

DIVING BEHAVIOR OF SUBADULT AND ADULT HARBOR SEALS IN PRINCE WILLIAM SOUND, ALASKA

KATHRYN J. FROST¹

Alaska Department of Fish and Game,
1300 College Road,
Fairbanks, Alaska 99701, U.S.A.
E-mail: kjfrost@eagle.ptialaska.net

MICHAEL A. SIMPKINS

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

LLOYD F. LOWRY¹

Alaska Department of Fish and Game,
1300 College Road,
Fairbanks, Alaska 99701, U.S.A.

ABSTRACT

Satellite-linked depth recorders (SDRs) were attached to 47 harbor seals in Prince William Sound, Alaska, during 1992–1996. Parameters describing diving effort, diving focus, and focal depth (depth bin to which diving was focused) were calculated from binned data on maximum dive depth and time spent at depth, and analyzed using repeated-measures mixed models. This analysis method accounted for individual variability, temporal autocorrelation, and the binned nature of SDR data, which are often ignored using standard statistical techniques. Results indicated that diving effort remained steady from September to April, when seals spent 68%–75% of their overall time in the water. Time spent in the water declined to 60% in May and to about 40% in July. Seals spent the most time in the water at night and the least in the morning. The diving of all seals in all months was highly focused. Overall, diving was focused to one depth bin approximately 75% of the time. Diving was more focused for females than for males and subadults. Focal dive depth was deepest in winter and shallowest during May–July. Focal depth and diving focus varied by region. Collinearity between month and region in the focal depth model suggests that seals move in winter to regions where prey are found deeper in the water column. Variations in diving behavior presumably result from combinations of regional bathymetry, seasonal cycles

¹ Current address: University of Alaska, School of Fisheries and Ocean Sciences, Fairbanks, Alaska 99775, U.S.A.

in type or depth distribution of prey, and seal life-cycle events such as reproduction and molting.

Key words: harbor seal, *Phoca vitulina richardsi*, Prince William Sound, diving behavior, satellite telemetry, repeated-measures mixed models.

In many parts of the world pinniped populations have increased as predicted after protection from over-exploitation (e.g., Olesiuk *et al.* 1990). However, large declines in populations of harbor seals (*Phoca vitulina richardsi*) and Steller sea lions (*Eumetopias jubatus*) have been documented in parts of Alaska (Pitcher 1990, Loughlin *et al.* 1992). These declines occurred despite implementation of the 1972 Marine Mammal Protection Act, which stopped or limited several types of human-caused mortality. Likewise, since the 1970s some species of sea birds have also declined in the Gulf of Alaska and Bering Sea regions (Anderson and Piatt 1999). These unanticipated declines have prompted monitoring and assessment of marine mammal, sea bird, and fish population trends in these regions.

Harbor seals are one of the most abundant and widely distributed marine mammals in Prince William Sound, Alaska, hauling out and/or pupping at more than 50 sites. Since 1984, harbor seal numbers in Prince William Sound have declined by about 60%, with only part of this decline attributable to the 1989 *Exxon Valdez* oil spill (Frost *et al.* 1994, 1999). A change in the trophic structure of the ecosystem, and hence the availability of prey, is among the hypothesized causes for the harbor seal decline. Determining how harbor seals depend on seasonal or area-specific concentrations of prey may provide insight into the causes of the observed changes in abundance. In addition, harbor seals may act as important indicators of the status of other marine species.

To evaluate the food limitation hypothesis, information is needed not only about the diet of harbor seals, but also about seasonal or annual changes in feeding behavior and the habitats used for feeding. Satellite-linked telemetry can be used to gather the latter types of information (e.g., Stewart *et al.* 1989). Satellite-linked depth recorders (SDRs) have been deployed on a variety of marine mammals, providing insights into both large-scale horizontal movements and diving behavior in these animals (e.g., Heide-Jørgensen *et al.* 1992, Heide-Jørgensen and Dietz 1995, Nordøy *et al.* 1995, Stewart *et al.* 1996, Merrick and Loughlin 1997, Lowry *et al.* 1998). However, unlike time-depth recorders (TDRs), which record and store information about individual dives, many SDRs sum dive information into bins over 6-h blocks of time. The binned nature of the SDR data, as well as substantial variability in diving behavior of individual seals, have made SDR data poorly suited to standard analysis techniques. These difficulties have often resulted in the application of simple summary statistics to SDR data and/or in the presentation of data for each individual, without a suitable means of combining data for groups of individuals (e.g., Mate *et al.* 1994, 1995; Davis *et al.* 1996; Stewart *et al.* 1996). The inferences about diving behavior that can be drawn from either

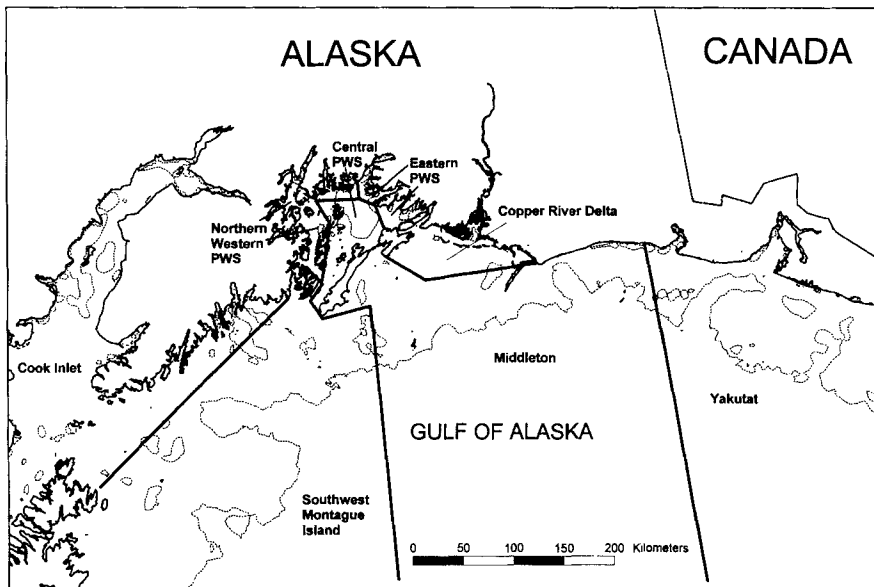


Figure 1. Map of Prince William Sound study area showing major harbor seal haul-outs (solid triangles) and 200 m depth contour (dotted line).

summary statistics or individual descriptions are limited. Temporal autocorrelation in SDR data has also been largely ignored in these summary analyses.

In this paper we present a statistically robust method for analyzing SDR data that accounts for individual variability among animals, temporal autocorrelation, and the binned nature of the data. We use this method to analyze the diving behavior of harbor seals in Prince William Sound, Alaska, using a large SDR dataset collected during 1992–1997 (Lowry *et al.* 2001). We specifically address patterns in diving behavior related to sex and age of the seal, time of day, month, and region.

METHODS

Data Collection

Harbor seals in Prince William Sound were captured in nets near haul-outs and outfitted with 0.5-w SDRs (Wildlife Computers, Redmond, WA; version 3.10 software) as described by Lowry *et al.* (2001). Seals weighing >50 kg were instrumented with tags that measured $14.8 \times 10.0 \times 3.8$ cm and weighed about 750 g in air. For lighter seals we used tags that measured $11.9 \times 5.1 \times 4.5$ cm and weighed 385 g. The larger tags had a projected capacity of about 100,000 transmissions, whereas the small tags were rated for approximately 30,000 transmissions. SDRs were equipped with a salt-water switch and transmitted only when a seal was at the surface.

Seals were tagged in spring (late April–May) and fall (late September). SDRs

attached in spring were not duty-cycled and transmitted continuously, because we expected that tags would be shed during the annual molt in August, long before the batteries failed. To conserve battery power, tags attached in the fall were programmed to not transmit during hours of poor satellite coverage (2200–0300 local time). In addition, small tags attached in the fall were duty-cycled one day on and one day off, or one day on and two days off.

The SDRs sampled time and pressure (depth) every 10 sec and summarized and stored this information in bins representing four 6-h histogram periods per day: 2100–0259 (night), 0300–0859 (morning), 0900–1459 (midday), and 1500–2059 (evening), local time (GMT – 10 h). All 47 SDRs collected data about the maximum depth and the duration of each dive. The SDRs measured depth from 0 to 490 m, with depth resolution of 2 m. There is considerable instrument noise and inaccuracy in assigning depths to dives that are near the 2-m resolution of the pressure sensor. Thus, we chose a depth equal to twice the resolution of the instrument (4 m) as the minimum depth to be considered a dive. Maximum dive depths were accumulated in user-defined bins as follows: 4–20 m, 21–50 m, 51–100 m, 101–150 m, 151–200 m, and >200 m. Thirty-five of 47 SDRs also stored “time-at-depth” which recorded the amount of time a seal spent per 6-h period within these same depth bins. In addition, a 0-m bin recorded time spent at the surface and dry, and a 0–4-m bin recorded the time the seal was wet and swimming shallower than 4 m.

Dive and location data from SDRs were relayed *via* satellite receivers operated by Service ARGOS (Argos 1990). Location data were screened and erroneous records identified as described by Lowry *et al.* (2001). Dive data from SDRs were extracted using the software program SATPAK 3.0 (Wildlife Computers). This software used an error-checking algorithm to validate messages. Histogram messages were sorted by date, period, and type, and duplicate messages were removed.

Diving Behavior Analysis

We analyzed diving behavior of seals in Prince William Sound with respect to sex and age of the seal, month, time of day, and geographical region. Seal location data were initially assigned to eight regions as follows: eastern Prince William Sound, northern and western Prince William Sound, central Prince William Sound, southwestern Montague Island, Copper River Delta, Middleton Island, Yakutat, and Cook Inlet (Fig. 1). Tagged seals were rarely found within four of these regions (eastern PWS, southwestern Montague, Yakutat, and Cook Inlet). These data-poor regions were not used in the final analysis because they contained too few observations (<1.5% of seal locations were within the region) or data were available from only a few seals of a single age or sex class. Data were not analyzed for year effect because of unequal distribution of age and sex categories across years. Seals were classified as adults or subadults according to their weight. Males <55 kg and females <47 kg were

considered to be subadults, based on historical age/weight data from the northern Gulf of Alaska (Pitcher and Calkins 1979).

Harbor seal SDR data were analyzed for diving effort, diving focus, and focal depth. SDRs provided several possible measures of diving effort, including number of dives, total duration of dives, and time spent in the water per 6-h data collection period. We chose "time-in-water" as the most representative effort variable. Data on number and duration of dives do not include any dives shallower than 4 m, yet seals spend considerable time in such shallow water. SDRs were programmed so that Bin 0 of the time-at-depth data recorded the proportion of time the sensor was dry during each period. Time-in-water was therefore calculated as 6 h minus time in Bin 0 for each period. Time-in-water values ranged from 0 h, for periods during which a seal was continually hauled out, to 6 h, for periods during which a seal was always in the water.

Diving focus was defined as the dominance of one depth bin in the maximum dive-depth data for a 6-h period. Diving focus (F) was calculated as the inverse of Simpson's Diversity Index, (Simpson 1949, Washington 1984, Krebs 1999):

$$F = \sum \{[n_i(n_i - 1)]/[N(N - 1)]\}$$

where n_i = number of dives to depth bin i , and N = total number of dives. The maximum value for focus, $F = 1$, indicated that all dives were to the same depth bin. A focus value of $F > 0.5$ indicated that dives in a period were primarily to one depth bin, while $F = 0.167$ indicated that dives were evenly distributed among the six depth bins. Because we used the "finite correction factor" [$n(n - 1)$ and $N(N - 1)$] in calculating dominance of bins, a smaller sample size required more relative focus to get the same value of F (*i.e.*, the analysis was more conservative for a small sample size). Also, Simpson's Diversity Index incorporates the distribution of bin use. When dives were allocated over several depth bins (instead of only two), proportionately more dives to the main depth bin were required to get a focus value of $F > 0.5$.

We defined focal depth as the dominant depth bin for a 6-h period, during which the seal's diving was primarily focused to that depth bin ($F > 0.5$). The term "focal depth", used in this context, has no relationship to "focal length" or other such optical terms. Seals were not considered to exhibit any depth preference when their diving was not focused to one depth bin, so focal depths were not determined for periods with $F < 0.5$.

Separate diving focus and focal depth analyses were conducted for "any time-in-water" and "time-in-water > 3 h" data sets to explore the effect of time-in-water on diving focus and focal depth. Bin data were summarized by standard 6-h periods, regardless of an individual's behavior, and some data represented periods when seals were diving less than half the time (time-in-water < 3 h). These low time-in-water periods could have represented the beginning or ending of a diving bout, or sporadic diving around a haul-out which might differ from diving while foraging. It was our intent to investigate foraging

behavior, so we compared diving focus and focal depth between high-effort (time-in-water > 3 h) periods and all periods. The "high time-in-water" and "any time-in-water" analyses produced consistent results, and we therefore used "any time-in-water" in subsequent analyses. This made it possible to include data from 12 additional seals in diving-focus and focal-depth analyses. SDRs from those seals provided maximum dive-depth data, but did not provide the time-at-depth data required to calculate time-in-water.

In addition to the time-in-water, focus, and focal-depth variables described above, a time series variable was created which combined the Julian date and time period for each record (time series = Julian date + time period/4). In cases where data from one seal spanned two years, the time series values in the second year were in sequence with those of the first year (*e.g.*, 31 December 1995 period 3 = 365.75; 1 January 1996 period 2 = 366.5). This time-series variable was used for calculating, and correcting for, the effect of temporal autocorrelation on statistical models of diving behavior.

Statistical Analysis

Repeated-measures mixed models for time-in-water, diving focus, and focal depth were created using the MIXED procedure in SAS (version 6.12, SAS Institute Inc.; Littell *et al.* 1996). We selected random subsets of 100 records from the databases for each seal for inclusion in each analysis, where each record included data from one 6-h period. For seals with less than 100 records, all data were included in analyses. Subsetting the data greatly reduced computation time, and also balanced the impact on the model of seals with many or few records. This was particularly important since non-duty-cycled SDRs transmitted substantially more data than did the duty-cycled units, and without subsetting might have disproportionately influenced the analyses. An alternative approach would involve an analysis with data from each seal weighted differently, however such an approach would not reduce computation time, which was prohibitive without subsetting.

Since the repeated-measures analysis (which accounted for temporal autocorrelation in the data) was very computation-intensive, the best model for each analysis was first determined using forward stepwise procedures with variation between individual seals as a random effect but without repeated-measures analysis. Denoting individual variation as a random effect modeled the variation in behavior between individual seals as randomly distributed around a mean of zero for all seals. Thus, an "average" seal would have no impact on the model. Fixed effects (sex, age, month, period, and region) were added singly to each model, using Akaike's Information and Schwarz's Bayesian Criteria (Carlin and Louis 1996) to determine the order of entry into the model.

Models with the maximum number of significant fixed effects were chosen for further analysis by including repeated-measures within the MIXED procedure. A spherical spatial autocorrelation model was used with time series and a column of ones as the dimensions, and individual seals as subjects, in

the model. Denoting seals as subjects in the model resulted in one global autocorrelation model being fit for all seals based on the autocorrelation found within the data for each seal (*i.e.*, data from seal X was not autocorrelated with data from seal Y). The random effect of variation among individual seals was maintained in the repeated-measures analysis. In several cases, parameters that had been significant in the mixed model were no longer significant in the repeated-measures mixed model. In those cases, non-significant fixed effects were removed one at a time to determine the final models that had the maximum number of significant fixed effects.

RESULTS

We analyzed data from 47 seals (25 females, 22 males, 27 adults, and 20 subadults) captured between 1992 and 1996 (see Appendix 1 in Lowry *et al.* 2001). Forty-five were captured and tagged in central Prince William Sound, one in eastern Prince William Sound, and one in northern Prince William Sound (Fig. 1). Seals were tagged during spring (April or May) and fall (September). SDRs attached in spring ($n = 21$) operated for an average of 64 d (range 39–81), before being shed during the annual molt. Fall SDRs ($n = 26$), which were attached after the molt was completed, operated for an average of 179 d (range 40–312).

Time-in-Water

The subset of time-in-water data used in the statistical analysis contained 2,522 records, each of which represented one 6-h period, for a total of 15,132 h of diving by 35 seals. This subset excluded data from poorly represented regions and included ≤ 100 randomly selected records/seal, reducing the original database by 50% (from 4,995 records). Month and time period were significant fixed effects in the repeated-measures mixed model for time-in-water. Sex, age class (*i.e.*, adult or subadult), and geographic region did not significantly affect time-in-water (Table 1). Time-in-water was similar throughout September–April (68%–75% of each 6-h period spent in the water), then declined steadily from 60% in May to 40% in July (Table 1, Fig. 2A). Seals spent the least time in the water diving in the morning (0300–0900) (Fig. 2B). Time-in-water increased throughout the day and was highest at night (2100–0300) (Table 1). At night seals spent approximately 80% of their time diving during September through April (range 77%–84%), compared to 50% in July. Seals spent about 19% less time diving in the early morning than they did at night.

Diving Focus

The subset of diving focus data used in the statistical analysis contained 3,163 records, for a total of 18,978 h of diving by 47 seals. This subset excluded data from poorly represented regions and included ≤ 100 randomly

Table 1. Stepwise mixed models statistics and parameter estimates for time-in-water model for harbor seals in Prince William Sound, Alaska ($n = 2,522$ 6-h periods, 35 seals). Covariance parameters for random effects and temporal autocorrelation are compared to the "total error variance" that would have been present in a simple fixed-effects model (total error variance = random effect variance + autocorrelation + residual variance).

Stepwise mixed models statistics (with random seal effect but no repeated measures)					
Variables in model	Type III <i>F</i> -statistic		<i>P</i>		
Sex	0.46		0.50		
Age	1.38		0.24		
Month	11.51		0.0001		
Period	14.67		0.0001		
Region	1.38		0.25		
Month, period	11.89, 15.72		0.0001, 0.0001		
Parameter estimates from best repeated-measures mixed model for time-in-water					
Fixed effect	Time-in-water (min)	SE	df	<i>t</i>	<i>P</i>
Intercept	263.6614	11.053	34	23.85	0.0001
Month					
January	-10.7778	13.697	2474	-0.79	0.431
February	7.9979	14.541	2474	0.55	0.582
March	-14.9388	16.071	2474	-0.93	0.353
April	-5.0566	16.031	2474	-0.32	0.753
May	-44.2030	13.549	2474	-3.26	0.001
June	-74.4995	14.328	2474	-5.2	0.0001
July	-112.2920	19.937	2474	-5.63	0.0001
September	9.1771	15.089	2474	0.61	0.543
October	6.8952	11.972	2474	0.58	0.565
November	6.6206	12.332	2474	0.54	0.591
December	0				
Period					
2100-0300	28.3274	8.721	2474	3.25	0.001
0300-0900	-26.7608	5.218	2474	-5.13	0.0001
0900-1500	-14.06	5.240	2474	-2.68	0.007
1500-2100	0				
Covariance parameter				Parameter estimate	Proportion of total error variance
Seal (random effect variance)				651.90	0.054
Sill-Nugget (repeated-measures/autocorrelation)				1,607.79	0.134
Residual variance				9,773.61	0.812
Total error variance				12,033.30	1.000
Range (spherical model, repeated-measures) = 15.0 d					

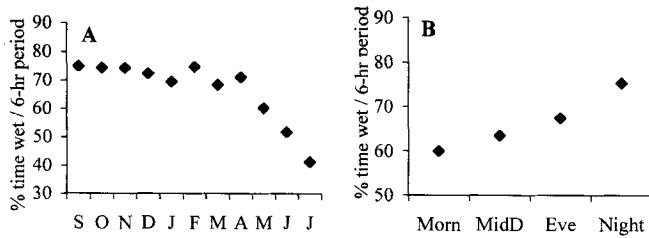


Figure 2. Modeled estimates of time-in-water for 35 satellite tagged harbor seals in Prince William Sound, Alaska, by month (A) and time of day (morning, midday, evening, night) (B). For ease of graphic presentation, data are adjusted from minutes to % time wet per 6-h period. Monthly estimates of time-in-water are average values for all periods of the day combined, and estimates for time of day are averages for all months combined (from Table 1).

selected records/seal, reducing the original database by 38% (from 5,133 records). Data were available from 12 seals that did not have time-at-depth data, in addition to the 35 seals included in the time-in-water analysis. Diving focus was significantly affected by time of day, region, and the interaction of sex and age (*i.e.*, sex-age class, Table 2). The diving of all seals was highly focused even before the effects of analysis variables were considered (model intercept $F = 0.69$, Table 2). The lowest focus predicted by the model was $F = 0.54$ for adult male seals in northwestern Prince William Sound, indicating that even the lowest focus values reflected a strong focus to one depth bin. Overall, diving was focused to one depth bin ($F > 0.5$) during approximately three quarters of the 6-h data periods recorded for all seals. Focus was not significantly affected by month.

Seal diving was most focused during midday (0900–1500) and secondarily at night (Fig. 3A). Adult female diving was the most focused of all demographic classes, and adult male diving was the least focused (Fig. 3B). Seal diving was most focused in the very shallow Copper River Delta and the least focused in Prince William Sound where bathymetry was highly variable (Fig. 3C).

Focal Depth Bin

The subset of focal depth data used in the statistical analysis contained 2,485 records, for a total of 14,910 h of diving by 47 seals. This subset excluded records with diving focus < 0.5 , as well as data from poorly represented regions including ≤ 100 records/seal, reducing the original diving focus database by 52% (from 5,133 records). Month and region were significant fixed effects in the model using data for any time-in-water (Table 3). However, collinearity between month and region, combined with lower sample size, resulted in month and region not being significant together in the model using only data with time-in-water > 3 h. We used the “any time-in-water” model, since it overcame collinearity problems. This model indicated that the

Table 2. Stepwise mixed models statistics and parameter estimates for diving focus models of harbor seals in Prince William Sound. Estimate is for any time-in-water ($n = 3,163$ 6-h periods, 47 seals). Covariance parameters for random effects and temporal autocorrelation are compared to the "total error variance" that would have been present in a simple fixed-effects model (total error variance = random effect variance + autocorrelation + residual variance).

Variables in model	Stepwise mixed models statistics (with random seal effect but no repeated measures)		df	SE	Diving focus	t	P
	Type III F-statistic	P					
Sex	14.70	0.0001					
Age	1.24	0.266					
Month	2.21	0.015					
Period	20.30	0.0001					
Region	7.98	0.0001					
Sex, period	14.43, 20.23	0.0001, 0.0001					
Sex, period, region	13.34, 20.10, 7.54	0.0003, 0.0001, 0.0001					
Sex, month, period, region	12.56, 2.36, 19.29, 8.63	0.0004, 0.0090, 0.0001, 0.0001					
Sex, age, month, period, region	12.07, 1.44, 2.37, 19.24, 8.70	0.0005, 0.2304, 0.0085, 0.0001, 0.0001					
Parameter estimates from best repeated-measures mixed model for diving focus							
Fixed effect	Diving focus	SE	df	t	P		
Intercept	0.6872	0.041	43	16.57	0.0001		
Sex*Age							
Adult female	0.1599	0.044	3110	3.65	0.0001		
Subadult female	-0.0213	0.050	3110	-0.43	0.670		
Adult male	-0.0909	0.045	3110	-2	0.046		
Subadult male	0						
Period							
2100-0300	0.0446	0.016	3110	2.78	0.005		
0300-0900	0.0169	0.010	3110	1.7	0.089		
0900-1500	0.0731	0.010	3110	7.08	0.0001		
1500-2100	0						

Table 2. Continued.

Fixed effect	Diving focus	SE	df	t	P
Region					
Northwest PWS	-0.0544	0.034	3110	-1.61	0.108
Central PWS	-0.0486	0.025	3110	-1.98	0.048
Copper River Delta	0.0933	0.037	3110	2.53	0.011
Middleton	0				
Covariance parameter					
Seal (random effect variance)			Parameter estimate	Proportion of total error variance	
Sill-Nugget (repeated-measures/autocorrelation)			0.0084	0.132	
Residual variance			0.0091	0.144	
Total error variance			0.0459	0.724	
Range (spherical model, repeated-measures) = 24.2 d			0.0634	1.000	

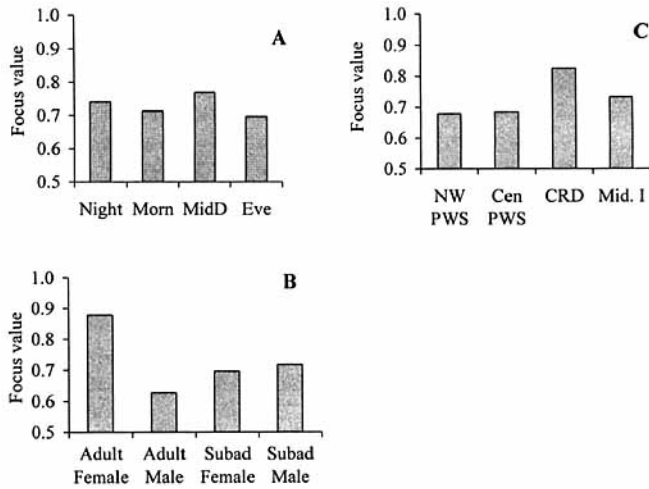


Figure 3. Modeled estimates of diving focus for 47 satellite-tagged harbor seals in Prince William Sound, Alaska, by time of day averaged across all regions and sex-age classes (A), sex-age class for all times of day and regions (B), and region for all times of day and all age-sex classes combined (C). Graphed estimates are average values of parameter estimates in Table 2.

focal depth bin was deepest during midwinter (February) and shallowest in spring (Fig. 4A). Focal depth was deepest in central Prince William Sound and shallowest in Copper River Delta (Fig. 4B).

Random Effects and Temporal Autocorrelation

For each analysis a random effect for seal was included in the model. The model error terms included two parts: a temporal autocorrelation component for repeated measurements of a seal, and an independent component (residual error). Each seal was assumed to have the same autocorrelation parameters. This model fitted considerably better, as judged by likelihood equations, when compared to a simple fixed-effects model. The error variance of a simple fixed-effects model would include deviations from the model that we had accounted for by including temporal autocorrelation and the random effects of individual differences in seal behavior. Temporal autocorrelation accounted for 13%–26% of the total variance (random effect variance + autocorrelated error variance + independent error variance, Table 1–3). The estimated range of autocorrelation for the model errors was 9.9–24.2 d. The estimated variance of the random effects for seals for each analysis (normal distribution, mean = 0) accounted for 5%–30% of the total error variance (Table 1–3).

DISCUSSION

The modeling and statistical approach we present here was developed to overcome some of the problems inherent in analysis of temporally autocorre-

Table 3. Stepwise mixed models statistics and parameter estimates for focal depth models of harbor seals in Prince William Sound. Estimate is for any time-in-water and for focused diving ($F > 0.5$, $n = 2,485$ 6-h periods, 47 seals). Covariance parameters for random effects and temporal autocorrelation are compared to the "total error variance" that would have been present in a simple fixed-effects model (total error variance = random effect variance + autocorrelation + residual variance).

Stepwise mixed models statistics (with random seal effect but no repeated measures)					
Variables in model	Type III <i>F</i> -statistic		<i>P</i>		
Sex	1.12		0.290		
Age	0.99		0.321		
Month	6.51		0.0001		
Period	1.70		0.164		
Region	27.69		0.0001		
Month, region	4.77, 21.76		0.0001, 0.0001		
Parameter estimates from best repeated measures model for focal depth					
Fixed effect	Focal depth bin	SE	df	<i>t</i>	<i>P</i>
Intercept	1.3455	0.108746	46	12.37	0.0001
Month					
January	0.1009	0.090	2425	1.13	0.260
February	0.2425	0.097	2425	2.5	0.012
March	-0.0265	0.110	2425	-0.24	0.810
April	-0.1036	0.113	2425	-0.92	0.358
May	-0.1934	0.101	2425	-1.92	0.055
June	-0.1668	0.106	2425	-1.57	0.115
July	-0.0366	0.127	2425	-0.29	0.772
September	0.0339	0.101	2425	0.34	0.736
October	-0.0614	0.080	2425	-0.77	0.443
November	-0.0050	0.082	2425	-0.06	0.952
December	0				
Region					
Northwest PWS	-0.0510	0.106	2425	-0.48	0.632
Central PWS	0.1440	0.073	2425	1.98	0.048
Copper River Delta	-0.3443	0.109	2425	-3.16	0.002
Middleton	0				
Covariance parameter			Parameter estimate	Proportion of total error variance	
Seal (random effect variance)			0.16	0.296	
Sill-Nugget (repeated-measures/autocorrelation)			0.14	0.259	
Residual variance			0.24	0.444	
Total error variance			0.54	1.000	
Range (spherical model, repeated-measures) = 9.9 d					

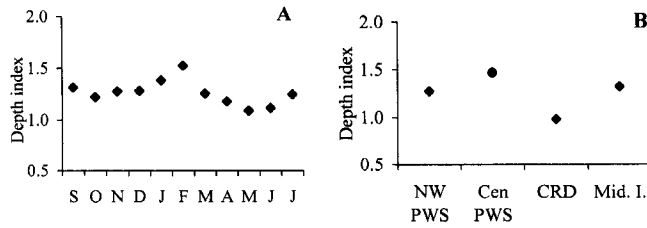


Figure 4. Modeled estimates of focal diving depth by month for all areas combined (A) and region averaged across all months (B), from parameter estimates in Table 3. Parameter estimates for this analysis are in units of depth bins where bins are numbered from 0 (4–20 m) to 5 (>200 m). In this figure, a depth index value of 1 corresponds to the 20–50-m bin, and a value of 2 to the 50–100-m bin.

lated SDR bin-type data with substantial individual variability among seals. Individual variability and temporal autocorrelation were significant factors in all three aspects of our analysis, accounting for a substantial part of the total error variance. Temporal autocorrelation in the data was detected over periods of many days. Individual variability, as measured by the random effects fit, encompassed a significant portion of the variation seen in the sample as a whole. Not surprisingly the focal-depth analysis demonstrated the strongest autocorrelation, as well as the greatest seal-to-seal variance. This is consistent with the facts that harbor seals often dive repeatedly to the bottom to feed, these feeding dives are often geographically clumped, and individual seals may use different areas and habitats for feeding (Boness *et al.* 1994, Ries *et al.* 1997, Tollit *et al.* 1998, Lesage *et al.* 1999, Lowry *et al.* 2001).

One problem with analyzing binned data is that the actual depth of any given dive is unknown. Some studies have analyzed data on a bin-by-bin basis, essentially studying diving behavior within each bin separately (Heide-Jørgensen and Dietz 1995, Heide-Jørgensen *et al.* 1998, Burns *et al.* 1999, Teilmann *et al.* 1999). Others have incorporated information from all bins by calculating a “mean depth” for each histogram period based on the assumption that the average depth of dives within each bin was equal to the bin midpoint (Mate *et al.* 1995, Merrick and Loughlin 1997, Burns and Castellini 1998, Folkow and Blix 1999). Results of comparisons between TDR and binned SDR data for Weddell seal pups suggest this assumption is reasonable (Burns and Castellini 1998). However, while foraging can be inferred from TDR dive profiles, foraging cannot be readily inferred from binned SDR data. For this reason, it is particularly important to explore ways of restricting analyses to subsets of the data that are more likely to represent foraging.

Many studies of harbor seal dive behavior have been conducted in regions where seals dive and forage in relatively shallow areas (<50 m, Boness *et al.* 1994, Coltman *et al.* 1997, Tollit *et al.* 1998, Lesage *et al.* 1999). In Prince William Sound the horizontal foraging ranges of seals are fairly similar to those for harbor seals in other areas (Lowry *et al.* 2001), but the bathymetry is highly variable. Depths of <50–>200 m are available to seals within just a few kilometers of their haul-outs. Thus, seals using the same haul-out may

forage in very different water depths and habitats within a short period. When summary statistics from bin data (e.g., mean depth) are summed over periods without regard to diving focus (e.g., Merrick and Loughlin 1997, Folkow and Blix 1999), the results may be misleading. For example, summary histograms may imply non-selective use of the water column if seals usually dive to the bottom but water depth varies. In fact, diving in such an instance is highly focused but the habitat is variable. In contrast, the approach we used directly accounted for differences in focus and variability between individuals. We suggest that bin-type data can be more informative if an assessment of diving focus is conducted. Estimates of focal depth, together with information about bathymetry and prey availability, are likely to be more useful than summary statistics in determining when, where, and upon what animals are feeding.

Time-in-water measured for seals in this study is within the range of values reported for harbor seals in other areas, for example 61%–93% in Moray Firth, Scotland (Thompson *et al.* 1998), and 76%–93% in the Dutch Wadden Sea (Ries *et al.* 1997), but somewhat lower than reported values of 90% or more for hooded seals (*Cystophora cristata*; Folkow and Blix 1999), northern elephant seals (*Mirounga angustirostris*; Le Boeuf *et al.* 1989), and southern elephant seals (*M. leonina*; Campagna *et al.* 1995). During September through April seals in this study spent more than two-thirds of their time in the water; then, time in the water decreased linearly to only 40% by July. The decline in time-in-water during May–July indicates that harbor seals spend more time hauled out as they become involved in activities such as pupping, breeding, and molting, a pattern also seen in other phocids (Lowry *et al.* 1980, Burns 1981, Thompson *et al.* 1989).

Merrick and Loughlin (1997) suggested that Steller sea lions in the Gulf of Alaska spent less time foraging and more time on land in spring and summer because prey were more abundant near haul-outs. In Prince William Sound some harbor seal prey are more abundant, and occur closer to shore, in summer than at other times of year. Energy-rich capelin (*Mallotus villosus*) and eulachon (*Thaleichthys pacificus*) winter offshore, but approach the coast to spawn in spring and early summer (Barraclough 1964, Anthony *et al.* 2000). Sand lance (*Ammodytes hexapterus*) swim above the sand in dense schools only during summer, when they are also highest in energy content (Robards *et al.* 1999). Salmon (*Oncorhynchus* spp.) smolt move offshore in spring, and adults return to nearshore areas to spawn in summer. In this study time-in-water decreased during May–July for seals of both sexes and a broad range of weights (28–105 kg). Pitcher (1986) showed that Prince William Sound harbor seal blubber thickness, and the percent of body weight made up by hide and blubber, increased during May–July. This suggests that in spring and summer harbor seals can obtain more energy with less time spent foraging than they can at other times of year.

Our analysis indicates that age and sex affect diving focus, with adult females showing greater focus than adult males or subadults (Fig. 3B). However, it is unclear whether adult females were really more focused in their diving, or whether regional bathymetry and the age and sex composition of our sample

influenced these results. Ten of 15 adult females were tagged in the shallow Port Chalmers region of southcentral Prince William Sound. Two other adult females were tagged at haul-outs only a few kilometers away which were also surrounded by shallow water. Nonetheless, within a 25-km radius of these haul-outs, females had access to water depths exceeding 250 m. More than 90% of the at-sea locations for harbor seals departing from and returning to the same haul-out in Prince William Sound were within 25 km of that haul-out (Lowry *et al.* 2001). Thus, it would appear that model results indicating high focus by adult females were not simply an artifact of sample distribution.

Harbor seals spend most of their time within 50 km of their haul-outs and are generally considered to feed in shallow, nearshore waters (Brown and Mate 1983, Thompson 1993, Suryan and Harvey 1998, Lowry *et al.* 2001). Studies in both North America (Boness *et al.* 1994, Coltman *et al.* 1997, Lesage *et al.* 1999) and Europe (Bjorge *et al.* 1995, Tollit *et al.* 1998) report modal dive depths of 60 m or less. Although some seals we tagged made dives to at least 480 m (Frost and Lowry, unpublished data), our analysis of seals diving in Prince William Sound and the nearby Gulf of Alaska indicated focal depths between 20 and 100 m (depth index 1–2, Fig. 4). This apparent preference for 20–50-m and 50–100-m depth bins was exhibited in all months, and all regions except the Copper River Delta where bottom depths rarely exceed 20 m and diving was consequently shallower. The varied bathymetry within central, northern, and western Prince William Sound made it difficult to determine when focal depths were limited by bathymetry in those regions, but seals diving around Middleton Island certainly had access to all six depth bins. Focal depth was somewhat greater in winter than in summer (Fig. 4A), suggesting that prey were less accessible in shallow nearshore waters at this time. The modal depth of Steller sea lions foraging in the northern Gulf of Alaska was also deeper in winter than in summer (Merrick and Loughlin 1997).

Diving effort as defined in this study included all time a seal was wet, even when it was near the surface in water <4 m. This is similar to VHF tagging studies where effort includes all time the transmitter is underwater (*e.g.*, Ries *et al.* 1997), but in contrast to many SDR and TDR studies which have restricted analyses to dives greater than some minimum depth, usually 4–12 m (Boness *et al.* 1994, Le Boeuf *et al.* 1996, Coltman *et al.* 1997, Burns and Castellini 1998, Folkow and Blix 1999, Lesage *et al.* 1999). For large, deep-diving phocids such as elephant seals, it is unlikely that exclusion of time spent in such shallow water significantly biases interpretation of diving behavior, because more than 90% of their time is spent making prolonged deep dives (Le Boeuf *et al.* 1989). However, we suggest that exclusion of very shallow dives may greatly underestimate diving effort by harbor seals, and potentially bias conclusions about foraging. Fifty-four percent of the total dives of harbor seals in the St. Lawrence estuary in eastern Canada, and 20% of the dives by male harbor seals at Sable Island, Nova Scotia, were <4 m deep (Coltman *et al.* 1997, Lesage *et al.* 1999). In this study not all SDRs were programmed to record dives <4 m in a separate bin, but from the 13 that did, it is apparent that seals spent 40%–60% of their time during September–

May in water <4 m (Frost and Lowry, unpublished data). Without additional sensors, SDRs provide no indication of what seals are doing in such shallow water. However, when Lesage *et al.* (1999) deployed stomach-temperature sensors on seals with TDRs, they found that 40% of the documented feeding events were at depths <4 m.

Like most other TDR and SDR-based studies, our analyses of diving focus and focal depth included only data for dives >4 m. This approach likely reduced inaccuracies due to dives near the resolution of pressure sensors and noise introduced by wave height, but it also quite clearly eliminated a substantial proportion of the total dives made by a seal (Lesage *et al.* 1999). Thus, it is likely that our focal depth analysis overestimates the preferred diving depths of harbor seals in the study area. While many of the dives made by seals in such shallow water may simply be associated with going to and from haul-outs, or with time spent near the surface between other dives, clearly some foraging may occur at this depth. Future studies of the diving behavior of species such as the harbor seal would be greatly facilitated by using instruments with pressure sensors that are more accurate at shallow depths. If this is done, it will be possible to distinguish avoidance of shallow water (*e.g.*, Tollit *et al.* 1998) from the simple absence of useful data.

Seasonal changes in focal depth, in combination with movements data for these same seals (see Lowry *et al.* 2001) suggest that deeper diving during winter coincided with movements to offshore areas of the Gulf of Alaska. We think it is likely these changes occurred as energy-rich prey such as eulachon, herring (*Clupea pallasii*), and salmon, which spawn nearshore but move to deeper water or offshore at other times of year, became less available. Recent and historical information on harbor seal diets in Prince William Sound and adjacent areas of the Gulf of Alaska indicate that pollock (*Theragra chalcogramma*) are a major dietary component in September–April (Pitcher 1980; Frost and Lowry, unpublished data). Small pollock of the size classes eaten by harbor seals are generally found in the Gulf of Alaska in near-bottom waters 150–200 m deep (Lowry *et al.* 1988, Muigwa 1989, Sample and Bakkala 1989).

Seasonal differences in time-in-water and focal depth were not reflected in diving focus, which showed no significant seasonal change. Seals concentrated their diving within only a few depth bins at all times of year, and dives were not distributed randomly among all available depth bins for any month. The focused nature of harbor seal diving is consistent with seals foraging on benthic prey or prey concentrated in layers within the water column. Seasonal changes in focal depth presumably reflect prey layers migrating vertically, and/or seals migrating horizontally and foraging in areas of different bathymetry.

Regional differences in diving focus reflect regional bathymetry. Seal diving was less focused in regions characterized predominantly by deeper water, such as central and northwestern Prince William Sound, and more focused in regions characterized by shallow water, such as Copper River Delta. When diving in shallow water, a seal can choose from only one or two depth bins, thus the focus variable is constrained to be greater than 0.5. In deep water, however,

a seal can choose from all six depth bins, and the focus variable can range as low as 0.167. It is notable that the intercept for the diving focus model is 0.69, and the minimum diving focus predicted for any sex-age, period, or region is 0.54. Thus, even in regions where all six depth bins occur, there is a strong tendency for seals to focus their diving effort within one or two depth bins. Harbor seals in Scotland showed similarly high focus in their diving, with more than 90% of the telemetered seals exhibiting a relatively high use of one depth category (Tollit *et al.* 1998).

Harbor seal diving behavior was significantly linked to time of day, as reflected in significant changes in time-in-water and focus among the four 6-h time periods. Time-in-water increased steadily from a low in the morning (0300–0900) to a high at night (2100–0300). Seals spent 55 min more per 6-h period in the water at night than in early morning. Diving was more focused at night, and secondarily in midday, suggesting that seals were targeting prey at particular depths. Similar nocturnal foraging behavior has been observed for harbor seals in other areas of North America and in Europe (Thompson *et al.* 1989, Olesiuk *et al.* 1990, Boness *et al.* 1994). Such diurnal differences in diving behavior by many pinnipeds may reflect the behavior of diel migrating prey, which are more accessible at night (Le Boeuf *et al.* 1989, Hindell *et al.* 1991, Goebel *et al.* 1991, Folkow and Blix 1999). We did not detect a change in focal depth by time of day, as would be expected if seals were foraging on prey that have a diel vertical migration.

Our data on the diving behavior of harbor seals have significant implications for aerial surveys used to assess seal abundance. Many surveys are conducted during the molting period in August–September, and there may be considerable annual variation in survey dates due to weather and tides (Harvey *et al.* 1990, Olesiuk *et al.* 1990, Thompson and Harwood 1990, Frost *et al.* 1994). The abrupt increase in time-in-water between July and September (>30% increase) suggests that the timing of surveys may have a substantial effect on the number of seals counted. In fact, aerial survey data collected from mid-August to mid-September in Prince William Sound clearly demonstrate how large this effect can be. Frost *et al.* (1999) determined that counts made in mid-September would be 45% lower than counts in mid-August. In northeast Scotland harbor seal counts were also substantially lower in September than they were in June–August (Thompson *et al.* 1997). Thus, it is essential that surveys conducted to assess population trends be standardized for date, or the analysis must incorporate the effect of date (Frost *et al.* 1999).

ACKNOWLEDGMENTS

This study was conducted as part of the *Exxon Valdez* Oil Spill Restoration Program, funded by the *Exxon Valdez* Oil Spill Trustee Council. Many people assisted in the capture and tagging of seals. We especially thank Jay Ver Hoef, Rob DeLong, and Brian Fadely, and also Vladimir Burkanov, Jennifer Burns, Maggie and Mike Castellini, Tracey Gotthardt, Shane Kanatous, Dan Reed, Bob Small, Ken Taylor, Pam Tuomi, and Randy Zarnke. The Captain, Glen

Hodge, and the crew of the research vessel *Pacific Star* provided excellent logistic support. Jay Ver Hoef assisted with data analyses. Ken Pitcher, Jennifer Burns, and Richard Merrick provided useful comments on a draft of the manuscript. This study was conducted under authorization of National Marine Fisheries Service Scientific Research Permits 770 and 1000 issued to the Alaska Department of Fish and Game.

LITERATURE CITED

- ANDERSON, P. J., AND J. F. PIATT. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189: 117–123.
- ANTHONY, J. A., D. D. ROBY AND K. R. TURCO. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *Journal of Experimental Marine Biology and Ecology* 248:53–78.
- ARGOS. 1990. User's manual. Satellite based data collection and location system. Service Argos, Toulouse, France.
- BARRACLOUGH, W. E. 1964. Contribution to the marine life history of the eulachon *Thaleichthys pacificus*. *Journal of the Fisheries Research Board of Canada* 21:1333–1337.
- BJORGE, A., D. THOMPSON, P. HAMMOND, M. FEDAK, E. BRYANT, H. AAREFJORD, R. ROEN AND M. OLSEN. 1995. Habitat use and diving behaviour of harbour seals in a coastal archipelago in Norway. Pages 211–223 in I. Walloe and O. Ulltang, eds. *Whales, seals, fish and man*. Elsevier Press, Norway.
- BONESS, D. J., W. D. BOWEN AND O. T. OFTEDAL. 1994. Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal. *Behavioral Ecology and Sociobiology* 34:95–104.
- BROWN, R. F., AND B. R. MATE. 1983. Abundance, movements, and feeding habits of harbor seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon. *Fishery Bulletin*, U.S. 81:291–301.
- BURNS, J. J. 1981. The ribbon seal. Pages 89–109 in S. H. Ridgway and R. J. Harrison, eds. *Handbook of marine mammals*. Volume 2. Seals. Academic Press Inc., London.
- BURNS, J. M., AND M. A. CASTELLINI. 1998. Dive data from satellite tags and time-depth recorders: A comparison in Weddell seal pups. *Marine Mammal Science* 14:750–764.
- BURNS, J. M., M. A. CASTELLINI AND J. TESTA. 1999. Movements and diving behavior of weaned Weddell seal (*Leptonychotes weddellii*) pups. *Polar Biology* 21:23–36.
- 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.
- CARLIN, B. P., AND T. A. LOUIS. 1996. Bayes and empirical Bayes methods for data analysis. Chapman and Hall, London.
- COLTMAN, D. W., W. D. BOWEN, D. J. BONESS AND S. J. IVERSON. 1997. Balancing foraging and reproduction in the male harbour seal, an aquatically mating pinniped. *Animal Behaviour* 54:663–678.
- DAVIS, R. W., G. A. J. WORTHY, B. WÜRSIG AND S. K. LYNN. 1996. Diving behavior and at-sea movements of an Atlantic spotted dolphin in the Gulf of Mexico. *Marine Mammal Science* 12:569–581.
- FOLKOW, L. P., AND A. S. BLIX. 1999. Diving behavior of hooded seals (*Cystophora cristata*) in the Greenland and Norwegian Seas. *Polar Biology* 22:61–74.
- FROST, K. J., L. F. LOWRY, E. SINCLAIR, J. M. VER HOEF AND D. C. McALLISTER. 1994. Impacts on distribution, abundance, and productivity of harbor seals. Pages 97–

- 118 in T. R. Loughlin, ed. *Marine Mammals and the Exxon Valdez*. Academic Press, San Diego, CA.
- FROST, K. J., L. F. LOWRY AND J. M. VER HOEF. 1999. Monitoring the trend of harbor seals in Prince William Sound, Alaska, after the *Exxon Valdez* oil spill. *Marine Mammal Science* 15:494–506.
- GOEBEL, M. E., J. L. BENGTON, R. L. DELONG, R. L. GENTRY AND T. R. LOUGHLIN. 1991. Diving patterns and foraging locations of female northern fur seals. *Fishery Bulletin*, U.S. 89:171–179.
- HARVEY, J. T., R. F. BROWN AND B. R. MATE. 1990. Abundance and distribution of harbor seals (*Phoca vitulina*) in Oregon, 1975–1983. *Northwestern Naturalist* 71: 65–71.
- HEIDE-JØRGENSEN, M. P., AND R. DIETZ. 1995. Some characteristics of narwhal, *Monodon monoceros*, diving behaviour in Baffin Bay. *Canadian Journal of Zoology* 73:2120–2132.
- HEIDE-JØRGENSEN, M. P., B. S. STEWART AND S. LEATHERWOOD. 1992. Satellite tracking of ringed seals *Phoca hispida* off northwest Greenland. *Ecography* 15:56–61.
- HEIDE-JØRGENSEN, M. P., P. RICHARD AND A. ROSING-ASVID. 1998. Dive patterns of belugas (*Delphinapterus leucas*) in waters near eastern Devon Island. *Arctic* 51:17–26.
- HINDELL, M. A., D. J. SLIP AND H. R. BURTON. 1991. Diving behaviour of adult male and female southern elephant seals. *Australian Journal of Zoology* 39:595–619.
- KREBS, C. J. 1999. Species diversity measures. Pages 410–454 in *Ecological methodology*. Second edition. Addison-Wesley Educational Publishers, Menlo Park, CA.
- LE BOEUF, B. J., Y. NAITO, A. C. HUNTLEY AND T. ASAGA. 1989. Prolonged, continuous, deep diving by northern elephant seals. *Canadian Journal of Zoology* 67:2514–2519.
- LE BOEUF, B. J., P. A. MORRIS, S. B. BLACKWELL, D. E. CROCKER AND D. P. COSTA. 1996. Diving behavior of juvenile northern elephant seals. *Canadian Journal of Zoology* 74:1632–1644.
- LESAGE, V., M. O. HAMMILL AND K. M. KOVACS. 1999. Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Canadian Journal of Zoology* 77:74–87.
- LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP AND R. D. WOLFINGER. 1996. SAS system for mixed models. SAS Institute Inc., Cary, NC.
- LOUGHLIN, T. R., A. S. PERLOV AND V. A. VLADIMIROV. 1992. Range-wide survey and estimation of total numbers of Steller sea lions in 1989. *Marine Mammal Science* 8:220–239.
- LOWRY, L. F., K. J. FROST AND J. J. BURNS. 1980. Variability in the diet of ringed seals, *Phoca hispida*, in Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 37:2254–2261.
- LOWRY, L. F., K. J. FROST AND T. R. LOUGHLIN. 1988. Importance of walleye pollock in the diets of marine mammals in the Gulf of Alaska and Bering Sea, and implications for fishery management. Pages 701–226 in *Proceedings of the International Symposium on the Biology and Management of Walleye Pollock*, November 1988, Anchorage, AK. Alaska Sea Grant Report 89–1.
- LOWRY, L. F., K. J. FROST, R. DAVIS, D. P. DEMASTER AND R. S. SUYDAM. 1998. Movements and behavior of satellite-tagged spotted seals (*Phoca largha*) in the Bering and Chukchi seas. *Polar Biology* 19:221–230.
- LOWRY, L. F., K. J. FROST, J. M. VER HOEF AND R. DELONG. 2001. Movements of satellite-tagged harbor seals in Prince William Sound, Alaska, 1992–1997. *Marine Mammal Science* 17:000–000.
- MATE, B. R., K. M. STAFFORD, R. NAWOJCHIK AND J. L. DUNN. 1994. Movements and dive behavior of a satellite-monitored Atlantic white-sided dolphin (*Lagenorhynchus acutus*) in the Gulf of Maine. *Marine Mammal Science* 10:116–121.
- MATE, B. R., K. A. ROSSBACH, S.L. NIEUKIRK, R. S. WELLS, A. B. IRVINE, M. D. SCOTT

- AND A. J. READ. 1995. Satellite-monitored movements and dive behavior of a bottlenose dolphin (*Tursiops truncatus*) in Tampa Bay, Florida. *Marine Mammal Science* 11:452–463.
- MERRICK, R. L., AND T. R. LOUGHLIN. 1997. Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. *Canadian Journal of Zoology* 75:776–786.
- MUIGWA, N. M. 1989. Vertical distribution patterns of prespawning and spawning pollock (*Theragra chalcogramma*) in Shelikof Strait. Pages 403–432 in *Proceedings of the International Symposium on the Biology and Management of Walleye Pollock*, November 1988, Anchorage, AK. Alaska Sea Grant Rep. 89–1.
- NORDØY, E. S., L. FOLKOW AND A. S. BLIX. 1995. Distribution and diving behaviour of crabeater seals (*Lobodon carcinophagus*) off Queen Maud Land. *Polar Biology* 15: 261–268.
- OLESIUK, P. F., M. A. BIGG AND G. M. ELLIS. 1990. Recent trends in the abundance of harbour seals, *Phoca vitulina*, in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 47:992–1003.
- PITCHER, K. W. 1980. Food of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. *Fishery Bulletin*, U.S. 78:544–549.
- PITCHER, K. W. 1986. Variation in blubber thickness of harbor seals in southern Alaska. *Journal of Wildlife Management* 50:463–466.
- PITCHER, K. W. 1990. Major decline in number of harbor seals, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. *Marine Mammal Science* 6:121–134.
- PITCHER, K. W., AND D. G. CALKINS. 1979. Biology of the harbor seal, *Phoca vitulina richardsi*, in the Gulf of Alaska. U.S. Department of Commerce, NOAA, Outer Continental Shelf Environmental Assessment Program Final Report 19:231–310.
- RIES, E. H., I. M. TRAUT, P. PAFFEN AND P. W. GOEDHART. 1997. Diving patterns of harbour seals (*Phoca vitulina*) in the Wadden Sea, the Netherlands and Germany, as indicated by VHF telemetry. *Canadian Journal of Zoology* 75:2063–2068.
- ROBARDS, M. D., J. F. PIATT AND G. A. ROSE. 1999. Maturation, fecundity, and intertidal spawning of Pacific sand lance in the northern Gulf of Alaska. *Journal of Fish Biology* 54:1050–1068.
- SAMPLE, T. M., AND R. G. BAKKALA. 1989. Assessment of walleye pollock of the eastern Bering Sea based on bottom trawl surveys. Pages 457–469 in *Proceedings of the International Symposium on the Biology and Management of Walleye Pollock*, November 1988, Anchorage, AK. Alaska Sea Grant Rep. 89-1.
- SIMPSON, E. H. 1949. Measurement of diversity. *Nature* 163:688.
- STEWART, B. S., S. LEATHERWOOD, P. K. YOCHER AND M.-P. HEIDE-JØRGENSEN. 1989. Harbor seal tracking and telemetry by satellite. *Marine Mammal Science* 5:361–375.
- STEWART, B. S., E. A. PETROV, E. A. BARANOV, A. TIMONIM AND M. IVANOV. 1996. Seasonal movements and dive patterns of juvenile Baikal seals, *Phoca sibirica*. *Marine Mammal Science* 12:528–542.
- SURYAN, R. N., AND J. T. HARVEY. 1998. Tracking harbor seals (*Phoca vitulina richardsi*) to determine dive behavior, foraging activity, and haul-out site use. *Marine Mammal Science* 14:361–372.
- TEILMANN, J., E. W. BORN AND M. ACQUARONE. 1999. Behaviour of ringed seals tagged with satellite transmitters in the North Water polynya during fast-ice formation. *Canadian Journal of Zoology* 77:1934–1946.
- THOMPSON, P. M. 1993. Harbour seal movement patterns. *Journal of Zoology*, London 217:281–294.
- THOMPSON, P. M., AND J. HARWOOD. 1990. Methods for estimating the population size of common seals, *Phoca vitulina*. *Journal of Applied Ecology* 27:924–938.
- THOMPSON, P. M., M. A. FEDAK, B. J. MCCONNELL AND K. S. NICHOLAS. 1989. Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). *Journal of Applied Ecology* 26:521–535.

- THOMPSON, P. M., D. J. TOLLIT, D. WOOD, H. M. CORPE, P. S. HAMMOND AND A. MACKAY. 1997. Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland. *Journal of Applied Ecology* 34:43–52.
- THOMPSON, P. M., A. MACKAY, D. J. TOLLIT, S. ENDERBY AND P. S. HAMMOND. 1998. The influence of body size and sex on the characteristics of harbour seal foraging trips. *Canadian Journal of Zoology* 76:1044–1053.
- TOLLIT, D. J., A. D. BLACK, P. M. THOMPSON, A. MACKAY, H. M. CORPE, B. WILSON, S. M. VAN PARIJS, K. GRELLIER AND S. PARLANE. 1998. Variations in harbour seal *Phoca vitulina* diet and dive-depths in relation to foraging habitat. *Journal of Zoology*, London 244:209–222.
- WASHINGTON, H. G. 1984. Diversity, biotic and similarity indices: A review with special relevance to aquatic ecosystems. *Water Resources* 18:653–694.

Received: 22 June 2000

Accepted: 26 January 2001