



## Comparative Diving Patterns of Pinnipeds and Seabirds

Jason F. Schreer; Kit M. Kovacs; R. J. O'Hara Hines

*Ecological Monographs*, Vol. 71, No. 1 (Feb., 2001), 137-162.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9615%28200102%2971%3A1%3C137%3ACDPOPA%3E2.0.CO%3B2-N>

*Ecological Monographs* is currently published by The Ecological Society of America.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

## COMPARATIVE DIVING PATTERNS OF PINNIPEDS AND SEABIRDS

JASON F. SCHREER,<sup>1,3</sup> KIT M. KOVACS,<sup>1,4</sup> AND R. J. O'HARA HINES<sup>2</sup>

<sup>1</sup>Department of Biology, University of Waterloo, Waterloo, Ontario, Canada N2L 3G1

<sup>2</sup>Department of Statistics and Actuarial Science, University of Waterloo, Waterloo, Ontario, Canada N2L 3G1

**Abstract.** General ecological information resulting from modern dive studies has been limited because analyses and conclusions are study- and species-specific. In this work, a series of unrelated divers was studied and compared using the same analytical procedures. More than 230 000 dives from 12 species were analyzed, and ~140 000 of these dives were classified according to dive shape. The species included one cormorant, three penguins, two eared seals, five true seals, and a walrus. Dive profiles could generally be characterized as one of four shapes: square, V, skewed right, or skewed left. In light of this, a universal shape classification protocol was developed that also offers potential solutions for “on board” memory limitations and transmission constraints for archival time–depth recorders and satellite-linked time–depth recorders. Comparisons of dive data recorded with different sample intervals indicated the need for a standardization relative to mean dive duration (i.e., an equal number of data points per dive). Comparative analyses across these dive types and the different species revealed that square dives were always, and by far, the most abundant dive type, usually followed by V dives, and then the skewed dives. The percentage of time that the animals spent at the bottom of square dives (~50%), as well as the variation in depth during this bottom time (~15%) were also quite uniform across species, indicating that similar foraging patterns were being used, at least relative to the shape of dives. Observed differences across species revealed that larger divers generally dived deeper and longer than did smaller ones, although fur seals and walrus were exceptions, with more limited diving performance than expected based on body size. Also, smaller divers had a tighter coupling between dive depth and duration than did larger ones, indicating that they may be more duration limited. Few other dive variables (e.g., the rate at which dive duration increases with depth, the percentage of dives within each dive type, the percentage of bottom time, the coefficient of variation of depth during bottom time, and the mean wiggle distance per depth during square dives) were affected by body size, but instead physical (water depth) and ecological (type of prey) constraints appeared to play major roles. Analyses using calculated aerobic dive limit (cADL) indicated that generic calculations are problematic and that estimates of diving metabolic rate can drastically influence cADL and resultant findings. However, even using crude estimators, comparisons of cADL across dive types indicated that square dives and V dives most often exceeded the cADL for large and small divers, respectively. This indicates that square dives and V dives may be the predominant foraging dive types for larger and smaller divers, respectively, as animals would be expected to push their limits most during this activity. However, the abundance of square dives within the small divers (>60%) indicates that these dives may have a foraging role as well. Functional analyses of the determined dive types were in general agreement with those from previous work indicating that the various dive types have foraging (benthic and pelagic), traveling, exploring, resting, and processing functions. However, for most species, except Weddell seal and southern elephant seal (rare but likely important), skewed dives were rare and are likely to be of little importance to these animals' diving regimes. Overall similarities in the dive patterns of the various species suggest that these animals exploit the aquatic environment in a similar way.

**Key words:** *calculated aerobic dive limit; dive profile; dive shape; functional analysis; fur seal; penguin; quantitative analysis; seabird; seal; time–depth recorder; universal classification method.*

### INTRODUCTION

Although aquatic mammals and birds breathe air, many spend a considerable amount of time underwater

Manuscript received 30 November 1998; revised 26 August 1999; accepted 19 October 1999; final version received 20 December 1999.

<sup>3</sup> E-mail: jfschree@sciborg.uwaterloo.ca

<sup>4</sup> Present address: Norwegian Polar Institute, 9005 Tromsø, Norway.

performing functions such as traveling, foraging, and food processing. To understand the ecology of these animals, one must study their underwater behavior. Many studies of diving behavior have utilized some sort of time–depth recorder (TDR) and have primarily grouped dives subjectively, according to perceived similarities in maximum depth and duration (e.g., Kooyman 1968, Croxall et al. 1991, Chappell et al. 1993a). It is perhaps inappropriate to base classification

analyses solely on the combination of maximum depth and duration because both of these variables may display strong diel variation (e.g., Bengtson and Stewart 1992, Boyd et al. 1994, Schreer and Testa 1996) that can obscure the determination of behavioral groupings. For example, an animal may perform similar behavior (e.g., foraging) at different times of day. If its prey migrate vertically, the animal under study will forage at different depths throughout the day depending on the location of its prey. Therefore, even though the shape of a dive (depth vs. time) may remain similar (due to optimizing time at the prey patch) and may indicate comparable behavior, depth and duration could vary drastically.

Several studies have included dive shape as a means of grouping diving behaviors (e.g., Le Boeuf et al. 1988, 1992, Hindell et al. 1991*b*, Bengtson and Stewart 1992, Schreer and Testa 1993, 1995, 1996, Jonker and Bester 1994, Brillinger et al. 1995, Campagna et al. 1995, Schreer et al. 1995, 1998, Brillinger and Stewart 1997, Burns et al. 1997, Burns and Schreer, *in press*). Many of these works have relied solely or primarily on subjective comparisons of dive profiles, which introduces human bias and reduces reproducibility. A few studies have attempted quantitative classification of diving patterns (Hindell et al. 1991*b*, Schreer and Testa 1993, 1995, 1996, Boyd et al. 1994, Brillinger et al. 1995, Schreer et al. 1995, 1998, Brillinger and Stewart 1997, Burns et al. 1997, Burns and Schreer, *in press*), although the individual classification protocols for these analyses have varied considerably (e.g., principal component analysis, discriminant function analysis, cluster analysis [various algorithms], artificial neural networks, shape-fitting algorithms, as well as combinations, some of which included maximum depth and duration), making interspecific comparisons difficult.

Gentry and Kooyman (1986) was one of the first comparative studies across many species that used similar methods. This work resulted in a dramatic increase in our knowledge about the diving behavior of fur seals and diving animals in general. However, a thorough analysis of dive shape was not performed in this work, and the comparisons focused on a closely related and highly similar group of animals. By studying the diving behavior of several unrelated species simultaneously, one can make a better assessment of possible dive functions. That is, due to convergent evolution, dive functions of unrelated species should be similar if they have similar ecological niches.

In this study, dive data from 12 different species of diving, air-breathing vertebrates from five different families were classified using the same methods. Patterns were compared across species and, through these comparisons, behavioral functions for the observed dive types were proposed. Differences and similarities within and across species should shed more light on how these animals exploit the marine environment.

## METHODS

Previously acquired time–depth recorder (TDR) data sets were compiled for this study (Table 1). These included 12 different species: Blue-eyed Shag (*Phalacrocorax atriceps*, specific race was South Georgia Shag, *P. a. georgianus*), Adélie Penguin (*Pygoscelis adeliae*), Royal Penguin (*Eudyptes schlegeli*), Gentoo Penguin (*Pygoscelis papua*), Galápagos fur seal (*Arctocephalus galapagoensis*), Antarctic fur seal (*Arctocephalus gazella*), harp seal (*Phoca groenlandica*), grey seal (*Halichoerus grypus*), hooded seal (*Cystophora cristata*), Weddell seal (*Leptonychotes weddellii*), southern elephant seal (*Mirounga leonina*), and walrus (*Odobenus rosmarus*). Table 1 can be consulted for direction to specific methods of device attachment and deployment.

A dive was defined as a series of depths over time, starting and ending with depth equal to zero. Due to erroneous drift of the zero depth in TDRs and possible effects of wave action, a depth of two times the resolution of the TDR was considered to be representative of the surface. Only dives with a maximum depth greater than this depth were analyzed. Also, because this work involves the determination of dive shape (depth vs. time), only dives with at least five depth readings were analyzed for shape because fewer readings resulted in considerable degradation of the precision of even the simplest geometric shapes (J. F. Schreer, *unpublished data*).

### Classification

Classification analyses evolved throughout this study, resulting in a robust, universal method for summarizing dive data with regard to shape that allows direct comparisons across different species and studies. The evolution of the dive analysis is of considerable educational value to researchers analyzing dive data, and is presented in detail in Schreer (1997: Chapter 4). The universal method consists of five steps: (1) dives for different individuals, species, and studies are standardized to a similar sampling frequency; (2) dives are pooled within a species (except for southern elephant seal); (3) each dive is compared to four simple shapes (*square*, *V*, *skewed right*, and *skewed left*, as identified by cluster analyses on numerous species (Schreer 1997, Schreer et al. 1998) and is assigned a group membership or probability of belonging to each category; (4) hybrids, dives intermediate to two or more shapes and consequently having two or more of its highest group memberships that are very similar, are identified and separated or omitted; and (5) a hierarchical classification of each shape group is performed using variables that provide fine-scale information about the dive shape.

*Standardization of sampling frequency.*—Sampling frequency has been shown to affect dive analysis results. Using data resampled at different sampling in-

TABLE 1. Recording and processing information for each species.

| Species                     | <i>n</i>              |      | Period sampled      | Sam-<br>pling<br>inter-<br>val<br>(s) | Mean<br>no.<br>obs.<br>per dive† | <i>n</i>                |                         |                         | Sources or related<br>publications                      |
|-----------------------------|-----------------------|------|---------------------|---------------------------------------|----------------------------------|-------------------------|-------------------------|-------------------------|---|
|                             | Indi-<br>vid-<br>uals | Days |                     |                                       |                                  | ≥5 obs.<br>per dive     | Minus<br>hybrids        |                         |   |
| Blue-eyed Shag              | 2                     | 7    | Jan–Feb             | 1<br><b>6</b>                         | 74<br><b>16</b>                  | 692<br><b>588</b>       | 588<br><b>489</b>       | 574<br><b>477</b>       | Bevan et al. (1997),<br>Boyd and Croxall<br>(1996)‡     |
| Adélie Penguin              | 36                    | 45   | Dec–Jan             | 1; 5<br><b>5</b>                      | 59; 12<br><b>12</b>              | 28 904<br><b>27 568</b> | 22 897<br><b>22 267</b> | 20 283<br><b>19 567</b> | Chappell et al.<br>(1993a,b)                            |
| Royal Penguin               | 6                     | 5    | Nov–Dec             | 2<br><b>10</b>                        | 59<br><b>14</b>                  | 3 763<br><b>3 274</b>   | 3 185<br><b>2 826</b>   | 2 785<br><b>2 473</b>   | Hindell et al. (1996)§                                  |
| Gentoo Penguin              | 2                     | 2    | Nov                 | 2<br><b>10</b>                        | 65<br><b>17</b>                  | 830<br><b>767</b>       | 742<br><b>553</b>       | 700<br><b>482</b>       | ‡,§   |
| Galápagos fur seal          | 32                    | 144  | Feb–Apr;<br>Jul–Nov | 5<br><b>10</b>                        | 22<br><b>13</b>                  | 83 404<br><b>75 974</b> | 52 149<br><b>44 333</b> | 45 266<br><b>38 393</b> | Horning (1992), Horn-<br>ing and Trillmich<br>(1997a,b) |
| Antarctic fur seal          | 4                     | 27   | Jan–Feb             | 5                                     | 15                               | 6 658                   | 4 455                   | 3 853                   | Boyd and Croxall<br>(1992), Boyd et al.<br>(1994)‡,§    |
| Harp seal                   | 6                     | 15   | Feb–Mar             | 10<br><b>20</b>                       | 28<br><b>17</b>                  | 11 038<br><b>8 841</b>  | 6 835<br><b>4 998</b>   | 5 926<br><b>4 389</b>   | Lydersen and Kovacs<br>(1993, 1996)                     |
| Grey seal                   | 5                     | 9    | Jan                 | 10                                    | 17                               | 1 480                   | 1 091                   | 1 058                   | Lydersen et al. (1994)                                  |
| Hooded seal                 | 2                     | 4    | Mar                 | 10<br><b>20</b>                       | 25<br><b>16</b>                  | 366<br><b>304</b>       | 193<br><b>140</b>       | 160<br><b>115</b>       | Kovacs et al. (1996)                                    |
| Weddell seal                | 7                     | 195  | Jan–Aug             | 60                                    | 16                               | 55 176                  | 40 166                  | 33 127                  | Testa (1994), Schreer<br>and Testa (1995,<br>1996)      |
| Southern elephant<br>seal ♀ | 5                     | 80   | Nov–Jan             | 30<br><b>90</b>                       | 43<br><b>15</b>                  | 22 042<br><b>21 913</b> | 21 893<br><b>21 752</b> | 19 769<br><b>19 134</b> | Hindell et al. (1991a,b,<br>1992)                       |
| Walrus                      | 1                     | 13   | Jul–Aug             | 10<br><b>30</b>                       | 38<br><b>14</b>                  | 1 663<br><b>1 479</b>   | 1 386<br><b>1 342</b>   | 1 363<br><b>1 325</b>   | Wiig et al. (1993)                                      |
| Southern elephant<br>seal ♂ | 4                     | 148  | Nov–Feb;<br>Apr–Jun | 30<br><b>90</b>                       | 52<br><b>18</b>                  | 14 976<br><b>14 256</b> | 14 190<br><b>14 023</b> | 13 318<br><b>12 917</b> | Hindell et al. (1991a,b,<br>1992)                       |

Note: Species with a second set of results (in boldface) from data sampled at a slower sampling interval were resampled so that the number of observations per dive was approximately equal for all species.

† For dives with ≥5 observations (obs.) per dive.

‡ Data from I. L. Boyd.

§ Data not previously published.

tervals from the same original data set, Boyd (1993) found that, as sampling interval increased (and sampling frequency decreased), mean maximum depth, duration, and postdive surface interval increased, whereas the number of dives detected decreased. A similar trend was found when resampling data sets from Adélie Penguin and Galápagos fur seal (Schreer 1997: Table 4.2). Furthermore, sampling interval was also found to affect dive shape and, consequently, the percentage of dives classified within each shape category (Table 2). As the sampling interval increased, the percentage of square dives decreased, whereas the percentage of V, skewed-right, and skewed-left dives increased. The reduction in the number of depth readings per dive (increased sampling interval) would cause true inflection points at the bottom of square dives to be missed, making them appear more triangular in shape. Therefore, fewer square dives and more V, skewed-right, and skewed-left dives would be detected. To correct for these differences, each data set was resampled so that on av-

erage, dives within each species had a similar number of depth readings per dive (Table 1).

*Pooling dives.*—Although it has been shown that the diving behavior among individuals within a species can have considerable variation (Hindell et al. 1991b, Testa 1994, Burns et al. 1997, Burns and Schreer, *in press*), within this work, small numbers of individuals and the lack of additional distinguishing parameters (e.g., physiological measures such as hematocrit, hemoglobin concentration, plasma lactate concentration, etc.; Burns et al. 1997, Burns and Schreer, *in press*) made any explanation of individual variability difficult. Therefore, data from individuals within a species were pooled. The only exception was that southern elephant seal were separated into male and female samples because of their exceptional sexual size dimorphism.

*Shape comparison.*—Having performed cluster analyses following Schreer and Testa (1995, 1996), Schreer (1997), and Schreer et al. (1998) on all 12 species, similarities in the dive patterns were found across the

TABLE 2. Effect of sampling interval on dive shape percentages.

| Interval (s)       | Total no. dives | Mean no. obs. per dive | Dives with $\geq 5$ obs. |      | Square dive |      | V dive   |      | Skewed-right dive |      | Skewed-left dive |      |
|--------------------|-----------------|------------------------|--------------------------|------|-------------|------|----------|------|-------------------|------|------------------|------|
|                    |                 |                        | <i>n</i>                 | %    | <i>n</i>    | %    | <i>n</i> | %    | <i>n</i>          | %    | <i>n</i>         | %    |
| Adélie Penguin     |                 |                        |                          |      |             |      |          |      |                   |      |                  |      |
| 1                  | 2571            | 57                     | 2348                     | 91.3 | 1706        | 72.7 | 555      | 23.6 | 68                | 2.9  | 19               | 0.8  |
| 2                  | 2512            | 30                     | 2282                     | 90.8 | 1613        | 70.7 | 584      | 25.6 | 63                | 2.8  | 21               | 0.9  |
| 3                  | 2463            | 20                     | 2202                     | 89.4 | 1470        | 66.8 | 646      | 29.3 | 66                | 3.0  | 18               | 0.8  |
| 4                  | 2440            | 16                     | 2149                     | 88.1 | 1370        | 63.8 | 681      | 31.7 | 74                | 3.4  | 24               | 1.1  |
| 5                  | 2406            | 13                     | 2060                     | 84.0 | 1219        | 59.2 | 739      | 35.9 | 76                | 3.7  | 25               | 1.2  |
| 10                 | 2354            | 7                      | 1650                     | 70.1 | 629         | 38.1 | 912      | 55.3 | 78                | 4.7  | 28               | 1.7  |
| Galápagos fur seal |                 |                        |                          |      |             |      |          |      |                   |      |                  |      |
| 5                  | 10469           | 14                     | 7052                     | 67.4 | 4996        | 70.8 | 1089     | 15.4 | 333               | 4.7  | 629              | 8.9  |
| 10                 | 9361            | 8                      | 5626                     | 60.1 | 3799        | 67.5 | 1088     | 19.3 | 306               | 5.4  | 430              | 7.6  |
| 15                 | 8465            | 6                      | 4722                     | 55.8 | 3083        | 65.3 | 1011     | 21.4 | 289               | 6.1  | 334              | 7.1  |
| 20                 | 7741            | 5                      | 3733                     | 48.2 | 2246        | 60.2 | 925      | 24.8 | 251               | 6.7  | 306              | 8.2  |
| 25                 | 7126            | 5                      | 2619                     | 36.8 | 1496        | 57.1 | 668      | 25.5 | 211               | 8.1  | 239              | 9.1  |
| 30                 | 6587            | 4                      | 1615                     | 24.5 | 837         | 51.8 | 385      | 23.8 | 184               | 11.4 | 204              | 12.6 |

Note: Data were resampled at different sampling intervals from a subsample of dive records for Adélie Penguin and Galápagos fur seal.

species that indicated the need for a unified method for classifying and comparing dive profiles. Additional variables (e.g., swim velocity, stomach temperature, jaw movements, heart rate, and three-dimensional dive behavior), that have only recently begun to be measured, may allow dive patterns within and across species to be better discriminated with clustering techniques. However, with only depth and time being measured, as is the case for the data presented in this study, dives will generally fall into one of four shapes (*square*, *V*, *skewed right*, and *skewed left*) and cluster analyses of dive data across species will generally show similar patterns. Therefore, to allow more direct comparisons across species, a method first presented by Schreer and Testa (1996) and further developed here was used. This method compares each dive to four simple geometric shapes (*square*, *V*, *skewed right* and *skewed left*) that have been adjusted to reflect realistic dive profiles (Fig. 1). For example, a “square-like” shape with bottom time equal to half of the dive duration was used as opposed to a truly square shape that would have an animal diving from the surface to the maximum depth of the dive in 0 time.

Using this procedure, in addition to fuzzy clustering theory developed by Bezdek (1981), summarized in

Kamel and Selim (1994), and explored as a dive analysis tool in Schreer et al. (1998), a new shape fitting protocol was developed. Dive profiles, scaled to equivalent depth, were compared to the four shapes as in Schreer and Testa (1996). For each dive, four shapes were generated with the number of depth values equal to that of the dive. The similarity of each shape to the dive was determined by calculating the Euclidean distance between the dive and the generated shape. Then to determine which shape was most similar to the dive, a group membership ( $M$ ), as outlined in Kamel and Selim (1994) and described in Schreer et al. (1998), was calculated by

$$M_{ij} = 1 / \sum_{l=1}^c (d_{ij}/d_{il})^{2/(m-1)}$$

for  $d_{il} > 0$ ,  $\forall i, j$ , where  $c = 4$  (the number geometric shapes),  $m$  is the fuzziness parameter ( $m > 1$ ), and  $d_{ij}$  is the Euclidean distance between the  $i$ th dive pattern vector and the  $j$ th geometric shape vector. If  $d_{il} = 0$  then  $M_{il} = 1$  and  $M_{ij} = 0$  for  $j \neq l$ . This results in four “probabilities” (one for the similarity of the dive profile to each shape) that sum to one.

*Hybrids.*—Group memberships were used to deter-

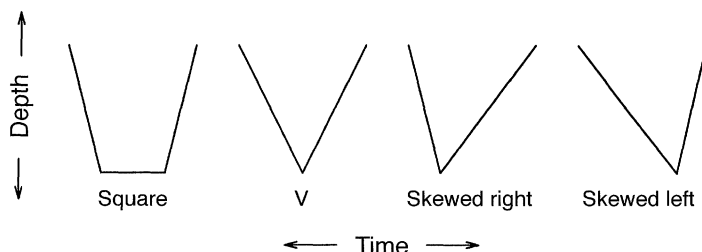


FIG. 1. Shapes used for the dive shape classification protocol. The four simple geometric shapes (square, V, skewed right, and skewed left) have been adjusted to reflect realistic dive profiles. Square is 25% descent, 50% bottom time, and 25% ascent; V is 50% descent, 50% ascent; skewed right is 25% descent, 75% ascent; and skewed left is 75% descent, 25% ascent.

TABLE 3. Dive variables used for comparisons across species and to determine the subdivisions of dive types.

| Dive variable                   | Definition  | Source                     |
|---------------------------------|---|----------------------------|
| Maximum depth (m)               | Maximum depth reading during the dive   | ...                        |
| Duration (min)                  | Duration between first and last reading of the dive, plus one sampling interval   | ...                        |
| Depth per duration (m/min)      | Maximum depth divided by duration   | Schreer and Testa (1995)   |
| Bottom time (min)               | Time interval between first and last depths $\geq 80\%$ of the dive's maximum depth   | Dive Analysis†             |
| Wiggle count (no.) ‡            | Number of ascent-to-descent occurrences during bottom time that differ by more than two times the resolution of the TDR§  | Dive Analysis†             |
| Mean wiggle distance (m)        | Average depth difference between the deepest and shallowest points of a wiggle  | Dive Analysis†             |
| Mean vertical velocity (m/s)    | Average rate of depth change: (descent rate + ascent rate) divided by 2 (descent rate is average rate of travel between start of the dive and beginning of bottom time; ascent rate is average rate of travel between end of bottom time and end of the dive) | This study; Dive Analysis† |
| Postdive surface interval (min) | Time between end of a dive and beginning of the subsequent dive   | This study; Dive Analysis† |

† Dive Analysis manual (Version 4.0) and program (Version 4.08), Wildlife Computers, Redmond, Washington, USA.

‡ For comparisons of all variables related to wiggle count (i.e., wiggle count, wiggle count per bottom time, mean wiggle distance, and mean wiggle distance per depth), only dives with at least one wiggle were compared.

§ TDR = time-depth recorder.

mine which dives had shapes that were intermediate to two or more geometric shapes. This was done because hybrids would probably display characteristics of more than one dive type and would blur differences between the types. The elimination of hybrids was accomplished by comparing the first and second highest group memberships for each dive. If the highest group membership was not at least 25% higher than the second highest group membership, the dive was considered to be a hybrid and not used in the comparative analyses of dive shape.

*Hierarchical classifications.*—Following the four shape classification and after omitting hybrids, several dive variables were also used to determine if any further divisions were warranted within a dive type. Variables were decided upon that provide fine-scale information about the dive shape and information on the surface interval following a dive. These included depth per duration, mean vertical velocity, bottom time, bottom time per duration, postdive surface interval, postdive surface interval per duration, percentage of dives with wiggles, wiggle count, wiggle count per bottom time, mean wiggle distance, mean wiggle distance per depth, and standard deviation and coefficient of variation of the depth during bottom time (see Table 3 for definitions). For example, it has been suggested that square dives represent pelagic and benthic foraging (e.g., Le Boeuf et al. 1988, 1992, Hindell et al. 1991b, Schreer and Testa 1996). Therefore, several variables that describe the variability in depth during the bottom time were analyzed with histograms to determine if any multimodality existed. The presence of strong multimodality would suggest that more than one type of behavior was occurring. A possible difference in the variability of depth values during bottom time could

indicate pelagic or benthic foraging (high variability, pelagic; low variability, benthic).

#### *Dive comparisons*

Once all dives were classified, dive variables (Table 3) were compared within and across species. Although exploratory analyses such as cluster analysis are valid techniques for examining this type of data, techniques that provide tests of significance, such as analysis of variance (ANOVA) or contingency table analysis, are inappropriate or invalid because of the large number of dives per animal and the small number of individuals per species. Therefore, differences in these patterns were visually analyzed. Additional comparisons were performed on square dives only, using bottom time, bottom time per duration, percentage of dives with wiggles, wiggle count, wiggle count per bottom time, mean wiggle distance, mean wiggle distance per depth, and the standard deviation and coefficient of variation of the depth readings during bottom. Diel patterns within dive types were also visually analyzed and compared within and across species. For all of these analyses, only dive types with >30 observations per group were used. The only exception to this was for the hooded seal, which had dive types represented by <30 dives, but still a relatively large percentage of all their dives (because of the small number of hooded seal dives in the total sample).

#### *Aerobic dive limit*

Dive durations within each dive type were compared to the calculated aerobic dive limit (cADL) for that species. The aerobic dive limit (ADL) is defined as the maximum duration of a breath-hold without any increase in plasma lactate levels above resting during

TABLE 4. Life history information about the various species relevant to the interpretation of their diving records in this study.

| Species<br>(sex)          | Mass (kg)  |                                 | Primary prey                               | Distribution  | Relevant details   | Sources   |
|---------------------------|------------|---------------------------------|--|---|--|---|
|                           | Literature | This study<br>(mean $\pm$ 1 SD) |  |   |  |   |
| Blue-eyed Shag<br>(♂, ♀)  | 2.2        | 2.4 $\pm$ 0.2                   | Benthic fish                               | Southern S. America ( <i>P. atriceps</i> ); South Georgia and nearby islands ( <i>P. georgianus</i> ) | Adults brooding and rearing chicks; also implanted with heart rate loggers; foot-propelled pursuit-diver; shags observed were South Georgia Shag, often considered race of Blue-eyed Shag                      | Burger (1991), del Hoyo et al. (1992), Bevan et al. (1997); I. L. Boyd, <i>personal communication</i>         |
| Adélie Penguin<br>(♂, ♀)  | 5.0        | 3.8 $\pm$ 0.3                   | Krill                                      | Circumpolar (S)   | Adults during late incubation and chick care periods; at-sea periods lasting up to 26 h; from 10 min to 5 h to begin foraging; not limited by water depth  | Burger (1991), Chappell et al. (1993a)  |
| Royal Penguin (?)         | 5.3†       | 5.3‡                            | Krill and amphipods                        | Macquarie Is. (S. of New Zealand)   | Breeding adults; sometimes considered a subspecies of Macaroni Penguin ( <i>E. chrysolophus</i> ); off-shore pelagic feeder  | del Hoyo et al. (1992), Hindell et al. (1996)   |
| Gentoo Penguin (?)        | 5.5        | 5.5‡                            | Krill and fish                             | Subantarctic  | Breeding adults; at-sea periods last ~14 h; inshore feeder that may forage for benthic prey  | Burger (1991), Williams et al. (1992), Robinson and Hindell (1996); I. L. Boyd, <i>personal communication</i> |
| Galápagos fur seal<br>(♀) | 30         | 29.0 $\pm$ 3.2                  | Cephalopods and fish                       | Galápagos Is.   | Lactating females; continuous swimming and diving while at sea for ~16 h; diving bouts start and end ~2 h before and after being ashore; nocturnal foraging  | Kooyman and Trillmich (1986), Jefferson et al. (1993), Horning and Trillmich (1997a,b)                        |
| Antarctic fur seal<br>(♀) | 35         | 34.4 $\pm$ 2.9                  | Krill and fish                             | Antarctic convergence   | Lactating females; also implanted with heart rate loggers; foraging trips ~3–5 days  | Jefferson et al. (1993), Boyd and Croxall (1992); I. L. Boyd, <i>personal communication</i>                   |
| Harp seal<br>(♀)          | 120        | 138.2 $\pm$ 6.7                 | Pelagic and benthic fish and crustaceans   | Arctic and N. Atlantic  | Lactating, ice breeding females on drifting pack-ice; during 12-d lactation period; probably feeding during lactation; mean at-sea period is 3.9 h; water depth of ~63 m, but to at least 106 m (deepest dive) | Jefferson et al. (1993), Lydersen and Kovacs (1993, 1996)   |
| Grey seal<br>(♀)          | 240        | 201.6 $\pm$ 29.9                | Benthic and pelagic fish and invertebrates | Subarctic to cold temperate in N. Atlantic  | Lactating, ice-breeding females; probably feeding during lactation; maximum water depth of 19 m; often benthic feeders   | Jefferson et al. (1993), Lydersen et al. (1994)   |
| Hooded seal<br>(♂)        | 350        | 353.5 $\pm$ 51.6                | Cephalopods and fish                       | Arctic and N. Atlantic  | Reproductive males; during breeding season ~85% of their time hauled out; shallow water depth (50–70 m); probably not feeding, but performing energy-expensive activity when at sea                            | Jefferson et al. (1993), Kovacs et al. (1996)   |

TABLE 4. Continued.

| Species (sex)              | Mass (kg)  |                              | Primary prey          | Distribution    | Relevant details   | Sources  |
|----------------------------|------------|------------------------------|-----------------------|-----------------|--|--|
|                            | Literature | This study (mean $\pm$ 1 SD) |                       |                 |  |  |
| Weddell seal (♀)           | 425        | 339.2 $\pm$ 42.8§            | Fish                  | Circumpolar (S) | Gestating females diving within pack ice; movements of up to 1500 km (in total)  | Jefferson et al. (1993), Testa (1994)  |
| Southern elephant seal (♀) | 600        | 394.0 $\pm$ 65.1             | Cephalopods and fish  | Circumpolar (S) | Adult females after annual molt or following the breeding season; most seals used foraging grounds > 1000 km from Macquarie Is. and took 2–4 wk to get there; most females thought to perform only pelagic dives | Hindell et al. (1991b), Jefferson et al. (1993)  |
| Walrus (♂)                 | 1900       | 1500                         | Benthic invertebrates | Circumpolar (N) | Adult male; water depth <100 m; 30 m in vicinity of the tagging site   | Jefferson et al. (1993), Fay and Burns (1988), Gjertz and Wiig et al. (1992), Wiig et al. (1993) |
| Southern elephant seal (♂) | 4000       | 2272.5 $\pm$ 909.0           | Cephalopods and fish  | Circumpolar (S) | Same as female southern elephant seal, except that males are thought to perform both pelagic and benthic dives   | Hindell et al. (1991b), Jefferson et al. (1993)  |

† Mass estimated from interspecific length vs. mass regression. Lengths are from del Hoyo et al. (1992).

‡ Mass taken from the published literature.

§ Mass estimated from intraspecific length/girth regression (J. Ward Testa, *personal communication*).

|| Mass estimated from intraspecific length/girth regression (Hindell et al. 1991b).

or following a dive (Kooyman 1989). It can be determined directly by measuring postdive plasma lactate concentrations or calculated by dividing total body oxygen stores (TBO<sub>2</sub>) by diving metabolic rate (DMR); see Burns and Castellini (1996) for a recent review. Because of considerable speculation regarding the calculation of cADL, and especially the estimate of DMR, three different models were used. To estimate DMR, 2  $\times$  standard metabolic rate (SMR) was used for all groups, but additionally, 1  $\times$  SMR was used for phocids and odobenids, and 4  $\times$  SMR was used for seabirds and otariids. Standard metabolic rate was calculated as  $SMR = 13.0(M_b)^{0.729}$  (Aschoff and Pohl 1970, Kooyman 1989) for seabirds, and as  $SMR = 10.1(M_b)^{0.25}$  (Kleiber 1961) for marine mammals, where  $M_b$  is body mass (in kilograms) and SMR is in milliliters of O<sub>2</sub> per minute. Standard metabolic rate and DMR were divided by mass to scale them to a unit mass (in milliliters of O<sub>2</sub> per minute per kilogram). Available mass-specific O<sub>2</sub> stores (in milliliters of O<sub>2</sub> per kilogram) for the various groups were 58 for seabirds, 60 for phocids, 40 for otariids (Kooyman 1989), and 34 for odobenids (Wiig et al. 1993). The resulting equations for cADL (minutes), mass-specific O<sub>2</sub> stores/mass-specific DMR, were  $cADL_{\text{phocids}(2 \times \text{SMR})} = 2.97(M_b)^{0.25}$ ,  $cADL_{\text{phocids}(1 \times \text{SMR})} = 5.94(M_b)^{0.25}$ ,

$cADL_{\text{otariids}(2 \times \text{SMR})} = 1.98(M_b)^{0.25}$ ,  $cADL_{\text{otariids}(4 \times \text{SMR})} = 0.99(M_b)^{0.25}$ ,  $cADL_{\text{birds}(2 \times \text{SMR})} = 2.23(M_b)^{0.271}$ ,  $cADL_{\text{birds}(4 \times \text{SMR})} = 1.12(M_b)^{0.271}$ ,  $cADL_{\text{odobenids}(2 \times \text{SMR})} = 1.68(M_b)^{0.25}$ , and  $cADL_{\text{odobenids}(1 \times \text{SMR})} = 3.37(M_b)^{0.25}$ . These equations are undoubtedly overly simple, but they are an attempt to allow for more meaningful interspecific comparisons.

Additionally, the potential effect of ADL on surface time was assessed by determining the relationship between dive duration and postdive surface interval. This was done through both linear (least squares regression) and nonlinear (LOWESS smoother that performs a series of locally weighted linear regressions) procedures (SYSTAT 1992).

#### Functional analyses

Using these analyses (i.e., interspecific similarities and differences) and comparing these results to previous studies on pinnipeds and seabirds, we proposed possible functions for the various dive types. In addition, life history information (mass, reproductive status, primary prey, etc.) for the various species and conditions and locations of the studies were used to propose possible functions of the dive types and to compare diving patterns across species.



TABLE 5. Dive statistics (mean  $\pm$  1 SD): maximum depth (Depth) and duration (Dur.) for all dives pooled, and by dive shape.

| Species                  | All      |               |                | Square dive |                  |               |                |
|--------------------------|----------|---------------|----------------|-------------|------------------|---------------|----------------|
|                          | <i>n</i> | Depth (m)     | Dur. (min)     | <i>n</i> †  | Percent-<br>age‡ | Depth (m)     | Dur. (min)     |
| Blue-eyed Shag           | 489      | 22 $\pm$ 19   | 1.6 $\pm$ 0.8  | 477         | 98.4             | 22 $\pm$ 20   | 1.6 $\pm$ 0.8  |
| Adélie Penguin           | 22 267   | 20 $\pm$ 13   | 1.0 $\pm$ 0.4  | 19 567      | 76.2             | 16 $\pm$ 10   | 0.9 $\pm$ 0.3  |
| Royal Penguin            | 2 826    | 49 $\pm$ 28   | 2.3 $\pm$ 0.7  | 2 473       | 63.9             | 38 $\pm$ 22   | 2.2 $\pm$ 0.7  |
| Gentoo Penguin           | 553      | 89 $\pm$ 38   | 2.9 $\pm$ 0.7  | 482         | 67.6             | 81 $\pm$ 26   | 2.7 $\pm$ 0.5  |
| Galápagos fur seal       | 44 333   | 37 $\pm$ 19   | 2.1 $\pm$ 0.7  | 38 393      | 72.0             | 36 $\pm$ 18   | 2.3 $\pm$ 0.8  |
| Antarctic fur seal       | 4 455    | 27 $\pm$ 21   | 1.2 $\pm$ 0.5  | 3 853       | 81.1             | 26 $\pm$ 17   | 1.3 $\pm$ 0.4  |
| Harp seal                | 4 998    | 49 $\pm$ 25   | 5.6 $\pm$ 2.0  | 4 389       | 67.5             | 57 $\pm$ 21   | 6.4 $\pm$ 1.8  |
| Grey seal                | 1 091    | 10 $\pm$ 3    | 2.8 $\pm$ 1.3  | 1 058       | 97.3             | 10 $\pm$ 3    | 2.9 $\pm$ 1.3  |
| Hooded seal              | 140      | 39 $\pm$ 17   | 5.5 $\pm$ 3.9  | 115         | 45.2             | 41 $\pm$ 18   | 6.1 $\pm$ 3.3  |
| Weddell seal             | 40 166   | 199 $\pm$ 129 | 15.8 $\pm$ 6.1 | 33 127      | 50.6             | 207 $\pm$ 118 | 16.4 $\pm$ 6.0 |
| Southern elephant seal ♀ | 21 752   | 442 $\pm$ 182 | 21.9 $\pm$ 4.9 | 19 134      | 72.6             | 399 $\pm$ 150 | 22.4 $\pm$ 4.7 |
| Walrus                   | 1 342    | 24 $\pm$ 12   | 6.8 $\pm$ 1.6  | 1 325       | 97.3             | 24 $\pm$ 12   | 6.9 $\pm$ 1.6  |
| Southern elephant seal ♂ | 14 023   | 436 $\pm$ 117 | 26.4 $\pm$ 6.4 | 12 917      | 85.0             | 444 $\pm$ 101 | 27.1 $\pm$ 5.8 |

Notes: Only dives with  $\geq 5$  depth readings per dive were analyzed. Values in boldface were not used in comparisons because sample sizes were  $< 30$  (except for the hooded seal; see *Methods, Dive comparisons*).

† Hybrid dives were excluded for shape classification.

‡ Percentages are the number of dives of each type, minus hybrids, divided by *n* (all dives minus hybrids).

## RESULTS

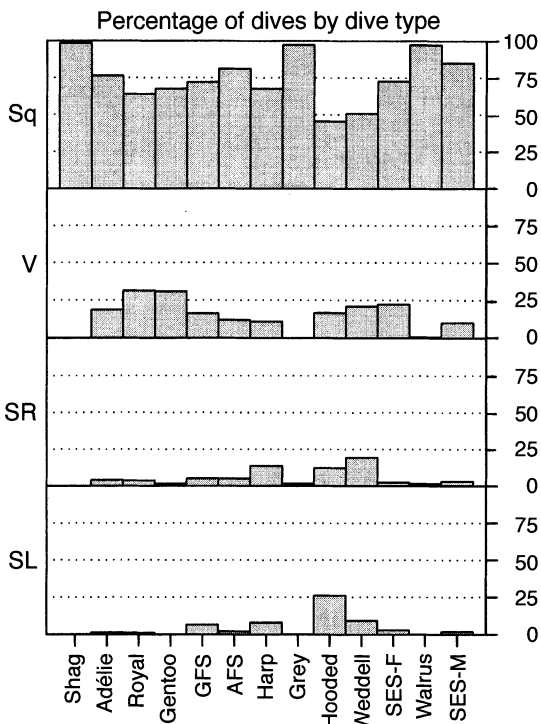


FIG. 2. Percentage of dives distributed by dive types. Here, and in subsequent figures, units are identified in the top label, and scale numbers are on the right-hand axis, rather than on the traditional left-hand axis. Species are organized from smallest (left) to largest (right): Shag, Blue-eyed Shag; Adélie, Adélie Penguin; Royal, Royal Penguin; Gentoo, Gentoo Penguin; GFS, Galápagos fur seal; AFS, Antarctic fur seal; Harp, harp seal; Grey, grey seal; Hooded, hooded seal; Weddell, Weddell seal; SES-F, female southern elephant seal; walrus; SES-M, male southern elephant seal. Dive-type abbreviations: Sq, square dive; V, V dive; SR, skewed-right dive; SL, skewed-left dive.

The species included in this study varied considerably in mass (2–2000 kg) and life stage (lactating females, gestating females, reproducing males, adults brooding and rearing chicks, etc.; Table 4). As well, recording protocols and length and annual timing of coverage varied considerably across species (Table 1). Analyzing the depth records for the 12 species resulted in 230 992 dives, of which 169 770 had five or more depth readings. When several of the data sets were resampled at larger sampling intervals, this number decreased to 156 435. Excluding hybrids from the resampled data reduced the number of dives to 137 310.

### Dive comparisons

Square dives were invariably, and markedly, the most abundant dive type (Fig. 2; for specific values, see Table 5). V dives were usually the next most abundant, followed by the skewed dives, although this trend was not always consistent for all of the species. Percentages of dive types did not appear to be influenced by body size, but rather by water depth and preferred prey. That is, limited water depth and possible benthic foraging increased the percentage of square dives (e.g., Blue-eyed Shag, grey seal, and walrus; Table 4).

Mean maximum dive depth and duration generally increased with body mass within pinnipeds and seabirds (Fig. 3; for specific values, see Tables 4 and 5). The trend for both groups combined was very weak for maximum depth, but could still be seen for duration. The walrus was a strong exception, with very shallow, short dives for its mass. The hypothesized behavior and the water depth during the study also seemed to be of considerable importance in affecting mean maximum depth and duration (also see Table 4). Maximum depth and duration patterns across dive types indicated that

TABLE 5. Extended.

| V dive       |                |                  | Skewed-right dive |                |                  | Skewed-left dive |               |                  |
|--------------|----------------|------------------|-------------------|----------------|------------------|------------------|---------------|------------------|
| Percent-age‡ | Depth (m)      | Dur. (min)       | Percent-age‡      | Depth (m)      | Dur. (min)       | Percent-age‡     | Depth (m)     | Dur. (min)       |
| <b>0.6</b>   | <b>15 ± 4</b>  | <b>0.9 ± 0.2</b> | <b>0.4</b>        | <b>24 ± 10</b> | <b>1.5 ± 0.4</b> | <b>0.6</b>       | <b>8 ± 1</b>  | <b>0.7 ± 0.1</b> |
| 18.5         | 34 ± 16        | 1.3 ± 0.4        | 4.1               | 18 ± 8         | 1.0 ± 0.3        | 1.2              | 19 ± 10       | 1.0 ± 0.4        |
| 31.3         | 73 ± 27        | 2.6 ± 0.6        | 3.7               | 40 ± 17        | 2.1 ± 0.6        | 1.1              | 23 ± 10       | 1.9 ± 0.5        |
| 30.7         | 113 ± 50       | 3.3 ± 0.8        | <b>1.5</b>        | <b>18 ± 17</b> | <b>1.5 ± 0.4</b> | <b>0.2</b>       | <b>47</b>     | <b>3</b>         |
| 16.2         | 46 ± 22        | 1.9 ± 0.7        | 5.2               | 31 ± 18        | 1.9 ± 0.7        | 6.6              | 28 ± 17       | 1.7 ± 0.6        |
| 11.9         | 49 ± 34        | 1.4 ± 0.6        | 5.1               | 14 ± 7         | 1.0 ± 0.3        | 1.9              | 16 ± 11       | 0.9 ± 0.4        |
| 10.9         | 46 ± 26        | 3.9 ± 1.3        | 13.7              | 40 ± 25        | 4.9 ± 1.7        | 7.9              | 26 ± 21       | 4.0 ± 1.8        |
| <b>0.3</b>   | <b>13 ± 2</b>  | <b>1.2 ± 0.3</b> | <b>1.8</b>        | <b>12 ± 4</b>  | <b>1.5 ± 0.7</b> | <b>0.6</b>       | <b>13 ± 2</b> | <b>1.9 ± 1.5</b> |
| 16.5         | 38 ± 18        | 3.3 ± 2.3        | 12.2              | 48 ± 15        | 6.2 ± 3.8        | 26.1             | 36 ± 17       | 4.3 ± 3.0        |
| 20.9         | 252 ± 140      | 14.2 ± 5.5       | 19.2              | 180 ± 99       | 16.8 ± 6.1       | 9.3              | 128 ± 91      | 13.4 ± 6.2       |
| 22.3         | 579 ± 205      | 20.7 ± 4.9       | 2.4               | 477 ± 205      | 21.6 ± 6.7       | 2.7              | 338 ± 132     | 21.3 ± 5.9       |
| <b>0.7</b>   | <b>35 ± 17</b> | <b>4.8 ± 1.2</b> | <b>1.5</b>        | <b>21 ± 11</b> | <b>5.2 ± 1.0</b> | <b>0.5</b>       | <b>21 ± 9</b> | <b>4.3 ± 0.5</b> |
| 10.1         | 405 ± 145      | 22.2 ± 6.1       | 3.1               | 405 ± 161      | 29.1 ± 9.2       | 1.8              | 356 ± 145     | 22.5 ± 9.0       |

V-shaped dives were usually the deepest, skewed-left dives were the shallowest, and both of these dive types were relatively short. The rate at which duration changed with depth (slope, Fig. 4A) did not appear to be affected by body size, but divers that were limited by water depth or those that dived to the bottom (benthic foragers; i.e., Blue-eyed Shag, walrus, and harp, grey, and hooded seal) increased dive duration more

rapidly with an increase in maximum depth than did the other species. The amount of variability in duration due to changes in maximum depth ( $r^2$ , Fig. 4B) was affected by body size; it decreased with increasing body size in a fairly regular pattern for all dives combined. This pattern was also seen for square dives, but was weaker or not apparent for the other dive types (probably because of small sample sizes). A comparison of

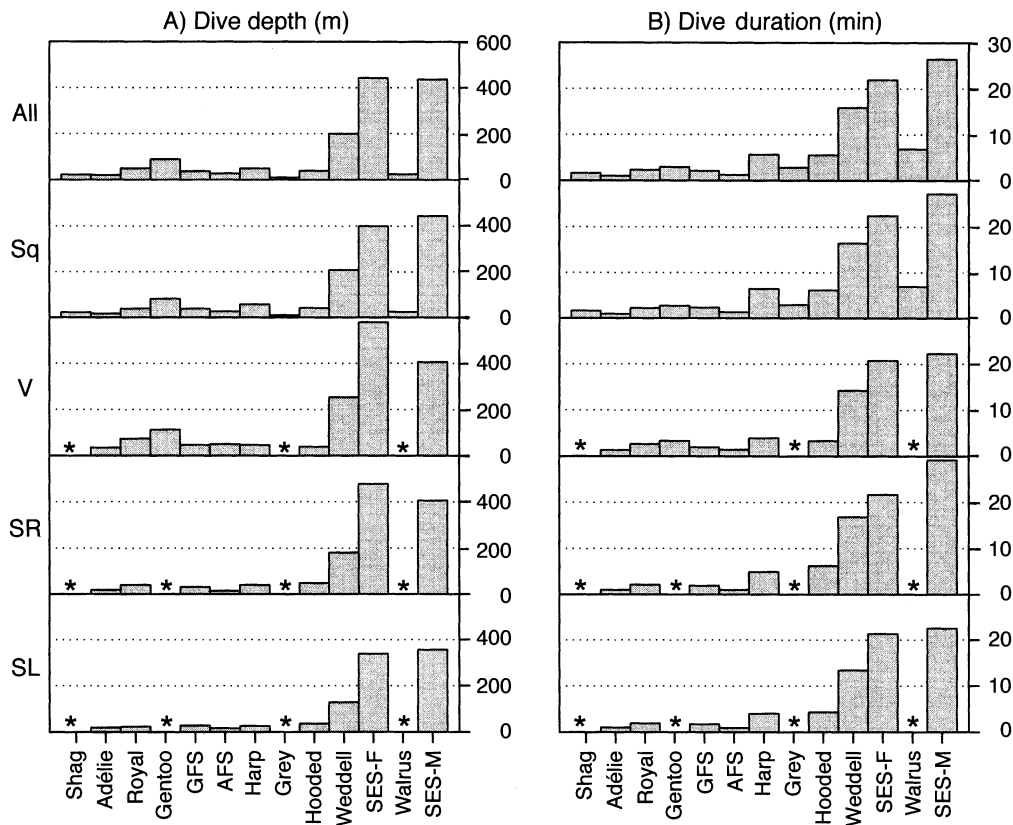


FIG. 3. Mean values for (A) maximum depth (m) and (B) duration (min). Stars (\*) denote insufficient data to calculate statistics. Abbreviations are as in Fig. 2.

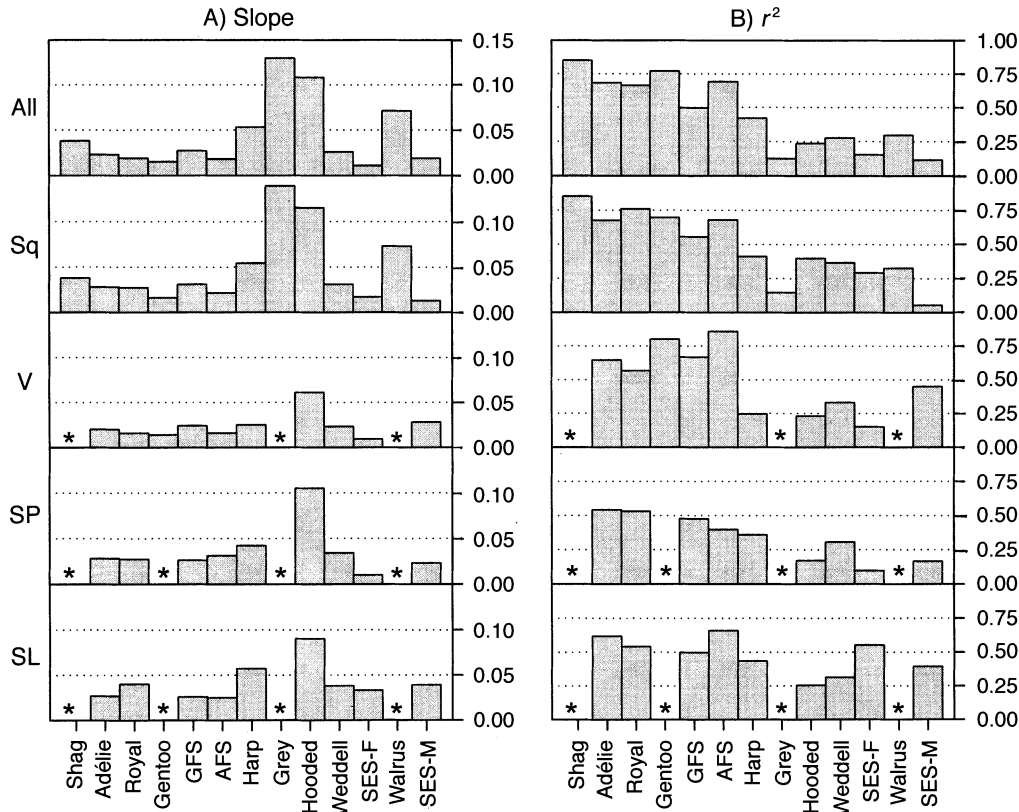


FIG. 4. (A) Slope and (B)  $r^2$  describing the relationship between maximum depth (independent variable) and duration (dependent variable). Stars (\*) denote insufficient data to calculate statistics. Abbreviations are as in Fig. 2.

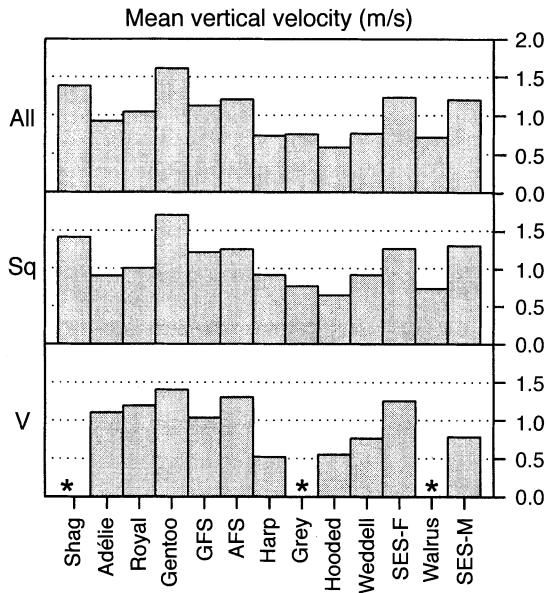


FIG. 5. Mean vertical velocity (m/s). Stars (\*) denote insufficient data to calculate statistics. Abbreviations are as in Fig. 2.

mean vertical velocity across species revealed a weak trend toward higher rates for smaller divers (Fig. 5).

The amount of bottom time for square dives generally increased with mass in a pattern similar to that for duration (Fig. 6A). However, when bottom time was scaled to duration for square dives, it was generally similar across species (41–74%; 41–53% when excluding the four highest values), but was higher for benthic foragers (Blue-eyed Shag, grey seal, and walrus; Fig. 6B, Table 4). Comparison of dive variables describing the bottom of square dives indicated similarities and differences (Fig. 7). Standard deviation of depth during bottom time generally increased with mass, considering seabirds and pinnipeds separately, probably through differences in diving depth. When scaled to depth, however, the coefficient of variation showed little variation around 15%. The percentage of dives with wiggles indicated very low and high values for benthic foragers and pelagic foragers, respectively. Wiggle counts within dives with wiggles showed little variation above one. When scaled to bottom time, a decreasing trend occurred, but this pattern probably resulted from increases in bottom time and duration with body size. Mean wiggle distance showed a pattern similar to standard deviation of depth during bottom time and maximum depth, but, when scaled to depth,

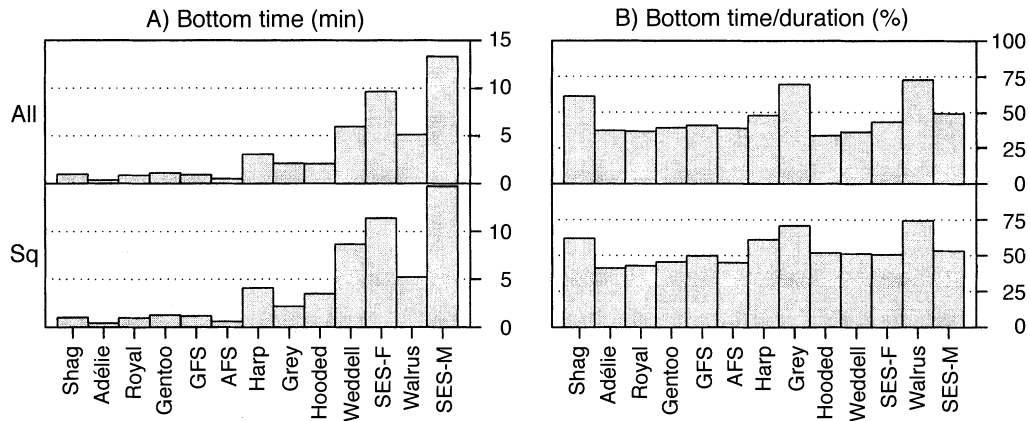


FIG. 6. Mean values for (A) bottom time and (B) bottom time/duration. Abbreviations are as in Fig. 2.

displayed little variation across species (similar to the coefficient of variation and generally at 15%).

The length of the postdive surface interval generally increased with increasing body size, similar to duration, but when postdive surface interval was scaled to duration, it generally decreased with increasing size (Fig. 8). This trend, however, was not apparent for all dive types, and no obvious trend was observed across dive types. Increasing dive duration generally did not affect the postdive surface interval for most species (Fig. 9), although a weak pattern could be seen across species, indicating that smaller divers increased the postdive surface interval more rapidly with increasing duration than did larger ones. Also, Blue-eyed Shag and Antarctic fur seal showed a relatively rapid increase in postdive surface interval with increasing duration, although only Blue-eyed Shag had a strong relationship between these variables. Similar trends were also seen when postdive surface interval and duration were plotted along with a LOWESS smoother (Fig. 10). All species generally showed a weak increase in postdive surface interval with increasing duration, although there was considerable scatter around the curves. As indicated by the linear regression results, Blue-eyed Shag and Antarctic fur seal showed the strongest increases, although Weddell and hooded seal also showed fairly strong increases. Several of the species had inflections at certain durations, although, except for Blue-eyed Shag and Antarctic fur seal, these were quite weak.

#### *Hierarchical classifications*

Five of the species had sufficient multimodality in one or more dive variables to warrant subdivisions of dive types (for schematics, see Schreer 1997: Fig. 4.9). Walrus square dives were divided into three groups based on mean vertical velocity ( $<0.6$  m/s,  $\geq 0.6$  but  $<1.0$  m/s, and  $\geq 1.0$  m/s). Male southern elephant seal square dives and Antarctic fur seal V dives were each divided into two groups based on mean vertical velocity

(southern elephant seal:  $<1$  m/s and  $\geq 1$  m/s, Antarctic fur seal:  $<0.8$  m/s and  $\geq 0.8$  m/s), as were harp seal square and V dives (square:  $<0.5$  m/s and  $\geq 0.5$  m/s, V:  $<0.48$  m/s and  $\geq 0.48$  m/s). Weddell seal square dives were divided into two groups based on depth per duration ( $<4$  m/s and  $\geq 4$  m/s).

Relevant dive variables for the hierarchical groups indicated some differences between dive types (Table 6). Dives with high values for mean vertical velocity (Antarctic fur seal, harp seal, walrus, and male southern elephant seal) and depth per duration (Weddell seal) were generally more abundant (opposite for walrus), deeper, longer (opposite for southern elephant seal), and had longer bottom times and bottom time per durations (no change for Weddell seal) than dives with low values. The other parameters were more variable. The percentage of dives with wiggles did not vary with mean vertical velocity for harp seal, whereas it decreased with increasing mean vertical velocity for walrus (although values were very small), and was higher for larger criteria values for southern elephant and Weddell seal. Wiggle count and wiggle count per bottom time showed little variation. Mean wiggle distance and mean wiggle distance per maximum depth were higher and lower, respectively, for higher criteria values for harp and Weddell seal, whereas southern elephant seal had the opposite relationship for mean wiggle distance and an even stronger relationship for mean wiggle distance per maximum depth. Standard deviation of depth during bottom time varied in a similar fashion to maximum depth, whereas the coefficient of variation was lower for harp and Weddell seal, higher for walrus, and did not change for southern elephant seal, for higher criteria values.

#### *Diel patterns*

All species exhibited some sort of diel pattern, although these patterns varied considerably across species (Fig. 11). Patterns within a species were generally consistent across dive types, although there were sev-

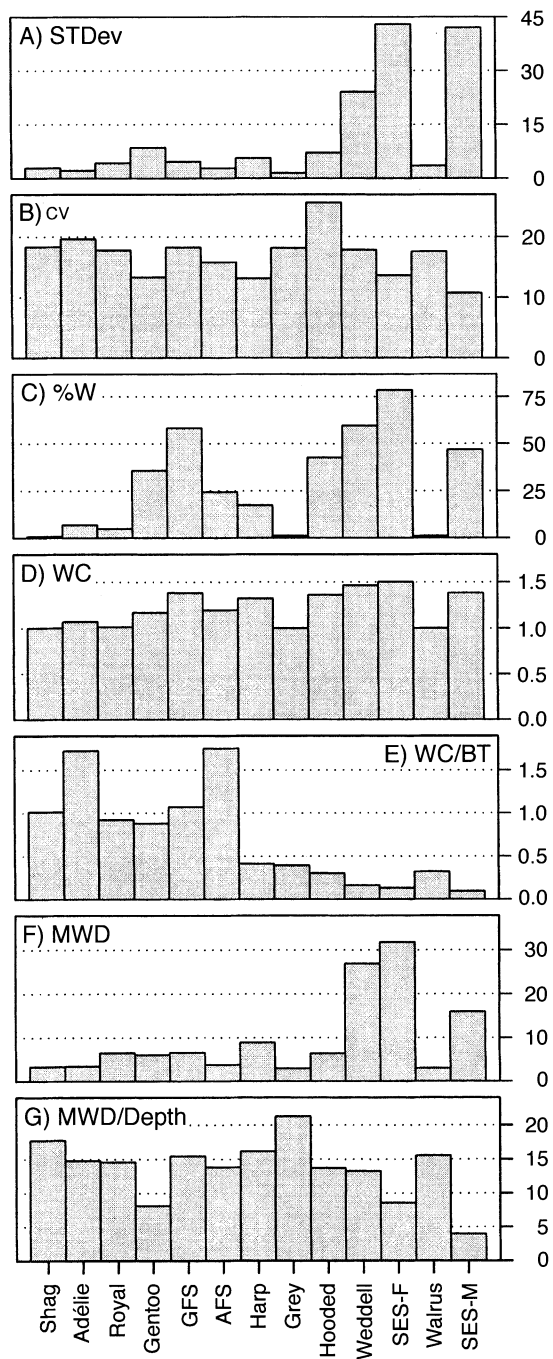


FIG. 7. Statistics for the bottom time of square dives. Mean values for (A) standard deviation of depth (m) and (B) coefficient of variation (%) of depth during bottom time. (C) Percentage of dives with wiggles. For dives with wiggles: (D) wiggle count, (E) wiggle count/bottom time (no./min), (F) mean wiggle distance (m), (G) mean wiggle distance/maximum depth (%). Abbreviations are as in Fig. 2. Definitions are as in Table 3.

eral exceptions. All species dived more at certain times of the day, but there were no consistent trends across all species. Some subgroups, however, showed similar patterns: all seabirds dived almost exclusively during the day, and both fur seals dived almost entirely at night. In general, species thought to be pelagic foragers dived deeper and longer during the day (i.e., Weddell seal, female southern elephant seal, and Royal, Adélie, and Gentoo penguins), whereas benthic foragers (obligate or facultative; i.e., Blue-eyed Shag, male southern elephant seal, walrus, and grey seal) or species performing behaviors other than foraging (i.e., grey, harp, and hooded seal) showed little to no diel patterns in maximum depth and duration (see Table 4). These patterns were difficult to interpret for the fur seals because they dived almost exclusively at night. However, Antarctic fur seal showed a tendency toward shallow, shorter dives during the night, whereas Galápagos fur seal showed the opposite trend. It needs to be noted that some of these interpretations are very limited by the small number of dives during certain times of day for several species.

Diel patterns for hierarchical subdivisions showed a general trend toward deeper and longer dives for higher values of depth per duration and mean vertical velocity (Fig. 11). For male southern elephant seal and harp seal, less diel variation in maximum depth was observed for higher values of mean vertical velocity. For Weddell seal, less diel variation in maximum depth was observed for lower values of depth per duration. Diel patterns for the two groups of V dives for Antarctic fur seal are not shown because there were too few dives to show patterns adequately.

#### Calculated aerobic dive limit

Calculated aerobic dive limits (cADL), with  $DMR = 2 \times SMR$ , indicate that seabirds and fur seals rarely exceeded their cADL, whereas larger phocids exceeded their cADL for a majority of their dives (Table 7). When  $DMR = 4 \times SMR$  was used for fur seals and seabirds, a considerable percentage of dives exceeded the cADL, except for Antarctic fur seal and Adélie Penguin, for which dives still rarely exceeded their cADLs. When  $DMR = 1 \times SMR$  for the phocids and odobenids, only 1–20% of the dives exceeded the cADL, except for harp, grey, and hooded seal and walrus, for which no dives exceeded the cADL. Among the dive types, square dives generally had the largest percentage of dives greater than the cADL. However, for Adélie, Royal, and Gentoo penguins and Antarctic fur seal, V dives exceeded the cADL most often. Further, for Weddell and southern elephant seal ( $DMR = 1 \times SMR$ ), skewed-right dives exceeded the cADL as often or more often than did square dives. As previously mentioned, assessing the effect of dive duration on postdive surface interval using both linear and nonlinear models revealed little regarding cADL (Figs. 9 and 10). For those species in which inflections could be observed

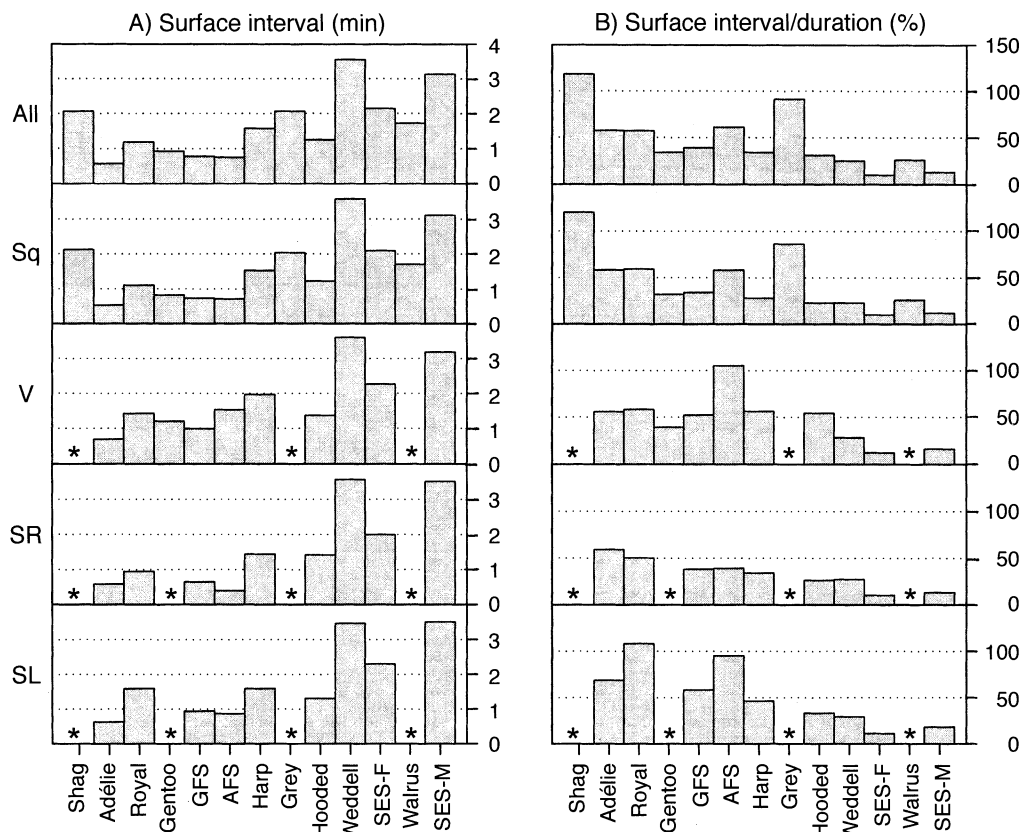


FIG. 8. Mean values for (A) postdive surface interval (min) and (B) postdive surface interval/duration (%). Postdive surface interval was limited to  $\leq 30$  min. Stars (\*) denote insufficient data to calculate statistics. Abbreviations are as in Fig. 2.

(strong inflection: Blue-eyed Shag, Antarctic fur seal; weak inflection: Adélie, Royal, and Gentoo penguins), the locations of these changes were more similar to cADL calculated with  $4 \times$  SMR than with  $2 \times$  SMR.

#### DISCUSSION

There were several strong similarities in diving patterns across very different species, indicating the use of similar behavioral regimes. Dive profiles (scaled to equivalent depth and duration) could generally be characterized as one of four shapes: square, V, skewed right, and skewed left. In addition, square dives were always, and by far, the most abundant dive type. V dives were usually the next most abundant dive type, followed by the skewed dives.

#### *Dive type functions*

It is very difficult to discuss general trends in dive type functions across species because these functions may not be consistent from one species to another. In any regard, most probable functions of the dive types will be proposed and possible variants will be noted.

*Square dives.*—Almost all of the studies that have grouped diving behavior according to shape have indicated that some of the profiles had some sort of

square-like shape. Square dives have been suggested to represent foraging because they are very abundant, occur in bouts or series, generally have a uniform depth within a bout, and often exhibit diel variation in maximum depth (Le Boeuf et al. 1988, 1992, Hindell et al. 1991b, Schreer and Testa 1996). Also, the mere shape of a square dive suggests that it may have a foraging function because the animal is maximizing the percentage of the time spent at a particular depth (i.e., the bottom of the dive where the prey may reside), and is descending rapidly and directly to this depth. Square dives for the species observed here were always, and by far, the most abundant dive type, often occurred in bouts, had uniform depths within a bout, and exhibited diel variation in maximum depth (within several of the species: Royal Penguin, Galápagos fur seal, Antarctic fur seal, southern elephant seal, and Weddell seal). Diel patterns may not have been observed for square dives in the other species because (1) the sample sizes were too small (Blue-eyed Shag and hooded seal); (2) these dives may have represented a myriad of functions for species that were not primarily foraging (grey, harp, and hooded seal); or (3) the species primarily feed on benthic prey and therefore would not exhibit diel variation in maximum depth because their prey do not

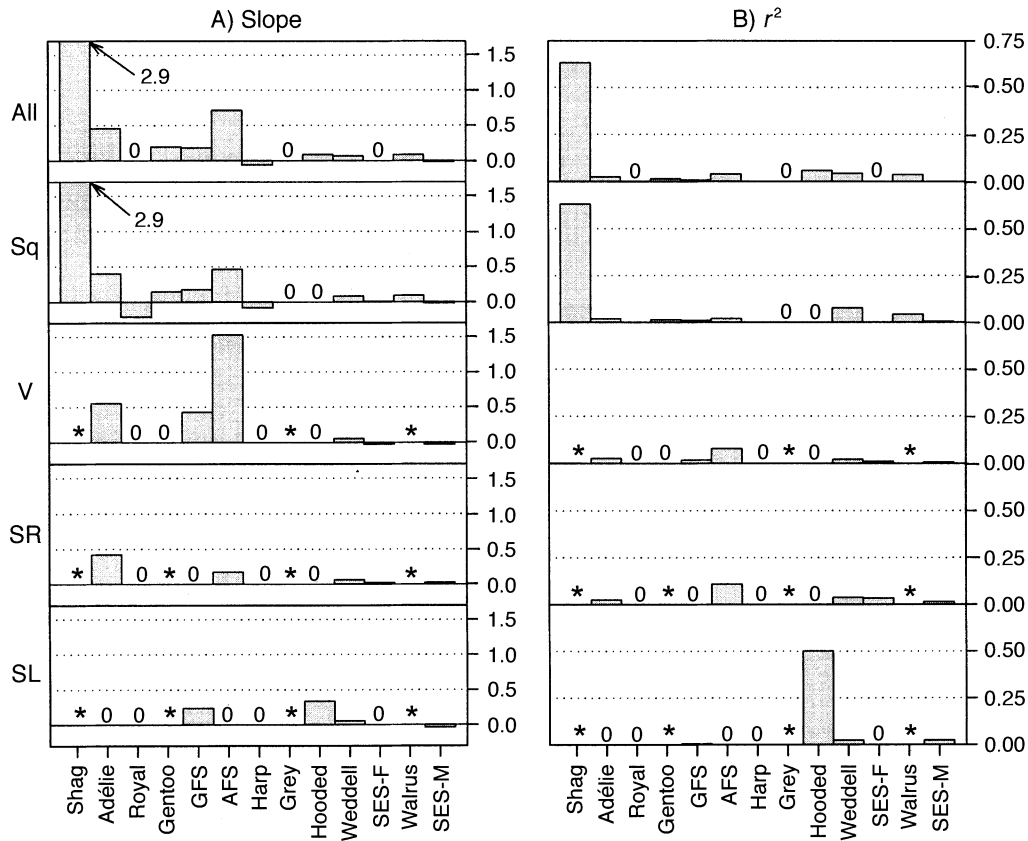


FIG. 9. (A) Slope and (B)  $r^2$  of the relationship between duration (independent variable) and postdive surface interval (dependent variable). Postdive surface interval was limited to  $\leq 30$  min. Stars (\*) denote insufficient data to calculate statistics. A "0" denotes a value not significantly different from zero ( $P > 0.05$ ). Abbreviations are as in Fig. 2.

migrate vertically (Blue-eyed Shag, grey seal, walrus; square dives with mean vertical velocity  $\geq 1$  for male southern elephant seal). In addition, regardless of the problems associated with calculating cADL, square dives generally exceeded the cADL more than did other dives types (at least for the phocids), further supporting a function as important as foraging, in which pushing physiological limits may be necessary.

Other functions suggested for square dives are specifically benthic or pelagic foraging (Le Boeuf et al. 1988, 1992, Hindell et al. 1991b, Schreer and Testa 1996), exploring, or traveling (Kooyman 1968, Schreer and Testa 1996). Dives thought to be benthic usually have fewer wiggles than do pelagic dives, and exhibit weaker or no diel variation in maximum depth because benthic prey have a much more limited vertical range. Walrus, grey seal, and Blue-eyed Shag are all thought to be primarily benthic foragers (Fay and Burns 1988, Croxall et al. 1991, del Hoyo et al. 1992, Jefferson et al. 1993, Wiig et al. 1993, Bevan et al. 1997), and all of these species had very few wiggles and no diel pattern toward deeper dives during the day. Male southern elephant seals have also been thought to perform some benthic foraging. In this species, square dives of males

had fewer and smaller wiggles than those of their female counterparts. As well, when male southern elephant seal square dives were subdivided based on mean vertical velocity, dives with higher values had less diel variation in maximum depth and smaller mean wiggle distance, despite deeper maximum depth. Square dives for the other species probably represented pelagic foraging, with higher numbers of wiggles and stronger diel variation in maximum depth.

Some square dives may also have an exploratory or traveling function, as previously proposed for Weddell seal (Kooyman 1968, Schreer and Testa 1996) and supported by results from this study. These were dives that had long durations relative to maximum depth (rectangular: square dives with depth per duration  $< 4$ ). They would be useful for traveling because the seal spent a large amount of time below the surface reducing drag (Williams and Kooyman 1985), within aerobic limits, and traveling potentially in a horizontal direction (Schreer and Testa 1996). (However, a horizontal line within a profile of depth vs. time indicates only that the animal was not moving up or down for a period of time, and not necessarily that it was moving horizontally.) These dives had little or no diel variation in

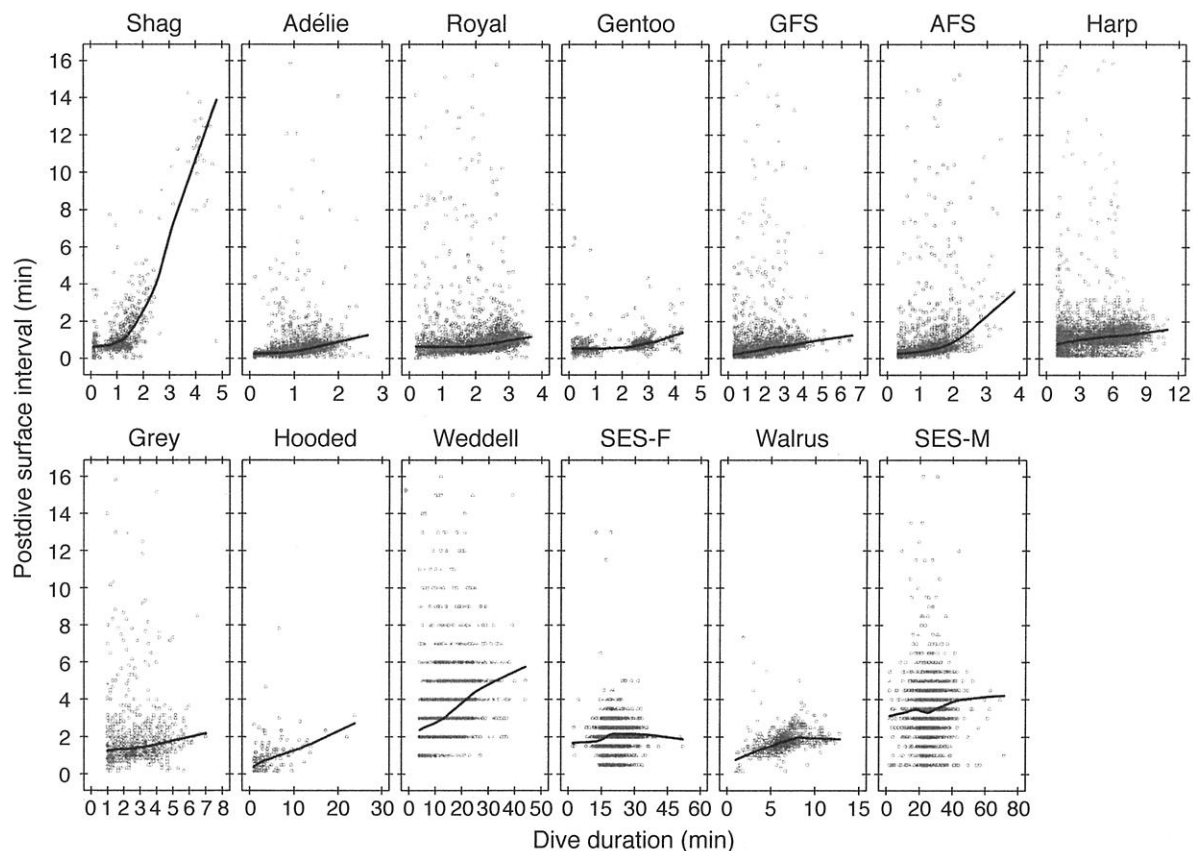


FIG. 10. Postdive surface interval vs. duration, smoothed by the LOWESS method. For Adélie Penguin, Galápagos fur seal, Weddell seal, and female and male southern elephant seal, a subsample of ~5500 dives was used. Postdive surface interval was limited to  $\leq 16$  min. Abbreviations are as in Fig. 2.

maximum depth and fewer wiggles (compared to deeper square dives), suggesting that pelagic foraging was not likely. However, shallow-benthic foraging cannot be ruled out.

*V dives.*—Most studies of dive profiles have also indicated that some of the dives had a V or spiked shape. These dives have been thought to represent predator avoidance (Hindell et al. 1991b), travel (Hindell et al. 1991b, Le Boeuf et al. 1992, Campagna et al. 1995), or exploration (Hindell et al. 1991b, Bengtson and Stewart 1992, Schreer and Testa 1996). In these dives, the animal dives deep below the surface and follows a direct path, perhaps to avoid predators, search for a prey patch, or get a better acoustical or visual image of its surroundings. The relative deepness of the V dives found for most species in this work is consistent with these suggestions. Also, the relatively short durations for these dives and the relative low percentage of dives greater than the cADL for phocids is consistent with maximizing depth while staying within duration limits.

However, the V dives for several species may also have a foraging function (Boyd and Croxall 1992, Burns et al. 1997, Burns and Schreer, *in press*). The

relatively large percentage of V dives performed by Royal and Gentoo penguins, strong diel variation in maximum depth and duration (stronger than square dives: Adélie, Royal, and Gentoo penguins), and the relatively high percentage of dives with durations greater than the cADL ( $DMR = 4 \times SMR$ ) for Adélie, Royal, and Gentoo penguins and Antarctic fur seal support this conclusion. All of these species are relatively small and would be more duration limited than the larger species. Therefore, when performing foraging dives to relatively great depths, smaller animals may have to sacrifice bottom time in order to remain within aerobic limits, causing these dives to have more of a V shape. Weddell and female southern elephant seals also showed strong diel variation in maximum depth and duration for V dives, but unlike Adélie, Royal, and Gentoo penguins, which had longer mean durations for V dives relative to square dives, their V-shaped dives had relatively shorter durations, suggesting a more exploratory function.

*Skewed-left dives.*—Skewed-left dives have been indicated as a dive type in far fewer studies than have square or V dives (Le Boeuf et al. 1988, 1992, Hindell et al. 1991b, Jonker and Bester 1994, Schreer and



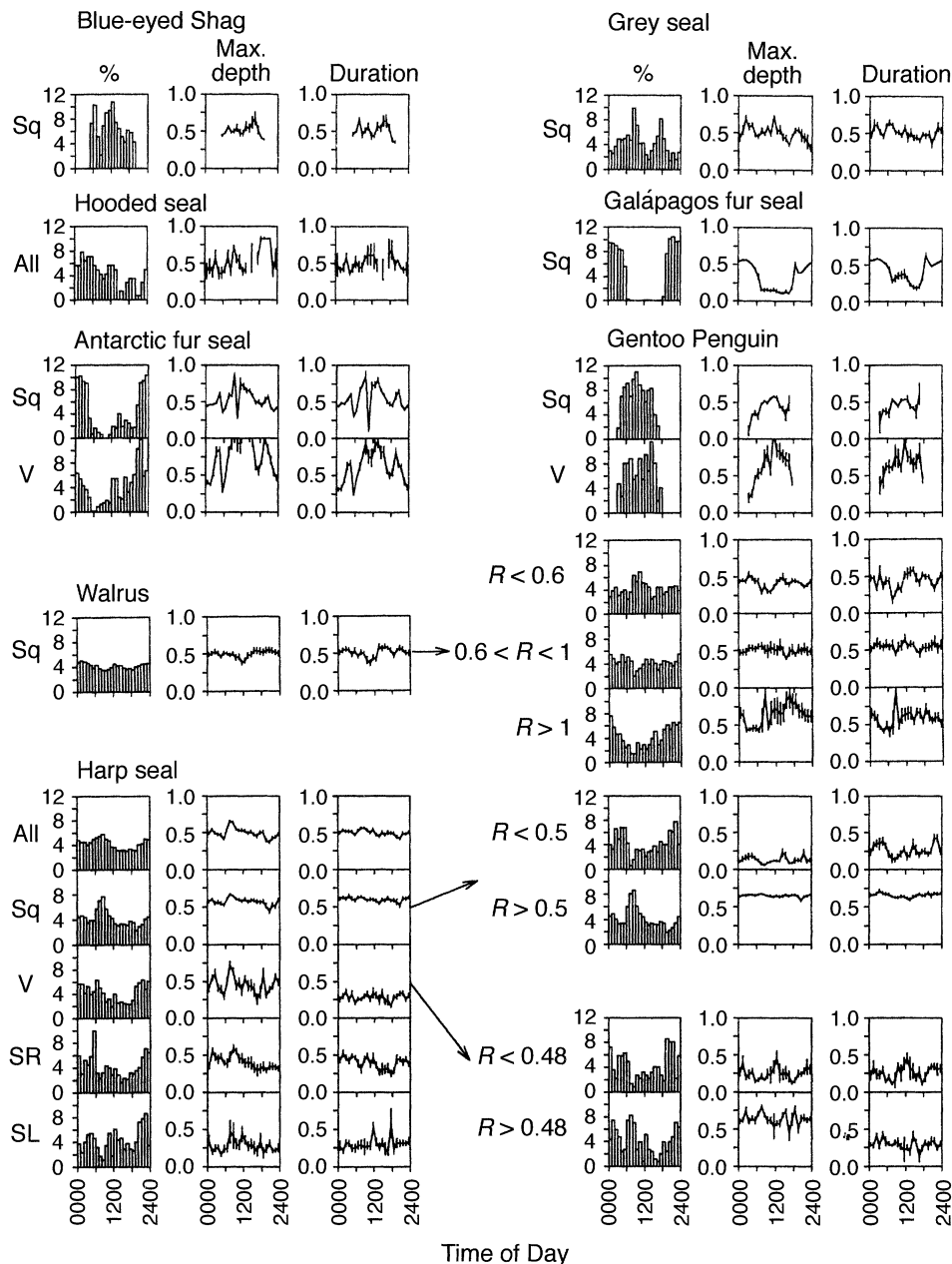


FIG. 11. Diel variation in percentage dive frequency, standardized maximum depth (mean  $\pm$  1 SE), and standardized duration (mean  $\pm$  1 SE) for Blue-eyed Shag, hooded seal, Antarctic fur seal, walrus, harp seal, grey seal, Galápagos fur seal, Gentoo Penguin; and female (F) and male (M) southern elephant seal, Royal Penguin, Adélie Penguin, and Weddell seal. Patterns are shown for each dive type (square, V, skewed right, and skewed left) and for any additional dive types that resulted from the hierarchical classifications. Dive types with too few observations to show patterns adequately, or with patterns very similar to previously displayed types, are not shown. Maximum depth and duration were standardized for each species, with the mean equal to 0.5 and one standard deviation equal to 0.25.  $R$  is mean vertical velocity (m/s);  $Q$  is maximum depth/duration (m/min).

Testa 1995, 1996, Burns et al. 1997, Crocker et al. 1997, Schreer et al. 1998, Burns and Schreer, *in press*), and are nearly absent for many of the species examined here: Blue-eyed Shag, Adélie Penguin (consistent with cluster analyses from Schreer et al. 1998), Royal Penguin, Gentoo Penguin, Antarctic fur seal, grey

seal, walrus, and male southern elephant seal (<2% of all dives). These dives have been suggested to represent exploration before a bout of square, foraging dives (Schreer and Testa 1996), resting or food processing (Hindell et al. 1991b, Le Boeuf et al. 1992, Schreer and Testa 1996, Crocker et al. 1997), foraging

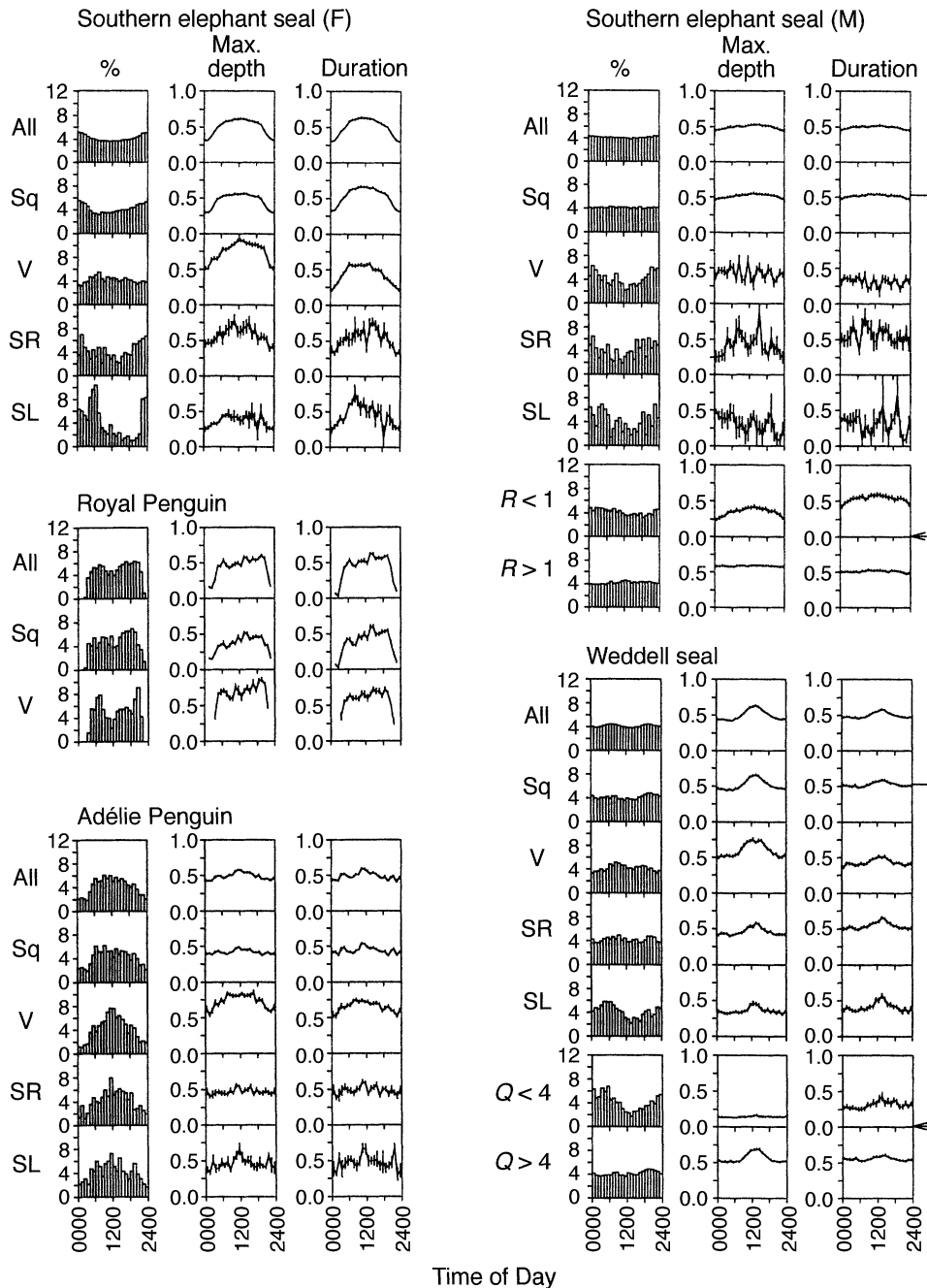


FIG. 11. Continued.

where prey are pursued vertically as well as horizontally (Chappell et al. 1993a), or they may simply be a result of the animal following the bottom away from a haul-out site (Schreer and Testa 1996). In any event, these dives are relatively rare and they exceed 5% of all dives in only four species (Galápagos fur seal and harp, hooded, and Weddell seal). This suggests that skewed-left dives may be fairly unimportant to most species. However, despite the rarity of these dives, the suggestion of the seemingly important functions of

resting, sleeping, or processing of food or anaerobic metabolites underwater in northern and southern elephant seal has been explored and substantiated by several studies (Hindell et al. 1991b, Le Boeuf et al. 1992, Crocker et al. 1997). It is thought that the period of slow descent represents the time when a seal stops swimming and slowly sinks. Oxygen saved through reduced locomotion could be used to process food. This suggestion has been substantiated by swim velocity profiles, which have shown very slow velocities

TABLE 6. Dive statistics (mean  $\pm$  1 SD) for dive types of five species resulting from a hierarchical classification.

| Parameter  | Antarctic fur seal |               | Harp seal       |                 |               |               |
|--|--------------------|---------------|-----------------|-----------------|---------------|---------------|
|  | V dive             |               | Square dive     |                 | V dive        |               |
|  | $R < 0.8$          | $R \geq 0.8$  | $R < 0.5$       | $R \geq 0.5$    | $R < 0.48$    | $R \geq 0.48$ |
| $n$  | 110                | 348           | 425             | 2539            | 222           | 255           |
| Percentage of dives <sup>†</sup>                         | 24                 | 76            | 14              | 86              | 47            | 53            |
| Maximum depth (m)  | 14 $\pm$ 5         | 60 $\pm$ 32   | 14 $\pm$ 13     | 64 $\pm$ 10     | 25 $\pm$ 18   | 65 $\pm$ 14   |
| Duration (min)   | 0.9 $\pm$ 0.3      | 1.6 $\pm$ 0.6 | 3.9 $\pm$ 1.8   | 6.9 $\pm$ 1.3   | 3.8 $\pm$ 1.6 | 4.0 $\pm$ 1.1 |
| Bottom time (min)  |                    |               | 1.8 $\pm$ 1.5   | 4.5 $\pm$ 1.4   |               |               |
| Bottom time per duration (%)                             |                    |               | 45.3 $\pm$ 22.1 | 64.0 $\pm$ 10.7 |               |               |
| Percentage of dives with wiggles (%)                     |                    |               | 17.4            | 17.3            |               |               |
| Wiggle count <sup>‡</sup>                                |                    |               | 1.1 $\pm$ 0.3   | 1.4 $\pm$ 0.7   |               |               |
| Wiggle count per bottom time <sup>‡</sup>                |                    |               | 0.6 $\pm$ 0.3   | 0.4 $\pm$ 0.2   |               |               |
| Mean wiggle distance <sup>‡</sup>                        |                    |               | 3.6 $\pm$ 2.1   | 9.8 $\pm$ 6.1   |               |               |
| Mean wiggle distance per max. depth (%) <sup>‡</sup>     |                    |               | 22.0 $\pm$ 7.8  | 15.1 $\pm$ 8.8  |               |               |
| Standard deviation of depth during bottom time           |                    |               | 2.2 $\pm$ 1.4   | 6.2 $\pm$ 4.2   |               |               |
| Coefficient of variation of depth during bottom time (%) |                    |               | 26.7 $\pm$ 17.4 | 10.8 $\pm$ 8.3  |               |               |

Note:  $R$ , mean vertical velocity (m/s);  $Q$ , maximum depth divided by duration (m/min).

<sup>†</sup> The number of dives for one subshape divided by all dives of that shape.

<sup>‡</sup> Only calculated for dives with wiggles.

<sup>§</sup> Too few observations to calculate statistics.

|| Only calculated for square dives.

during part of the descent phase of these dives (Le Boeuf et al. 1992, Hindell and Burton 1993, Crocker et al. 1997), body composition measurements that indicate buoyancy-dependent drifting during descent, and a temporal correlation with square (foraging) dives (Crocker et al. 1997). It seems plausible that these dives do represent resting or processing in elephant seal and perhaps Weddell seal, because these species dive nearly continuously for several months (Le Boeuf et al. 1988, 1989, Hindell et al. 1991b, Schreer and Testa 1996). For the other species, however, this function seems unlikely. Many of the species (Blue-eyed Shag, Adélie Penguin, Royal Penguin, Gentoo Penguin, Galápagos fur seal, and Antarctic fur seal) generally dived continuously for <24 h and therefore could either rest at the surface or when hauled out.

*Skewed-right dives.*—Skewed-right dives are also fairly rare in studies of dive shape (Kooyman and Gentry 1986, Chappell et al. 1993a, Jonker and Bester 1994, Schreer and Testa 1995, 1996, Burns et al. 1997, Crocker et al. 1997, Schreer et al. 1998, Burns and Schreer, *in press*) and, not surprisingly, were nearly absent for several of the species here (Blue-eyed Shag, Gentoo Penguin, grey seal, and walrus: <2% of all dives). These dives have been suggested to represent exploration (Kooyman and Gentry 1986, Jonker and Bester 1994, Schreer and Testa 1996), traveling (Jonker and Bester 1994), food processing (Schreer and Testa 1996, Crocker et al. 1997), foraging where prey are pursued vertically as well as horizontally (Chappell et al. 1993a), or they may simply be a result of the animal following the bottom back to a haul-out

site (Schreer and Testa 1996). In any event, these dives are relatively rare and they exceed 10% of all dives in only three species (harp, hooded, and Weddell seal). This suggests that skewed-right dives may not be a terribly important component of most of the species' diving regimes and are simply hybrid dives (e.g., an aborted square foraging dive that has become an exploratory dive) or random dives with no specific function or with multiple functions. However, for Weddell seal, which had the highest percentage of this dive type and the longest dive records, it has been suggested that these dives may allow the seal to process food when hauling out is unlikely. In Weddell seal, skewed-right dives were most common farthest from the initial haul-out sites (Schreer and Testa 1996). A similar suggestion has also been made for female northern elephant seal during late pregnancy (Crocker et al. 1997). However, the relatively high percentage of skewed-right dive durations that exceeded the cADL for both of these species is highly curious for dives that may have a processing function. A possible explanation would be that a decrease in oxygen consumption during these dives (similar to skewed-left dives) would extend the ADL for this dive type.

#### Comparisons across species

Comparing diving patterns across species is complicated because of differences in sampling regimes, life stage, number of individuals and dives, and length of coverage. Although variation in sampling intervals could be adjusted for by resampling, differences in life stage, number of individuals (1–36), total number of dives (366–83 404), and length of coverage (2–195 d)

TABLE 6. Extended.

| Weddell seal    |                 | Walrus          |                    |                | Southern elephant seal ♂ |                 |
|-----------------|-----------------|-----------------|--------------------|----------------|--------------------------|-----------------|
| Square dive     |                 | Square dive     |                    |                | Square dive              |                 |
| $Q < 4.0$       | $Q \geq 4.0$    | $R < 0.6$       | $0.6 \leq R < 1.0$ | $R \geq 1.0$   | $R < 1.0$                | $R \geq 1.0$    |
| 1947            | 14 814          | 519             | 494                | 276            | 3250                     | 7735            |
| 12              | 88              | 40              | 38                 | 22             | 30                       | 70              |
| $25 \pm 19$     | $232 \pm 104$   | $20 \pm 7$      | $24 \pm 11$        | $31 \pm 17$    | $369 \pm 104$            | $476 \pm 81$    |
| $11.0 \pm 6.2$  | $17.1 \pm 5.6$  | $6.4 \pm 1.5$   | $7.2 \pm 1.5$      | $7.4 \pm 1.5$  | $28.5 \pm 7.1$           | $26.5 \pm 5.1$  |
| $6.2 \pm 5.3$   | $9.0 \pm 3.9$   | $4.4 \pm 1.6$   | $5.6 \pm 1.4$      | $6.0 \pm 1.4$  | $13.2 \pm 5.3$           | $15.3 \pm 4.6$  |
| $51.7 \pm 24.6$ | $51.4 \pm 11.1$ | $67.2 \pm 14.4$ | $77.4 \pm 5.7$     | $81.5 \pm 5.4$ | $45.3 \pm 10.2$          | $56.7 \pm 8.6$  |
| 15.8            | 65.2            | 1.7             | 0.6                | 0.3            | 31.8                     | 52.8            |
| $1.5 \pm 0.9$   | $1.5 \pm 0.7$   | §               | §                  | §              | $1.3 \pm 0.6$            | $1.4 \pm 0.7$   |
| $0.2 \pm 0.1$   | $0.2 \pm 0.1$   | §               | §                  | §              | $0.1 \pm 0.0$            | $0.1 \pm 0.0$   |
| $9.1 \pm 4.9$   | $27.4 \pm 19.5$ | §               | §                  | §              | $29.0 \pm 28.4$          | $12.6 \pm 14.2$ |
| $22.3 \pm 8.3$  | $12.9 \pm 8.5$  | §               | §                  | §              | $8.6 \pm 8.5$            | $2.8 \pm 3.5$   |
| $5.1 \pm 3.2$   | $26.8 \pm 18.1$ | $2.1 \pm 2.1$   | $3.5 \pm 2.6$      | $6.2 \pm 3.0$  | $32.5 \pm 20.6$          | $46.6 \pm 30.6$ |
| $32.1 \pm 17.6$ | $16.0 \pm 12.9$ | $13.2 \pm 13.3$ | $17.8 \pm 12.8$    | $25.0 \pm 9.5$ | $10.8 \pm 8.9$           | $10.7 \pm 7.5$  |

remained. These sorts of problems exist for all interspecific, interstudy comparisons and, short of collecting equal amounts of data under similar conditions for all species (usually logistically and financially impossible), they must simply be considered when making comparisons. Gentry and Kooyman (1986) was the first comprehensive study that addressed many of these problems by using similar equipment, study design, and analytical procedures on numerous species within a single family, Otariidae. However, this leads to an additional problem with any interspecific comparison: exaggerated similarity due to phylogenetic relatedness. In the present work, because the 12 species studied represent two different classes (Aves and Mammalia) and five different families (Spheniscidae, penguins; Phalacrocoracidae, cormorants/shags; Phocidae, seals; Otariidae, fur seals; and Odobenidae, walrus), all of which may have re-invaded the ocean at different times, most observed similarities are probably due to convergent evolution.

*Diving capacity.*—The body size of the species had an impact on diving patterns as expected. This has also been shown for larger interspecific comparisons using maximum depth and duration (Piatt and Nettleship 1985, Cooper 1986, Prince and Harris 1988, Burger 1991, Boyd and Croxall 1996, Schreer and Kovacs 1997). Larger animals would be expected to be able to dive longer and, hence, deeper because they can store more oxygen (more blood) and use this oxygen more slowly (lower mass-specific metabolic rate). Within both main groups, larger seabirds and pinnipeds dived deeper and longer than did smaller ones. This trend was also seen over all 13 groups, but the relationship was considerably weaker. Fur seals, which are considerably larger than penguins, do not dive deeper or longer than the larger penguins. Schreer and Kovacs (1997) also observed this for maximum depth and du-

ration. Otariids, which often prey on food items that are similar to those of penguins, such as krill and cephalopods, may not need to dive deeper or longer than penguins because their prey occur at similar depths. In contrast, if otariids have higher DMRs and lower TBO<sub>2</sub>s than phocids and seabirds, their shorter and shallower diving patterns may be the result of physiological limitations. Other species that would be expected to dive deeper and longer, based on their body size, are walrus and grey, harp, and hooded seal. The seals are all known to dive considerably deeper and longer than the dives analyzed here (Schreer and Kovacs 1997); and the performances reported here are almost certainly due to limited water depth. It is likely that walrus are also able to dive to greater depths and for longer durations than have been recorded, but have little reason to do so because of the abundance of their benthic prey in shallow waters (Fay and Burns 1988).

*Dive shape.*—The percentages of dives within each dive type across species were surprisingly similar, with square dives being always, and by far, the most abundant, V dives being the next most abundant dive type, and the skewed dives being the least abundant. Even more surprising was that bottom time per duration and the variation in depth during bottom time (coefficient of variation and mean wiggle distance per depth for square dives with wiggles) among square dives were extremely consistent across species. This indicates that similar foraging strategies are used across different species, with regard to optimizing time at the prey patch and vertical pursuit distances from this patch. The only explanations for the differences observed in the percentage and bottom time per duration of square dives were the type of foraging performed, water depth, and life stage (e.g., the main activity during the recording periods). The three species with the highest percentage and bottom time per duration of square dives (Blue-

TABLE 7. Calculated aerobic dive limits (cADL) and the percentage of dives that exceed these values, by dive shape.

| Species                  | Mass (kg)† | cADL (min) | 2 × SMR                  |       |      |      |      |      |
|--------------------------|------------|------------|--------------------------|-------|------|------|------|------|
|                          |            |            | Dives exceeding cADL (%) |       |      |      |      |      |
|                          |            |            | All                      | Shape | Sq   | V    | SR   | SL   |
| Blue-eyed Shag           | 2.4        | 2.83       | 5.3                      | 6.3   | 6.4  | 0.0  | 0.0  | 0.0  |
| Adélie Penguin           | 3.8        | 3.20       | 0.0                      | 0.0   | 0.0  | 0.0  | 0.0  | 0.0  |
| Royal Penguin            | 5.3        | 3.50       | 1.9                      | 2.5   | 1.3  | 5.4  | 0.0  | 0.0  |
| Gentoo Penguin           | 5.5        | 3.54       | 7.6                      | 12.0  | 1.2  | 36.5 | 0.0  | 0.0  |
| Galápagos fur seal       | 29.0       | 4.59       | 0.1                      | 0.3   | 0.4  | 0.1  | 0.3  | 0.1  |
| Antarctic fur seal       | 34.4       | 4.80       | 0.0                      | 0.0   | 0.0  | 0.0  | 0.0  | 0.0  |
| Harp seal                | 138.2      | 10.18      | 0.2                      | 0.4   | 0.5  | 0.0  | 0.0  | 0.6  |
| Grey seal                | 201.6      | 11.19      | 0.0                      | 0.0   | 0.0  | 0.0  | 0.0  | 0.0  |
| Hooded seal              | 353.5      | 12.88      | 1.6                      | 4.3   | 5.8  | 0.0  | 7.1  | 3.3  |
| Weddell seal             | 339.2      | 12.75      | 41.2                     | 68.7  | 74.3 | 59.0 | 74.7 | 47.4 |
| Southern elephant seal ♀ | 394.0      | 13.23      | 85.6                     | 97.9  | 99.0 | 95.4 | 94.8 | 95.6 |
| Walrus                   | 1500.0     | 10.46      | 4.2                      | 4.7   | 4.8  | 0.0  | 0.0  | 0.0  |
| Southern elephant seal ♂ | 2272.5     | 20.51      | 80.0                     | 88.3  | 92.4 | 60.9 | 82.9 | 57.6 |

Notes: SMR = standard metabolic rate. "All" includes every dive recorded. For the shape comparison, only dives with at least five observations per dive are used, and hybrids are excluded; dive types are analyzed separately by shape, and with all types pooled under "Shape" (Sq, square, V, V-shaped; SR, skewed right; SL, skewed left). See *Methods, Aerobic dive limit* for a description of calculations.

† Masses are from Table 4.

eyed Shag, grey seal, and walrus) were all benthic foragers. Also, male southern elephant seals, which are also thought to perform some benthic foraging, had the fourth highest percentage of square dives. Additionally, when square dives for male southern elephant seals were split using mean vertical velocity, dives with higher values (suspected to be benthic dives because of the lack of diel variation in maximum depth and the smaller mean wiggle distance despite deeper maximum depth) had higher bottom time per duration. This suggests that when animals are able to dive to the bottom, while remaining within their physiological depth limit (because of limited travel time to and from the bottom depth, and not a direct limit due to hydrostatic pressure), they can spend more time at the bottom of the dive. These higher values would make dive profiles appear more "square" and, hence, more square dives would be detected. Also, because these animals are diving to non-moving benthic sites, less time would be needed for exploratory dives (i.e., searching for prey sites). This is substantiated by the very low numbers of V-shaped dives for the four above-mentioned species.

Contrary to the high percentages just mentioned, hooded seal had the fewest square dives and the smallest bottom time per duration among all dives combined. This was the one species that was suspected not to be foraging during the measurement period (Kovacs et al. 1996), which would be consistent with the low percentage of square dives and smallest bottom time per duration. Weddell seal also had a low percentage of square dives and bottom time per duration, but were observed for >6 mo during the overwinter, gestation period, which would indicate that foraging must have been of primary importance. However, the length of these records may explain the lower percentage of

square dives observed. Because the long recording periods sampled so much of these animals' behavior, it is possible that behavior recorded for Weddell seal was simply missed for other species because of their relatively short lengths of coverage. Also, unlike the penguins and fur seals that forage for only hours or days at a time, the Weddell seal spends months in the open ocean and therefore may need more time for exploring (V dives), resting/processing (skewed dives), or other nonforaging activities.

*Depth vs. duration.*—The rate at which duration changed with depth (slope) did not appear to be affected by body size, but divers that were limited by water depth or that dived to the bottom (i.e., Blue-eyed Shag, walrus, and harp, grey, and hooded seal) increased dive duration more rapidly with an increase in maximum depth than did the other species. The amount of variability in duration due to changes in maximum depth ( $r^2$ ) was affected by body size, and decreased with increasing body size in a fairly regular pattern for all dives. This pattern was also seen for square dives, but was weaker or not apparent for the other dive types, probably because of small sample sizes. Boyd and Arnbom (1991) have shown that, for southern elephant seal, dive duration increases rapidly with increasing depth to a point when the rate of increase becomes much slower (i.e., at a certain point, increasing depth does not result in longer dives). If this finding applies to all divers, those that are limited by depth (i.e., benthic foragers and those in relatively shallow water) would only be using the first part of the curve where duration increases rapidly with increasing depth (i.e., large slopes for duration vs. depth). Divers that are diving to all depths within their abilities (i.e., pelagic foragers) could follow the entire curve shown in Boyd and Arnbom (1991) and therefore would, on average,

TABLE 7. Extended.

| 1 × SMR (in italics) and 4 × SMR (in boldface) |                          |             |             |             |             |              |
|--|--------------------------|-------------|-------------|-------------|-------------|--------------|
| cADL (min)                                     | Dives exceeding cADL (%) |             |             |             |             |              |
|  | All                      | Shape       | Sq          | V           | SR          | SL           |
| <b>1.42</b>                                    | <b>36.1</b>              | <b>44.4</b> | <b>45.0</b> | <b>0.0</b>  | <b>50.0</b> | <b>0.0</b>   |
| <b>1.60</b>                                    | <b>4.9</b>               | <b>6.9</b>  | <b>3.8</b>  | <b>20.5</b> | <b>3.5</b>  | <b>5.6</b>   |
| <b>1.75</b>                                    | <b>58.2</b>              | <b>77.0</b> | <b>70.4</b> | <b>91.6</b> | <b>69.6</b> | <b>70.4</b>  |
| <b>1.77</b>                                    | <b>58.4</b>              | <b>92.9</b> | <b>93.6</b> | <b>94.6</b> | <b>28.6</b> | <b>100.0</b> |
| <b>2.30</b>                                    | <b>20.4</b>              | <b>40.4</b> | <b>46.0</b> | <b>28.9</b> | <b>27.9</b> | <b>17.5</b>  |
| <b>2.40</b>                                    | <b>1.0</b>               | <b>1.6</b>  | <b>1.1</b>  | <b>5.7</b>  | <b>1.0</b>  | <b>0.0</b>   |
| <i>20.37</i>                                   | <i>0.0</i>               | <i>0.0</i>  | <i>0.0</i>  | <i>0.0</i>  | <i>0.0</i>  | <i>0.0</i>   |
| <i>22.38</i>                                   | <i>0.0</i>               | <i>0.0</i>  | <i>0.0</i>  | <i>0.0</i>  | <i>0.0</i>  | <i>0.0</i>   |
| <i>25.76</i>                                   | <i>0.0</i>               | <i>0.0</i>  | <i>0.0</i>  | <i>0.0</i>  | <i>0.0</i>  | <i>0.0</i>   |
| <i>25.49</i>                                   | <i>3.8</i>               | <i>6.3</i>  | <i>7.4</i>  | <i>3.3</i>  | <i>7.3</i>  | <i>4.7</i>   |
| <i>26.46</i>                                   | <i>15.6</i>              | <i>17.8</i> | <i>19.3</i> | <i>12.7</i> | <i>20.5</i> | <i>19.3</i>  |
| <i>20.91</i>                                   | <i>0.0</i>               | <i>0.0</i>  | <i>0.0</i>  | <i>0.0</i>  | <i>0.0</i>  | <i>0.0</i>   |
| <i>41.01</i>                                   | <i>1.6</i>               | <i>1.7</i>  | <i>1.6</i>  | <i>0.5</i>  | <i>8.7</i>  | <i>3.9</i>   |

increase duration more slowly with depth (smaller slopes).

In addition, depth and duration are probably more tightly coupled in smaller divers because these animals are more duration- and velocity-limited than are larger ones. Smaller divers have equal or greater mean vertical velocity than larger divers, and yet are not expected to swim as fast because inertia is greater for small objects and drag increases with surface area ( $L^2$ ), whereas power increases with muscle volume ( $L^3$ ). Further, smaller divers have smaller oxygen stores and higher mass-specific metabolic rates, so they cannot stay submerged as long. As a result, duration and depth should be more tightly coupled for smaller divers. Larger divers have more time during each dive to adjust swimming velocity to increase or decrease the resulting maximum depth, and have a wider range of available speeds. The facts that smaller divers exceed their cADL more often (DMR = 1 × SMR for phocids and 4 × SMR for seabirds and otariids) and increase their post-dive surface interval more rapidly with increasing duration than do larger divers indicate a stronger duration limit. However, considering the indirect and highly assumptive nature of much of the supporting evidence, and that the diving capacity of an animal should be closely linked to its routine behavior and foraging needs, no differences in these values among adults of the different species would be expected.

*Aerobic dive limit.*—Comparison of cADLs and the percentage of the dives that exceeded these values must be tentative because many assumptions and estimates need to be made in order to calculate ADL. The percentage of dives within a functional group that exceed cADL may still be useful, however, because the differences are relative and should be consistent within a species. The finding that square dives most often exceed the estimated ADL is probably realistic. Square dives are likely to represent foraging, and a diver would be expected to maximize the length of these dives even at a cost. Also, consistent with the suggestion that some

of the smaller divers may also forage when performing V dives and that foraging dives may appear more V shaped when pushing duration limits, Adélie, Royal, and Gentoo penguins and Antarctic fur seal exceeded their estimated ADLs most often when performing these dives.

There has been considerable speculation regarding the calculation of ADL, and direct postdive plasma lactate levels have only been collected for Weddell seal (Kooyman et al. 1980, 1983, Burns and Castellini 1996), Emperor Penguin, *Aptenodytes forsteri* (Ponganis et al. 1997b), Baikal seal, *Phoca sibirica* (Ponganis et al. 1997a), California sea lion, *Zalophus californianus* (Ponganis et al. 1997c), and beluga whale, *Delphinapterus leucas* (Shaffer et al. 1997). In these species, it has generally been shown that ADL can be accurately estimated from calculations of TBO<sub>2</sub> and DMR (but see Burns and Castellini 1996). This technique has been used by many researchers to calculate ADL for a wide variety of species without further calibration (e.g., Gentry et al. 1986, Feldkamp et al. 1989, Hindell et al. 1992, Chappell et al. 1993a, Wiig et al. 1993, Boyd and Croxall 1996, Schreer and Kovacs 1997). In addition to this shortcoming, the variables needed to calculate ADL are rarely measured directly, being estimated instead. TBO<sub>2</sub> has been measured for a few species (e.g., Kooyman 1989), but it is usually only estimated when calculating ADL. DMR has also rarely been measured, and it has been found to vary with dive type and duration (Kooyman et al. 1973, 1980, 1983, Castellini et al. 1992, Ponganis et al. 1993, Hurley 1996). Metabolic rates during a dive have never been measured under natural conditions (Boyd 1997). DMR is of considerable concern because these values have varied considerably in the literature (e.g., 2–10 × SMR; Kooyman et al. 1973, Nagy et al. 1984, Kooyman and Ponganis 1990, Burger 1991, Castellini et al. 1992, Chappell et al. 1993a, b, Costa 1993) and have a direct and significant effect on the cADL. For ex-

ample, if a DMR of  $4 \times \text{SMR}$  is used instead of  $2 \times \text{SMR}$ , the cADL is halved.

From the calculations performed here, the impact of different DMRs is clearly evident. Using  $\text{DMR} = 2 \times \text{SMR}$ , it appears that the largest phocids, Weddell and male and female southern elephant seal, exceed the cADL for a majority of their dives, whereas relatively tiny seabirds rarely do so. Recalculating the results with  $\text{DMR} = 4 \times \text{SMR}$  for seabirds and otariids and  $\text{DMR} = 1 \times \text{SMR}$  for phocids improves the biological validity of the findings, but some strong anomalies still remain (e.g., Gentoo Penguin with  $\sim 90\%$  and harp, grey, and hooded seal with  $0\%$  of their dives exceeding the cADL). This is also supported by inflections observed for the LOWESS-smoothed relationship of postdive surface interval vs. duration, where the locations of these changes were more similar to cADL calculated with  $4 \times \text{SMR}$  rather than  $2 \times \text{SMR}$  (see Blue-eyed Shag, Antarctic fur seal, and Adélie, Royal, and Gentoo penguin). Even though DMRs of  $2 \times \text{SMR}$  are by far most commonly used for calculating ADL (e.g., Eliassen 1960, Kooyman et al. 1973, Baudinette and Gill 1985, Gentry et al. 1986, Feldkamp et al. 1989, Kooyman 1989, Kooyman and Ponganis 1990, Burger 1991, Castellini et al. 1992, Costa 1993, Williams et al. 1993, Schreer and Kovacs 1997), it appears that lower and higher DMRs are more appropriate for phocids and seabirds/otariids, respectively. The few studies that have directly measured DMR or estimated DMR with field metabolic rates (using doubly labeled water) support this finding with higher DMRs for birds (e.g.,  $6.6\text{--}9.8 \times \text{SMR}$  for African Penguin, *Spheniscus demersus*, Nagy et al. 1984;  $8.2 \times \text{SMR}$  for Adélie Penguin, Chappell et al. 1993a, b) and lower DMRs for seals (e.g.,  $1 \times \text{SMR}$  for Weddell seal, Castellini et al. 1992). However, even these directly measured values vary considerably across species (e.g.,  $1.6 \times \text{SMR}$  for Common Murre, *Phalacrocorax carbo*, Croll and McLaren 1993;  $2.2 \times \text{SMR}$  for Gentoo Penguin, Bevan et al. 1995) and behavior (Castellini et al. 1992, Ponganis et al. 1993, Hurley 1996).

Further, comparisons with direct measures of ADL also indicate that no simple generic rule exists for a group of species. For example,  $4 \times \text{SMR}$  for California sea lion (2.3 min for both directly measured [Ponganis et al. 1997b] and cADL) and  $1 \times \text{SMR}$  for Baikal seal ( $\sim 15$  min for both directly measured [Ponganis et al. 1997a] and cADL) appear appropriate, whereas 2, not  $4 \times \text{SMR}$  is appropriate for Emperor Penguin ( $5.6_{\text{direct}}$  [Ponganis et al. 1997c] and  $5.2_{2 \times \text{SMR}}$  min). For Weddell seal, a strong developmental effect is seen in ADL and DMR where pups fit well with  $4 \times \text{SMR}$  ( $4.4_{\text{direct}}$  [Burns and Castellini 1996] and  $5.0_{\text{cADL}}$  min), yearlings with  $2 \times \text{SMR}$  (10.0 min for both directly measured [Kooyman et al. 1983] and cADL), and adults with  $1 \times \text{SMR}$  ( $22.0_{\text{direct}}$  [Kooyman et al. 1980] and  $25.8_{\text{cADL}}$  min).

If the cADL results produced here are compared to postdive surface interval vs. duration (Figs. 9 and 10),

it indicates that these cADLs are not reflected behaviorally. The linear relationships between postdive surface interval and duration (Fig. 9) indicate that for all species, except perhaps Blue-eyed Shag and Antarctic fur seal, the duration of the dive has little or no effect on the subsequent postdive surface interval. This lack of relationship has been observed by others (Boyd and Croxall 1996, Boyd 1997) and suggests that most species rarely exceed their actual ADL. Analysis of postdive surface interval vs. duration smoothed with the LOWESS method (Fig. 10) shows that several species exhibit an increase in postdive surface interval with an increase in dive duration. However, except for Blue-eyed Shag, Antarctic fur seal, and perhaps Weddell and hooded seal, the increase is very small and inflections are weak. Another study using similar data for adult Weddell seal found a more pronounced inflection point, although data were processed differently (e.g., only dives with post dive surface intervals  $> 1$  min and  $< 20$  min were used, and individual variation was assessed; Burns 1999). It is clear that different methods for estimating ADL can drastically influence findings drawn from the results, and that one must be very tentative when making conclusions based on uncorroborated ADL estimates.

#### Comparisons with previous work

For all of the species studied here except Royal Penguin, previous work had been conducted on either the same data sets used here or on different dive data. Many of these works involved some sort of dive classification using primarily maximum depth and duration, although the shape of the dive profile was used directly or peripherally in a few studies (Table 8). Dives from Royal Penguin, Galápagos fur seal, grey seal, hooded seal, and walrus have not been previously classified (Kooyman and Trillmich 1986, Fay and Burns 1988, Wiig et al. 1993, Lydersen et al. 1994, Folkow and Blix 1995, Horning and Trillmich 1997b). Studies that did attempt shape classification generally had findings similar to those presented here. Major differences in findings and conclusions are rare and most are probably attributable to different analytical procedures.

In Weddell seal, in addition to the dive types found here, a flat-bottomed benthic foraging dive type was proposed (Schreer and Testa 1996). However, even in that study, this dive type could not be distinguished using quantitative methods; it was only indicated as a dive type through subjective visual analyses. Also, this dive type was rare, accounting for only 1.8% of all the dives. Skewed dives for Adélie Penguin have been considered to be a type of foraging dive in which prey are pursued vertically as well as horizontally (Chappell et al. 1993a). There is no concrete evidence to contradict this here, but the lack of diel variation in maximum depth for both skewed dive shapes suggests that they may not have a foraging function (although Adélie Penguin square dives also showed very little diel variation

TABLE 8. Previous dive classifications.

| Species                | Classification criteria  | Sources  |
|------------------------|--|--|
| Blue-eyed Shag         | 1) short and shallow ( $\leq 2$ min and $< 20$ m)<br>2) long and deep ( $> 2$ min and $> 35$ m)  | Croxall et al. (1991), Wanless et al. (1992), Bevan et al. (1997)              |
| Adélie Penguin         | 1) short ( $< 0.33$ min or no abrupt inflections in descent and ascent rate)<br>2) long and deep ( $\geq 20$ m, $\geq 1$ min, or abrupt inflections in descent and ascent rate)<br>2a) mean depth 13–15 m<br>2b) mean depth 34–46 m<br>2 <sub>variations</sub> ) square, V, skewed-right, and skewed-left shapes.  | Chappell et al. (1993a)  |
| Gentoo Penguin         | 1) shallow ( $< 21$ m)<br>2) deep ( $> 30$ )   | Williams et al. (1992)   |
| Antarctic fur seal     | Dive classification<br>1) V-shaped<br>2) square-shaped<br><br>Bout classification<br>1) short (17 min)<br>2) long (80 min)<br>3) shallow (12 min, near surface)<br>4) deep (19 min, 40–50 m)   | Boyd and Croxall (1992)<br><br>Boyd et al. (1994)                              |
| Harp seal              | 1) shallow, short (means of 5 m and 0.5 min)<br>2) intermediate (means of 49 m and 4.6 min)<br>3) deep, long (means of 63 m and 7.2 min)   | Lydersen and Kovacs (1996)   |
| Weddell seal           | Original classification (1968)<br>1) short, shallow ( $< 100$ m and 5 min)<br>2) long ( $< 200$ m and $> 20$ min)<br>3) deep ( $> 200$ m and 8–15 min)<br><br>Shape classification (1995, 1996)<br>1) square-shaped<br>1a) many wiggles during bottom time<br>1b) no or few wiggles during bottom time<br>1c) rectangular (long and shallow)<br>2) V-shaped<br>3) skewed-right shaped<br>4) skewed-left shaped | Kooyman (1968)<br><br>Schreer and Testa (1995, 1996)                           |
| Southern elephant seal | 1) square-shaped<br>1a) many wiggles during bottom time<br>1b) no or few wiggles during bottom time (rare for females, more common for males)<br>2) parabolic-shaped, V-shaped<br>3) skewed-right shaped<br>4) skewed-left shaped<br>5) short, shallow ( $< 1.5$ min)<br>6) hybrids  | Hindell et al. (1991b),<br>Jonker and Bester (1994),<br>Compagna et al. (1995) |

Note: Dives from Royal Penguin, Galápagos fur seal, grey seal, hooded seal, and walrus have not been previously classified.

in maximum depth). For Antarctic fur seal, in contrast to the 81% square dives found here, Boyd and Croxall (1992) found that most Antarctic fur seal dives had a V shape, whereas square dives were rare. However, the work done by Boyd and Croxall (1992) and that conducted here utilized different data sets; therefore, these conflicting determinations may be real. Further, many of the attributes of V dives in our study indicate a foraging function. Two differences between this work and some of the previous work on southern elephant seal were that we could not discriminate a specific ben-

thic foraging dive type for females and the separation of male square dives into pelagic and benthic dives was done on the basis of the mean vertical velocity, not the number or size of wiggles during bottom time (Hindell et al. 1991b, Jonker and Bester 1994, Campagna et al. 1995). The lack of a benthic square dive type for females may be realistic, because other work has also found that this sort of dive was not present in female records (Hindell et al. 1991b, Jonker and Bester 1994) or it was very rare (Campagna et al. 1995). As for the subdivision of square dives made by males, there was



no evidence found here to separate these dives based on the number and size of wiggles, although the separation based on the mean vertical velocity may have resulted in a similar subdivision.

#### *Utility of quantitative shape analysis*

It has been shown here and by many others (e.g., Le Boeuf et al. 1988, 1992, Hindell et al. 1991b, Schreer and Testa 1996) that dives classified on the basis of shape may represent meaningful behavioral groupings. However, this type of classification may not be applicable to all species. Three species in this study (Blue-eyed Shag, grey seal, and walrus) essentially had only one dive type that represented >97% of all their dives. For these species, it was useful to learn that almost all of their dives had a square shape, although this was already known by simply looking at the dive profiles. Therefore, either these species only perform one type of diving behavior or other criteria are needed for dive classification. It should be noted, however, that in all three species, only a small number of dives (<2000) from few individuals (<6) were collected over a short time range (<14 d), which undoubtedly presents a limited view of their overall diving regime.

Another limitation of the shape classification is that it only uses two variables, depth and time. Dive types and functions are inferred from two-dimensional patterns when the actual three-dimensional activity during these dives is unknown. Despite these limits, shape classification is a logical progression from simple maximum depth and duration patterns, and has given us a glimpse of not only how deep and long animals dive, but also what they do during the dives. Further, the shape-fitting method presented here is useful for mitigating dive analyses through automation and increased objectivity and for facilitating interspecific and cross-study comparisons through a universal and parsimonious approach. It also offers potential solutions for "on board" memory limitations and transmissions constraints for archival time-depth recorders and satellite-linked time-depth recorders by conveying meaningful dive information with a relatively small number of parameters (Schreer 1999). Additional variables (e.g., velocity, stomach temperature, heart rate, and three-dimensional movements) will give more information about what an animal is doing while diving, and will undoubtedly help in determining more representative dive types and more accurate functions for these types. However, the quantitative techniques presented here should also be useful for analytical interpretations of these additional data.

#### *Conclusion*

In conclusion, this work has shown that there are strong similarities in diving patterns across unrelated species, indicating the utility of a universal classification approach. Performing broad interspecific comparisons and assessing similarities as well as anomalies

within and across species has further elucidated possible behavioral functions and ecological implications of diving patterns. Considering the quantity and quality of data that have been, and currently are being, collected on diving endotherms, current and future studies should utilize interspecifically robust procedures for interpreting these data. Only through a comparative approach can general ecological models be generated and tested.

#### ACKNOWLEDGMENTS

This work could not have been accomplished without the generosity of several of our colleagues who provided us with raw TDR data. We thank Ian L. Boyd, Mark A. Chappell, Mark A. Hindell, Markus Horning, Christian Lydersen, J. Ward Testa, and Øystein Wiig, who all invested considerable time and funds to collect dive data on the various species. This work was supported by the Natural Sciences and Research Council of Canada, the Ontario Graduate Scholarship Program, and the University of Waterloo Graduate Scholarship Program. This manuscript benefitted from reviews by Mark Horsburgh, Dan P. Costa, Gerald L. Kooyman, and three anonymous reviewers. J. F. Schreer thanks XOQ.

#### LITERATURE CITED

- Aschoff, S., and H. Pohl. 1970. Rhythmic variation in energy metabolism. *Federation Proceedings* **29**:1541–1552.
- Baudinette, R. V., and P. Gill. 1985. The energetics of 'flying' and 'paddling' in water: locomotion in penguins and ducks. *Journal of Comparative Physiology B* **155**:373–380.
- Bengtson, J. L., and B. S. Stewart. 1992. Diving and haulout behavior of crabeater seals in the Weddell Sea, Antarctica, during March 1986. *Polar Biology* **12**:635–644.
- Bevan, R. M., I. L. Boyd, P. J. Butler, K. Reid, A. J. Woakes, and J. P. Croxall. 1997. Heart rates and abdominal temperatures of free-ranging South Georgian shags, *Phalacrocorax Georgianus*. *Journal of Experimental Biology* **200**:661–675.
- Bevan, R. M., A. J. Woakes, P. J. Butler, and J. P. Croxall. 1995. Heart rate and oxygen consumption of exercising gentoo penguins. *Physiological Zoology* **68**:855–877.
- Bezdek, J. C. 1981. *Pattern recognition with fuzzy objective function algorithms*. Plenum, New York, New York, USA.
- Boyd, I. L. 1993. Selecting sampling frequency for measuring diving behavior. *Marine Mammal Science* **9**:424–430.
- Boyd, I. L. 1997. The behavioural and physiological ecology of diving. *Trends in Ecology and Evolution* **12**:213–217.
- Boyd, I. L., and T. Arnomb. 1991. Diving behaviour in relation to water temperature in the southern elephant seal: foraging implications. *Polar Biology* **11**:259–266.
- Boyd, I. L., J. P. Y. Arnould, T. Barton, and J. P. Croxall. 1994. Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. *Journal of Animal Ecology* **63**:703–713.
- Boyd, I. L., and J. P. Croxall. 1992. Diving behaviour of lactating Antarctic fur seals. *Canadian Journal of Zoology* **70**:919–928.
- Boyd, I. L., and J. P. Croxall. 1996. Dive durations in pinnipeds and seabirds. *Canadian Journal of Zoology* **74**:1696–1705.
- Brillinger, D. R., and B. S. Stewart. 1997. Elephant seal movements: dive types and their sequences. Pages 275–288 in T. G. Gregoire et al., editors. *Modelling longitudinal and spatially correlated data: methods, applications, and future directions*. Lecture Notes in Statistics. Volume 122. Springer, New York, New York, USA.
- Brillinger, D., B. S. Stewart, and A. Wang. 1995. Computer-assisted, automatic evaluation of two-dimensional profiles (time vs. depth) of time-series data for diving marine mam-

- mals. Abstracts from the 11th Biennial Conference on the Biology of Marine Mammals, Orlando, Florida USA, 14–18 December 1995.
- Burger, A. E. 1991. Maximum diving depth and underwater foraging in alcids and penguins. Pages 9–15 in W. A. Montevecchi and A. J. Gaston, editors. Studies of high-latitude seabirds. 1. Behavioural, energetic, and oceanographic aspects of seabird feeding ecology. Canadian Wildlife Service, Occasional Paper, Number 68.
- Burns, J. M. 1999. The development of diving behavior in juvenile Weddell seals: pushing physiological limits in order to survive. *Canadian Journal of Zoology* **77**:737–747.
- Burns, J. M., and M. A. Castellini. 1996. Physiological and behavioral determinants of the aerobic dive limit in Weddell seal (*Leptonychotes weddellii*) pups. *Journal of Comparative Physiology B* **166**:474–483.
- Burns, J. M., and J. F. Schreer. *In press*. Changes in the behavioral repertoire of Weddell seal pups diving in McMurdo Sound, Antarctica. In W. Davidson, editor. Antarctic ecosystems: models for wider ecological understanding. Caxton Press, Christchurch, New Zealand.
- Burns, J. M., J. F. Schreer, and M. A. Castellini. 1997. Physiological effects on individual dive patterns and foraging strategies in yearling Weddell seals. *Canadian Journal of Zoology* **75**:1796–1810.
- Campagna, C., B. J. Le Boeuf, S. B. Blackwell, D. E. Crocker, and F. Quintana. 1995. Diving behaviour and foraging location of female southern elephant seals from Patagonia. *Journal of Zoology, London* **236**:55–71.
- Castellini, M. A., G. L. Kooyman, and P. J. Ponganis. 1992. Metabolic rates of freely diving Weddell seals: correlations with oxygen stores, swim velocity and diving duration. *Journal of Experimental Biology* **165**:181–194.
- Chappell, M. A., V. H. Shoemaker, D. N. Janes, T. H. Bucher, and S. K. Maloney. 1993a. Diving behavior during foraging in breeding Adélie penguins. *Ecology* **74**:1204–1215.
- Chappell, M. A., V. H. Shoemaker, D. N. Janes, S. K. Maloney, and T. L. Bucher. 1993b. Energetics of foraging in breeding Adélie penguins. *Ecology* **74**:2450–2461.
- Cooper, J. 1986. Diving patterns of cormorants Phalacrocoracidae. *Ibis* **128**:562–570.
- Costa, D. P. 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia. *Symposia. Zoological Society of London* **66**:293–314.
- Crocker, D. E., B. J. Le Boeuf, and D. P. Costa. 1997. Drift diving in female northern elephant seals: implications for food processing. *Canadian Journal of Zoology* **75**:27–39.
- Croll, D. A., and E. McLaren. 1993. Diving metabolism and thermoregulation in common and thick-billed murre. *Journal of Comparative Physiology B* **163**:160–166.
- Croxall, J. P., Y. Naito, A. Kato, P. Rothery, and D. R. Briggs. 1991. Diving patterns and performance in the Antarctic blue-eyed shag *Phalacrocorax atriceps*. *Journal of Zoology, London* **225**:171–199.
- del Hoyo, J., A. Elliot, and J. Sargatal. 1992. Handbook of the birds of the World. Volume 1. Lynx Edicions, Barcelona, Spain.
- Eliassen, E. 1960. Cardiovascular responses to submersion asphyxia in avian divers. *Acta Universitatis Bergensis. Series Mathematica. Rerumque Naturalium* **2**:1–100.
- Fay, F. H., and J. J. Burns. 1988. Maximum feeding depth of walruses. *Arctic* **41**:239–240.
- Feldkamp, S. D., R. L. DeLong, and G. A. Antonelis. 1989. Diving patterns of California sea lions, *Zalophus californianus*. *Canadian Journal of Zoology* **67**:872–883.
- Folkow, L. P., and A. S. Blix. 1995. Distribution and diving behaviour of hooded seals. Pages 193–202 in A. S. Blix, L. Wallace, and Ø. Ultang, editors. Whales, seals, fish, and man. Proceedings of the International Symposium on the Biology of Marine Mammals in the North East Atlantic, Tromsø, Norway, 29 November to 1 December 1994.
- Gentry, R. L., D. P. Costa, J. P. Croxall, J. H. M. David, R. W. Davis, G. L. Kooyman, P. Majluf, T. S. McCann, and F. Trillmich. 1986. Synthesis and conclusions. Pages 220–264 in R. L. Gentry and G. L. Kooyman, editors. Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, New Jersey, USA.
- Gentry, R. L., and G. L. Kooyman. 1986. Fur seals: Maternal strategies on land and at sea. Princeton University Press, Princeton, New Jersey, USA.
- Gjertz, I., and Ø. Wiig. 1992. Feeding of walrus *Odobenus rosmarus* in Svalbard. *Polar Record* **28**:57–59.
- Hindell, M. A. and H. R. Burton. 1993. Swimming speed and diving behaviour of adult female southern elephant seals. Page 61 in Abstracts from the 10th Biennial Conference on the Biology of Marine Mammals, Galveston, Texas, USA, 11–15 November 1993.
- Hindell, M. A., H. R. Burton, and D. J. Slip. 1991a. Foraging areas of the southern elephant seal, *Mirounga leonina*, as inferred from water temperature data. *Australian Journal of Marine and Freshwater Research* **42**:115–128.
- Hindell, M. A., M.-A. Lea, and C. L. Hull. 1996. The effects of flipper bands on adult survival rate and reproduction in the royal penguin, *Eudyptes schlegeli*. *Ibis* **138**:557–560.
- Hindell, M. A., D. J. Slip, and H. R. Burton. 1991b. The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia: Phocidae). *Australian Journal of Zoology* **39**:595–619.
- Hindell, M. A., D. J. Slip, H. R. Burton, and M. M. Bryden. 1992. Physiological implications of continuous, prolonged, and deep dives of the southern elephant seal (*Mirounga leonina*). *Canadian Journal of Zoology* **70**:370–379.
- Horning, M. 1992. Die ontogenese des tauchverhaltens beim Galápagos seebären *Arctocephalus galapagoensis* (Heller 1904). Dissertation. Universität Bielefeld, Bielefeld, Germany.
- Horning, M., and F. Trillmich. 1997a. Development of hemoglobin, hematocrit, and erythrocyte values in Galápagos fur seals. *Marine Mammal Science* **13**:100–113.
- Horning, M., and F. Trillmich. 1997b. Ontogeny of diving behaviour in the Galápagos fur seal. *Behaviour* **134**:1211–1257.
- Hurley, J. A. 1996. Metabolic rate and heart rate during trained dives in adult California sea lions. Dissertation. Department of Biology, University of California, Santa Cruz, California, USA.
- Jefferson, T. A., S. Leatherwood, and M. A. Webber. 1993. FAO species identification guide: Marine mammals of the world. Food and Agriculture Organization, Rome, Italy.
- Jonker, F. C., and M. N. Bester. 1994. The diving behaviour of adult southern elephant seal, *Mirounga leonina*, cows from Marion Island. *South African Journal of Antarctic Research* **24**:75–93.
- Kamel, M. S., and S. Z. Selim. 1994. New algorithms for solving the fuzzy clustering problem. *Pattern Recognition* **27**:421–428.
- Kleiber, M. 1961. The fire of life. An introduction to animal energetics. Wiley, New York, New York, USA.
- Kooyman, G. L. 1968. An analysis of some behavioral and physiological characteristics related to diving in the Weddell seal. Pages 227–261 in G. A. Llano and W. L. Schmidt. Biology of the Antarctic Seas. Antarctic Research Series. Volume 3. American Geophysical Union, Washington, D.C., USA.
- Kooyman, G. L. 1989. Diverse divers: physiology and behavior. Springer-Verlag, Berlin, Germany.
- Kooyman, G. L., M. A. Castellini, R. W. Davis, and R. E. Maue. 1983. Aerobic diving limits of immature Weddell seals. *Journal of Comparative Physiology B* **151**:171–174.

- Kooyman, G. L., and R. L. Gentry. 1986. Diving behavior of South African fur seals. Pages 142–152 in R. L. Gentry and G. L. Kooyman, editors. *Fur seals: Maternal strategies on land and at sea*. Princeton University Press, Princeton, New Jersey, USA.
- Kooyman, G. L., D. H. Kerem, W. B. Campbell, and J. J. Wright. 1973. Pulmonary gas exchange in freely diving Weddell seals. *Respiration Physiology* **17**:283–290.
- Kooyman, G. L., and P. J. Ponganis. 1990. Behavior and physiology of diving in emperor and king penguins. Pages 229–242 in L. S. Davis and J. T. Darby, editors. *Penguin biology*. Academic Press, San Diego, California, USA.
- Kooyman, G. L., and F. Trillmich. 1986. Diving behavior of Galápagos fur seals. Pages 186–195 in R. L. Gentry and G. L. Kooyman, editors. *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton, New Jersey, USA.
- Kooyman, G. L., E. A. Wahrenbrock, M. A. Castellini, R. W. Davis, and E. E. Sinnett. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior. *Journal of Comparative Physiology B* **138**:335–346.
- Kovacs, K. M., C. Lydersen, M. Hammill, and D. M. Lavigne. 1996. Reproductive effort of male hooded seals (*Cystophora cristata*): estimates from mass loss. *Canadian Journal of Zoology* **74**:1521–1530.
- Le Boeuf, B. J., D. P. Costa, A. C. Huntley, and S. D. Feldkamp. 1988. Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Canadian Journal of Zoology* **66**:446–458.
- Le Boeuf, B. J., Y. Naito, T. Asaga, D. Crocker, and D. P. Costa. 1992. Swim speed in a female northern elephant seal: metabolic and foraging implications. *Canadian Journal of Zoology* **70**:786–795.
- Lydersen, C., M. O. Hammill, and K. M. Kovacs. 1994. Activity of lactating ice-breeding grey seals, *Halichoerus grypus*, from the Gulf of St. Lawrence, Canada. *Animal Behaviour* **48**:1417–1425.
- Lydersen, C., and K. M. Kovacs. 1993. Diving behaviour of lactating in harp seal, *Phoca groenlandica*, females from the Gulf of St. Lawrence, Canada. *Animal Behaviour* **46**:1213–1221.
- Lydersen, C., and K. M. Kovacs. 1996. Energetics of lactation in harp seals (*Phoca groenlandica*) from the Gulf of St. Lawrence, Canada. *Journal of Comparative Physiology B* **166**:295–304.
- Nagy, K. A., W. R. Siegfried, and R. P. Wilson. 1984. Energy utilization by free-ranging jackass penguins, *Spheniscus demersus*. *Ecology* **65**:1648–1655.
- Piatt, J. F., and D. N. Nettleship. 1985. Diving depths of four alcids. *Auk* **102**:293–297.
- Ponganis, P. J., G. L. Kooyman, E. A. Baranov, P. H. Thorson, and B. S. Stewart. 1997a. The aerobic submersion limit of Baikal seals, *Phoca sibirica*. *Canadian Journal of Zoology* **75**:1323–1327.
- Ponganis, P. J., G. L. Kooyman, and M. A. Castellini. 1993. Determinants of the aerobic dive limit of Weddell seals: analysis of diving metabolic rates, postdive and tidal PO<sub>2</sub>, and blood and muscle oxygen stores. *Physiological Zoology* **66**:732–749.
- Ponganis, P. J., G. L. Kooyman, L. N. Starke, C. A. Kooyman, and T. G. Kooyman. 1997b. Postdive blood lactate concentrations in emperor penguins, *Aptenodytes forsteri*. *Journal of Experimental Biology* **200**:1623–1626.
- Ponganis, P. J., G. L. Kooyman, L. M. Winter, and L. N. Starke. 1997c. Heart rate and plasma lactate responses during submerged swimming and trained diving in California sea lions, *Zalophus californianus*. *Journal of Comparative Physiology B* **167**:9–16.
- Prince, P. A., and M. P. Harris. 1988. Food and feeding ecology of breeding Atlantic alcids and penguins. *Proceedings of the International Ornithological Congress XIX*:1195–1204.
- Robinson, S. A., and M. A. Hindell. 1996. Foraging ecology of gentoo penguins *Pygoscelis papua* at Macquarie Island during the period of chick care. *Ibis* **138**:722–731.
- Schreer, J. F. 1997. Diving behavior of air-breathing vertebrates: allometry, classification, and interspecific comparisons. Dissertation. University of Waterloo, Waterloo, Ontario, Canada.
- Schreer, J. F. 1999. A universal method for summarizing dive data: potential solutions for “on board” memory limitations, transmission constraints, and analysis difficulties. Page 167 in Abstracts of the 13th Biennial Conference on the Biology of Marine Mammals, 28 November–3 December 1999, Maui, Hawaii, USA.
- Schreer, J. F., and K. M. Kovacs. 1997. Allometry of diving capacity in air-breathing vertebrates. *Canadian Journal of Zoology* **75**:339–358.
- Schreer, J. F., K. M. Kovacs, and R. J. O’Hara Hines. 1995. Quantitative analyses of marine mammal diving behavior. Page 102 in Abstracts of the 11th Biennial Conference on the Biology of Marine Mammals, 14–18 December 1995, Orlando, Florida, USA.
- Schreer, J. F., R. J. O’Hara Hines, and K. M. Kovacs. 1998. Classification of dive profiles: a comparison of statistical clustering techniques and unsupervised artificial neural networks. *Journal of Agricultural, Biological, and Environmental Statistics* **3**:383–404.
- Schreer, J. F., and J. W. Testa. 1993. Statistical classification of diving behavior: quantitative analyses of Weddell seal diving. Page 96 in Abstracts of the 10th Biennial Conference on the Biology of Marine Mammals, 11–15 November 1993, Galveston, Texas, USA.
- Schreer, J. F., and J. W. Testa. 1995. Statistical classification of diving behavior. *Marine Mammal Science* **11**:85–93.
- Schreer, J. F., and J. W. Testa. 1996. Classification of Weddell seal diving behavior. *Marine Mammal Science* **12**:227–250.
- Shaffer, S. A., D. P. Costa, T. M. Williams, and S. H. Ridgway. 1997. Diving and swimming performance of white whales, *Delphinapterus leucas*: an assessment of plasma lactate and blood gas levels and respiratory rates. *Journal of Experimental Biology* **200**:3091–3099.
- SYSTAT. 1992. SYSTAT for Windows: Statistics. Volume 5. SYSTAT, Evanston, Illinois, USA.
- Testa, J. W. 1994. Overwinter movements and diving behavior of female Weddell seals (*Leptonychotes weddellii*) in the SW Ross Sea, Antarctica. *Canadian Journal of Zoology* **72**:1700–1710.
- Wanless, S., M. P. Harris, and J. A. Morris. 1992. Diving behaviour and diet of the blue-eyed shag at South Georgia. *Polar Biology* **12**:713–719.
- Wiig, Ø., I. Gjertz, D. Griffiths, and C. Lydersen. 1993. Diving patterns of an Atlantic walrus *Odobenus rosmarus rosmarus* near Svalbard. *Polar Biology* **13**:71–72.
- Williams, T. D., D. R. Briggs, J. P. Croxall, Y. Naito, and A. Kato. 1992. Diving patterns and performance in relation to foraging ecology in the gentoo penguin, *Pygoscelis papua*. *Journal of Zoology, London* **227**:211–230.
- Williams, T. M., W. A. Friedl, and J. E. Haun. 1993. The physiology of bottlenose dolphins (*Tursiops truncatus*): heart rate, metabolic rate and plasma lactate concentration during exercise. *Journal of Experimental Biology* **179**:31–46.
- Williams, T. M. and G. L. Kooyman. 1985. Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. *Physiological Zoology* **58**:576–589.