Diving behavior of immature Steller sea lions (*Eumetopias jubatus*)

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Abstract—Understanding the ontogenetic relationship between juvenile Steller sea lions (*Eumetopias jubatus*) and their foraging habitat is key to understanding their relationship to available prey and ultimately their survival. We summarize dive and movement data from 13 young-of-the-year (YOY) and 12 yearling Steller sea lions equipped with satellite dive recorders in the Gulf of Alaska and Aleutian Islands (n=18), and Washington (n=7) from 1994 to 2000. A total of 1413 d of transmission ($\bar{}$=56.5 d, range: 14.5–104.1 d) were received. We recorded 222,073 dives, which had a mean depth of 18.4 m (range of means: 5.8–67.9 m; SD=16.4). Alaska YOY dived for shorter periods and at shallower depths (mean depth=7.7 m, mean duration=0.8 min, mean maximum depth=25.7 m, and maximum depth=252 m) than Alaska yearlings ($\bar{}$=16.6 m, 0=1.1 min, $\bar{x}$= 63.4 m, 288 m), whereas Washington yearlings dived the longest and deepest (mean depth=39.4 m, mean duration=1.8 min, mean maximum depth=144.5 m, and maximum depth= 328 m). Mean distance for 564 measured trips was 16.6 km; for sea lions ≤10 months of age, trip distance (7.0 km) was significantly less than for those >10 months of age (24.6 km). Mean trip duration for 10 of the 25 sea lions was 12.1 h; for sea lions ≤10 months of age, trip duration was 7.5 h and 18.1 h for those >10 months of age.

We identified three movements types: long-range trips (>15 km and >20 h), short-range trips (<15 km and <20 h) during which the animals left and returned to the same site, and transits to other haul-out sites. Long-range trips started around 9 months of age and occurred most frequently around the assumed time of weaning, whereas short-range trips happened almost daily (0.9 trips/day, n=426 trips). Transits began as early as 7 months of age, occurred more often after 9 months of age, and ranged between 6.5 and 454 km. The change in dive characteristics coincided with the assumed onset of weaning. These yearling sea lion movement patterns and dive characteristics suggest that immature Steller sea lions are as capable of making the same types of movements as adults.

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Steller sea lions range throughout the North Pacific Ocean rim and are declining in numbers in most of Alaska and Russia (Loughlin et al., 1992; Loughlin and York 2000). Studies of mitochondrial DNA suggest that at least two stocks exist: an eastern stock (California through southeast Alaska) and a western stock (Prince William Sound and areas west) (Bickham et al., 1996; Loughlin, 1997). For the western U.S. stock (west of 144°W), counts of adults and juveniles have fallen from about 110,000 individuals in the late 1970s to about 25,000 individuals in 2000—a decline of almost 80%. Although the numbers of sea lions that died were greater from the late 1970s to the early 1990s than at present, the rate of decline has remained high. As a result of this decline the U.S. government designated the western stock as "endangered" in 1997 under the U.S. Endangered Species Act; the eastern stock is designated as "threatened." Reasons for the decline in numbers are unknown but may be linked to reduced availability of prey caused indirectly by environmental changes or commercial fishing activities, or both (Loughlin and Merrick, 1989; Merrick, 1995). Severe environmental perturbations and commercial fishing, both resulting in changes in the abundance or availability of prey, have been implicated in the alteration of pinniped foraging behavior and declines in pinniped abundance (e.g. Trillmich and Ono, 1991; Melin, 2002). One method for studying the effect of reduced prey availability on pinnipeds is to measure diving behavior and foraging ecology by using either a time-depth-recorder (Kooyman et al., 1983; Gentry and Kooyman, 1986) from which dive data are retrieved after the animal returns from a feeding trip (e.g. Goebel et al., 1991; Boyd et al., 1994; Werner and Campagna, 1995), or by using a satellite-linked time-depth recorder (SLTDR; the newer version is called a "satellite dive recorder" SDR), which transmits dive and transmitter-status information to orbiting satellites and thus eliminates the need to recapture the animal (e.g. Merrick et al., 1994).

Few data are available concerning the foraging ecology of Steller sea lions. Merrick et al. (1994) and Merrick and Loughlin (1997) presented information on the dive characteristics and foraging

Table 1

Satellite transmitter number (PTT number), deployment location, age, sex, and morphometric measures of 25 Steller sea lions studied for diving behavior in Alaska and Washington, 1994–2000. The ten ST-10 and ST-16 SDRs we deployed that transmitted time-line messages are shown with **. 1 = Washington State area; 2 = Kodiak area; 3 = Shumagin Islands; 4 = Unimak Pass area; 5 = Sequam area. n/d = no data obtained. PTT number is the satellite transmitter identification number. Est. = estimated.

PTT number	Location code (regional)	Age (months)	Sex	Deployment date	Length of transmission (d)	Mass (kg)	Girth (cm)	Length (cm)
14073	1	12	M	6/8/95	51.67	86.26	n/d	151
14084	1	11	F	5/5/99	50.22	77.18	102	159
14085	1	19	M	1/5/00	14.50	154.36	133	193
14087	1	16	F	10/3/97	68.99	122.45	113	171
14089	1	16	F	10/3/97	55.58	111.11	122	173
21103**	1	22	M	3/30/00	63.80	139.23	128	192
21106**	1	22	M	3/30/00	83.28	143.31	119	192
14071	2	6	M	12/2/94	19.61	92.00	n/d	n/d
14074	2	6	M	12/6/94	53.13	79.80	n/d	n/d
14077	2	18	M	12/9/94	39.63	n/d	n/d	n/d
14078	2	18	F	12/7/94	57.99	n/d	n/d	n/d
14079	2	7	F	1/14/96	27.11	94.90	115	155
14080	2	7	M	1/16/96	79.04	106.20	115	156
14170**	2	21	M	3/12/00	93.99	Est. 95–105	n/d	150
21094**	2	9	M	3/12/00	66.40	62.20	90	145
14076	3	21	F	3/1/96	52.21	103.70	111	n/d
14081	3	9	M	3/2/96	45.02	n/d	144	n/d
14072	4	22	F	4/13/95	56.35	116.10	n/d	n/d
14075	4	8	F	2/25/96	31.76	104.00	123	140
14164**	4	9	M	3/8/00	97.61	79.60	n/d	n/d
14167**	4	9	F	3/9/00	29.67	100.20	n/d	155
14111**	5	9	F	2/29/00	61.71	87.00	108.5	151
14114**	5	9	F	2/29/00	52.53	85.80	108	157
14116**	5	9	F	2/29/00	56.61	76.20	102.5	148
14163**	5	9	M	2/29/00	104.14	109.00	113	156

behavior of a small sample of Steller sea lions in Alaska; Loughlin et al. (1998) provided similar information for Steller sea lions off the Kuril Islands, Russia. Merrick et al. (1990) and Brandon (2000) presented information on female pup-attendance behavior of sea lions with VHF radio-transmitters off the Kuril Islands and Alaska, respectively. These studies showed that during the breeding season, adult female Steller sea lions generally spent about half their time at sea on relatively brief (18–20 h) foraging trips. Dives tended to be shallow ($\bar{x}$=21 m), brief ($\bar{x}$=1.4 min), and frequent (about 13/h). Observations during winter showed that females with suckling yearlings (17–22 months of age) had feeding trips of about 2.3 days, whereas those with young-of-the-year (5–10 months of age) had trips lasting 0.9 of a day; time on shore for lactating females of both groups averaged 14.2 hours (Porter, 1997). Baba et al. (2000) were able to follow a yearling Steller sea lion for 5 months using two location-only satellite transmitters; one was attached to the top of the head and the other on the back. This animal traveled from Hokkaido to Sakhalin Island and throughout the southern Okhotsk Sea. No dive data were obtained.

Our objective is to present a description of the diving behavior of juvenile Steller sea lions for the western stock of Steller sea lions in Alaska and the eastern stock in Washington state. We deployed SDRs on juvenile Steller sea lions over a broader geographical range in Alaska and over a wider range of dates, providing a more comprehensive picture of the diving behavior of young Steller sea lions. Additionally, SDRs are now smaller and of higher quality, so that more detailed information on diving behavior is available. We then provide in the "Discussion" section a comparison of the accounts in the present study to those we published earlier on adult female diving behavior (e.g. Merrick and Loughlin, 1997).

Materials and methods

We captured 25 free-ranging Steller sea lions of both sexes from approximately 6–22 months of age at rookeries and haul-out sites in the Aleutian Islands and Gulf of Alaska (Table 1, Fig. 1) throughout the year from 1994 to 2000, and during 1995–2000 at Shilshole Marina in Puget Sound, near Seattle, Washington. Animal age was estimated by using

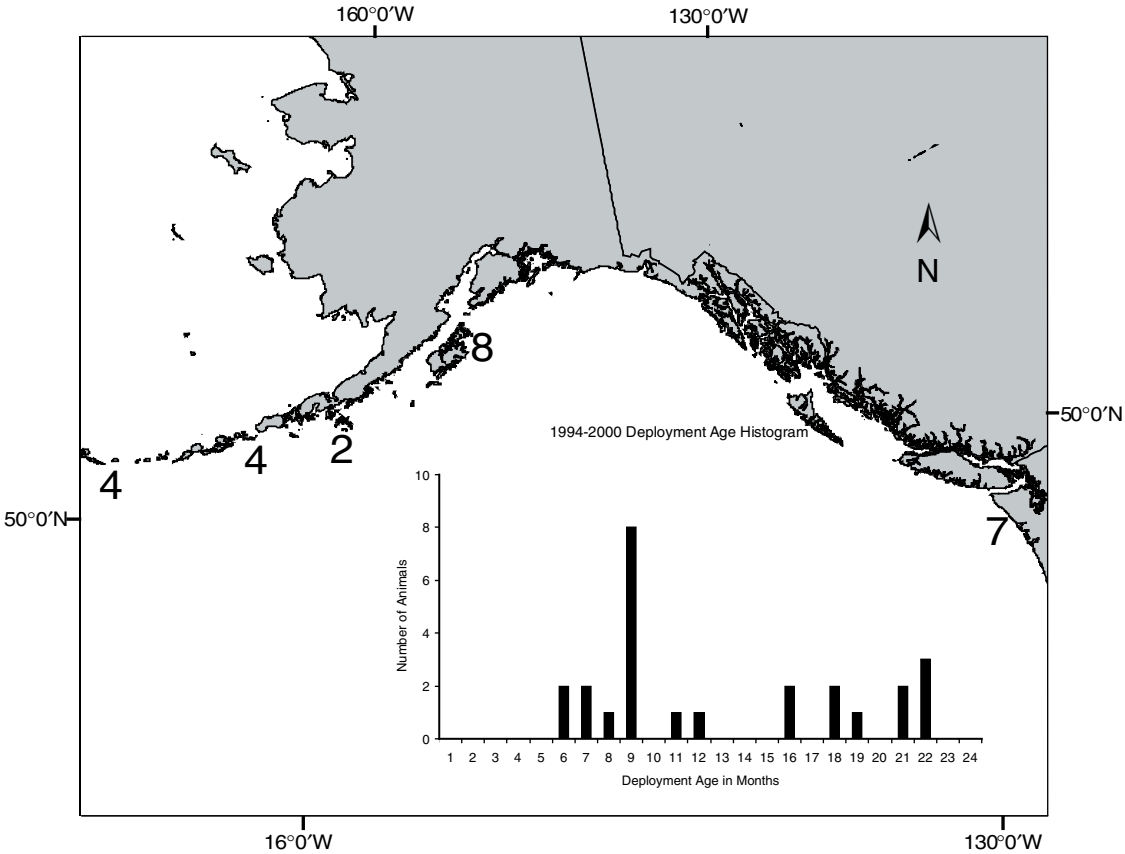


Figure 1

Locations where satellite dive recorders (SDRs) were deployed on 25 Steller sea lions in Alaska and Washington between 1994–2000. "Deployment age" is the age of the sea lions when satellite transmitters were attached.

mid-June as the presumed birth date (Pitcher and Calkins, 1981) and published accounts of mass, standard length, and girth at age (Calkins et al., 1998). Some juveniles before 1996 were chemically immobilized with Telazol[tm] injected intramuscularly by a dart fired from a pneumatic gun (Loughlin and Spraker, 1989). Those animals were not weighed; therefore exact dosage levels were not determined. However, dosages were most likely between 1.5 and 2.5 mg/kg. Once a sea lion was immobilized, intramuscular injection of 3–10 cc of Dopram was administered to stimulate respiration and facilitate recovery. After 1996, young sea lions were captured on land with a hoop net and physically restrained. During all years a SLTDR or SDR was glued to the pelage on the animal's back with fast-setting epoxy resin (Loughlin et al., 1987), and two plastic cattle ear tags with the same identification numbers were attached, one to each front flipper. The instruments were not recovered and were expected to be shed during or before molt.

Instrument description and programming

We used 0.5-watt ST-6 SLTDRs (packaged by Wildlife Computers, Redmond, WA), which provide dive depth, dive duration, and transmitter status. Further development by Wildlife Computers resulted in 0.25-watt ST-10 and ST-16 SDRs which could provide five messages: 1) dive depth, 2) dive duration, 3) transmitter status, 4) proportion of time at depth, and 5) a time line. Messages are sent at prescribed intervals; transmission interval at sea is every 43 sec and on land it is every 1 min 28 sec. The number of transmissions (and thus messages received) while the sea lion is at sea depends on the length of exposure of the instrument's salt-water switch at the surface. Location data are not sent by the transmitter but are calculated by Service-Argos, Inc. from the received message. Additional information on these instruments and their capabilities can be found in Merrick et al. (1994). The satellite tracking system (Argos) is described in detail in Fancy et al. (1988) and Stewart et al. (1989). Additional information can be obtained from the manufacturer at their web site (www.wildlifecomputers.com).

The ST-6 SLTDR stored, summarized, and transmitted dive data as histograms. Individual dives and surface intervals were not provided; therefore sampling frequency for measuring dive behavior was not a consideration (e.g. Boyd, 1993). Software programming of the SLTDR subdivided each day into four 6-h periods (2100–0300 h, 0300–0900 h, 0900–1500 h, and 1500–2100 h local time). Frequency histo-

grams were summarized separately for dive depth and dive duration for each of the four time periods. The SLTDRs recorded dive depth information in six separate "bins": 4–10 m, 10–20 m, 20–50 m, 50–100 m, 100–250 m, and >250 m. We used 4 m as the minimum depth for a dive based on earlier studies in Alaska (Merrick et al., 1994). Dive-duration bins were 0–60 sec, 60–120 sec, 120–180 sec, 180–240 sec, 240–360 sec, and >360 sec.

The ST-10 and ST-16 units used the same 6-h periods as the ST-6. However, the ST-10 and ST-16 SDRs subdivided dive depth information into 14 bins: 4 m; 4–6 m, 6–10 m, 10–20 m, 20–34 m, 34–50 m, 50–74 m, 74–100 m, 100–124 m, 124–150 m, 150–174 m, 174–200 m, 200–250 m, and >250 m. Dive duration also contained 14 bins at one-minute intervals (e.g. 1–2 min, 2–3 min, 3–4 min, etc.). The 14 time-at-depth bins coincided with dive-depth bins (e.g. 0, 4, 4–6, 6–10, etc. and the last was >200). However, the first bin was set to zero to determine if an animal was on land based on the proportion of dry readings of the salt-water switch during a 6-hour period. Time-at-depth was calculated as the proportion of time that dives occurred within a particular depth bin of a 6-h period while the sea lion was at sea (e.g. if an animal was at sea for 3 hours during a 6-h period and spent half its dive time in bin 50–74, the value in bin 50–74 would be 25%).

We deployed ten ST-10 and ST-16 SDRs (Table 1) which transmitted time-line messages in bins of 20-min periods (there are 72 periods of 20-min each in a 24-h day). These messages provide information on whether the instrument was wet or dry >10 min of a 20-min period for each of the 72 periods. Time-line messages thus allow calculation of time spent at sea and on land.

Maximum dive depth in a 24-h period, from midnight GMT to midnight GMT, was provided in the status message. This is a separate message that provides information on transmitter status, including a pressure offset, battery status, number of transmissions to date, at-surface data, date, time, ID of message, and a saltwater conductivity reading. All 25 transmitters that we deployed transmitted a status message.

The ST-6 SLTDRs were on 24 h/day and transmitted a maximum of 400 transmissions/day. To save battery power the instrument had a 6-h haul-out period; that is, it would turn off only if the transmitter was "dry" for 6 hours, indicating that the animal was on land. The ST-10 and ST-16 SDRs had 3-h haul-out periods; the ST-10 had a maximum of 250 transmissions/day, and the ST-16 had a maximum of 325/day. Both the ST-10 and ST-16 had duty cycles of 4 h on and 2 h off during a 24-h period to distribute transmissions during different times of the day and to ensure recording of information in all bins. All duty cycles started at midnight, with an offset of +13 h from GMT for Alaska.

Location data

Locations were estimated by the Service-Argos, Inc. classification scheme, where location class (LC) 3 is accurate to <150 m, LC 2 is accurate 150 m–≤350 m, LC 1 is accurate 350 m–1000 m, and LC 0 is accurate >1000 m. LCs A and B have no assigned accuracy range (Service-Argos, 1984; Keating, 1994). However, after our analysis, Vincent et al. (2002) used an algorithm published by McConnell et al. (1992) to filter satellite locations and found that both filtered and unfiltered LC A locations were of a similar accuracy to LC 1 locations for four gray seals (*Halichoerus grypus*). Because of the large variance in our samples associated with LC A locations, we excluded them (and the LC Bs) from our analyses. We sorted location data by date and time line to determine the locations for each trip.

Data analysis

Data analysis followed that of Merrick et al. (1994) and Merrick and Loughlin (1997). Analysis of the number of dives was prepared by summing counts of dives from the histograms. Median depths and durations of dives were calculated by using the range midpoint of a bin (e.g. 7 m for a 4–10 m bin) as the depth for all dives in the bin. We recognize that this approach invokes a possible error for dive profiles in large increment bins (e.g. 50–100 m) where the mean dive depth is the same, 75 m, regardless of whether the animal made most of its dives between 51 and 60 m or if it made most of its dives between 90 and 100 m. This error is inherent in the data collection process and could not be eliminated with the instruments used in our study. We also recognize that more locations will be recorded when the animals are at the surface for long periods or when transiting to different locations. However, because of the repetitive transmission of the histogram data and the usual short duration of short-range trips, there should be no inherent behavior-based bias in the dive data reported. Differences in dive depth and duration between locations were tested by using the Pearson chi-square tests or analysis of variance (ANOVA) (F-statistic), and P-value differences less than 0.05 were considered significant. Analysis of trip distance and duration were analyzed by using a repeated measures ANOVA, and because the distances were skewed, they were log-transformed to examine differences among groups.

Trips were defined and measured for distance by using an integrated process of the SDR data. For animals deployed with ST6 SDRs, which did not contain time line data sets (n=15), trip distances were extracted by using a combination of the dive histogram, duration histogram, and land or sea data sets to estimate arrival and departure times as well as locations calculated at sea or on land. Once arrival and departure times were estimated, the location data were examined to confirm that all locations calculated during that trip were wet locations. We then had all locations for an individual trip and from those locations we filtered out all A and B locations and imposed a swim speed filter (3 m/s). Finally, we reported the maximum straight-line distance from the departure site. For animals with ST10/16 SDRs, we were able to extract arrival and departure times from the time-line messages. However, if a day of time-line data was not received, we referenced the time-at-depth data, depth, and duration histograms to reconstruct the missing day of data. Once arrival and departure times were calculated we then followed the protocol stated above.

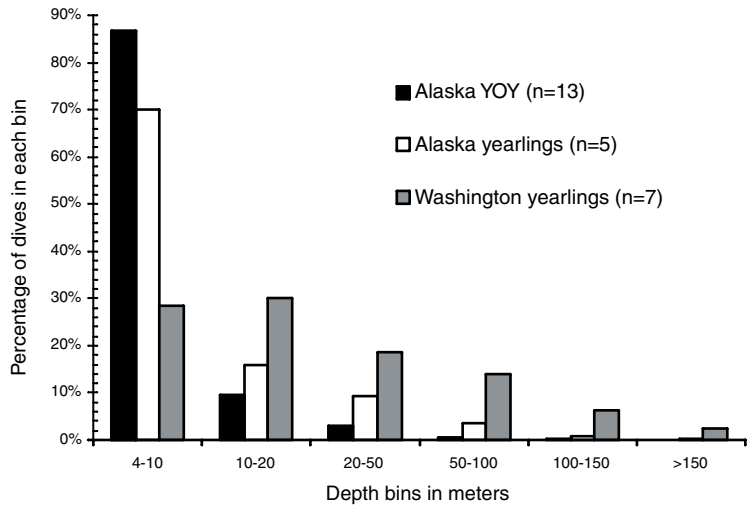


Figure 2

Percentage of dives occurring in each dive-depth bin for Alaska young-of-the-year (YOY), Alaska yearling, and Washington yearling Steller sea lions. Twenty-five animals are represented from 1994 to 2000 and a total of 222,073 dives.

Results

We report on SDR data obtained from 25 (13 male, 12 female) young-of-the-year and juvenile (estimated ages of <2 yr) Steller sea lions from Washington state, Gulf of Alaska, and Aleutian Islands, Alaska (Table 1). Most (22 of 25) were caught during October–March 1995–2000 and the remainder during May–July (Table 1). Mean number of days of transmission received from the SDRs was 56.8 d (range 14.5–104.1 d).

Dive characteristics

We recorded over 222,073 dives for young-of-the-year and juvenile Steller sea lions which had a mean dive depth of 18.4 m (range of means: 6.1–67.0 m; SD=16.23). Alaska young-of-the-year dived to shallower depths and for shorter periods (mean depth=7.7 m, SD=1.7; mean duration=0.8 min, SD=0.1; mean maximum depth=25.7 m, SD=16.9; and maximum depth=252 m) than did Alaska yearlings (mean depth=16.6 m, SD=10.9; mean duration=1.1 min, SD=0.4; mean maximum depth=63.4 m, SD=37.7; and maximum depth=288 m), whereas Washington yearlings dived the deepest and the longest (mean depth=39.4 m, SD=14.9; mean duration=1.8 min, SD=0.6; mean maximum depth=144.5 m, SD=32.6; and maximum depth=328 m). Alaska animals dived to much shallower depths (mean depth=10.3 m) than animals from Shilshole, WA. There was no significant difference in the mean dive depths among locations in Alaska (P=0.8). Alaska animals, in comparison to the Washington animals, had a significantly greater proportion of dives in the 4–10 m depth bin (70%, P<0.001) than in the deeper depth bins.

We compared the proportion of dives in the shallowest bin (depth bin 4–10 m) for animals captured in Washington state versus Alaska using a generalized linear model with a binomial link function (McCullagh and Nelder, 1989). The proportion of shallow dives was significantly greater (P<0.001) among the Alaskan animals (81.4%) than among the Washington state animals (43.8%). Among the Washington state animals, the proportions of dives in the 1020 m depth bin (20.4%) and the 20–50 m depth bin (19.4%) were similar; proportions of dives in the deeper depth bins were progressively fewer (Fig. 2). Maximum and mean-maximum dive depth were also greater for young sea lions from Washington that dived to 141.5 m (SE=11.4) mean-maximum depth versus 33.8 m (SE=7.2) for Alaska sea lions (F=63.4, 23 and 24 df; P<0.001) (Table 2). We plotted the maximum depth for each 24-h period by the number of days in which the Argos satellite received a status message (which contains maximum depth for 24 hours) and found that with one exception (PTT 14078), Washington yearlings consistently dived deeper than their Alaska counterparts (Fig. 3, A and B). Two of three Alaska young-of-the-year were shallow divers and the third dived to 250 m once and beyond 100 m on numerous occasions late in the tracking period (Fig. 3C). The maximum depth for all sea lions that we studied was 328 m for a juvenile sea lion that was equipped with a SDR at Shilshole, WA (PTT 21106); the deepest dive for a yearling Alaska sea lion was 288 m (PTT 14078) (Fig. 3).

Mean dive duration was 1.1 min for all young sea lions (n=226,497 dives). Dive duration was significantly longer for Shilshole sea lions ($\bar{x}$=1.75 min; range: 0.95–3.10) compared to Alaska sea lions ($\bar{x}$=0.85 min; range: 0.61–1.86; F=24.5, 23 and 24 df; P<0.001). Few dives were greater

Table 2

Summary of dive parameters from satellite dive recorders (SDRs) deployed on Steller sea lions in Washington and Alaska, 1994–2000. "PTT" is the satellite transmitter identification number.

	PTT	Mean max. dive depth (m)	Mean max. dive depth (*n*)	Max. depth (m)	Mean depth (m)	Mean depth (*n*)	Mean duration (min)	Mean duration (*n*)
Washington	14073	77.68	38	168	31.99	10,746	0.96	11,241
	14084	154.12	34	288	47.29	5183	1.69	5047
	14085	187.67	12	280	67.94	1991	3.10	2025
	14087	164.37	53	256	33.21	14,287	1.69	14,572
	14089	144.00	46	200	44.76	9682	1.82	9659
	21103	124.22	18	256	23.59	6920	1.40	5431
	21106	159.09	44	328	26.92	11,839	1.61	11,647
Alaska	14071	10.44	18	12	7.20	1541	0.61	1732
	14074	11.07	30	20	7.24	3044	0.72	2954
	14077	28.57	21	144	9.67	4745	0.81	5146
	14078	125.74	23	288	35.00	4186	1.82	3657
	14079	12.80	20	44	7.13	7546	0.71	8482
	14080	15.80	59	24	7.60	17,236	0.96	18,056
	14170	41.87	47	180	10.23	17,741	0.91	19,447
	21094	48.90	31	152	11.67	9745	0.79	9388
	14076	51.69	26	144	9.29	11,593	0.86	12,739
	14081	11.76	34	20	7.25	8717	0.70	9013
	14072	68.98	49	100	18.69	12,597	1.06	11,931
	14075	8.00	15	12	7.01	5424	0.67	4869
	14164	26.09	44	60	9.46	16,352	0.96	16,426
	14167	20.73	11	60	7.01	2985	0.81	3022
	14111	17.76	25	40	6.44	10,919	0.72	10,903
	14114	13.75	16	16	5.84	5846	0.68	6256
	14116	24.24	17	40	6.70	7359	0.73	7739
	14163	65.55	49	252	10.94	13,849	0.82	15,204
Mean		62.42		135.36	18.42		1.10	
SE		11.50		3.23	3.23		0.11	

than 6 min (Fig. 4). There was a significant positive linear relationship between dive duration and dive depth (r^2=0.89, F=7.06, 1 and 23 df, P<0.001), and a significant positive relationship between sea lion mass at the time of capture and mean dive duration (r^2=0.46, F=3.86, 1 and 20 df, P<0.001) but not girth (r^2=0.10, F=1.62, 1 and 14 df, P=0.22). The relationship between dive duration and dive depth for males was not different from that for females (F=1.16, 2 and 21 df, P=0.33). The positive relationship between dive duration and mass was likely driven by the greater mass of the male sea lions because the relationship was not statistically significant when the analysis was restricted to females.

Dive depth and duration showed an interesting ontogenetic trend. Alaska animals 7–10 months old typically had a mean dive duration of <1 min and a mean dive depth of about 10 m; by 11–12 months of age both increased, almost doubling in most cases (Fig. 5). Although sample size was small, this ontogeny of diving to deeper depths for longer periods at about 11–12 months of age was evident in the percentage of time at depth (Fig. 6). There was a higher proportion of time spent in the deeper depth bins during May and June (at age 11 and 12 months, respectively) than when younger, and the proportion of time hauled out was reduced for the older animals. Interestingly, the decrease in dive depth and dive duration for two Washington animals at 23 months of age (Fig. 5) corresponded with movement from inside Puget Sound to deeper waters off the Washington coast.

The greatest proportion of all diving (37%) occurred during 2100–0300 h; the least (about 16%) during 0900–1500 h (Fig. 7). There were no periods when young-of-the-year or juvenile sea lions from any location did not dive. The frequency distribution of dives was similar in all time periods for all age groups from Alaska and Washington (Fig. 7).

Distance and duration of trips at sea

Mean distance of trips at sea for 564 measured trips of the 25 study animals was 16.6 km (SD=44.9 km; range:

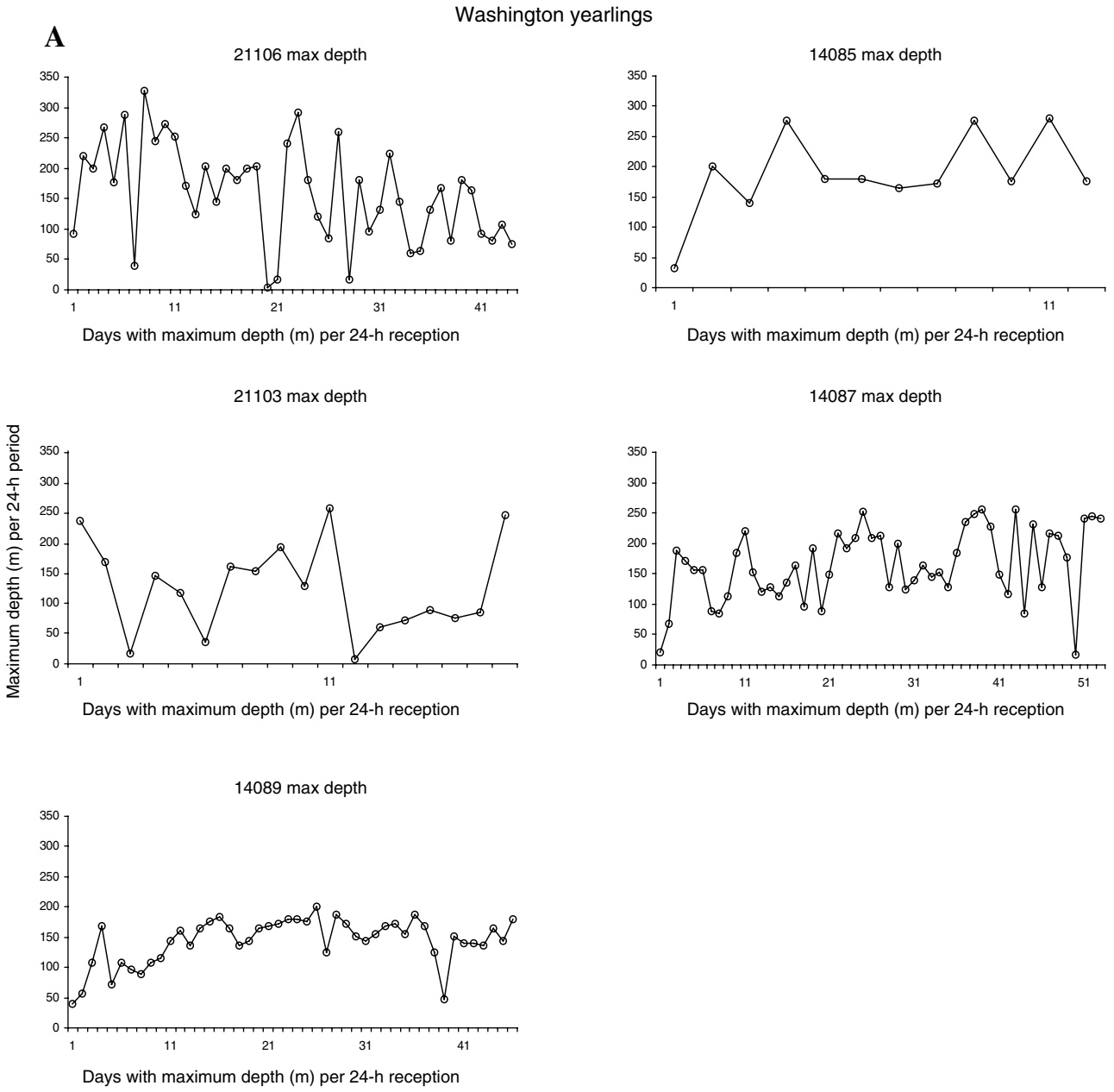


Figure 3

Summaries of the maximum depth (m) for each 24-h period (○) in which a status message containing maximum depth information was received by the Argos satellite for 13 of the 25 SDR-equipped Steller sea lions. For example, the Argos satellite received a status message from SDR 21106 for about 44 days, yet the SDR was operational for a total of 83 days (A; see Table 1). These 13 were chosen to compare yearlings of comparable age in Washington (**A**), and Alaska (**B**), and to provide typical examples of Alaska young-of-the-year (**C**).

<1–447.3 km; median=4.2 km). For sea lions ≤10 months of age, the mean distance of all trips was 7.0 km (n=257 trips; range=0.1–260.7 km; SD=19.0 km; median=2.7 km) (Fig. 8); for sea lions >10 months of age, the mean distance of all trips was 24.6 km (n=307; range: <1–447.3 km; SD=57.2 km; median=5.6 km) (Fig. 8). Averaged across individual animals, the mean distance of trips at sea ranged between 2.3 and 55.6 km; for the younger animals this range was 4–17 km and 2–55 km for the older animals. The repeated-measures ANOVA on the logarithm of trip distance showed that the older sea lions traveled significantly farther (P<0.001) than younger animals and that there were neither signifi-

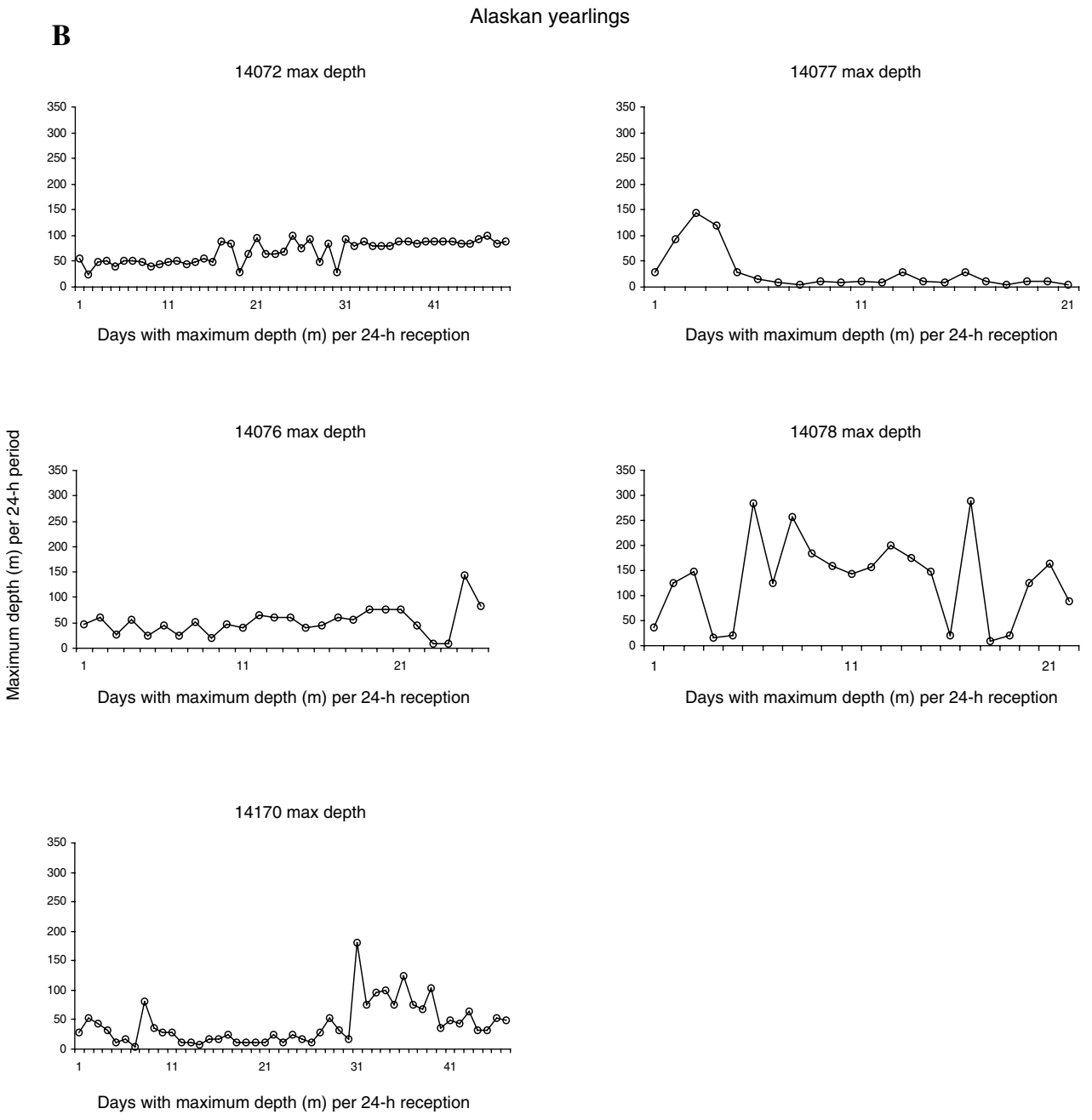
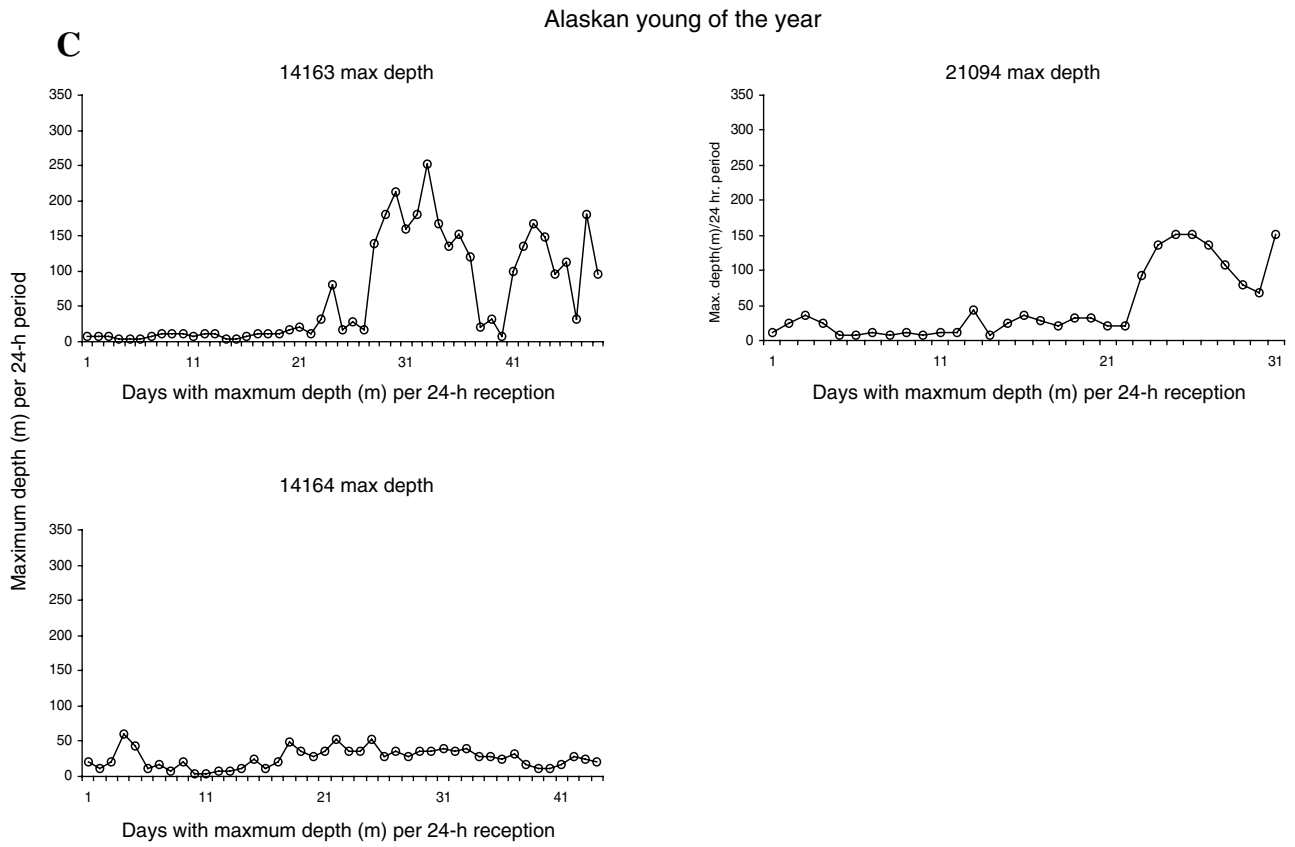


Figure 3 (continued)

cant gender (P = 0.6) nor gender × age interaction effects (P=0.19).

Trip distance increased with age. For example, we captured a 9-month-old male sea lion (bearing transmitter identification number PTT 21094, Table 1) near Kodiak Island in March 200. It had short trip distances (<10 km) which tended to concentrate near the capture site and nearshore (Fig. 8). As the animal matured through April and May, trip distance progressively increased until the sea lion was swimming over 50 km offshore beyond the 100-m depth contour and had a maximum dive depth >150 m (Table 2; Fig. 8).

Trip duration was measured for 10 of 25 animals with SDRs containing time-line data (it was not possible to calculate trip duration for 15 SDRs with the earlier SLTDRs that did not transmit time-line data). Mean trip duration for these 10 animals was 12.1 hours (n=544; SD=23.83 h; range: 1–344 h; median=7.3 h). For animals ≤10 months



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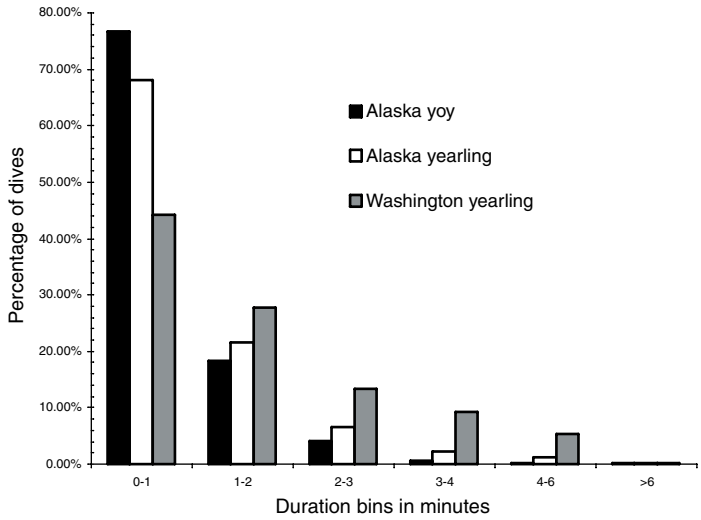

Figure 4

Percentage of dives occurring in each duration bin for Alaska young-of-the-year (YOY), Alaska yearling, and Washington yearling Steller sea lions. Twenty-five animals are represented from 1994 to 2000 with a total of 226,497 dives.

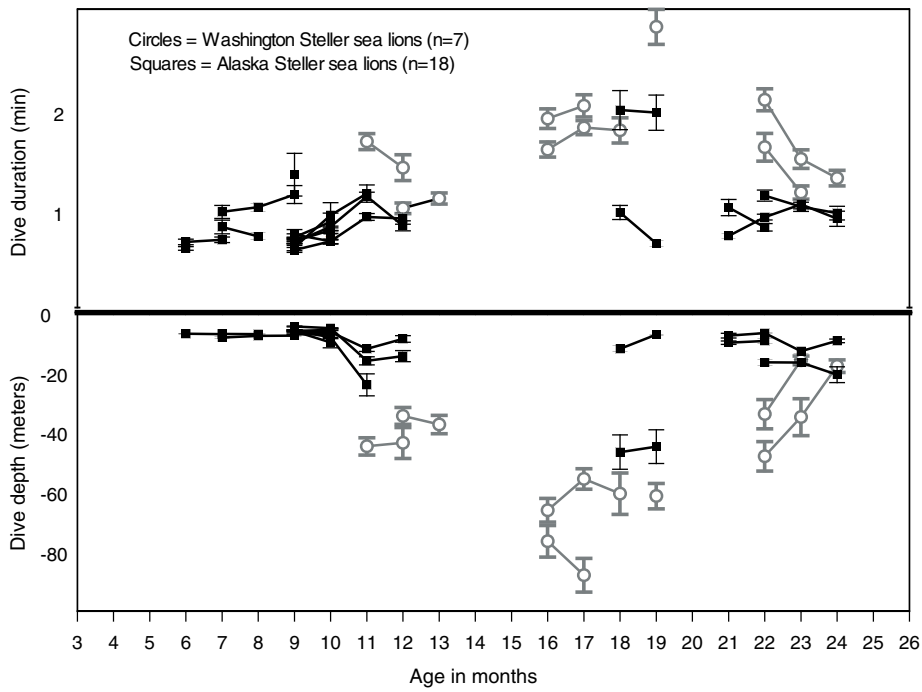

Figure 5

Mean dive depth and duration as a function of age in months for Washington and Alaska Steller sea lions. Error bars represent the standard error. Each connected symbol represents one individual sea lion monitored over several months.

of age, the mean trip duration was 7.5 hours (n=307; SD=7.5 h; range: 1–81.3 h; median=6 h) and for sea lions >10 months of age, the mean duration of all trips was 18.1 hours (n=237; SD=34.2 h; range: 1–344 h; median=10.3 h). Averaged across individual animals, the mean duration of trips at sea ranged between 6.2 to 21.4 hours; this range was 6.2 to 17.2 hours for the younger animals and 10.3 and 21.4 hours for the older animals. The analysis of the repeated-measures ANOVA on the logarithm of trip duration showed that the older sea lions had longer trip durations (P<0.001). We could not test for gender and gender × age effects because there were no measured trip durations for females >10 months. Among the younger animals, there was no gender difference in mean trip duration (P=0.11).

Types of movement

We identified three types of movements for the sea lions at sea: long-range trips (>15 km and >20 h), short-range trips (<15 km and <20 h), and transits to other haul-out sites (Fig. 9). Long-range trips most likely were foraging trips and began around 9 months of age. These trips had a mean of 48.7 km (SD=55.7 km; max=240.8 km) and may coincide with the assumed onset of weaning; they represented 6% of all trips to sea. The most numerous trips (88%) were short-range foraging trips ($\bar{x}$=3.6 km; SD=0.4; max=21.0 km), which happened almost daily (0.9 trips/d, n=426 trips). Transits were movements from one haul-out site to another haul-out site; these trips were characterized as the straight line distance from one haul-out site to another and began as early as 7 months of age but occurred more often after 9 months of age. Transit trips represented 6% of all trips at sea and had a mean distance of 66.6 km (SD=83.7 km; range: 6.5–341.9 km).

Discussion

The differences in diving behavior between young Steller sea lions in Washington and those off Alaska are intriguing. Possible reasons for these differences include variable habitat type, prey resources, or morphological or genetic differences. However, there is no evidence, based on morphology or genetics, to either support or refute differences in the diving behavior that we observed. The evidence of genetic differences between the western and eastern stock of Steller sea lions is based on mtDNA haplotype differences for a segment of the mitochondrial D-loop which does not code for any structural proteins (Bickham et al., 1996; Loughlin, 1997).

One morphological difference between the two stocks is a progressive increase in mass of Steller sea lion pups from east to west (Merrick et al., 1995), but whether this difference in mass continues with increasing age is unknown. Large animals typically dive deeper and longer than smaller (and younger) animals (Schreer and Kovacs, 1997). Larger animals have less drag per unit of mass and generally have more blood than smaller ones and thus are able to store more oxygen. Larger animals also have lower

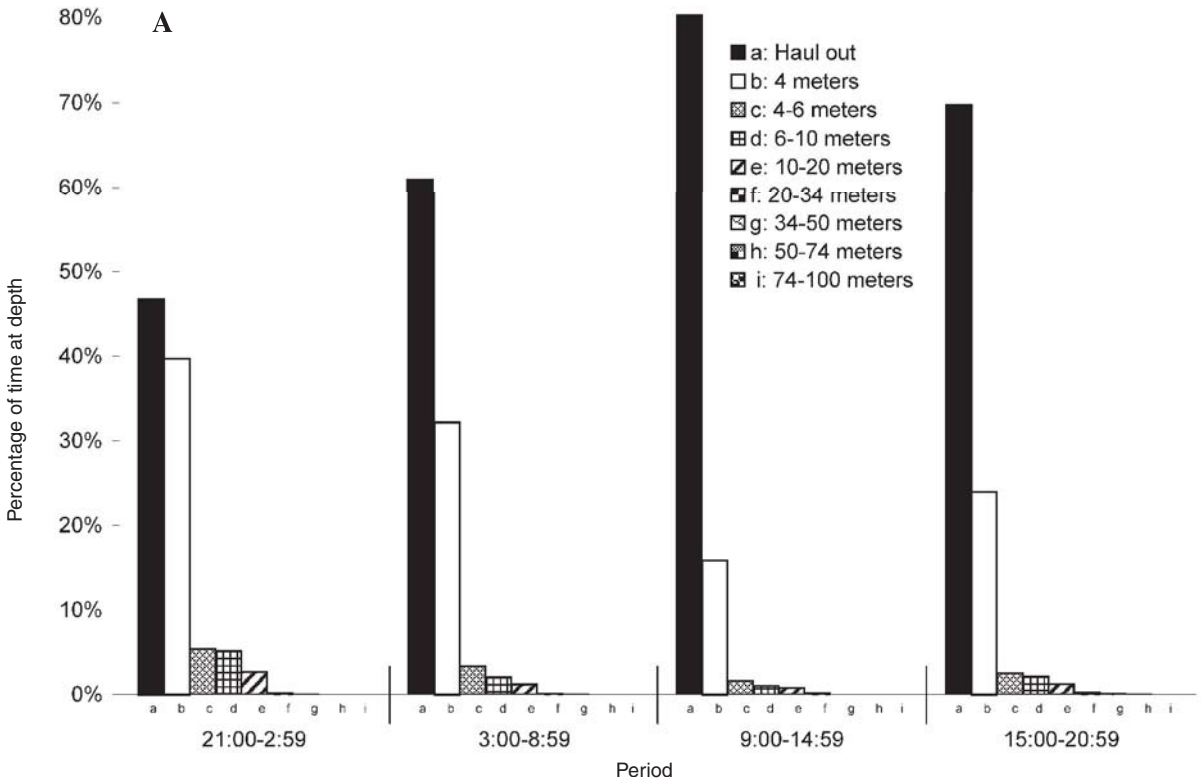

Figure 6

Percentage of time spent at depth for seven young-of-the-year Steller sea lions approximately (**A**) 7–10 months of age in Alaska, and percentage of time spent at depth for three young-of-the-year Steller sea lions approximately (**B**) 11–12 months of age (during May and June) in Alaska. This figure suggests that as young sea lions approach one year of age they tend to spend less time hauled out and that a greater proportion of their dives are deeper.

mass-specific metabolic rates than their smaller counterparts and thus expend less energy and use less oxygen stores (Schreer and Kovacs, 1997). Our sample size of sea lions of comparable age is small; however, we compared the mean mass of three Washington sea lions to the mean mass of three Alaska sea lions of approximately the same age (Table 1) and found that the Alaska animals had less mass than those in Washington (108 kg vs. 145 kg). Whether or not this difference in mass can account for the differences we saw in diving characteristics for animals of similar age (Fig. 3, A and B) is unknown.

The differences in diving characteristics between animals tracked in coastal waters of Puget Sound, Washington, and those tracked in Alaska waters are most likely linked to localized differences in prey habitat. The primary prey of Steller sea lions across their range are fish and cephalopods, both of which have a broad but predictable range in temporal, spatial, and seasonal nearshore availability. Typically, each species makes predictable migrations seasonally from pelagic to nearshore waters where they form large spawning concentrations. The prey are then further concentrated by local transition boundaries such as frontal zones and bathymetric features such as submarine channels (Sinclair et al., 1994). Steller sea lions appear to have the foraging flexibility to take advantage of both the predictable behavioral traits of these prey species, as well as the localized oceanographic conditions that enhance prey concentrations (Sinclair and Zeppelin, 2002).

The primary prey of Steller sea lions in Alaska waters is walleye pollock (*Theragra chalcogramma*), which is consumed year-round (Sinclair and Zeppelin, 2002). Walleye pollock is replaced as a dominant year-round prey item by Pacific whiting (*Merluccius productus*) in Pacific Northwest waters (Gearin et al., 1999). Both species are semidemersal and can be found from near surface waters to depths >1200 m, depending on localized conditions (Hart, 1973; Eschmeyer et al., 1983). The greatest abundances of both species are available to Steller sea lions in nearshore waters over the continental shelf and perhaps as the prey become more available during nighttime diurnal vertical movements.

The physical features of Puget Sound, along with its complex bathymetry and the extensive channels and canyons, provides extensive microhabitat for both predator and prey species to express the full extent of their depth range. In this respect, Puget Sound is comparable to the Gulf of Alaska where Pacific cod (*Gadus macrocephalus*) is the predominant winter prey item for Steller sea lions. Pacific cod is thought to be consumed during spawning when it ap-

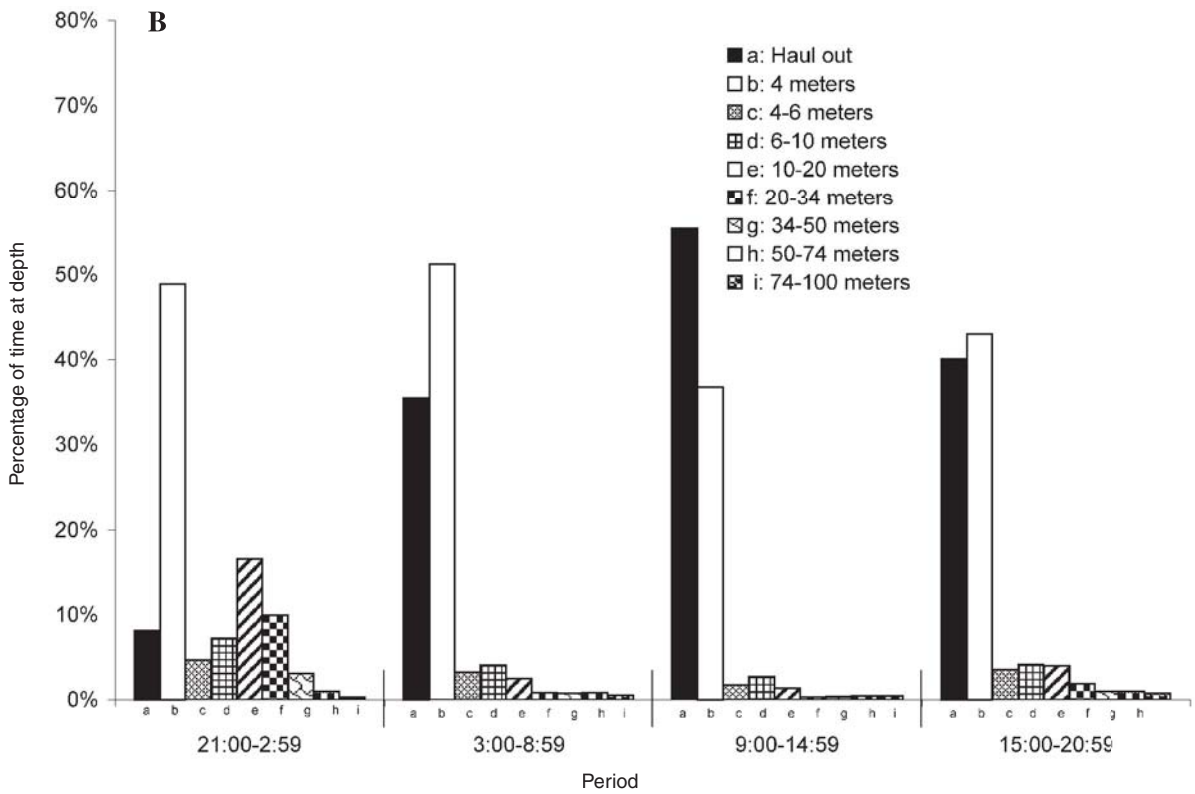

Figure 6 (continued)

pears to concentrate in the deep nearshore channels and gullies of the Gulf of Alaska (Sinclair and Zeppelin, 2002).

The differences in dive depths that we report also could be typical of the variability among individuals. Boveng et al. (1996) analyzed TDR data for six dive-related variables and found that dive duration was the least variable and vertical distance (dive depth) was the most variable among individual Antarctic fur seals (*Arctocephalus gazella*). In our study, there was high individual variability in both dive depth and maximum depth and little variability in dive duration—results similar to those of Boveng et al.'s (1996) study.

A female Steller sea lion nurses her pups during the day, stays with the pup for the first week, then goes to sea on foraging trips. Maternal pup-attendance patterns seem to vary over the sea lion's geographic range; the average range of time for foraging trips during lactation are from about 24 h to 2 d at the southernmost rookery at Año Nuevo Island, California (Higgins et al., 1988; Hood and Ono, 1997; but note that some of this variability may have been the result of El Niño conditions during part of the Higgins et al. study period), about 25 h at Lowrie Island, 19 h at Fish Island, 11 h for Chirikof Island, and 7 h in the Aleutian Islands (Brandon, 2000).

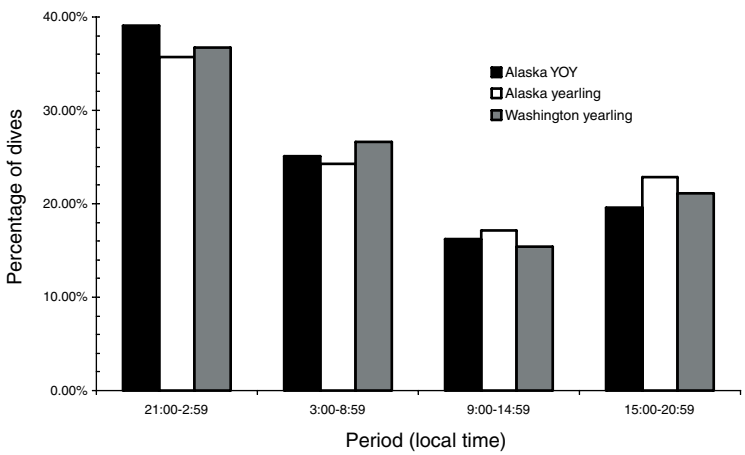

Figure 7

Percentage of dives occurring in each time bin for Alaskan young-of-the-year (YOY), Alaska yearling, and Washington yearling Steller sea lions. Twenty-five animals are represented from 1994 to 2000.

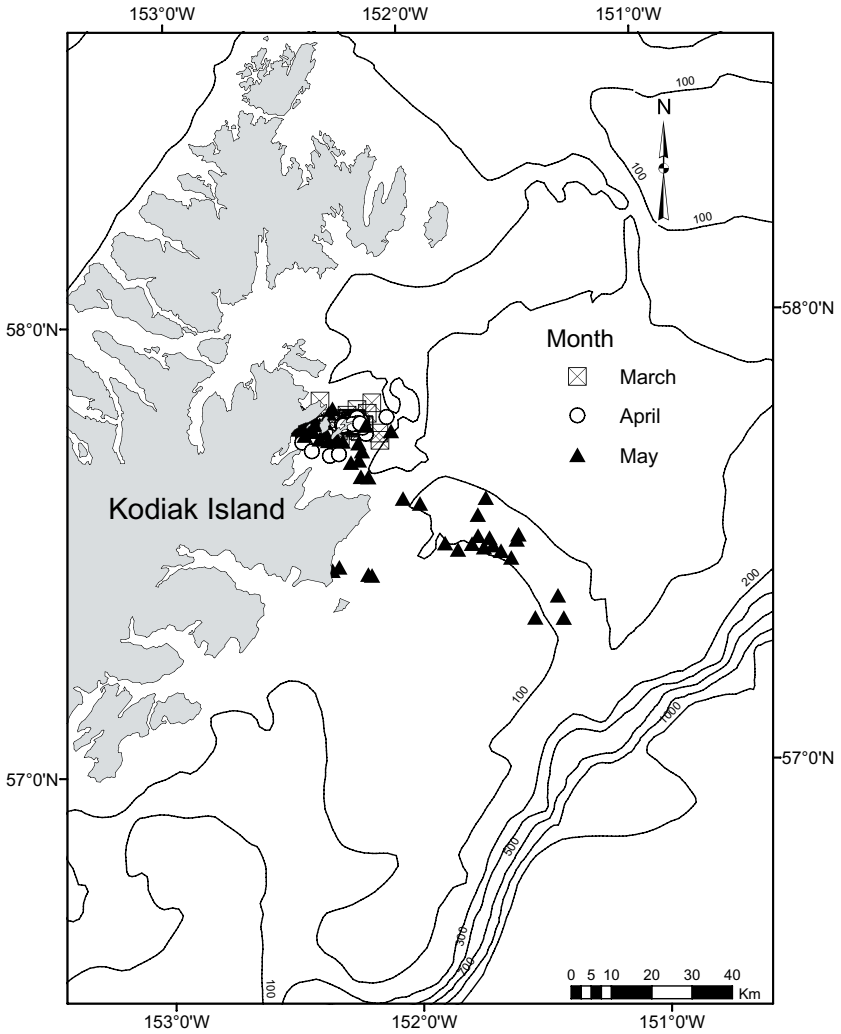

Figure 8

Figure showing the progressive increase in distance of locations from shore for a 9-month-old sea lion over time. This animal (identification number: PTT 21094) was equipped with a satellite transmitter near Kodiak Island in March 2000. Early trips were <15 km from shore in water <50 m in depth near the capture site. Trips became progressively greater as the animal matured through May 2000 when it was venturing over 50 km from shore in water >100 m in depth.

Ontogeny of diving ability has been studied in two other otariids. Baker and Donohue (2000) used data loggers (which they termed "time wet recorders") to measure time spent in the water and diving behavior of northern fur seal (*Callorhinus ursinus*) pups on St. Paul Island, Alaska. These pups began spending substantial time in the water at approximately 40–50 d of age that coincided with growth of the under fur and increases in sea surface temperature. Time spent in the water increased up to about 100 d of age; diving to depth did not occur until they were much older and about to migrate. Horning and Trillmich (1997) conducted an extensive study on the ontogeny of diving behavior in Galapagos fur seals (*Arctocephalus galapagoensis*), a species that weans no sooner than 2 years of age. They found that in young the development of diving behavior was closely linked to dependence on the mother and that substantial diving activity did not occur until one year of age; but even then the young fur seals were still nutritionally dependent on their mothers and did not dive as deep, or for as long, as mature females. The weaning date for Steller sea lions is unknown but is assumed to be between 4 and 12 months, and most pups are weaned just before the next breeding season (11–12 months) (Porter, 1997). The change in diving characteristics that we report is interesting in that it coincides with this period. Prior to weaning these pups forage in the company of their mother and learn to forage on their own; the need to dive deep for long periods to acquire food is compensated by nursing from the mother. Once weaning

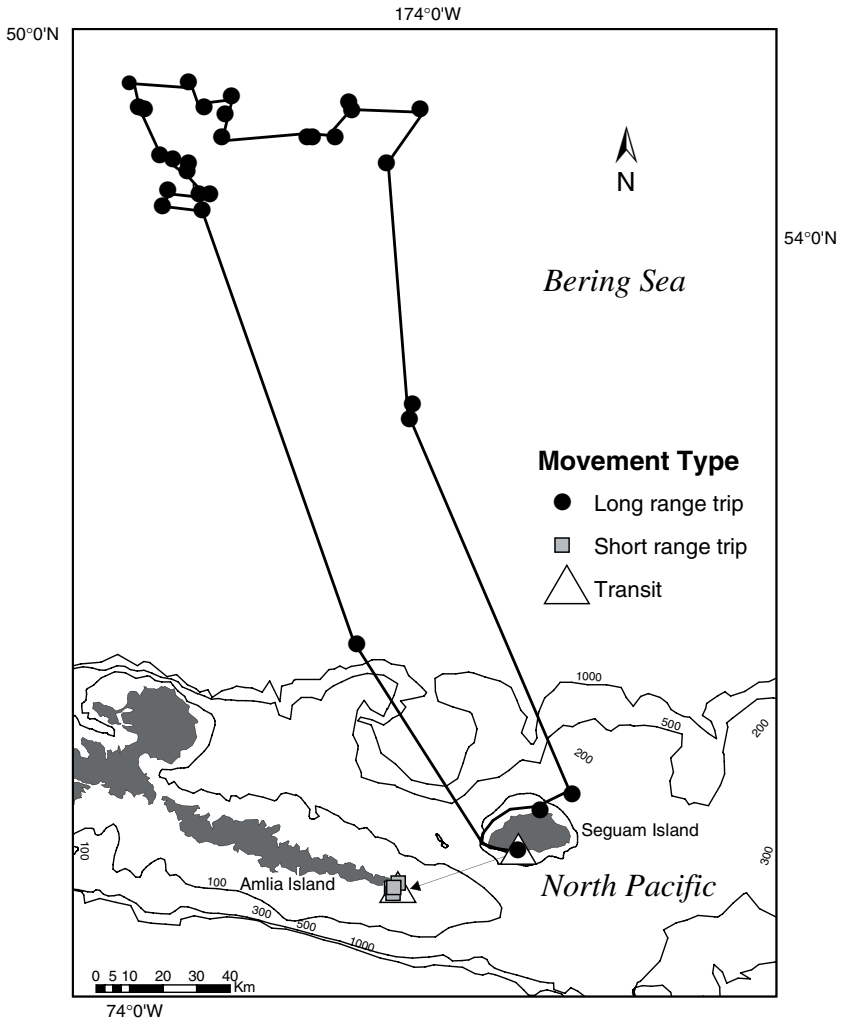

Figure 9

The three types of movement exhibited by two immature Steller sea lions captured at Turf Point, Seguam Island, Alaska, in 2000. A long-range trip (solid circles) >200 km is shown for PTT 14163 as it left and returned to Turf Point. A transit trip (open triangles) for PTT 14111 is shown as it left Turf Point and remained at the east end of Amlia Island where it went on numerous short-range trips (shaded squares).

occurs, the yearlings are forced to explore more areas to acquire food for needed energy. Dives become deeper and longer as these yearlings forage at different depths within the water column. Just before their first birthday, many of these young sea lions are capable of diving to the same depths and for the same duration as those of many adults; they also begin to forage at greater distances and for longer periods. Juveniles that we studied had a mean dive depth of 18.4 m and dive duration of 1.1 min compared to adult females in Alaska that had a mean dive depth of 21 m and dive duration of 1.4 min (Merrick and Loughlin, 1997). Maximum depth in our study was 328 m for a Washington juvenile and 288 m for an Alaska juvenile. Maximum depth information for adult females in Alaska was not provided by the instruments used by Merrick and Loughlin (1997); their maximum depths were characterized by bin data only. They showed that about 5% of dives by adult females in winter were greater than 250 m. In another study, adult females in Alaska were equipped with early-style SLTDRs that had features that recorded time-depth information and these SLTDRs showed that the females frequently dived to 200 m or more (Merrick et al., 1994).

Schreer and Kovacs (1997) summarized maximum dive depth and dive duration for air-breathing vertebrates and developed predictive allometric equations for both parameters based on body mass. We fitted our Steller sea lion body mass data to these equations to estimate maximum dive depth ($27.33M_b^{0.46}$), where M_b represents body mass in kilograms, and maximum dive duration ($6.22M_b^{0.10}$). We found that the maximum dive depth equation provided reasonably close estimates but that dive durations were typically overestimated (Table 3). In some cases measured and

Table 3

The recorded mass, recorded maximum dive depth, and recorded maximum dive duration for individual young Steller sea lions in Alaska and Washington from this study and the estimated maximum dive depth ($27.33M_b^{0.46}$) and estimate maximum dive duration ($6.22\ M_b^{0.1}$) based on allometric equations in Schreer and Kovacs (1997). PTT number is the satellite transmitter identification number. Est.= estimated. n/a = no data obtained.

PTT number	Mass (kg)	Maximum depth (m)	Est. maximum depth (m)	Maximum duration (min)	Est. maximum duration (min)
14073	86.26	168	212.38	>6	9.71
14084	77.18	288	201.79	>6	9.61
14085	154.36	280	277.57	>6	10.30
14087	122.45	256	249.52	>6	10.06
14089	111.11	200	238.61	4–6	9.96
21103	139.23	256	264.70	13	10.19
21106	143.31	328	268.24	>14	10.22
14071	92.00	12	218.77	2–3	9.78
14074	79.80	20	204.91	>6	9.64
14077	n/a	144	n/a	>6	n/a
14078	n/a	288	n/a	>6	n/a
14079	94.90	44	221.91	>6	9.81
14080	106.20	24	233.70	> 6	9.92
14170	Est. 95–105	180	Est. 222.02–232.48	> 14	Est. 9.81–9.91
21094	62.20	152	182.72	>14	9.40
14076	103.70	144	231.15	>6	9.89
14081	n/a	20	n/a	>6	n/a
14072	116.10	100	243.48	>6	10.01
14075	104.00	12	231.46	>6	9.90
14164	79.60	60	204.67	>14	9.64
14167	100.20	60	227.53	3–4	9.86
14111	87.00	40	213.22	8–9	9.72
14114	85.80	16	211.86	7–8	9.71
14116	76.20	40	200.60	5–6	9.59
14163	109.00	252	236.51	>14	9.94

estimated maximum dive depth values differed by large amounts (e.g. sea lion PTT 14071), perhaps because the deployment period was brief, before deep dives occurred. For others (e.g. PTT 14074) the difference may have been due to the young animal's continued dependence on the female for nourishment; deeper dives do not occur until weaning. In addition, we note that our dive duration data were stored in bins of 1-min intervals (from 1 to 6 min in the early instruments and from 1 to 14 min in the recent ones); the exact duration of each dive is unknown.

Movement patterns also suggest that the swimming ability of juvenile sea lions is comparable to that of adults. It is not unusual for young sea lions to travel distances as great as 1784 km from the natal rookery; as they approach adulthood they generally remain within 500 km of their natal rookery (Raum-Suryan et al., 2002). In our study some young sea lions traveled several hundred kilometers between sites while presumably searching for food or venturing from the natal rookery site.

Further analysis of our SDR data is warranted to more fully understand sea lion diving behavior and its relationships with oceanographic parameters, daily and season change, and behavioral features as discussed by Fedak et al. (2001). The time allocation at depth (TAD) index described by them will be a useful method for interpretation of our SDR (and TDR) data. Further analysis of our SDR data is needed to determine if such a study is possible.

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