dives showed both strong and weak overlap (26% to 94%). The total overlap across methods was 68% for MDFA and ST, 75% for MDFA and GEO, and 78% for ST and GEO. The second cross-tabulation of just MDFA and ST dive types using five common dive types had a total overlap of 63%, although there was little overlap between rectangular dive types (MDFA5 with ST5a, 40%; and ST5a with MDFA5, 25%). *Chi*-square statistics

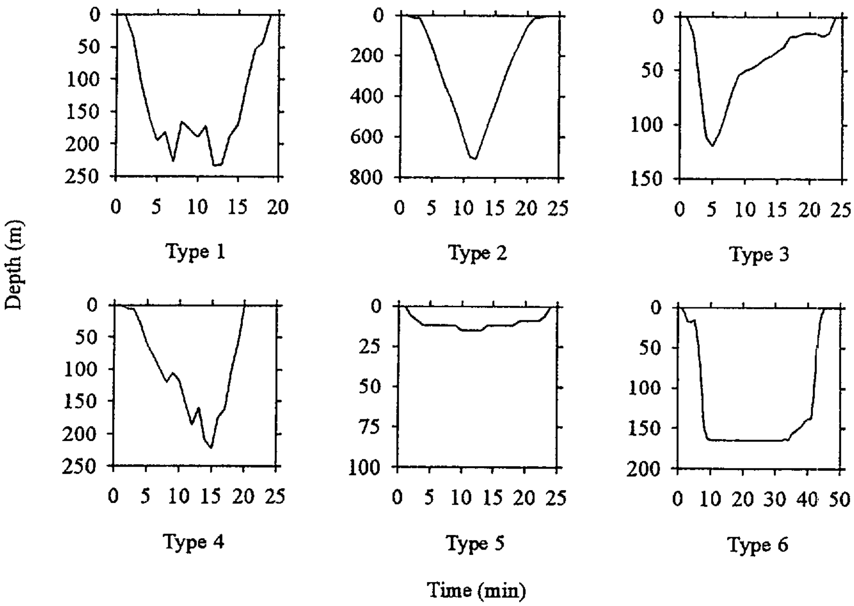


*Figure 4.* Examples of six types of Weddell seal dive profiles. Dive profiles are plotted from time-depth recorder data recorded every 60 sec. Time-depth recorder data collected from 15 adult female Weddell seals in McMurdo Sound, Antarctica, during 1986, 1990, and 1991.

indicated that dive types across all methods were strongly associated ($P < 0.0001$).

### *Behavior*

There were four dive types common to all methods (MDFA, ST, and GEO), and a fifth dive type common to two of the methods (MDFA and ST), which represented most of the observed behavior (98%). However, a sixth dive type determined manually and not rejected by MDFA may have also represented important behavior. Examples of the six dive types are shown in Fig. 4. Of the 1,399 dives used as the training set for the discriminant function analysis, 93% were indicated as a similar dive type by at least two of the methods. The remaining 7% of the dives were placed manually into groups. The total cross-validation error rate produced by discriminant function analysis was only 7.7%. Also, dives misclassified were almost always placed into a group that had been indicated by one of the methods.

The 39,119 dives classified into six groups resulted in 41% type 1 dives, 24% type 2 dives, 13% type 3 dives, 10% type 4 dives, 10% type 5 dives, and 2% type 6 dives. There was considerable variation in mean maximum depth and duration across dive types (Table 3), ranging from 97 ± 63 m to 285 ± 83 m and 12.9 ± 6.0 min to 30.1 ± 4.9 min. There was strong diel variation in mean maximum depth and mean duration over the 20,892 dives occurring

*Table 3.* Basic dive statistics for all dive types.

| Dive type | Number | Depth (m) | | Duration (min) | |
|---|---|---|---|---|---|
| | | Mean ± SD | Maximum | Mean ± SD | Maximum |
| 1 | 16,049 | 245 ± 100 | 627 | 16.5 ± 4.7 | 46 |
| 2 | 9,561 | 241 ± 138 | 726 | 12.9 ± 6.0 | 50 |
| 3 | 5,035 | 178 ± 90 | 723 | 17.0 ± 6.1 | 61 |
| 4 | 3,954 | 150 ± 92 | 723 | 12.9 ± 6.6 | 78 |
| 5 | 3,816 | 97 ± 63 | 549 | 15.2 ± 6.1 | 56 |
| 6 | 704 | 285 ± 83 | 531 | 30.1 ± 4.9 | 56 |
| Overall | 39,119 | 212 ± 117 | 726 | 15.4 ± 6.2 | 78 |

in the spring and fall ($P < 0.0001$) (Fig. 5A, B). For all dive types, significantly deeper dives occurred during the day than at night ($P < 0.007$). Type 1 and 2 dives showed the strongest diel variation, type 5 and 6 dives showed the weakest, and type 3 and 4 dives were intermediate (Fig. 6). All dive types were also significantly longer during the day than at night ($P < 0.0003$). Again, type 1 and 2 dives showed the strongest diel variation, type 5 and 6 dives showed the weakest, and type 3 and 4 dives were intermediate. The trend in dive frequency was a peak around 1800 and a larger peak around 0600 (Fig. 5C). Diel variation in dive frequency was more variable across dive types (Fig. 7). Type 1 and 2 dives were most frequent from 0600 to 1800 with a slight decrease in dive frequency around 1500. Type 3, 4, and 5 dives were most common around 0600 and 2100 with absolute lows around noon. Type 6 dives showed weaker and more variable trends in dive frequency with a low around 1600. Manual observations of the temporal placement of the various dive types indicated that type 1, 5, and 6 dives often occurred in bouts and type 2 dives often occurred just prior to or during bouts of these dive types. Also, type 4 dives often preceded bouts of type 1 dives, while type 3 dives often followed these bouts.

Seasonal trends were less apparent because large portions of the year were not represented (*e.g.*, most of spring) (Fig. 8A, B). The trend for mean maximum depth over all dives showed deeper dives during the summer. There was also

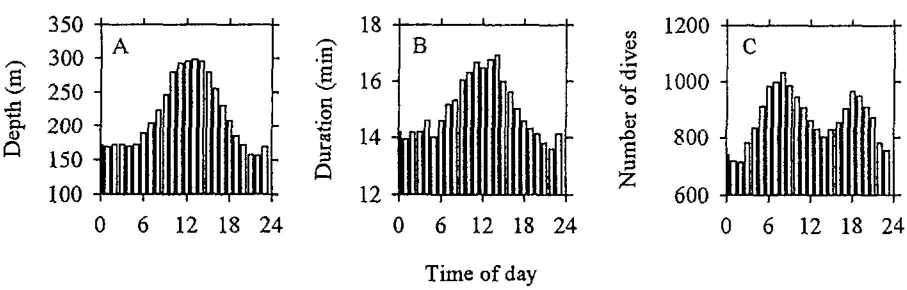


*Figure 5.* Mean maximum depth (A), mean duration (B), and frequency (C) of dives occurring in spring and fall. Time-depth recorder data collected from eight adult female Weddell seals in McMurdo Sound, Antarctica, during 1986, 1990, and 1991.

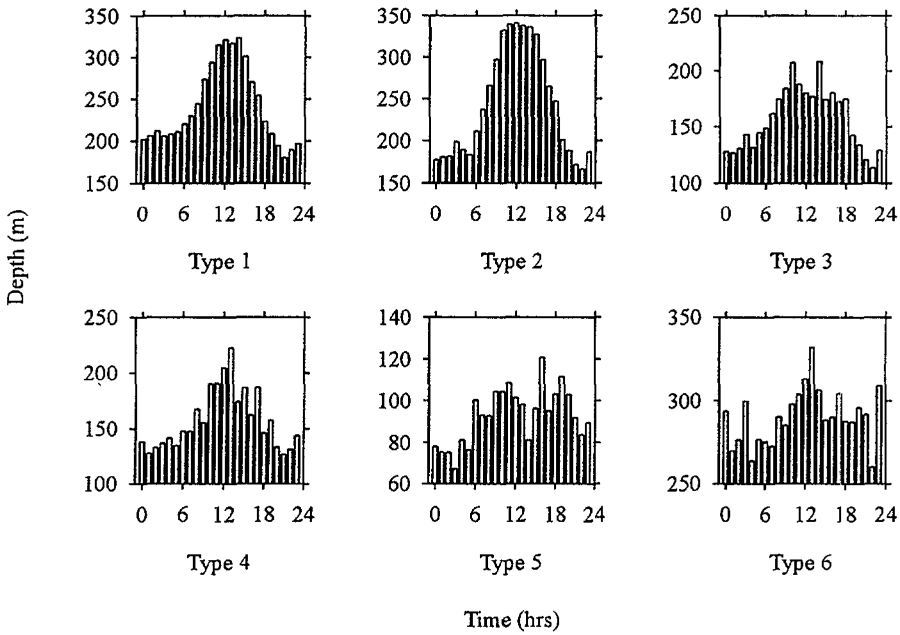


*Figure 6.* Diel variation in mean maximum depth for all six types of dive profiles occurring in spring and fall. Time-depth recorder data collected from eight adult female Weddell seals in McMurdo Sound, Antarctica, during 1986, 1990, and 1991.

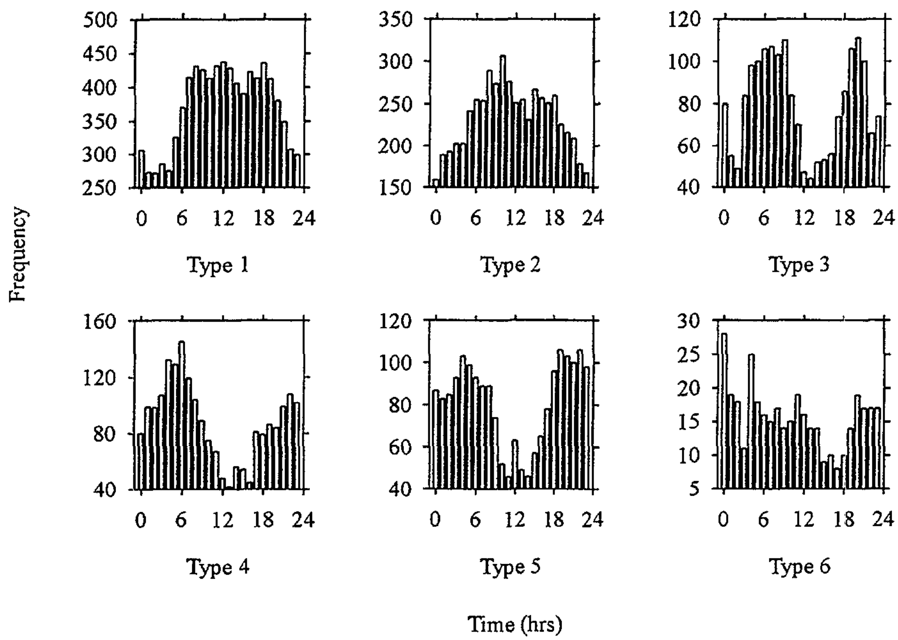


*Figure 7.* Diel variation in dive frequency for all six types of dive profiles occurring in spring and fall. Time-depth recorder data collected from eight adult female Weddell seals in McMurdo Sound, Antarctica, during 1986, 1990, and 1991.

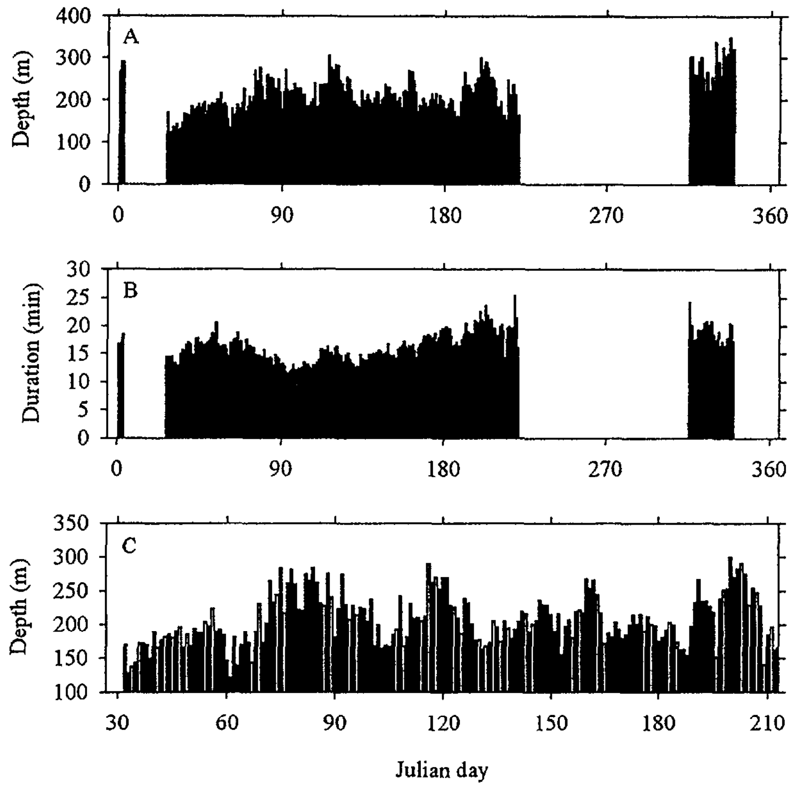


*Figure 8.* Daily mean variation in maximum depth and duration. (A) Daily mean maximum depths of all dives. (B) Daily mean durations of all dives. (C) Daily mean maximum depths from 1991 data (33,328 dives). Time-depth recorder data collected from 15 adult female Weddell seals in McMurdo Sound, Antarctica, during 1986, 1990, and 1991.

an oscillation between deep and shallow dives for the 1991 data that had a period of approximately 30 d, suggesting a lunar cycle (Fig. 8C). Daily mean maximum depths were significantly deeper during the periods around a full moon than those around a new moon ($P < 0.001$). All dive types, except type 6, showed a trend towards deeper dives during the summer, with a smaller peak around midwinter. Type 6 dives showed only the midwinter peak in mean maximum depth, although the pattern was very weak. Daily mean duration over all dives showed a trend for longer dives during the early summer, early fall, and late winter (remembering that the midsummer dives were not represented in the dive data). A steady increase in dive duration was also seen as the winter progressed, starting with a minimum in mid-fall and a maximum in late winter (Fig. 8B). All dive types, except type 6 which showed no discernable pattern, also showed a steady increase in dive duration as the winter progressed, with a peak in early summer. Daily proportions of dive types plotted against date were highly variable across dive types. Type 1 and 2 dives showed a peak in early summer and several peaks throughout the winter; type 3, 4, and 5 dives showed a winter peak and a late summer peak, and type 6 dives showed peaks in late summer and midwinter. Again, patterns were incomplete due to portions of the year not being represented.

The 24,299 dives for which locations could be determined were placed into five regions (Table 4, Fig. 2). There was considerable variation in the number of dives occurring in each region, with Region 1 being most frequently used (33%) followed by Region 4 (22%), Region 2 (19%), Region 3 (16%), and Region 0 (10%). Most dive types followed a similar pattern except type 3, which occurred at considerably higher numbers in Region 4 (36%), and type 6, which predominantly occurred in Region 1 (74%).

## Discussion

### *Dive Classification*

It is possible to classify diving behavior with several different methods. The validity of the various methods was substantiated by the similarities in dive classifications. Common dive types identified by all methods were square dives, triangular dives, skewed left and right dives, and dives with long durations relative to maximum depth (not in GEO). Pooling dives within each classification method into the four and five common dive types (*e.g.*, ST1 and ST5b into square dives) resulted in similar frequency distributions across all methods. Square dives generally were most abundant, followed by triangular dives, and then the other dive types. Differences in frequency of common dive types occurred because of the variation in sensitivity to different parameters across methods. Cluster analysis was more sensitive than manual/discriminant function analysis to skewness in triangular and square dive profiles, while analysis by geometric comparisons indicated that right-skewed dives were more skewed than left-skewed dives (*i.e.*, had a greater difference between descent and ascent rates). The lower frequency of square dives indicated by cluster analysis was due to the method's greater sensitivity to skewness.

These conclusions were substantiated by the results of the two-way cross-tabulation tables where *Chi*-square values indicated high overall associations across methods. Inspection of individual cells within the tables showed that only 72% of the square dives indicated by MDFA were also indicated as square by ST, while the converse relationship resulted in 88% overlap. This is consistent with the larger number of square dives indicated by MDFA and the higher sensitivity of ST to skewed dives, resulting in fewer square dives and more skewed dives. MDFA-determined skewed dives overlapped with ST-determined dives more than 80% of the time, while only approximately 30% of the ST-determined skewed dives were also indicated as skewed by MDFA. Cross-tabulation with dives from the GEO method indicated similar results. The cross-tabulation of five common dive types between MDFA and ST indicated similar results to those above for the first four common dive types, but had little overlapping across the rectangular dive types. The results of the cross-tabulation tables (four dive types) indicated that there was considerable overlap across

*Table 4.* Basic dive statistics for all dive types relative to region. The regions are described in the text.

| Dive type | | Region 0 | Region 1 | Region 2 | Region 3 | Region 4 | Overall |
|---|---|---|---|---|---|---|---|
| 1 | N (Row%/Col%) | 892 (9/39) | 3,114 (31/39) | 2,375 (23/51) | 1,509 (14/40) | 2,361 (23/43) | 10,281 (42) |
| | Depth ± SD | 259 ± 106 | 233 ± 99 | 270 ± 101 | 221 ± 103 | 216 ± 69 | 238 ± 97 |
| | Duration ± SD | 18.8 ± 5.2 | 16.2 ± 4.8 | 16.2 ± 4.7 | 13.2 ± 4.0 | 16.2 ± 3.6 | 16.3 ± 4.7 |
| 2 | N (Row%/Col%) | 517 (9/22) | 1,765 (31/22) | 1,203 (21/26) | 1,229 (21/32) | 1,051 (18/19) | 5,765 (24) |
| | Depth ± SD | 235 ± 133 | 216 ± 126 | 263 ± 136 | 261 ± 148 | 208 ± 132 | 236 ± 136 |
| | Duration ± SD | 13.3 ± 7.1 | 13.2 ± 5.7 | 13.3 ± 5.3 | 11.2 ± 4.1 | 11.5 ± 6.4 | 12.5 ± 5.7 |
| 3 | N (Row%/Col%) | 271 (9/12) | 935 (32/12) | 354 (12/7) | 339 (11/9) | 1,057 (36/19) | 2,956 (12) |
| | Depth ± SD | 191 ± 110 | 147 ± 89 | 173 ± 95 | 157 ± 77 | 190 ± 81 | 171 ± 90 |
| | Duration ± SD | 17.7 ± 7.5 | 16.7 ± 6.6 | 16.6 ± 6.6 | 13.3 ± 5.0 | 16.9 ± 5.3 | 16.5 ± 6.2 |
| 4 | N (Row%/Col%) | 256 (11/11) | 951 (38/12) | 373 (15/8) | 401 (16/11) | 508 (20/10) | 2,489 (10) |
| | Depth ± SD | 194 ± 111 | 146 ± 89 | 142 ± 81 | 139 ± 91 | 143 ± 86 | 149 ± 92 |
| | Duration ± SD | 16.1 ± 8.7 | 13.5 ± 6.2 | 12.0 ± 5.6 | 10.4 ± 5.6 | 12.3 ± 6.6 | 12.8 ± 6.6 |
| 5 | N (Row%/Col%) | 300 (13/13) | 911 (39/11) | 324 (14/7) | 308 (13/8) | 476 (21/9) | 2,319 (10) |
| | Depth ± SD | 106 ± 59 | 78 ± 58 | 111 ± 66 | 105 ± 48 | 116 ± 60 | 98 ± 61 |
| | Duration ± SD | 19.1 ± 7.0 | 14.3 ± 5.4 | 15.0 ± 6.6 | 10.7 ± 3.6 | 16.3 ± 5.2 | 14.9 ± 6.0 |
| 6 | N (Row%/Col%) | 81 (17/3) | 360 (74/4) | 36 (7/1) | 3 (0/0) | 9 (2/0) | 489 (2) |
| | Depth ± SD | 324 ± 93 | 275 ± 57 | 293 ± 86 | 254 ± 158 | 300 ± 129 | 285 ± 71 |
| | Duration ± SD | 32.6 ± 5.6 | 29.8 ± 4.7 | 26.6 ± 3.6 | 33.3 ± 7.8 | 30.1 ± 6.1 | 30.0 ± 5.0 |
| Overall | N (Row%) | 2,317 (10) | 8,066 (33) | 4,665 (19) | 3,789 (16) | 5,462 (22) | 24,299 (100) |
| | Depth ± SD | 221 ± 121 | 194 ± 113 | 240 ± 120 | 210 ± 124 | 194 ± 93 | 208 ± 114 |
| | Duration ± SD | 17.7 ± 7.6 | 16.0 ± 6.4 | 15.2 ± 5.6 | 12.1 ± 4.5 | 15.1 ± 5.5 | 15.2 ± 6.1 |

methods (68% to 78%); the discrepancies were caused by differences in sensitivity across classification methods. The high measures of association, the overlap within common dive types and across methods, and the similarities in dive-type frequencies suggest that the four similar dive types represent similar diving behavior. Rectangular dives had little overlap and perhaps should not have been separated from the square dive types. However, a similar dive type had been manually identified previously for Weddell seals (Kooyman 1968) and therefore may represent important behavior. The discrepancies in overlap occurred mostly when MDFA defined a dive as square while ST defined it as rectangular, and when ST defined a dive as skewed while MDFA defined it as rectangular. This is consistent with the higher sensitivity of ST to skewness and the higher sensitivity of MDFA to squareness.

That manual inspection of dive profiles suggested nine dive types, but the statistical methods indicated fewer, suggests three explanations for the dive types missing from the statistical classifications: (1) there were too few examples of the dive types in the data set for specific mathematical rules to be created, (2) the statistical methods are not sufficiently sensitive to classify all the dive types, or (3) these dive types were not sufficiently different from other types. Most likely it was the third, because although there were few MDFA6 dives, this dive type was classified with very few errors by discriminant function analysis, suggesting that it was sufficiently different from all other dive types. The extraneous dive types were probably extreme variations of other groups, but not sufficiently different to be their own group.

Cluster analysis aided by discriminant function analysis (ST) and manual/discriminant function analysis (MDFA) indicated similar dive types, each with some unique variations. The major difference between the two classification methods was that MDFA made more use of maximum depth and duration for separating dives, while ST only used shape until the second cluster analysis split ST5 dives into two groups, using the quotient of maximum depth divided by duration. Thus, a solely statistical analysis (ST) was able to find dive types similar to those found by manual inspection of dive profiles. These conclusions are encouraging for the use of both manual and statistical methods. Results from previous manual categorizations of diving behavior are probably very similar to those that would be found using statistical categorizations. The similarities between manual and statistical categorizations indicate that the statistical techniques are producing biologically valid results (*i.e.*, providing statistical algorithms with a matrix of numbers representing behavior produced similar results to manually identifying the behavior) and, with the added efficiency of statistical techniques (speed and data compression), suggest much potential.

The geometric shape method (GEO) classified dives quickly and statistically, but it was limited to only a few shapes regardless of what the data suggested. Interestingly, dives were grouped in a similar manner compared to the other methods. This simple method is useful in two ways and warrants further study. First, since only simple shapes with slight modifications were used, the method may be useful for quickly classifying an unknown data set without enforcing any previous knowledge from other data sets. This method also showed potential for creating complex dive prototypes (shapes that represent specific behavior) for well-studied species and using these prototypes to classify unclassified diving behavior. This would enable huge data sets (new and old) to be classified very quickly and consistently.

All the classification methods indicated dive types that suggest distinct behaviors, but the statistical methods expedited the process and reduced human bias. Of the methods used in this study, the most promising was found to be cluster analysis. It classified diving behavior quickly and statistically, and had the flexibility to provide different solutions to different problems (*e.g.,* multistage cluster analysis using different variables in each stage or different diving behavior of different animals). Cluster analysis (aided by discriminant function analysis) was also the only method able to determine statistically the number of groups within the data set. However, all methods tested had interesting results and warrant further study. New and/or additional variables (*e.g.*, velocity, shape, etc.) may allow these methods to become more effective at grouping observed bouts of natural behavior.

### *Behavioral Patterns*

Discussions of the patterns in Weddell seal diving behavior must be tentative because of the pooling across individuals and the simplicity of the analyses, although some strong trends were apparent. Other studies (Hindell *et al.* 1991, Testa 1994) have shown that individual variability can be considerable. The overall pattern of deeper dives during the day than at night was consistent with the results for Weddell seals during the summers of 1968, 1969, and 1971 in McMurdo Sound, Antarctica (Kooyman 1975) and further substantiate that vision is an important perceptive modality for navigation and foraging (Wartzok *et al.* 1992). The trend towards deeper dives during full moon periods also suggests this conclusion. The decrease in dive frequency around the midday hours suggests that more time was spent hauled out at this time, preferred foraging times occurred around dawn and dusk, or simply that the longer and deeper dives around midday allowed for fewer dives.

Seasonal trends were much less clear because of the gaps in the data set for many days throughout the year. The trend toward deeper dives during the summer may suggest that Weddell seals were exploiting different food sources, their preferred prey were residing at different depths, or low light levels during the winter were limiting their diving. Weddell seals have been shown to dive deeper during the spring and early summer (350–450 m) than in the late summer (50–200 m) and this was thought to reflect a change in preferred hunting depth (Kooyman 1975), although Testa (1994) found shallow, late-summer diving was performed when seals hauled out over shallower parts of McMurdo Sound. Selective pelagic feeding has been indicated for Weddell seals by the predominance of a single pelagic fish species (*Pleuragramma antarcticum*) in the summer diet during 1985 in the Eastern and Southern Weddell Sea, despite the presence of numerous demersal fish in the water column (Plotz 1986, Plotz *et al.* 1991). Temporal variation in prey availability and prey consumption have been indicated for Weddell seals by the absence of *P. antarcticum* in stomach contents in the spring of 1986, whereas it was the predominant prey species in the summer of 1985 (Plotz *et al.* 1991). Longer dive durations during the spring were expected due to deeper maximum depths, but the steady increase in dive duration as the winter progressed may have indicated that the seals were putting more effort into foraging in order to further build up fat reserves before the summer, or that their diving capacity changes as their condition improves.

*Behavioral Functions of Dive Types*

Square dives have been suggested to represent foraging dives in northern elephant seals (Le Boeuf *et al.* 1988), southern elephant seals (Hindell *et al.* 1991), and crabeater seals (*Lobodon carcinophagus*) (Bengtson and Stewart 1992). Type 1 dives performed by Weddell seals showed strong diel variation in maximum depth, occurred in bouts, and frequently had similar maximum depths within a bout suggesting that these were foraging dives. The strong tendency towards deeper dives during the day may indicate that the seals were pursuing pelagic prey that were exhibiting diel vertical migration. Diel variation in maximum depth has been observed in several air-breathing marine vertebrates including antarctic fur seals (*Arctocephalus gazella*) (Croxall *et al.* 1985, Boyd and Croxall 1992, Boyd *et al.* 1994), northern elephant seals (Le Boeuf *et al.* 1988), macaroni penguins (*Eudyptes chrysolophus*) (Croxall *et al.* 1988), gentoo penguins (*Pygoscelis papua*) (Croxall *et al.* 1988), southern elephant seals (Hindell *et al.* 1991), and crabeater seals (Bengtson and Stewart 1992). The high frequency of square dives in Weddell seal dive records is consistent with the high foraging effort expected for adult female seals building up fat reserves over winter.

Triangular, or spiked dives have been thought to represent predator avoidance (Hindell *et al.* 1991) and exploration (Hindell *et al.* 1991, Bengtson and Stewart 1992). Bengtson and Stewart (1992) suggested that by diving deep below the noise created by shifting ice flows rubbing and grinding against each other, crabeater seals were better able to listen for acoustical cues that could assist them in navigation. Type 2 dives performed by Weddell seals seemed to have a similar, exploratory function like that suggested for crabeater seals, because these dives frequently occurred just prior to and during bouts of type 1 dives (potential foraging dives) and type 5 dives (potential traveling dives, see below). These dives may also allow the seals to get a better visual image of the surroundings, enabling them to navigate more efficiently and detect prey above them. Under-ice photographs taken at depths of 200 m have revealed that light levels reaching these depths could be used to backlight swimming objects (Castellini, personal communication).

Skewed left dives have been thought to represent resting or sleeping underwater, with the period of slow descent representing time when the seal stopped swimming and was slowly sinking (Hindell *et al.* 1991, Le Boeuf *et al.* 1992). This explanation seems plausible for some of the type 4 dives performed by

Weddell seals since there was a slight peak around midwinter, which corresponds to an intense foraging period and perhaps longer intervals between haul-outs. However, the temporal placement of many skewed dives relative to other dives may suggest other explanations. Skewed left dives frequently occurred just prior to bouts of square dives (type 1) and had maximum depths similar to the maximum depths of the following square dives. Type 3 (skewed right) dives frequently followed bouts of square dives and also had maximum depths that were similar to the preceding square dives. These skewed dives may represent seals following the sea floor as they descend away from haul-out or resting sites and subsequently ascend back to the sites. This explanation may only be plausible when haul-out sites occur over shallow water (near land). These dives may also represent a type of exploration in which the seal slowly descends looking for a food source and having found one begins foraging (type 1 dives). The skewed right dives may represent the ending of a foraging bout in which the seal slowly ascends collecting cues for its next move. It is interesting to note that these skewed right dives are most common in the region (Region 4) farthest from the initial haul-out sites in the pack ice, which could suggest that they play a role in navigation under specific conditions, or food processing at the end of successful feeding.

Dives with long durations relative to maximum depth (rectangular) may represent exploratory or traveling dives. Kooyman (1968) suggested that Weddell seal dives greater than 20 min in duration and less than 200 m in maximum depth were exploratory dives which enabled seals to find distant breathing holes. Kooyman (1968) also suggested that these dives may have represented errors in navigation and that the long durations were accidental. In the present study the type 5 dives had shorter durations and often occurred in small bouts, suggesting that the seals were traveling. The calculated aerobic diving limit (ADL) for adult Weddell seals is about 16–20 min (Castellini *et al.* 1992) and is consistent with the 15.2-min mean durations for the type 5 dives occurring in this study. It is energetically more efficient for seals to swim fully submerged rather than near the surface because of the effects of drag (Williams and Kooyman 1985). This suggests that the most efficient way for a seal to travel is to spend as much time underwater as possible without exceeding its ADL. The observed mean duration of approximately 15 min for type 5 dives is consistent with an animal having an ADL of 16–20 min and traveling in an energy-efficient way. The shorter durations of these dives as compared to the exploratory dives (>20 min) found by Kooyman (1968) may have been possible because the dives recorded in this study occurred in pack ice, or well-known fast ice, and not with the intentionally isolated breathing holes in fast ice that were used by Kooyman's study animals.

Type 6 dives had very few or no wiggles, very long bottom times and durations, and weak diel variation in mean maximum depth and duration relative to type 1 dives. These dives may represent benthic foraging and are similar to dives purported to be benthic for southern elephant seals (Hindell *et al.* 1991) and northern elephant seals (Le Boeuf *et al.* 1992). The weak diel variation in maximum depth and duration are consistent with an animal foraging for a food source that does not exhibit vertical movements. The presence of benthic prey items in stomach contents (Plotz *et al.* 1991) and the increase in jaw movements at maximum dive depths (Bornemann *et al.* 1992) suggest that Weddell seals dive to the bottom and ingest prey in this area. Type 1 square dives were most likely typical pelagic foraging dives with long bottom times, wiggles, and strong diel variation in maximum depth. Type 1 dives were much more common than type 6 dives (41% and 2%, respectively) and are likely to be ecologically more important. The predominance of type 6 dives at two short time periods during late summer and midwinter suggest that these benthic dives only occur under specific conditions, most likely when the seals are foraging in relatively shallow waters (Testa 1994). The occurrence of almost all of these dives in coastal regions (91%: 17% in Region 0 and 74% in Region 1) clearly supports this conclusion.

These analyses have shown that it is possible to categorize Weddell seal diving behavior with several different methods that suggest possible first steps towards modelling diving behavior. The functional analyses of Weddell seal dive types indicated several patterns that may represent ecologically important behavior for these animals. However, the hypothesized functions of the dive types were highly speculative due to the limitations of the data (depth and time) and the methods which were built on largely non-biological assumptions. With recent advances in the study of diving behavior (*e.g.,* velocity meters, jaw sensors, and video cameras), new variables and information will aid our further understanding of the relationship of diving behavior to the ecology of marine mammals.

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