Dive shapes reveal temporal changes in the foraging behaviour of different age and sex classes of harbour seals (*Phoca vitulina*)

J. Baechler, C.A. Beck, and W.D. Bowen

Abstract: Classifying dives into two-dimensional shapes based on time and depth is an attempt to extract additional information about the behaviour of aquatic air-breathing predators. In some species, there is considerable circumstantial evidence that different dive shapes represent different behaviours. However, few studies have provided direct evidence of the relationship between dive shape and function. We classified over 283 000 dives of adults (31 males and 45 females) and suckling (13) and recently weaned (15) harbour seal (*Phoca vitulina*) pups into seven shapes using supervised discriminant function analysis. Changes in the percentage of U-shaped dives over time within adults and weaned pups were associated with changes in food intake derived from water-flux studies on subsets of the same individuals. The changes in the percentage of U-shaped dives were accompanied by roughly reciprocal changes in V-shaped dives, whereas there was little change in other dive shapes, indicating that V-shaped dives are not generally exhibited during foraging. Video of adult males (from an animal-borne video system) also showed that there was a strong but not exclusive association between foraging and U-shaped dives. Our results indicate that changes in the percentage of U-shaped dives may serve as a reasonable index of changes in foraging behaviour. However, behaviours of suckling pups and adult males during the breeding season cannot be easily inferred from dive shape alone.

Résumé : La classification des plongées en entités bidimensionnelles d'après leur durée et leur profondeur constitue une tentative d'extraction d'informations supplémentaires sur le comportement de prédateurs aquatiques à respiration aérienne. Chez certaines espèces, il y a de fortes preuves indirectes que les différentes formes de plongées représentent des comportements différents. Cependant, peu d'études ont fourni des preuves directes de l'existence d'un lien entre la forme des plongées et leur rôle. Nous avons classifié plus de 283 000 plongées de phoques communs (*Phoca vitulina*), adultes (31 mâles et 45 femelles), nourrissons (13) et juvéniles sevrés depuis peu (15), en sept formes au moyen d'une analyse supervisée des fonctions discriminantes. Les changements dans le temps du pourcentage des plongées en U chez les adultes et les juvéniles sevrés sont associés à des changements dans la consommation de nourriture, tels que perçus dans les résultats d'études sur le débit de l'eau mettant en cause des sous-groupes des mêmes individus. Les changements dans le pourcentage de plongées en U coïncident grosso modo avec des changements dans le pourcentage des plongées en V, alors qu'il y a peu de variations dans les plongées d'autres formes, ce qui indique que les plongées en V ne sont généralement pas utilisées durant la quête de nourriture. Des magnétoscopes installés sur les animaux ont permis d'obtenir des bandes vidéo de mâles adultes qui démontrent qu' il y a une corrélation forte, quoique non exclusive, entre la quête de nourriture et les plongées en U. Nos résultats indiquent que les changements dans le pourcentage des plongées en U peuvent servir d'indicateurs de modifications dans le comportement de quête de nourriture, mais ils ne peuvent servir de seuls indicateurs du comportement des nourrissons ni de celui des mâles adultes durant la saison de la reproduction.

[Traduit par la Rédaction]

Introduction

The use of time–depth recorders (TDRs) has greatly advanced our understanding of the diving behaviour of many species of air-breathing marine predators (e.g., Eckert et al. 1988; Boyd et al. 1994; Wilson et al. 1996; Coltman et al. 1997; Martin et al. 1998; Le Boeuf et al. 2000). TDRs measure depth at regularly timed intervals, providing a two-dimensional representation of each dive. For some time it has been recognized that these two-dimensional profiles could be classified into shapes and that these shapes might be associated with different behaviours (Le Boeuf et al. 1988; Hindell et al. 1991; Bengtson and Stewart 1992). Dive shapes can be classified in a number of ways (Schreer et al. 1998); fundamentally, they are distinguished as dives in which the animal travels from the surface to depth and then returns to the surface immediately, so called V-shaped dives, and dives in which a reasonable percentage of time is spent at the bottom of the dive, resulting in a U shape (also called trapezoidal or square-shaped dives).

In a number of pinniped species, behaviour has been inferred from different dive shapes (e.g., northern elephant

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seal, *Mirounga angustirostris*, Le Boeuf et al. 1988, 1992; southern elephant seal, *Mirounga leonina*, Hindell et al. 1991; crabeater seal, *Lobodon carcinophagus*, Bengtson and Stewart 1992; Weddell seal, *Leptonychotes weddellii*, Schreer and Testa 1996). For example, based on manual classification, Le Boeuf et al. (1988) identified six dive shapes and suggested that different shapes were exhibited by northern elephant seals for travelling, foraging, energy conservation, and digestion. Asaga et al. (1994) concluded that the type-D (U-shaped) dives of northern elephant seals are exhibited during foraging, because they occurred throughout the period spent at sea, except for the first and last few days when the seals were moving across the continental shelf. The mean characteristics of these dives changed in a manner consistent with seals foraging in the deep scattering layer, and the frequency of type-D dives was lowest during the day when type-C dives, thought to be associated with digestion, peaked. Crocker et al. (1994, 1997) also concluded that northern elephant seals drifted during some skew-shaped dives to rest and digest food.

However, few studies have provided direct evidence of the relationship between dive shape and function. In one of the first such studies, Lesage et al. (1999) used a combination of direct observation and stomach-temperature telemetry to provide evidence of the association between feeding and certain dive shapes. In the present study, we used supervised discriminant function analysis to classify dive shapes among four harbour seal (*Phoca vitulina*) sex and age classes. Our objective was to examine the dive shapes exhibited by different age and sex classes of harbour seals during and immediately following the breeding season. Our hypothesis was that the percentage of dive shapes exhibited by adult males, adult females, and suckling and weaned pups of both sexes would differ and that these differences would reflect known changes in diving behaviour within and among these classes.

Our harbour seal data are useful in this regard, because we have independent data on changes in the behaviour of adults and recently weaned pups. These data come from a series of studies in which harbour seals carrying TDRs were also given a stable hydrogen isotope to estimate food intake from measurements of water flux and changes in body energy stores (Coltman et al. 1998; Bowen et al. 2001; Muelbert et al. 2003). Further evidence comes from free-ranging adults fitted with both an animal-borne video system and a TDR (Bowen et al. 2003) and from gastric intubation of suckling pups (Muelbert and Bowen 1993; Muelbert 1998).

Materials and methods

Data for this study were collected on Sable Island, a vegetated sandbar located 290 km southeast of Halifax, Nova Scotia, Canada (43°90′N, 60°00′W), during the harbour seal breeding seasons (May–June) of 1989–1996 and the post-breeding periods of 1993 and 1994. Adults were captured in hand-held hinged-pole nets, whereas pups were captured by hand or in hoop nets. Prior to attaching TDRs, adults and pups were sedated with an intravenous injection of diazapam at doses of 0.5–0.7 and 0.2 mg/kg, respectively. TDRs were secured to an epoxy mount and glued to the fur on the mid-back of the seal using a 5-min epoxy (Boness et al. 1994). The TDRs and mounts fitted to adults and pups weighed

about 350 g (<0.4% of the initial body mass) and 150 g (<1.0% of the initial body mass), respectively.

Generally, TDRs were programmed to sample depth every 10 s, although units placed on females sampled depth every 7 s in 1989 and 1990. Upon recovery, dive records were corrected for drift in the calibration of the pressure transducer, using software provided by the manufacturer (Zero Offset Correction, Wildlife Computers Inc., Redmond, Wa.). Only dives to a depth ≥4 m were analyzed, to avoid including instrument noise in the dive data. Dive Analysis (Wildlife Computers) was used to calculate the following variables for each dive: depth, duration, bottom time (time spent at more than 85% of the maximum depth of the dive), wiggle count (the number of vertical movements within the bottom portion of the dive), and average ascent and descent rates. To discriminate between dives with and without bottom time, bottom times ≤0.20 s were set to zero. This criterion was used, because given our sampling frequency, only dives with >0.20 s spent at the bottom of a dive represented true time spent at depth. In addition to these variables, two new variables were created: skew (the ratio of average ascent rate/average descent rate) and bottom time/depth (BTD) (Schreer and Testa 1996).

Dive classification

Seven dive shapes were visually identified and 394 dives were then manually classified (approximately 20 randomly selected dives from 20 animals, stratified by sex and age class): four shapes had bottom time (U-shaped dives, wiggle dives, and right- and left-skewed U-shaped dives) and three did not (V-shaped dives and right- and left-skewed V-shaped dives). Dives ≤30 s in duration were omitted from the analysis, because at a TDR sampling rate of 10 s, such dives would appear to be V-shaped. These dives were usually to depths <4 m and therefore were mostly eliminated in initial data processing (see above).

Discriminant functions were derived from this training sample on the basis of the following dive variables: depth, duration, bottom time, average ascent rate, average descent rate, skew, and BTD. Wiggle count was the defining characteristic of wiggle-shaped dives and, thus, all dives with a wiggle count >0 were automatically classified as wiggle dives. The discriminant functions generated by this training set were then used to classify the remaining dives. Dives in the training sample were correctly classified 94.9% of the time, with a cross-validation level of 92.0% correct classifications.

To examine the effect of temporal changes in behaviour during the breeding or post-breeding period on the proportion of dive shapes exhibited, the dives of each individual were grouped into time periods. For males, we used two groups: dives occurring during the premating period (on or before 8 July) and dives occurring during the mating period (after 8 July) (Coltman et al. 1997). Female dives were grouped into three time periods: early lactation (0–6 d postpartum (dpp)), mid lactation (7–14 dpp), and late lactation (≥15 dpp) (Bowen et al. 1999). The dives of suckling pups were grouped into two periods (i.e., ≤11 dpp and >11 dpp) on the basis of the median record length, because there were insufficient data to use the same time periods used for adult females. The dives of weaned pups were also grouped into three weekly periods: 0–6 d post-weaning (dpw), 7–14 dpw, and

Table 1. Number of dives and days sampled (mean ± SE) for the four age and sex classes of harbour seals (*Phoca vitulina*) fitted with TDRs.

Class	n	Dives per animal	Total no. of dives	Days sampled
Weaned pups	15	5718.3 ± 438.63	73 589	21.2 ± 0.62
Suckling pups	13	701.1 ± 228.66	5 955	7.4 ± 1.44
Adult females	45	1024.1 ± 245.23	46 082	14.8 ± 1.00
Adult males	31	7356.2 ± 361.81	157 718	26.3 ± 0.88

Fig. 1. Proportion of dive shapes exhibited by 15 weaned pups during the first month of independence, 13 suckling pups, 45 lactating females, and 31 adult male harbour seals (*Phoca vitulina*) during the breeding season. Error bars are 1 SE; Rskew, right-skewed; Lskew, left-skewed.
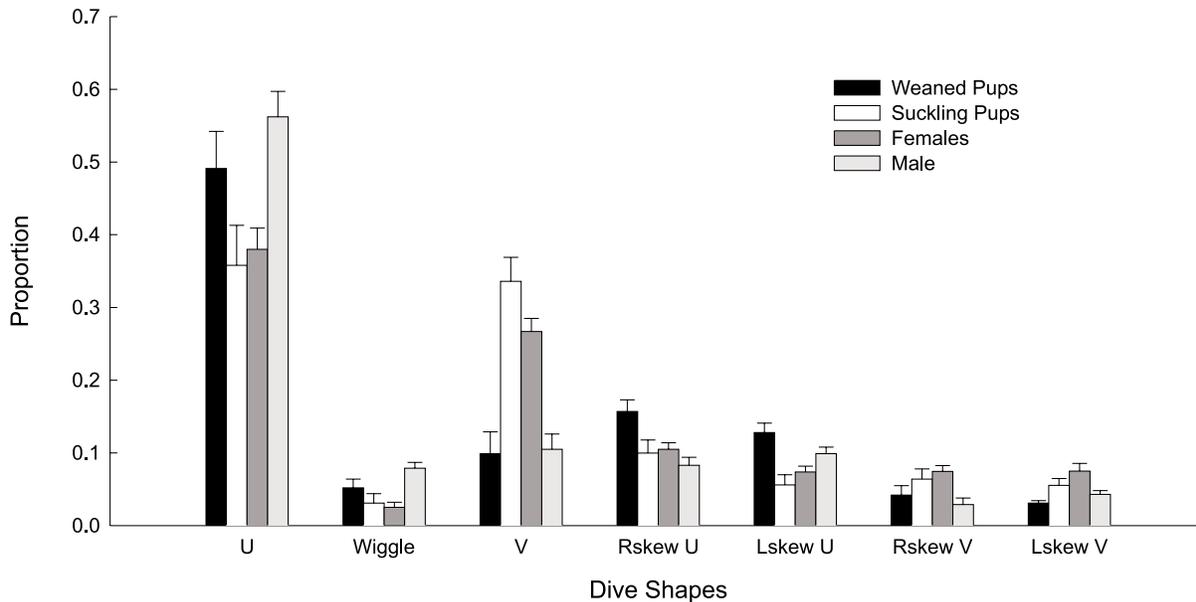
15–25 dpw. Only animals with dives present in each time period were included in the statistical analysis. As a result, sample sizes in this analysis are smaller than for the overall comparison among classes.

Statistical analyses were conducted using SPSS 10.0. The standard error is given as the measure of variability about the mean. Proportions were arcsine square-root transformed prior to analyses. Repeated-measures analysis of variance was used to compare the frequency of dive shapes among age and sex classes and to compare changes in the percentage of dive shapes over time within each age and sex class. In cases where the assumption of compound symmetry was violated in repeated-measures analyses, we used the Greenhouse–Gessier adjusted degrees of freedom (G–G) to assess significance.

Results

A total of 283 344 dives was recorded from 104 harbour seals, including 45 adult females, 31 adult males, 13 suckling pups, and 15 weaned pups (Table 1). Details of the characteristics of individual dives for these animals are found in Boness et al. (1994), Coltman et al. (1997), Muelbert (1998), and Bowen et al. (1999, 2001).

Dive shapes by age and sex class

The proportion of dive shapes exhibited by individuals differed significantly among the age and sex classes (G–G, $F_{[4.8,158.7]} = 9.45$, $P < 0.001$). However, the U-shaped dive was the most common shape exhibited by all four age and sex classes (Fig. 1). Suckling pups and adult females also exhibited a high percentage of V-shaped dives compared with weaned pups and adult males. The percentage of dive shapes exhibited by adult males and females differed significantly ($P = 0.035$), with males exhibiting a greater percentage of U-shaped dives than females but fewer V-shaped dives (Fig. 1). Of the four age and sex classes, wiggle dives were most commonly exhibited by adult males and least commonly exhibited by adult females. Dives with bottom time comprised a large percentage of the dives of weaned pups, with skewed U-shaped dives being more common for this group than for any other (Fig. 1). By contrast, dives without bottom time were most common among suckling pups. The percentage of dive shapes exhibited by weaned pups was more similar to that exhibited by adult males than to suckling pups, whereas adult females and suckling pups had similar percentages of each dive shape. Adult males and weaned pups exhibited a large percentage of bottom-time dives, whereas females and suckling pups exhibited a high percentage of V-shaped dives (Fig. 1).

Table 2. Multivariate analysis of dive-shape characteristics among sex and age classes of harbour seals fitted with TDRs.

Dive Shape	Description	MANOVA* $F_{[15,276]}$	P	Variable	Weaned pups (n = 15) Mean	SE	Suckling pups (n = 13) Mean	SE	Adult females (n = 45) Mean	SE	Adult males (n = 31) Mean	SE
U		9.52	<0.001	Depth (m)	18.86a,b	1.84	16.52a	1.47	16.75a	1.41	24.99b	1.41
				Duration (min)	2.50a	0.10	1.62b	0.12	2.12a	0.09	4.00c	0.10
				Bottom (min)	1.70a	0.06	0.93b	0.08	1.42c	0.07	2.71d	0.07
				Descent (m/s)	0.86a	0.03	0.89a	0.06	0.83a	0.06	0.67a	0.03
				Ascent (m/s)	−0.82a	0.03	−0.78a,b	0.06	−0.82a	0.06	−0.61b	0.02
	Wiggle	5.36	<0.001	Depth (m)	20.56a,b	2.26	15.16a,b	1.50	16.36b	1.15	22.43a	1.64
				Duration (min)	3.03a	0.27	1.69a,b	0.14	2.61a	0.11	3.89c	0.13
				Bottom (min)	1.92a	0.17	1.06b	0.07	1.80a	0.09	2.53c	0.09
				Descent (m/s)	0.85a	0.03	0.92a	0.10	0.81a	0.05	0.61a	0.03
				Ascent (m/s)	−0.78a	0.03	−0.96a	0.09	−0.83a	0.05	−0.57b	0.03
V		8.87	<0.001	Depth (m)	9.31a,b	0.72	9.97a	0.52	7.60b	0.37	7.39b	0.45
				Duration (min)	1.13a	0.03	0.98a,b	0.04	0.94b	0.02	1.37c	0.03
				Bottom (min)	0.22a	0.01	0.26a	0.01	0.25a	0.01	0.23a	0.01
				Descent (m/s)	0.43a	0.02	0.53a	0.04	0.45a	0.02	0.30b	0.01
				Ascent (m/s)	−0.39a	0.02	−0.50a	0.05	−0.44a	0.03	−0.29b	0.01
Right-skewed U		7.52	<0.001	Depth (m)	10.77a	0.74	8.54a	0.60	9.90a	0.72	9.49a	0.54
				Duration (min)	2.06a	0.06	1.24b	0.09	1.83a	0.13	2.92c	0.08
				Bottom (min)	1.36a	0.07	0.65b	0.05	1.04c	0.07	1.35a	0.05
				Descent (m/s)	1.43a	0.06	1.36a	0.11	1.27a	0.06	0.73b	0.04
				Ascent (m/s)	−0.58a	0.04	−0.43a	0.06	−0.48a	0.04	−0.21b	0.02
Left-skewed U		8.66	<0.001	Depth (m)	11.59a	0.81	9.30a,b	1.02	8.75b	0.61	9.16a,b	0.62
				Duration (min)	2.29a	0.09	1.37b	0.14	1.98a	0.09	3.14c	0.12
				Bottom (min)	1.15a	0.05	0.69b	0.06	0.91b	0.05	1.49c	0.09
				Descent (m/s)	0.29a	0.02	0.36a	0.04	0.23b	0.02	0.15c	0.01
				Ascent (m/s)	−1.13a	0.05	−1.22a	0.11	−0.88b	0.05	−0.57c	0.03
Right-skewed V		8.36	<0.001	Depth (m)	6.52a	0.34	5.75a	0.32	5.84a	0.19	5.69a	0.21
				Duration (min)	0.88a	0.04	0.61a	0.04	0.80a	0.04	1.13b	0.06
				Bottom (min)	0.05a	0.00	0.06a	0.01	0.04a,b	0.00	0.03b	0.00
				Descent (m/s)	0.90a,b	0.03	0.97a,b	0.06	1.01a	0.06	0.76b	0.03
				Ascent (m/s)	−0.22a,b	0.01	−0.28a	0.02	−0.22a,b	0.01	−0.21b	0.01
Left-skewed V		6.25	<0.001	Depth (m)	7.38a	0.46	6.63a	0.55	6.46a	0.38	6.74a	0.39
				Duration (min)	1.03a	0.04	0.77a	0.09	0.94a	0.05	1.54b	0.06
				Bottom (min)	0.03a	0.00	0.03a	0.01	0.03a	0.00	0.01b	0.00
				Descent (m/s)	0.22a	0.02	0.27a	0.04	0.22a	0.01	0.16b	0.01
				Ascent (m/s)	−0.76a	0.04	−0.78a	0.10	−0.67a	0.03	−0.52b	0.02

Note: Values followed by the same letter are not significantly different at the 0.05 significance level, using a Šidák post-hoc univariate test.

*Statistical results are from a multivariate analysis of variance of dive-shape characteristics by age and sex classes.

The characteristics of dive shapes differed significantly among age and sex classes (Table 2; MANOVA, $P < 0.001$ for all dive shapes). Dive shapes without bottom time were generally the shallowest dives, with pups (both weaned and suckling) having significantly deeper V-shaped dives than adults. Weaned pups also had the deepest skewed U-shaped dives, but post-hoc analysis showed that this difference was not significant (Table 2). Male harbour seals exhibited the longest dives across all seven dive shapes, followed by weaned pups. For all dive shapes, males had significantly slower rates of ascent and, in some cases, of descent compared with other groups, which may account for the longer dive durations in this group. Although there was some variability among dive shapes, the characteristics of dives by suckling pups were most similar to those of dives by adult females (Table 2).

Temporal changes in dive shapes within age and sex classes

The proportion of dive shapes exhibited by adult males differed significantly between the premating and mating periods (G–G, $F_{[2.1,125.1]} = 12.4$, $P < 0.001$). In both periods, U-shaped dives were most common (Fig. 2), however, there was a significant decrease in the percentage of U-shaped dives between the premating (62.5 ± 3.0%) and mating (44.6 ± 2.9%) periods ($t_{30} = 6.23$, $P < 0.001$). The percentage of all other dive shapes increased during the mating period, but only significantly so for V-shaped (9.2 ± 1.2 to 17.4 ± 3.0%, $t_{30} = -2.84$, $P = 0.008$) and left-skewed U-shaped (8.1 ± 1.0 to 13.3 ± 1.7%, $t_{30} = -2.21$, $P = 0.035$) dives.

The proportion of dive shapes exhibited by females differed significantly over the three periods of lactation (G–G, $F_{[3.8,113.0]} = 10.03$, $P < 0.001$; Fig. 2). The percentage of U-shaped dives increased significantly from early (16.7 ± 3.1%) to late (54.9 ± 6.9%) lactation ($F_{[2,60]} = 12.26$, $P < 0.001$), whereas the percentage of V-shaped dives decreased significantly (40.7 ± 3.2 to 13.7 ± 3.5%, $P < 0.001$). Left-skewed V-shaped dives also decreased significantly from 8.3 ± 1.1% during early lactation to 2.7 ± 0.7% during late lactation ($F_{[2,60]} = 4.82$, $P = 0.011$). The proportions of the four other dive shapes did not vary significantly throughout lactation (Fig. 2).

The proportion of dive shapes exhibited by suckling pups changed significantly between early and late lactation (G–G, $F_{[2.2,30.7]} = 3.45$, $P = 0.041$; Fig. 3). U-shaped dives increased significantly (26.0 ± 5.5 to 45.0 ± 6.9%, $t_7 = -2.54$, $P = 0.039$), with a corresponding decrease in the percentage of V-shaped dives (39.5 ± 6.3 to 24.2 ± 4.6%, $t_7 = 2.83$, $P = 0.025$). Overall, suckling pups exhibited more dive shapes with bottom time during the later stage of lactation. However, this increase was not significant when considering skewed dives with bottom-time individually (Fig. 3).

The proportion of dive shapes exhibited by weaned pups changed significantly over the first month post weaning (G–G, $F_{[4.4,65.8]} = 3.10$, $P < 0.018$; Fig. 2). U-shaped dives were most frequent in all three time-periods but increased from the initial (36.8 ± 6.1%) to the final (57.1 ± 4.3%) post-weaning period ($F_{[2,60]} = 4.06$, $P = 0.028$). The use of V-shaped and right-skewed V-shaped dives decreased significantly from 15.6 ± 2.6 to 8.0 ± 1.2% ($F_{[2,60]} = 4.87$, $P =$

0.015) and from 12.2 ± 2.8 to 2.8 ± 0.6% ($F_{[2,60]} = 3.38$, $P = 0.047$), respectively, over the three post-weaning periods.

Temporal changes in food intake

The significant increase over time in the percentage of U-shaped dives exhibited by lactating harbour seal females was associated with an almost 9-fold increase in both time spent in bouts of diving and estimated food intake by females from early to late lactation (Bowen et al. 2001). Food intake accounted for an average of 29% of the daily energy expenditure of females during late lactation but ranged from 0 to 100%, indicating the importance of foraging during this period (Bowen et al. 2001). Furthermore, there was a significant positive correlation between food intake and the percentage of U-shaped dives exhibited by 14 females during late lactation (Pearson's $r = 0.60$, $P = 0.02$).

Similarly, among pups, the percentage of U-shaped dives increased from about 40 to 58% of dives between the first and second 2-week period post weaning. During these periods, estimated food intake more than doubled from an average of 4.1 to 10.7 MJ/d in 14 of these same pups (Muelbert et al. 2002).

In adult males, the percentage of U-shaped dives decreased from over 60% of total dives during the premating period to about 45% of dives during the mating period, with a corresponding increase in the percentage of V-shaped dives and dives of several other shapes. Associated with the decrease in the percentage of U-shaped dives, food intake in 17 of these males declined from 25.6 to 15.6 MJ/d (Coltman et al. 1998).

Discussion

Classifying dives into two-dimensional shapes based on time and depth is an attempt to extract additional information about the behaviour of aquatic air-breathing predators. Dive-shape classification and inferences about the function of differently shaped dives have been used to investigate the behaviour of pinnipeds (Schreer et al. 2001), turtles (Hochscheid et al. 1999), penguins (Wilson et al. 1996), and cetaceans (Martin et al. 1998). Despite the popularity of this approach, few studies have attempted to validate the behavioural inferences arising from dive-shape analyses. Our results showed that the percentage of dive shapes exhibited by harbour seals differed within and among age and sex classes during the breeding season and the period immediately following the breeding season. These demographic and temporal differences reflect known changes in behaviour based on evidence that is independent of the dive data (see below).

Although, from four to seven dive shapes are generally recognized, two primary shapes are common across studies: the U-shaped dive and the V-shaped dive. The remaining shapes can be viewed as variations of these primary forms, differing in skewness (the ratio of rates of ascent and descent), the presence of wiggles, or the depth or duration of the dive. We have not attempted to assign functions to each of the seven dive shapes classified in this study. Rather, we focussed on evidence for the relationship between foraging and U-shaped dives, because these dives are usually the most commonly exhibited by the species studied

Fig. 2. Temporal changes in the proportion of dive shapes exhibited by 31 adult males (top panel), 21 adult females (middle panel), and 11 weaned harbour seal pups (bottom panel). Error bars are 1 SE; Rskew, right-skewed; Lskew, left-skewed.
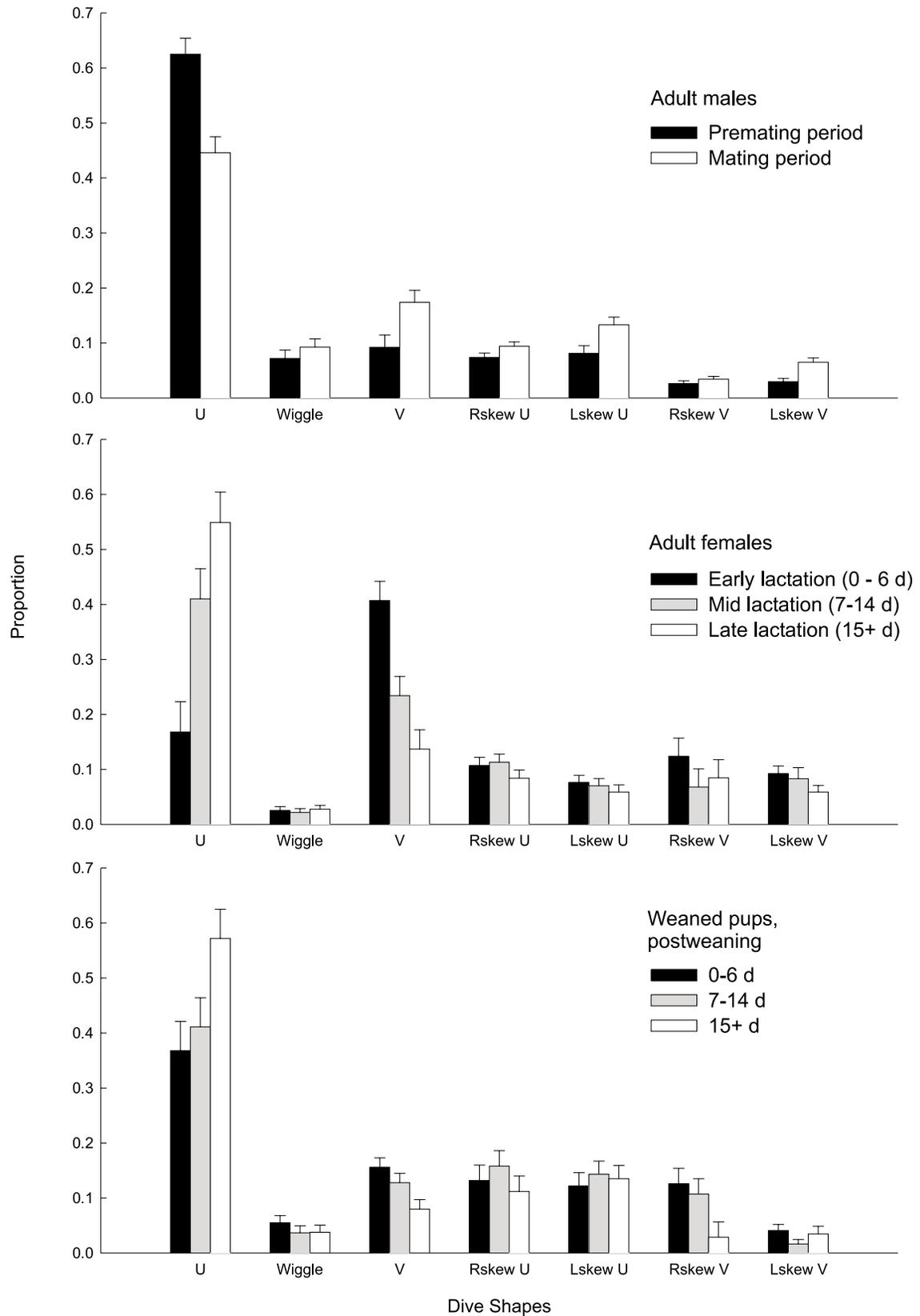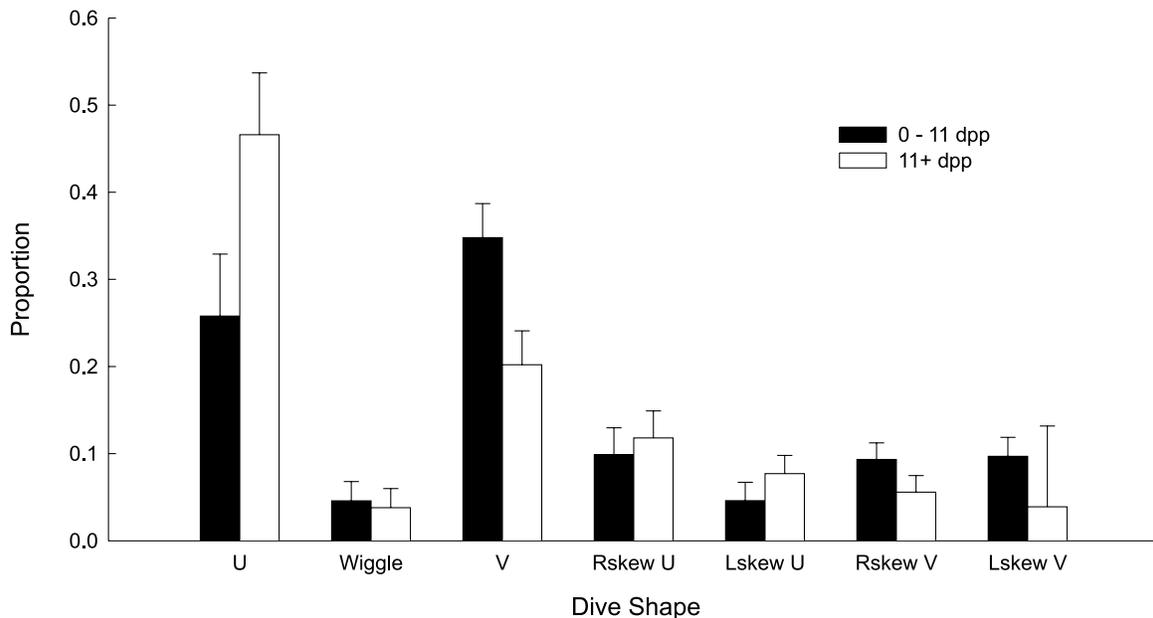
Fig. 3. Proportion of dive shapes exhibited by eight suckling harbour seal pups during the first and second half of lactation. Error bars are 1 SE; Rskew, right-skewed; Lskew, left-skewed.

to date and they varied significantly among classes of harbour seals.

U-shaped dives and dives exhibiting variants of this shape have been consistently attributed to foraging (e.g., Le Boeuf et al. 1988; Hindell et al. 1991; Asaga et al. 1994; Slip et al. 1994; Bjorge et al. 1995; Schreer and Testa 1996; Wilson et al. 1996; Martin and Smith 1998; Lesage et al. 1999). This seems reasonable, as the diver spends most time at the bottom of such dives where it is likely to encounter prey. Nevertheless, the evidence that U-shaped dives are associated only with foraging is largely circumstantial.

Direct evidence that U-shaped dives are exhibited during foraging comes from several sources. The first is stomach-temperature telemetry studies of harbour seals (Bjorge et al. 1995; Lesage et al. 1999). Lesage et al. (1999) found that 89% of feeding events were recorded during either U-shaped dives (48% during their types 1 and 5) or skewed U-shaped dives (41% during their types 3 and 4) and that only 11% occurred during V-shaped dives. The second source is temporal changes in the percentage of dive shapes (this study) and temporal changes in food intake from water-flux data of subsets of the same individuals used in the study (Coltman et al. 1998; Bowen et al. 2001; Muelbert et al. 2003). Finally, based on stomach-temperature data in African penguins (*Spheniscus demersus*), Wilson and Wilson (1995) concluded that prey was ingested only during U-shaped dives.

Evidence of the relationship between dive shape and foraging behaviour is more complex in adult males during the breeding season. Studies during the breeding season using an animal-borne video system showed that harbour seal males foraged only during U-shaped and other bottom-time dives (W.D. Bowen, D. Tully, D.J. Boness, B. Bulheier, and G. Marshall, unpublished data). However, these video data also show that harbour seal males exhibit U-shaped dives while performing behaviours other than foraging. U-shaped dives were also exhibited while travelling throughout their home range, a behaviour quite different from searching for prey, and

while performing roar vocalizations (Hanggi and Schusterman 1994), a reproductive behaviour. Another reproductive behaviour of males, the bubbly growl vocalization (Hanggi and Schusterman 1994), was usually associated with right-skewed U-shaped dives.

Among suckling pups, changes in the percentage of dive shapes between early and late lactation may represent both increased physiological capabilities and learned behaviour. Pups often accompany their mothers during diving (Bowen et al. 1999) and therefore their selection of dive shapes probably reflects those exhibited by females. In contrast with other age and sex classes, the U-shaped dives of suckling pups do not represent foraging behaviour, as pups are dependent on milk for all nutritional requirements. No food other than milk was found in the stomachs of 52 pups sampled by gastric intubation over the course of lactation (Muelbert and Bowen 1993). Thus U-shaped dives exhibited by suckling pups may look similar to the foraging dives of females but were not foraging dives. This illustrates the difficulty of assigning behaviours to specific dive shapes.

Although our data provide further evidence that U-shaped dives are exhibited during foraging, our results also indicate that it is unlikely that dive shapes will generally represent exclusive behaviours. Both data for adult male harbour seals from animal-borne video systems and stomach-temperature telemetry data (Lesage et al. 1999) provide support for this conclusion. Our results underscore the need both for caution when attempting to infer behaviour from dive shape and for further species-specific validation. After all, shapes are simply two-dimensional representations of behaviour performed in three dimensions. Several studies have taken the next logical step by investigating the three-dimensional properties of diving behaviour (Harcourt et al. 2000; Simpkins et al. 2001) and using swimming speed to investigate dive function (Le Boeuf et al. 1992; Lesage et al. 1999). Although these approaches are useful, ultimately assigning function to a dive shape will require direct observation of behaviour (e.g., using

animal-borne video systems). However, estimates of food intake coupled with changes in the percentage of different dive shapes can increase our confidence in the assignment of dive-shape function.

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