

SUMMER DIVING BEHAVIOR OF MALE WALRUSES IN BRISTOL BAY, ALASKA

CHADWICK V. JAY

SEAN D. FARLEY¹

GERALD W. GARNER²

United States Geological Survey,
Alaska Biological Science Center,
1011 East Tudor Road, Anchorage, Alaska 99503, U.S.A.
E-mail: chad.jay@usgs.gov

ABSTRACT

Pacific walruses (*Odobenus rosmarus divergens*) make trips from ice or land haul-out sites to forage for benthic prey. We describe dive and trip characteristics from time-depth-recorder data collected over a one-month period during summer from four male Pacific walruses in Bristol Bay, Alaska. Dives were classified into four types. Shallow (4 m), short (2.7 min), square-shaped dives accounted for 11% of trip time, and many were probably associated with traveling. Shallow (2 m) and very short (0.5 min) dives composed only 1% of trip time. Deep (41 m), long (7.2 min), square-shaped dives accounted for 46% of trip time and were undoubtedly associated with benthic foraging. V-shaped dives ranged widely in depth, were of moderate duration (4.7 min), and composed 3% of trip time. These dives may have been associated with navigation or exploration of the seafloor for potential prey habitat. Surface intervals between dives were similar among dive types, and generally lasted 1–2 min. Total foraging time was strongly correlated with trip duration and there was no apparent diel pattern of diving in any dive type among animals. We found no correlation between dive duration and postdive surface interval within dive types, suggesting that diving occurred within aerobic dive limits. Trip duration varied considerably within and among walruses (0.3–9.4 d), and there was evidence that some of the very short trips were unrelated to foraging. Overall, walruses were in the water for 76.6% of the time, of which 60.3% was spent diving.

Key words: time-depth-recorder, TDR, walrus, *Odobenus rosmarus*, diving, foraging, Bristol Bay.

Walruses (*Odobenus rosmarus*) consume primarily bivalve molluscs (Fay 1982). Their highly sensitive mystacial vibrissae and unique mouth parts make

¹ Present address: Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518.

² Deceased.

them well adapted for identifying, excavating, and feeding on benthic prey (Fay 1982, Kastelein and van Gaalen 1988, Kastelein and Gerrits 1990). Much of what is understood about how walruses search for and handle their prey comes from observations on captive animals (Fay 1982, Kastelein and Mosterd 1989) and foraging marks left in surface sediments by free-ranging animals rooting through the substrate in search of prey (Oliver *et al.* 1983, Nelson and Johnson 1987).

Walruses make trips from ice and land haul-out sites to forage; however, little is known of their dive behavior during these trips. Our current understanding of free-ranging walrus dive behavior is largely limited to surface observations of animals at close range (Fay 1982, Born and Knutsen 1997, Nowicki *et al.* 1997), dive data obtained from satellite-linked radio transmitters (Born and Knutsen 1992, 1997), and time-depth-recorder data collected from one Atlantic walrus (*O. r. rosmarus*) over a 14-d period from which simple dive statistics were reported (Wiig *et al.* 1993).

Time-depth-recorders (TDRs) can provide a nearly continuous record of the physical parameters associated with diving. This has enabled researchers to contrast foraging effort with food availability (Boyd *et al.* 1994, Francis *et al.* 1998), examine intraspecific foraging strategies (Thompson *et al.* 1998), and develop insights into the manner by which certain mammal species have adapted to the challenges imposed by life spent in a marine environment (Boyd 1997).

Pacific walruses (*O. r. divergens*) range over areas of the continental shelf in the Chukchi and Bering Seas. From late spring through fall, most adult males are segregated from adult female and young walruses. During this time males rest, between foraging trips, at coastal sites in Russia and Alaska (Fay 1982). Walruses using an established haul-out site in Bristol Bay, Alaska, (Cape Peirce) were the focus of this study because of the moderate within-season fidelity individual animals displayed to this site (C. Jay, unpublished data) and the comparative ease with which animals could be accessed. Using TDR data, we report here on the trip and dive characteristics of four walruses in Bristol Bay during the summer of 1997.

METHODS

TDR Deployment

An established walrus haul-out site in Bristol Bay, Alaska, (Cape Peirce) was surveyed in August 1997, and five adult male walruses were selected for study. Each animal was captured by chemical immobilization with an intramuscular injection of Telazol® (0.75–1.25 mg/kg, Wildlife Pharmaceuticals, Fort Collins, CO) administered by dart rifle (Extra-Long Range Projector, Palmer Chemical & Equipment Co., Douglasville, GA), and supplemented with small doses of Telazol® by hand injection as needed to maintain anesthesia. A TDR (Mk5 model, Wildlife Computers, Redmond, WA) was attached to the lateral side of one of the tusks of each animal with two 19 mm-

wide stainless steel bands. A dense piece of rubber (6 mm thick), with the same surface dimensions as the TDR, was placed between the TDR and tusk to allow for compression while the bands were tightened.

TDR components were cast in $7.8 \times 3.8 \times 2.1$ -cm hard epoxy with no external housing. The TDRs recorded depth every 10 sec (accuracy 1% of reading ± 1 m to 250 m) and temperature every 20 sec (± 0.1 C resolution from -2.5° to 22.7°C). Each TDR had 512 kb of memory and could sample for 39.5 d at the prescribed sampling rate. After approximately one month deployment, all TDRs were recovered after recapturing the animals when they were hauled out at the deployment site.

Data Analysis

Software provided by the TDR manufacturer was used to download data from each TDR, correct for drift in pressure transducer readings, identify dives from the pressure data, and measure dive parameters. After correcting for drift in the pressure transducer, negative depth readings (usually within -5 m) still occurred in the data. Temperature data associated with these anomalies indicated that some of these readings occurred due to the pressure transducer's sensitivity to sudden temperature change. Thus, all negative depth readings were adjusted to zero depth. Occasional positive depth readings were recorded when it was apparent that the animal was hauled out, and most likely occurred from the animal pressing the transducer against the substrate or another animal during haul-out periods (*e.g.*, Wiig *et al.* 1993).

The following dive parameters were examined: dive duration, bottom time, descent rate, ascent rate, and maximum dive depth. The start and end of a dive was delineated at a depth of ≤ 2 m. Only dives with at least two depth readings of ≥ 2 m were analyzed to avoid spurious dives. Bottom time was the time between the first and last depth readings equal to or greater than a user-defined percentage of the dive's maximum depth. To obtain an accurate measure of bottom time, this percentage was set to 90% for dives exceeding 10 m in depth and 65% for shallower dives, because small depth changes represented a proportionately smaller change in depth in deep dives than in shallow dives. Average descent and ascent rates were calculated from readings from the start of the dive to the start of bottom time, and the end of bottom time to the end of the dive, respectively.

Preliminary dive groups were identified using agglomerative cluster analysis (Everitt 1980). Dives were classified from the variables: bottom time/dive duration (relative bottom time), dive duration, and descent rate $-$ ascent rate ($\text{rate}_{\text{desc}} - \text{asc}$). Each variable was standardized to a mean of zero and standard deviation of one. The clustering method used a squared Euclidean distance measure and Ward's minimum variance fusion strategy. As clusters of dives were sequentially fused into larger clusters at each step of the algorithm, an estimate of the proportion of total variance that was explained by the clusters (R^2) was calculated. These estimates were used to determine the approximate number of dive groups that likely existed in the data. Following the cluster

analysis, a few clusters were manually fused because of their similarity in mean values of the classification variables, resulting in a new set of clusters. The effect of the manual fusion on cluster integrity was assessed by comparing results from separate discriminant analyses, one analysis using the new set of clusters and the other using the original set of clusters.

Subsequently, discriminant analysis was used to derive functions to assess which classification variables were most related to cluster separation, and secondarily, to refine dive assignments by reassigning some of the dives into different clusters (Klecka 1980). The analysis used the same variables that were used in the cluster analysis (relative bottom time, dive duration, and $\text{rate}_{\text{disc-asc}}$). The ability of the discriminant functions to adequately discriminate between clusters, and hence adequately classify dives, was assessed using split-sample cross-validation. The data were randomly split into two nearly equal subsets. The discriminant functions were derived from one subset (calibration data set), and their adequacy was assessed from misclassification rates that were calculated after classifying dives from the other subset (validation data set). Lastly, the functions were used to reassign some of the dives within the entire data set based on a dive's degree of similarity to each of the dive clusters.

The start of a trip was marked by a sudden decrease in ambient temperature that followed a prolonged period of no diving and relatively high temperatures. The end of a trip was marked by a sudden increase in ambient temperature that followed a sequence of gradually decreasing dive depths and relatively cold temperatures. A dive bout was defined as a group of two or more consecutive dives of the same type (defined by dive classification). The duration of outbound travel was defined as the time from the start of the trip to the start of the first bout of deep square-shaped diving. The duration of inbound travel was defined as the time from the end of the last bout of deep square-shaped diving to the end of the trip. The posttrip haul-out duration was defined as the time from the end of a trip to the start of the following trip.

Estimates of trip duration, outbound and inbound travel duration, and percent of trip time spent diving by dive type were calculated using all data. Estimates of posttrip haul-out duration excluded data from partial haul-out periods which occurred when an animal was captured for TDR deployment and recaptured for TDR recovery. Estimates of percent time on a trip were calculated using data only for the period during which trips with complete posttrip haul-out periods were observed (*i.e.*, only data from the start of the first trip to the start of the last trip in each animal).

Mean and standard errors for trip parameters, and percent of trip time diving by dive type, within and among animals were estimated. Within-animal mean and standard error estimates were calculated from simple univariate estimates. The mean among animals was calculated from the mean of animal means. However, the standard error of the mean of animal means was estimated using a generalized linear model that accounted for differences in numbers of trips among animals. Correlations between dive parameters were

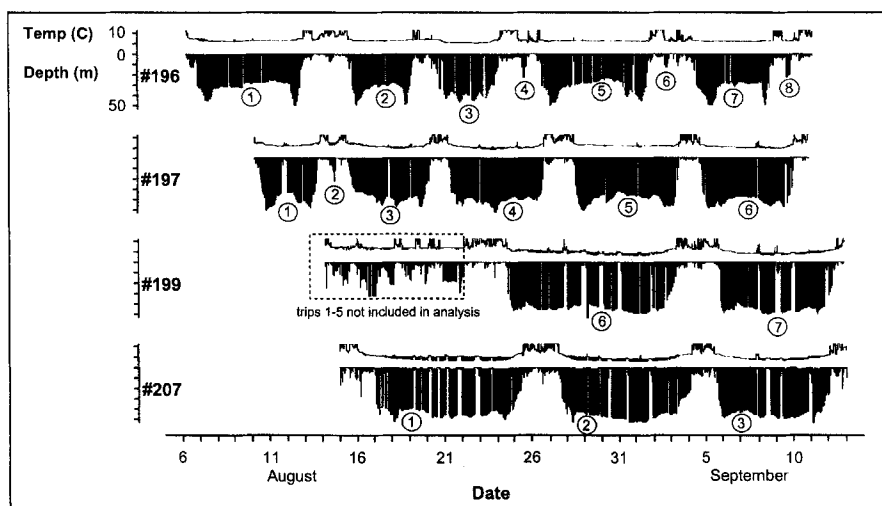


Figure 1. Depth and temperature profiles recorded from four adult male walrus in Bristol Bay, Alaska, between 6 August and 13 September 1997. Trips are indicated.

reported for descriptive purposes, and because parameters of sequential dives were autocorrelated, *P*-values were not reported for these correlations.

RESULTS

One TDR failed after eight days and its data are not presented. The remaining four TDRs functioned for 29–36 d. The first five trips of walrus #199 were excluded from analyses following dive classification because the animal exhibited behavior that we believe may have been abnormal, possibly from the effects of capture when the TDR was deployed. Shortly after capture, the animal made five short consecutive trips with short and shallow diving over a period of 7.6 d (Fig. 1), a behavior that was not subsequently observed in this animal nor at any time in the other three animals.

Dive Classification

In the cluster analysis 66% of the total variation among dives was explained by six clusters and explanatory power rapidly declined with subsequent cluster fusion by the clustering algorithm. Five clusters explained 5% less variation than the variation explained by six clusters. Consequently, the six clusters were chosen to represent preliminary dive groups. Following the analysis two pairs of clusters were manually fused because of their similarity in mean values of the classification variables, resulting in four new clusters. Separate discriminant analyses, one using the four new clusters and other using the original six clusters, indicated that information loss from manual fusion was minimal. Within-cluster misclassification rates were roughly similar between the four

new clusters and the six original clusters (0%–13% and 0%–7%, respectively), and the relationship between cluster separation and the classification variables was similar between the two sets.

In the discriminant analysis of the four new clusters, the clusters in the calibration data set ($n = 8,837$) explained 80%, 57%, and 1% of the variation in the scores of the first, second, and third discriminant functions (squared canonical correlations), respectively. The first discriminant function contained 76% of the total explanatory power of the three functions (relative percent variance), was highly correlated with dive duration (total canonical structure correlation $r = 0.90$), and only weakly correlated with relative bottom time ($r = -0.36$). The second discriminant function contained 24% of the explanatory power, was highly correlated with relative bottom time ($r = 0.92$), and only weakly correlated with dive duration ($r = 0.43$). The third discriminant function contained relatively no explanatory power (0%) and was highly correlated with rate_{dsc-asc} ($r = 0.99$).

The functions adequately discriminated between clusters as evidenced by within-cluster misclassification rates of only 0%–7% in the validation data set ($n = 8,886$, overall misclassification = 4%). Reclassification of the entire data set led to almost identical misclassification rates as those from the validation data set. At least 93% of the dives within each cluster retained their original cluster assignment. The greatest proportion of reassigned dives were reassignments between clusters 1 and 2, indicating that similarity was greatest between these clusters. None of the dives in cluster 4 were reassigned. Clusters 1–4 are hereafter referred to as dive types I–IV. Dive types I–IV contained a total of 4,730, 1,758, 9,463, and 725 dives, respectively (which excludes 537, 221, 239, and 50 dives from each dive type of the first five trips of walrus #199).

Dives

The frequency of maximum dive depth in each animal was bimodal with a paucity of depths from about 10 to 20–35 m (Fig. 2). Diving effort in deep water differed among walrus. The depth distribution of deep dives in walrus #197, #199, and #207 were similar, whereas walrus #196 had many more shallow dives than in the other three animals. Shallow dives consisted primarily of type I and II dives and deep dives consisted primarily of type III and IV dives (Fig. 3).

Type I dives were short in duration (median = 2.7 min), square-shaped, non-skewed, and shallow (median = 4 m) (Fig. 3). They occurred throughout most trips, but most frequently near the beginning and end of trips (Fig. 4). Walrus were typically engaged in type I diving for an average of 11% of the duration of each trip, and thus type I dives were the second most prevalent dive type (Table 1).

Type II dives were very short in duration (median = 0.5 min) (Fig. 3). Relative bottom time, descent rate, and ascent rate were probably not accurately measured in these dives because they were so short in duration and

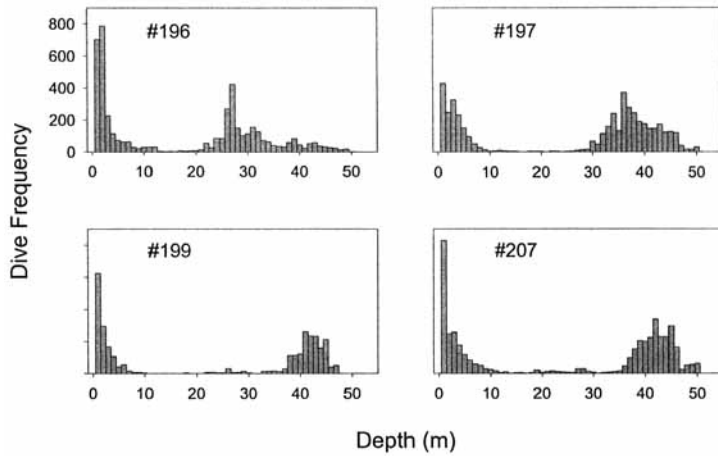


Figure 2. Maximum depth of all dives each walrus, all trips combined.

consequently few depth readings were recorded. The depth of most type II dives were at the shallowest depth of dive detection by the TDRs (2 m). Type II dives occurred throughout most trips, but with no apparent pattern of occurrence (Fig. 4), and together represented a relatively small proportion of total trip time (1%, Table 1).

Type III dives were long (median = 7.2 min) (Fig. 3), the longest lasted 15.2 min. They were typically square-shaped, non-skewed, and deep (median = 41 m), and had at least twice as fast descent and ascent rates as those in the other dive types (four times the ascent rate of type IV dives). They occurred throughout most trips, but less frequently during the beginning and end of trips (Fig. 4), and were by far the most prevalent dive type (represented an average of 46% of total trip time, Table 1). Type III dives were uncommon during a roughly 0.25-d period immediately after and prior to hauling out (outbound and inbound travel duration, Table 1).

Type IV dives were of moderate duration (median = 4.7 m) and had short bottom times (median = 1.0 min) (Fig. 3), and thus their profiles were typically V-shaped. Median bottom time was usually about one-quarter as long as dive duration; 25% of all type IV dives had 20-sec bottom times. Most type IV dives had a profile that was right-skewed (positive $\text{rate}_{\text{dsc}-\text{asc}}$) with a median descent rate about twice the median ascent rate. Type IV dives ranged widely in depth, but were usually deeper than 10 m. They made up a small proportion of total trip time (3%, Table 1), and occurred most often near the beginning and end of trips (Fig. 4).

Among all walruses combined, median bout duration, number of dives per bout, and duration of surface interval between dives were greater for type III dives than for the other dive types (Table 2). Surface intervals between dives in each dive type lasted up to 7.8 h. Long surface intervals were common; for example, all long trips (15 of 19 trips) contained 1–19 surface intervals of

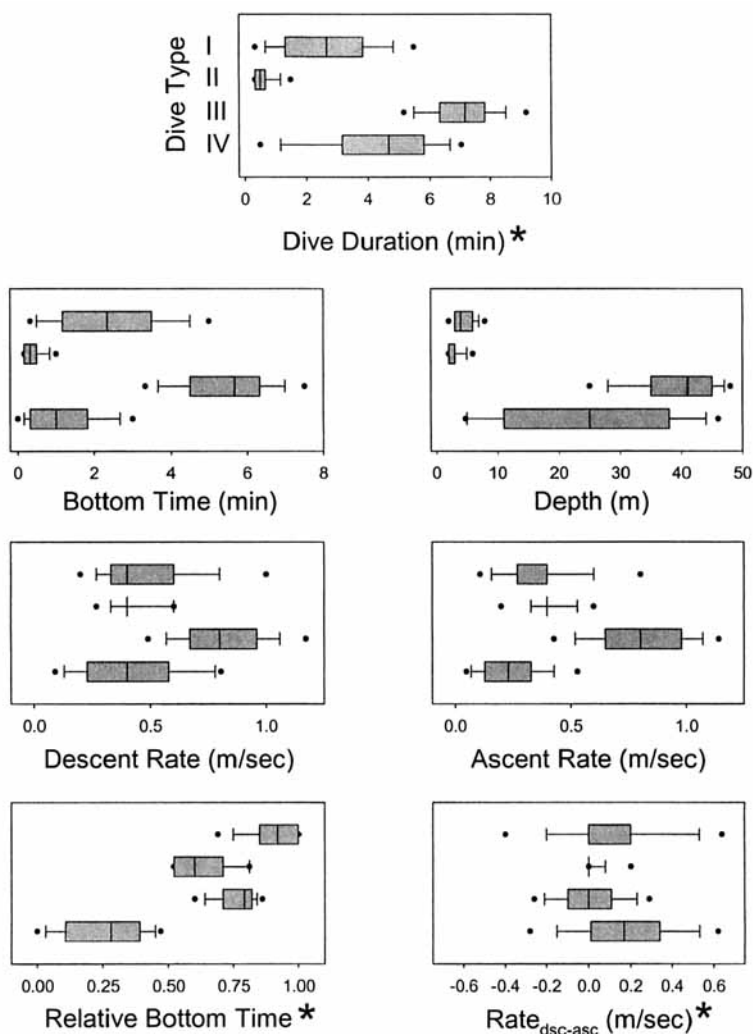


Figure 3. Box plots of dive parameters by dive type, all walrus combined. The 5th, 10th, 25th, 50th, etc., percentiles are indicated. Variables used to classify dives are indicated with an asterisk.

>1-h duration. Over 85% of the dives in type I and III dives were associated with bout diving (Table 2).

Dive duration and maximum dive depth were very weakly correlated within type III dives (each animal: $r = 0.31, 0.32, 0.31,$ and $0.39, n \geq 1,695$), but were moderately to strongly correlated within type IV dives (each animal: $r = 0.58, 0.82, 0.79,$ and $0.66, n \geq 53$). Type I and II dives had very narrow depth ranges so correlations are not reported. There was no apparent correlation between dive duration and postdive surface interval within dive types (each animal and dive type: $r \leq 0.27, n = 35-2,790$).

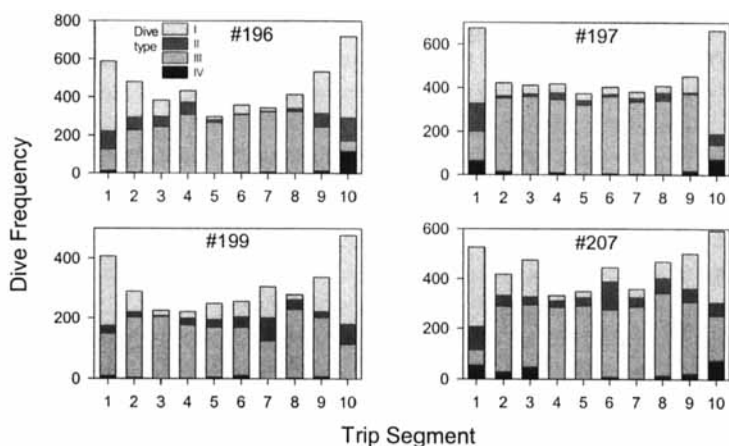


Figure 4. Frequency of dive types across trip segment, all trips combined each walrus.

Plots of dive frequency on hour of day indicated no apparent diel pattern of diving among animals within each dive type. Lack of a pattern among animals was supported by results from a log-linear model indicating significant differences among animals in dive frequencies in six 4-h classes (0100–0459, 0500–0859, *etc.*) analyzed separately by dive type ($\chi^2 \geq 71.3$, $df = 15$, $P < 0.0001$).

Trips

Observation periods, wherein complete trip and posttrip haul-out periods were observed for each animal, lasted from 18.9 to 34.7 d (Table 1). Trip duration varied considerably within and among walrus (Table 1, Fig. 1). Four trips lasted less than 0.6 d (mean = 0.4 d) and 15 trips lasted more than 3.6 d (mean = 6.6 d), indicating two potentially different trip types. Walrus #196 made eight trips with a mean duration of 3.4 d (three trips < 0.6 d, five trips 3.8–6.6 d); whereas, walrus #207 made three trips with a mean duration of 7.9 d (6.6–9.4 d). The mean duration of all trips was 6.0 d.

Combined travel duration for each trip (outbound + inbound, Table 1) ranged from 0.12 to 1.21 d and was not significantly correlated with trip duration ($r = 0.39$, $P = 0.11$, $n = 18$). Posttrip haul-out duration ranged from 0.37 to 2.59 d and increased with trip duration ($r^2 = 0.40$, $P = 0.01$, $n = 15$). Total dive duration for each dive type was significantly correlated with trip duration (type I–IV: $r = 0.82$, 0.79, 0.94, and 0.58, $P \leq 0.0096$, $n = 18$ –19).

Overall, walrus were on a trip for 76.6% of the time, of which 60.3% of that time was spent diving (Table 1). Less time was spent diving during short trips (<0.6 d) than long trips (>3.6 d). Furthermore, on average, short trips contained more type I dives and less type III dives than long trips, but this

Table 1. Summary of foraging trips made by 4 male walrus during summer in Bristol Bay, Alaska. Observation period is from start of first trip to end of last trip.

Animal (observa- tion period)	Trip	Trip duration (d)	Outbound travel duration (d)	Inbound travel duration (d)	Posttrip haul-out duration (d)
#196 [34.7 d]	1	6.59	0.09	0.41	2.59
	2	3.75	0.11	0.14	0.37
	3	4.50	0.12	0.35	1.16
	4*	0.57	0.20	0.12	0.64
	5	6.32	0.25	0.60	0.84
	6*	0.27	0.03	0.09	1.35
	7	4.65	0.09	0.44	0.51
	8*	0.55	0.41	0.14	—
	Mean (SE)	3.40 (0.92)	0.16 (0.04)	0.29 (0.07)	1.07 (0.29)
#197 [31.0 d]	1	3.68	0.19	0.56	0.57
	2*	0.42	— ^a	— ^a	0.69
	3	4.74	0.12	0.49	1.01
	4	5.46	0.23	0.21	1.74
	5	6.15	0.27	0.42	1.10
	6	5.34	0.35	0.48	—
	Mean (SE)	4.30 (0.85)	0.23 (0.04)	0.43 (0.06)	1.02 (0.20)
#199 ^b [18.9 d]	6	9.75	0.17	0.14	2.41
	7	6.74	0.23	0.26	—
	Mean (SE)	8.25 (1.50)	0.20 (0.03)	0.20 (0.06)	2.41 (—)
#207 [27.0 d]	1	9.37	1.05	0.17	2.10
	2	7.65	0.15	0.23	1.32
	3	6.58	0.18	0.18	—
	Mean (SE)	7.87 (0.81)	0.46 (0.29)	0.19 (0.02)	1.71 (0.39)
	Short* ($n = 4$)	0.44 (0.10)	0.21 (0.11)	0.11 (0.01)	0.84 (0.31)
	Long ($n = 15$)	6.59 (0.36)	0.25 (0.06)	0.30 (0.04)	1.58 (0.25)
All trips	5.95 (0.60)	0.26 (0.06)	0.28 (0.04)	1.55 (0.22)	

^a Unable to determine outbound or inbound travel duration because too few deep square-shaped dives were made.

^b First 5 trips of animal #199 were not analyzed because questionable whether normal behavior was exhibited.

was largely due to the diving characteristics of two of the four short trips; the other two short trips had diving characteristics similar to those of long trips.

DISCUSSION

During dive classification, dives were discriminated most by dive duration and relative bottom time. Relative bottom time represented the degree of squareness in the shape of the dive's profile. Although dives were adequately classified, there was clearly a gradient of dive forms in the data. Dive types I and II were the most difficult to discriminate between.

Many type I dives probably represented traveling behavior. Most of these dives occurred near the beginning and end of trips, tended to occur in bouts,

Table 1. Extended.

% time on trip	% of trip time diving by dive type				
	I	II	III	IV	All types
71.7	6.9	0.5	53.7	2.3	63.4
91.0	13.1	0.4	53.7	2.8	70.0
79.5	9.9	0.9	39.1	2.6	52.5
47.1	4.4	0.7	29.4	6.1	40.6
88.3	11.7	1.1	51.6	1.8	66.2
16.6	7.2	0.1	43.1	1.3	51.8
90.1	11.1	0.5	52.7	2.9	67.1
—	24.8	1.9	5.8	6.9	39.4
69.2 (10.5)	11.1 (2.2)	0.8 (0.2)	41.1 (5.9)	3.4 (0.7)	56.4 (4.3)
86.6	15.8	1.6	40.5	2.9	60.8
37.7	29.3	4.9	0.0	8.2	42.4
82.4	6.5	0.3	55.5	3.1	65.4
75.9	8.1	0.3	64.7	2.2	75.3
84.9	6.5	0.4	65.5	1.9	74.3
—	9.9	0.5	63.4	2.2	76.0
73.5 (9.1)	12.7 (3.6)	1.3 (0.7)	48.3 (10.4)	3.4 (1.0)	65.7 (5.3)
80.2	9.5	0.8	50.8	0.6	61.7
—	10.5	1.0	51.6	0.7	63.8
80.2 (—)	10.0 (0.5)	0.9 (0.1)	51.2 (0.4)	0.6 (0.0)	62.7 (1.0)
81.7	4.7	1.1	37.8	2.0	45.6
85.3	10.1	1.1	43.9	3.9	59.1
—	12.6	0.8	46.4	4.3	64.2
83.5 (1.8)	9.2 (2.3)	1.0 (0.1)	42.7 (2.6)	3.4 (0.7)	56.3 (5.5)
34.8 (13.2)	20.7 (6.4)	2.9 (0.5)	13.1 (10.9)	6.5 (1.8)	43.1 (3.9)
82.5 (2.3)	9.8 (0.9)	0.8 (0.1)	50.5 (2.1)	2.2 (0.2)	63.3 (2.0)
76.6 (8.1)	10.7 (1.8)	1.0 (0.3)	45.8 (5.0)	2.7 (0.5)	60.3 (3.1)

and were shallow and moderately short in duration. Shallow and short diving has been attributed to traveling behavior in other pinnipeds (Bengtson and Stewart 1992, Burns *et al.* 1997). Also, casual inspection of consecutive dive profiles indicated that many type I dives did not reach the sea floor since they occurred within minutes of much deeper type III dives.

It is difficult to ascribe a behavior to type II dives. They were very shallow (2 m) and brief in duration (0.5 min). Walruses commonly gather in small groups near coastal haul-outs and can be seen diving together just below the surface during social interactions (personal observation). Perhaps this kind of behavior was a source of type II dives. Type II dives occurred throughout trips, but made up only about 1% of the activity budget of the trips.

Type III dives were undoubtedly associated with foraging. They were square-shaped, had long bottom times, occurred in bouts, and were the most prevalent behavior during most trips, all of which is consistent with walruses' benthic foraging behavior (Fay 1982).

Table 2. Combined dive bout characteristics of 4 adult male walrus.

Dive type	Median bout duration (h)	Median number of dives in bout	Median surface interval between dives (min)	% of total dives contained in bouts
I	0.20	3	1.3	85.2
II	0.06	2	1.0	54.1
III	0.73	5	2.2	95.8
IV	0.20	2	1.7	25.5

Type IV dives (V-shaped) may have been associated with navigation or the exploration of bottom prey. It is likely that many type IV dives extended to the sea floor because most of these dives either extended to a similar depth and were in the immediate proximity of type III dives (foraging dives), or occurred in a series of gradually changing dive depth at the beginning and end of trips. V-shaped dives have been noted in other marine mammals, including the crabeater seal (*Lobodon carcinophagus*), Weddell seal (*Leptonychotes weddellii*), and Beluga whale (*Delphinapterus leucas*) (Bengtson and Stewart 1992, Schreer and Testa 1996, Martin *et al.* 1998). Bengtson and Stewart (1992) suggest that V-shaped diving in crabeater seals may have a navigational or exploratory function because they occur during periods of travel. They suggest crabeater seals may be better able to hear prey or other seals at a distance below the background noise of grinding ice at the surface. Schreer and Testa (1996) suggest that V-shaped dives observed in Weddell seals may serve a similar function as that suggested for crabeater seals, and may also serve to get a better visual image of their surroundings for navigation and prey detection. Our observations came from walrus in ice-free habitat and walrus are almost exclusively benthic feeders, so it is unlikely that type IV dives were associated with avoiding surface noise or searching the water column for prey. Apart from their potential role in navigation, V-shaped dives may have been used to explore the sea floor for prey and suitable foraging habitat, or in some cases may have resulted from aborted foraging dives.

The functional significance of a slow descent or ascent rate and the often right-skewed profile of type IV dives is unclear. Visual inspection of skewed dives showed that the skewed part of the dive was from protracted vertical travel within about 15 m of the surface. Skewed diving was apparently unrelated to the presence of a thermocline because they occurred in both mixed and stratified water columns as interpreted from concurrent temperature profiles. Skewed dives have been observed in other pinnipeds and the function of these are also unclear. Suggested causes for these in other pinnipeds include the animal sinking while resting below the surface, traveling along a sloped seafloor, exploring for food, navigating, or processing food after bouts of foraging (Hindell *et al.* 1991, Schreer and Testa 1996).

The proportion of dive types in short trips suggests that at least some short trips were unrelated to foraging. A short trip made by each of two animals

had unusually high proportions of type I dives and low proportions of type III dives. Consequently, diving during these trips was generally shallow and different than diving in all other trips. Some pinnipeds make short trips into the water to lower their body temperature (Francis *et al.* 1998), and perhaps these trips served a similar purpose.

Among all trips, total foraging time (type III diving) was strongly correlated with trip duration. This, and the lack of correlation between trip duration and combined outbound and inbound travel duration, suggests that increased trip duration was not associated with increased traveling time between foraging areas. Although total foraging time increased with trip duration, the tendency for posttrip haul-out durations to also increase with trip duration may dilute total foraging time over the course of several long trips. Walrus #207 made significantly longer trips than walrus #196, yet the sum of type III diving relative to the entire observation period in each walrus was similar (38% and 37% of the observation periods, respectively).

Our estimate of the proportion of trip time spent diving ($60\% \pm 3\%$) is substantially less than submergence estimates from visual observations of diving Atlantic walruses (81%, Born and Knutsen 1997) and other Pacific walruses (84%, Fay *et al.* 1997). Differences in observation methods could have contributed to this difference. We found that long surface intervals commonly occurred during trips. Many of the long surface intervals were probably associated with resting at the surface, which in male walruses is facilitated by the animal's inflation of pharyngeal pouches (Fay 1960). If visual observations in other studies missed similarly long surface intervals, then their estimates of submergence time would be overestimated. Also, because we were able to resolve only dives with a maximum depth of ≥ 2 m, our estimates of submergence time would be expected to be underestimated. However, Wiig *et al.* (1993) collected data over a 14-d period from an Atlantic walrus, using a TDR with similar dive resolution as our TDRs. During four diving periods, the walrus was submerged 76% of the time. Estimates of submergence for the 4 animals in our study ranged from 56% to 66%.

We found no correlation between dive duration and postdive surface interval (potential recovery time) in any of the dive types, which is consistent with findings from visual observations on free-diving Atlantic walruses (Born and Knutsen 1997, Nowicki *et al.* 1997), and the very weak correlation in TDR data from the Atlantic walrus observed by Wiig *et al.* (1993). Our recorded dive durations were usually within the theoretical aerobic dive limits of adult male walruses (10.5 min for 1,500 kg walrus, Wiig *et al.* 1993; 9.8 min for 1,100 kg walrus, Nowicki *et al.* 1997), thus it is likely that the walruses in our study were diving aerobically during foraging. The mean foraging dive duration of walruses in our study (type III dives, 7 min) is between the ranges of aerobic dive limits of otariids (3–6 min) and phocids (9–30 min) (Wells *et al.* 1999).

Wiig *et al.* (1993) reported a correlation between dive duration and maximum dive depth for all dives combined from TDR observations of a single Atlantic walrus ($r = 0.74$) (dives were not classified). However, we found only

a very weak correlation between dive duration and depth in type III dives ($r = 0.31-0.39$) suggesting that diving effort did not increase with depth during foraging in waters deeper than about 20 m. We found a moderate to strong correlation between dive duration and depth in type IV dives among animals ($r = 0.58-0.82$), but this was probably because of these dives having very short bottom times, and hence for this dive type, dive duration was largely dependent on transit time to and from the sea floor.

Among other pinnipeds, diel differences in dive behavior is usually associated with diel cycles in vertically migrating pelagic prey (Wells *et al.* 1999). Fay (1982) suggested, from a review of visual observations on walrus made by himself and previous investigators, that walrus do not forage with diel periodicity. This would seem reasonable since the benthic prey of walrus are sedentary and would not exhibit diel periodicity in their availability. A lack of diel periodicity in feeding by walrus is further supported here, wherein substantial foraging behavior was recorded over all hours of the day.

The Pacific walrus population ranges widely within the Chukchi and Bering Seas and is segregated by sex and age throughout much of the year. From late spring through fall, adult male walrus haul out primarily at coastal sites (*e.g.*, this study), while female and young walrus haul out predominantly on ice floes. During the breeding season in winter, the population is mixed and all animals inhabit the ice. It seems likely that foraging behaviors would vary seasonally and among segments of the population because of differences in local prey availability among haul-out locations. Therefore, future research on walrus diving behavior should extend efforts to other segments of the population (*e.g.*, adult females). Furthermore, the paucity of diving between 10 and 25 m by walrus in this study, which may have reflected a depth range of low prey abundance, exemplifies the need for concomitant information on prey distribution and abundance to better interpret observed foraging behaviors.

ACKNOWLEDGMENTS

USFWS Togiak National Wildlife Refuge kindly provided field lodging and logistical support for this work. We appreciated field assistance from M. McClaren and C. Wilson (TNWR). This paper was greatly improved by suggestions and comments from S. Innes and an anonymous reviewer. Walrus capturing and handling was conducted under USFWS permit no. PRT-801652.

LITERATURE CITED

- BENGTSON, J. L., AND B. S. STEWART. 1992. Diving and haulout behavior of crab-eater seals in the Weddell Sea, Antarctica, during March 1986. *Polar Biology* 12:635-644.
- BORN, E. W., AND L. Ø. KNUTSEN. 1992. Satellite-linked radio tracking of Atlantic walrus (*Odobenus rosmarus rosmarus*) in northeastern Greenland, 1989-1991. *Zeitschrift fuer Säugetierkunde* 57:275-287.
- BORN, E. W., AND L. Ø. KNUTSEN. 1997. Haul-out and diving activity of male Atlantic walrus (*Odobenus rosmarus rosmarus*) in NE Greenland. *Journal of Zoology (London)* 243:381-396.

- BOYD, I. L. 1997. The behavioural and physiological ecology of diving. *Trends in Ecology and Evolution* 12:213–217.
- BOYD, I. L., J. P. Y. ARNOULD, T. BARTON AND J. P. CROXALL. 1994. Foraging behavior of Antarctic fur seals during periods of contrasting prey abundance. *Journal of Animal Ecology* 63:703–713.
- BURNS, J. M., J. F. SCHREER AND M. A. CASTELLINI. 1997. Physiological effects on dive patterns and foraging strategies in yearling Weddell seals (*Leptonychotes weddellii*). *Canadian Journal of Zoology* 75:1796–1810.
- EVERITT, B. S. 1980. Cluster analysis. Halsted Press, New York, NY.
- FAY, F. H. 1960. Structure and function of the pharyngeal pouches of the walrus (*Odobenus rosmarus* L.). *Mammalia* 24:361–371.
- FAY, F. H. 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. U.S. Department of the Interior, Fish and Wildlife Service, North American Fauna, Number 74. Washington, DC. 279 pp.
- FAY, F. H., L. L. EBERHARDT, B. P. KELLY, J. J. BURNS AND L. T. QUAKENBUSH. 1997. Status of the Pacific walrus population, 1950–1989. *Marine Mammal Science* 13: 537–565.
- FRANCIS, J., D. BONESS, AND H. OCHOA-ACUZA. 1998. A protracted foraging and attendance cycle in female Juan Fernández fur seals. *Marine Mammal Science* 14: 552–574.
- HINDELL, M. A., D. J. SLIP AND H. R. BURTON. 1991. The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia: Phocidae). *Australian Journal of Zoology* 39:595–619.
- KASTELEIN, R. A., AND N. M. GERRITS. 1990. The anatomy of the Walrus head (*Odobenus rosmarus*). Part 1: The Skull. *Aquatic Mammals* 16.3:101–119.
- KASTELEIN, R. A., AND P. MOSTERD. 1989. The excavation technique for molluscs of Pacific Walruses (*Odobenus rosmarus divergens*) under controlled conditions. *Aquatic Mammals* 15.1:3–5.
- KASTELEIN, R. A., AND M. A. VAN GAALEN. 1988. The sensitivity of the vibrissae of a Pacific walrus (*Odobenus rosmarus divergens*) Part 1. *Aquatic Mammals* 14.3:123–133.
- KLECKA, W. R. 1980. Discriminant analysis. Sage Publications, Newbury Park, CA.
- MARTIN, A. R., T. G. SMITH AND O. P. COX. 1998. Dive form and function in belugas *Delphinapterus leucas* of the eastern Canadian High Arctic. *Polar Biology* 20:218–228.
- NELSON, C. H., AND K. R. JOHNSON. 1987. Whales and walruses as tillers of the sea floor. *Scientific American* 256:112–117.
- NOWICKI, S. N., I. STIRLING AND B. SJARE. 1997. Duration of stereotyped underwater vocal displays by male Atlantic walruses in relation to aerobic dive limit. *Marine Mammal Science* 13:566–575.
- OLIVER, J. S., P. N. SLATTERY, E. F. O'CONNOR AND L. F. LOWRY. 1983. Walrus, *Odobenus rosmarus*, feeding in the Bering Sea: A benthic perspective. *Fishery Bulletin, U.S.* 81:501–512.
- SCHREER, J. F., AND J. W. TESTA. 1996. Classification of Weddell seal diving behavior. *Marine Mammal Science* 12:227–250.
- 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.
- WELLS, R. S., D. J. BONESS AND G. B. RATHBUN. 1999. Behavior. Pages 324–422 in J. E. Reynolds III and S. A. Rommel, eds. *Biology of Marine Mammals*. Smithsonian Institution Press, Washington, DC.
- 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.

Received: 10 April 2000

Accepted: 12 December 2000