

Ontogeny of dive performance in pup and juvenile Steller sea lions in Alaska

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Abstract: Development of competent diving ability is critical to obtaining nutritional independence in marine mammals such as Steller sea lions (SSLs), *Eumetopias jubatus* (Schreber, 1776). We studied diving performance in pup (75) and juvenile (36) SSLs using satellite data recorders. In general, dives by SSLs were brief and shallow. Overall, 82.3% of dives were <2 min long and 86.9% of dives were <10 m deep. Long (>5 min) and deep dives (>100 m) constituted only 2.49% and 0.77%, respectively, of total dives. We used linear mixed-effects models to investigate the relationships between the response variables maximum-daily-depth, time-at-depth, mean-dive-duration, dive rate, and time-at-sea and the predictor variables age, sex, population (eastern and western Alaska populations), time-of-day, and month-of-year. All response variables except dive rate were positively related ($P < 0.05$) to age. Dive rate declined ($P < 0.001$) with age. Time-of-day, month, population, sex, and some first-order interactions were all significantly ($P < 0.05$) related to some measure of diving performance. With large samples we were able to identify significant relationships between the response variables and the predictor variables, even though the total amount of variation explained by the models was low, because most dives were short and shallow regardless of age, sex, population, time-of-day, or month-of-year. Depths and durations of dives by juvenile animals increased throughout the range of ages studied and were similar to or greater than those previously reported for juveniles and adult females. We expect maximum depths and durations to continue to increase with age until body mass plateaus at about 10 years of age. Therefore, we expect older animals to be more efficient foragers, as they would have greater aerobic dive limits as well as more experience locating and capturing prey.

Résumé : L'acquisition de la compétence dans la capacité de plongée est une étape cruciale vers l'indépendance alimentaire chez les mammifères marins tels que les lions de mer de Steller (SSL) (*Eumetopias jubatus* (Schreber, 1776)). Nous avons étudié la performance de plongée chez des petits (75) et des jeunes (36) SSL à l'aide d'enregistreurs de données reliés à des satellites. Les plongées des SSL sont en général de courte durée et de faible profondeur. Au total, 82,3 % des plongées durent <2 min et 86,9 % d'entre elles atteignent <10 m. Les plongées prolongées (>5 min) et profondes (>100 m) représentent respectivement 2,49 % et 0,77 % de l'ensemble des plongées. Des modèles linéaires à effets mixtes nous ont servi à analyser les relations entre les variables dépendantes (profondeur maximale journalière, temps en fonction de la profondeur, durée moyenne de plongée, taux de plongée et temps passé en mer) et les variables prédictives (âge, sexe, population (de l'est ou de l'ouest de l'Alaska), heure du jour et mois de l'année). Toutes les variables dépendantes, à l'exception du taux de plongée, sont en corrélation positive ($P < 0,005$) avec l'âge. La fréquence des plongées diminue ($P < 0,001$) en fonction de l'âge. L'heure du jour, le mois, la population, le sexe et quelques interactions de premier degré entre ces variables sont tous reliés de façon significative ($P < 0,05$) à une mesure quelconque de la performance de plongée. Dans les grands échantillons, il est possible d'identifier des relations significatives entre les variables dépendantes et les variables prédictives, bien que la fraction de la variation expliquée par les modèles soit faible parce que la plupart des plongées sont courtes et peu profondes, quels que soient l'âge, le sexe, la population, l'heure ou le mois. La profondeur et la durée des plongées des jeunes animaux augmentent en fonction directe des différents âges retenus dans notre étude; elles sont de même ordre ou plus élevées que celles signalées antérieurement chez les jeunes et les femelles adultes. Nous prévoyons que la profondeur maximale et la durée continuent

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à croître en fonction de l'âge jusqu'à ce que la masse corporelle atteigne un plateau vers l'âge de 10 ans. Nous nous attendons donc à ce que les animaux plus âgés recherchent leur nourriture de façon plus efficace puisqu'ils possèdent des limites aérobies de plongée plus importantes, ainsi qu'une expérience plus grande pour trouver et capturer leurs proies.

[Traduit par la Rédaction]

Introduction

The development of diving ability plays a major role in determining at what age a young pinniped can successfully forage and survive independently (Horning and Trillmich 1997). Diving ability may be a particularly important determinant of survival and (or) age of nutritional independence (weaning) during periods when prey abundance is low or when prey are dispersed or found deep in the water column (Trillmich and Limberger 1985; Merrick and Loughlin 1997). Knowledge of the progression of diving ability in relation to age is important in understanding the weaning and independent foraging strategies of pinnipeds. Nutritional independence of young at an early age will, in general, enhance population productivity because females can produce more offspring during their lifetime, while delayed weaning may increase survival of young (Pitcher et al. 1998) but decrease female productivity. Greater diving ability results in greater flexibility in exploiting various prey resources, thereby enhancing survival independent of maternal support.

Diving performance is constrained primarily by the ability to store oxygen in blood and muscle, metabolic rate, ability to metabolize aerobically, and locomotive efficiency while diving (Burns and Castellini 1996; Boyd 1997; Schreer and Kovacs 1997; Williams et al. 2000; Kanatous et al. 2002). Increasing body mass (with increasing age) provides a metabolic advantage, as oxygen storage in blood and muscle increases linearly with body mass while mass-specific metabolic rate increases only with body mass^{0.75} (Schreer and Kovacs 1997). The oxygen-carrying capacity of blood and muscle also increases with age, independently of mass, in young animals (Richmond 2004).

Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) (SSLs) are the largest otariid and would therefore be expected to have the ability to dive longer and deeper than other otariids. By 1 year of age, SSLs are larger than adult females of many otariid species (Schreer and Kovacs 1997; Winship et al. 2001). The increased oxygen stores and lower metabolic rates afforded by increased body mass primarily increase dive duration or the amount of time that can be spent under water without entering an anaerobic metabolic state (Burns et al. 1997). In general, increased dive duration is positively correlated with dive depth, as it provides more time to reach depth (Feldkamp et al. 1989; Horning and Trillmich 1997; Costa and Gales 2003).

SSLs are completely terrestrial for the first 2–3 weeks of their lives and then rapidly transition to an amphibious mode (Sandegren 1970). By 0.2 years of age they are well adapted to aquatic life and have been observed to disperse to haul-outs up to 120 km from their natal rookery (Raum-Suryan et al. 2004). SSLs and some other otariid pinnipeds have extended and variable periods (117 to 540 days) of energetic dependence on their mothers (Boness and Bowen 1996). Weaning occurs for many young SSLs around 1 year of age, although observations have frequently been made of suck-

ling animals in their second and even third year of life (Pitcher and Calkins 1981; Trites and Porter 2002; Alaska Department of Fish and Game, unpublished data). Little is known about the transition to energetic independence in young SSLs and whether weaning is a gradual or abrupt process.

The ontogeny of diving performance of SSLs is of particular interest because of the major decline of the genetically distinct (Bickham et al. 1996) western Alaskan population (animals born on rookeries from Prince William Sound west through the Aleutian Islands) that resulted in its “endangered” status. The cause(s) of this decline is unknown, although there were indications that suboptimal nutritional status may have played a role during at least a portion of the decline (Calkins et al. 1998; Pitcher et al. 1998). York (1994) and Pascual and Adkison (1994) concluded that chronically low juvenile survival was likely a primary driver in this decline. Additionally, Merrick (1995) and Merrick and Loughlin (1997) hypothesized that young animals are more vulnerable than adults to changes in prey distribution (e.g., a reduction in prey abundance in the upper water column) because of extended development of diving performance.

In contrast to the western population, SSLs in Southeast Alaska, which belong to the eastern population, have more than doubled in number since the late 1970s and are thought to be at a historically high level (Calkins et al. 1999; Alaska Department of Fish and Game, unpublished data). This provided an opportunity to compare the diving performance of young SSLs from two populations with contrasting population trajectories. Indications that animals from the western population were “working harder” at diving than those in the eastern population could be taken as support for the hypothesis that food limitation of pups and (or) juveniles was a factor in the decline of the western population at the time of this study.

Our primary objective was to document the ontogeny of diving performance in pup (<1 year of age) and juvenile (1–3 years of age) SSLs through the use of satellite data recorders (SDRs; Wildlife Computers, Inc., Redmond, Washington). We also evaluated the effects of gender, time of day, month of year, body mass, and population on various measures of diving performance. Finally, we evaluated the hypothesis that young SSLs may be particularly vulnerable to reductions of prey in shallow water because of limited diving ability (Merrick 1995; Merrick and Loughlin 1997). Data on dispersal, movement patterns, and haul-out use from a subset of these instrumented animals were reported in Raum-Suryan et al. (2004).

Methods

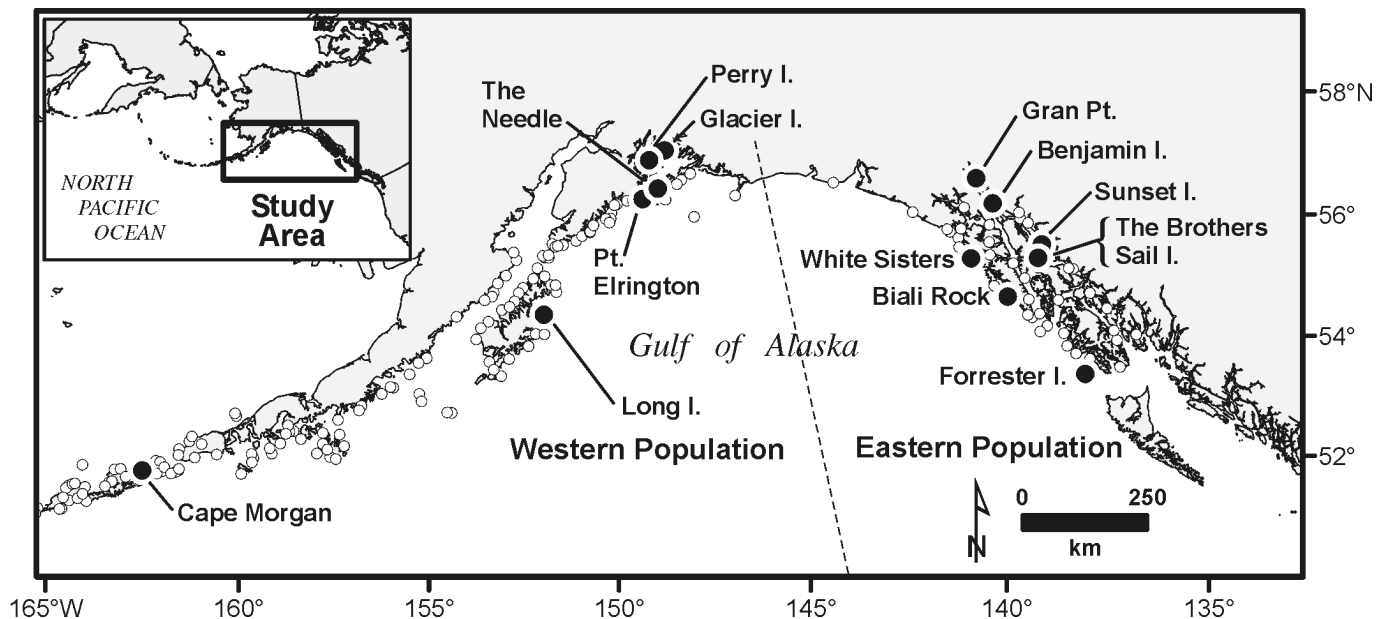
Captures and processing

We captured pup and juvenile SSLs by underwater noosing with SCUBA and with hoop nets on haul-outs and rookeries (Raum-Suryan et al. 2004). They were then immobilized

Table 1. Deployment of satellite data recorders (SDRs) on male (M) and female (F) Steller sea lion (*Eumetopias jubatus*) pups (0.13–0.92 years old) and juveniles (1.21–2.92 years old) in the western and eastern populations of Alaska (SEA, Southeast Alaska).

Region	Month of capture	No. of SDRs				Deployment duration (days) (mean (range))
		Pups		Juveniles		
		M	F	M	F	
Western population						
Prince William Sound	Apr. 2000	4	4	0	2	46.9 (10–77)
Prince William Sound	Aug. 2000	0	0	1	3	67.8 (51–103)
Kodiak Island	Mar. 2001	1	2	0	0	87.7 (59–106)
E. Aleutian Islands	Sept. 2001	0	2	0	0	29.0 (29)
Prince William Sound	Nov. 2001	1	4	3	2	110.8 (36–144)
Eastern population						
Central SEA	Mar. 1998	7	5	0	0	81.8 (30–143)
Southern SEA	July 1998	3	7	0	0	21.3 (11–34)
Northern SEA	Nov. 1998	5	5	0	0	44.7 (12–119)
Central SEA	Aug. 1999	4	6	0	0	5.7 (3–13)
Northern SEA	Jan. 2000	2	5	2	1	101.1 (60–181)
Central SEA	Sept. 2000	0	0	3	2	143.6 (82–190)
Central and northern SEA	May 2001	4	4	4	2	59.5 (25–91)
Central SEA	Aug. 2001	0	0	2	1	109.3 (68–184)
Central SEA	Nov. 2002	—	—	6	2	179.8 (91–252)

Fig. 1. Map of study area in Alaska showing division between eastern and western populations (dashed line) and sites (named locations) where pup and juvenile Steller sea lions (*Eumetopias jubatus*) were captured for this study. Open circles show locations of rookeries and haul-outs within the study area.



with gas anesthetic (Heath et al. 1997). Except for young pups, whose age was obvious, we estimated age from tooth eruption patterns and canine tooth length, a technique verified by examination of the teeth of 26 known-aged animals between the ages of 0.21 and 1.92 years. We attached SDRs with fast-drying epoxy to the pelage along the midline of the back of 75 pup (0.13–0.92 years) and 36 juvenile (1.21–2.92 years) SSLs captured from the eastern and western populations in Alaska between March 1998 and November 2002

(Table 1, Fig. 1). All research conformed to the guidelines of the Alaska Department of Fish and Game Animal Care and Use Committee (03-0002). These guidelines meet the principles and guidelines of the Canadian Council on Animal Care.

Satellite data recorders

SDRs, which have been used for numerous studies of diving animals, store and transmit dive data summaries (histo-

grams) to satellites, where they are processed through Argos (Stewart et al. 1989; Merrick et al. 1994; Burns and Castellini 1998; Loughlin et al. 2003). The SDRs used in this study recorded depth every 10 s from a pressure transducer and immersion status (submerged or dry) every 10 s from a conductivity sensor. The sampling rate of the conductivity sensors increased progressively to every 0.25 s as they approached the surface of the water. Data were summarized during four daily 6-h periods (night, 21:00–02:59:59; morning, 03:00–08:59:59; midday, 09:00–14:59:59; and evening, 15:00–20:59:59) and repeatedly transmitted to the Argos satellite system during the subsequent 24 h.

Over the course of this project, we modified SDR type and programming as technology improved, as we became more familiar with juvenile SSL behavior, and to permit data interchange with other SSL diving research projects. Three models of Wildlife Computers SDRs were used — ST-6, ST-10, and T-16 — which differed primarily in physical size, transmission output power (0.25–1.0 W), and expected battery lifetime (20 000 – 60 000 transmissions). Early SDRs (deployed March 1998 – September 2000, $n = 71$) were programmed to record individual dives reaching a minimum 2-m threshold, at 1 m resolution, with a maximum depth limit of 225–245 m (variable by individual SDR). Forty-seven were programmed to transmit on alternate days; the remainder transmitted daily. Later SDRs (deployed March 2001 – November 2002, $n = 40$) recorded individual dives reaching a minimum 4-m threshold, at 2 m resolution, with a maximum depth limit of 490 m, and all transmitted daily. Dive-depth histograms from the different SDR programs were standardized by discarding dives with maximum depth <4 m and combining bins, where necessary, to yield nine common bins.

We limited the dive data set to those values reporting behavior between SDR deployment and SDR failure. We conservatively identified SDR failure as complete data loss during active diving deeper than 10 m (suggesting technical failure or loss at sea), termination of regular data reception followed by sporadic dives deeper than 10 m (suggesting the SDR was attached to a live animal but suffered technical failure), or a period of shallow diving followed by complete data loss (suggesting either an SDR shed onto the intertidal zone or an animal's final haul-out before tag failure). SDRs operated for a mean of 72 days ($SD = 58$, range = 2–252, $n = 111$). Data from pups <0.4 years of age and juveniles 1.2–1.4 years of age were limited because of instrument loss during the annual molting period (August through November).

The basic measures obtained were as follows. (i) Maximum-daily-depth was the maximum depth recorded for an instrumented animal during a 24-h period. (ii) Time-at-depth was the number of minutes per 6-h period a sea lion spent diving below 4 m, using only those periods when the animal was at sea. (iii) Mean-dive-duration was the time spent diving below 4 m divided by the number of dives and was computed for each 6-h period an animal was at sea. (iv) Dive rate was the number of dives below 4 m per hour while the animal was at sea. (v) Time-at-sea was the number of hours per day an animal spent in the ocean versus being hauled out, using only those records that provided complete 24-h coverage.

Measurements of maximum-daily-depth (4795 observations), time-at-depth (21 020 observations), and time-at-sea

(21 020 observations) were obtained from all instrumented animals. Mean-dive-duration (11 301 observations) and dive rate (7477 observations) were limited to a subset of 32 animals because these measures were sensitive to differences in minimum dive-depth thresholds (2 or 4 m) among the different SDR programs (Table 1). None of the animals dove to maximum depths approaching the programmed limit of their SDR; therefore, the differences in programming for maximum depth were not critical.

Analysis

We used linear mixed-effects models (Littell et al. 1996) to investigate the relationships between the response variables (maximum-daily-depth, time-at-depth, mean-dive-duration, dive rate, and time-at-sea) and the predictor variables age, gender, population (eastern and western Alaska), and month-of-year. We added mass-at-capture to the maximum-daily-depth analysis to evaluate whether mass had an additional effect beyond age. Time-of-day (by 6-h period) was added as a predictor variable for analysis of time-at-depth and time-at-sea, for which we had a sufficiently large sample to evaluate the interactions with month-of-year and population. We used the natural logarithms of the response variables and the natural logarithm of age in all analyses. This ln-ln analysis assumed an underlying nonlinear relationship of the form $y = B_0(x^{B_1})$, where y is the response variable, x is the predictor, and B_0 and B_1 are the regression coefficients. This transformation yielded more symmetric residuals but had the effect of predicting a geometric mean response instead of an arithmetic mean response. We included ln(age), sex, population, month-of-year, time-of-day (when appropriate), and their two- and three-way interactions in the models as fixed effects; interactions containing ln(age) \times month were not included because age and month are confounded within animals. To account for the potential lack of independence of observations caused by using repeated responses from individual animals, animal ID was included as a random effect in the analyses. Therefore, variation among animals rather than variation among observations was used in computing standard errors of estimates (Littell et al. 1996). Autocorrelation of residuals within animals was modeled as a spatial process with the “distance” between observations a function of elapsed time (Littell et al. 1996). In some analyses, the autocorrelation was estimated to be 0; for these we included only the animal random effect. Initially, we included all predictor variables in the models and eliminated predictors one at a time based on Wald F statistics. We continued this process until only important (Wald P value <0.05) predictors remained. Lower order effects (i.e., main effects) with larger P values were retained in final models when they were contained in higher order interactions that had P values <0.05. Least-squares marginal means (Littell et al. 1996) were estimated for categorical effects retained in final models. Estimated geometric means and their confidence intervals were transformed back to the original response scale. To illustrate the proportion of variation explained by our regression models, we computed a generalization of the R^2 statistic (R^2_g). This generalization uses a deviance-based approach and has advantages over other proposed generalized R^2 measures (e.g., C^2 ; Cox and Snell 1989, pp. 208–209) (Ver Hoef 2003). Partial R^2_g is based on

Table 2. Summary of linear mixed-effects model used to investigate the relationships between maximum-daily-depth and age (ln-transformed), sex, population, month-of-year, and their interactions.

Effect	df	<i>F</i>	<i>P</i>	Partial R^2_g
Retained				
Age	1,159	48.33	<0.0001	0.071
Population	1,165	5.73	0.0178	0.027
Month-of-year	11,734	2.75	0.0017	0.026
Sex	1,160	3.59	0.0599	0.008
Population × month-of-year	11,734	2.71	0.0020	
Age × population	1,159	7.11	0.0085	
Sex × population	1,160	6.06	0.0149	
Age × sex	1,156	3.96	0.0482	
Removed				
Sex × month-of-year	11,690	1.36	0.1880	

Note: Presented are main effects and two-way interactions retained and those removed from the final model. Three-way interactions are not shown. The R^2_g for the complete model is 0.083. Partial R^2_g values are for the main effect and all interactions containing that effect.

Fig. 2. Maximum-daily-depth predicted by age using a linear mixed-effects model with sex (solid line, female; dashed line, male) and population (plot a, western population; plot b, eastern population) as factors. Actual data points from which predictions were computed are indicated by open circles.

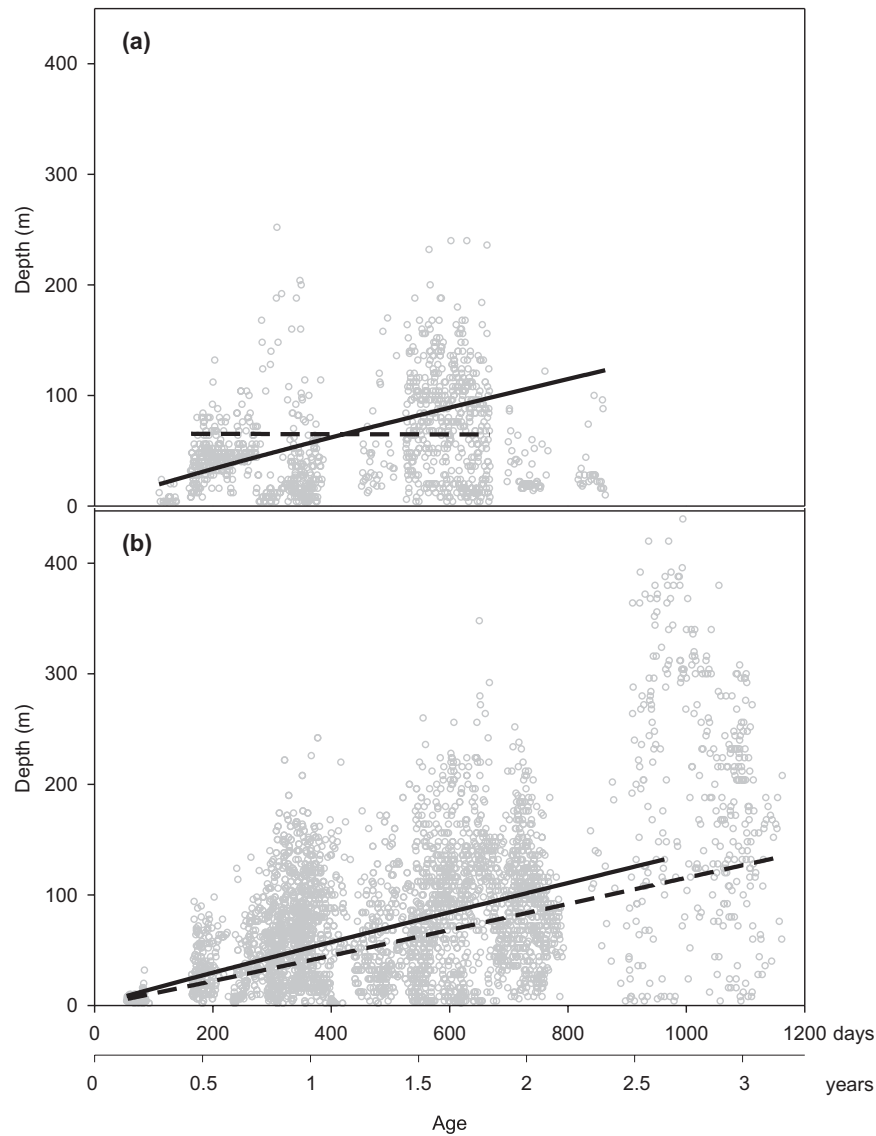
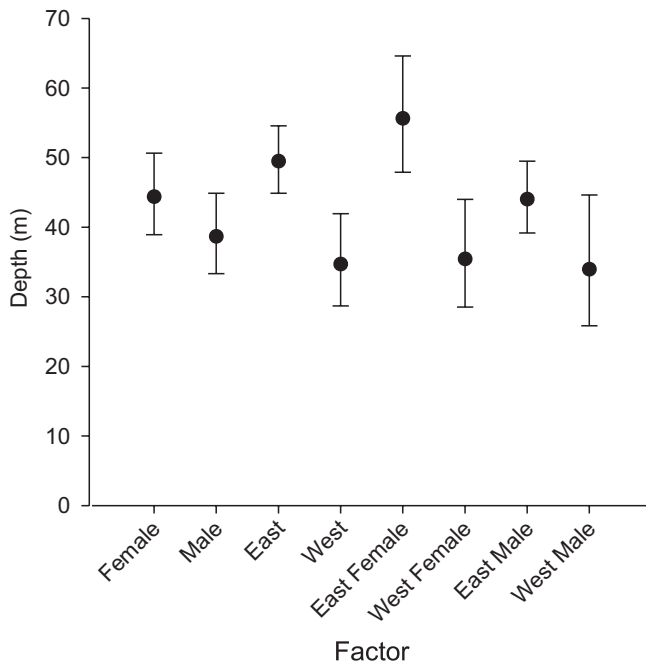


Fig. 3. Least-squares geometric means with 95% confidence intervals for maximum-daily-depth by sex and population. The graph is based on simplified analysis with some interactions omitted to illustrate relationships between maximum-daily-depth, gender, and population.



the same approach (G.W. Pendleton, unpublished). R^2_g is interpreted in the same way as the standard R^2 statistic.

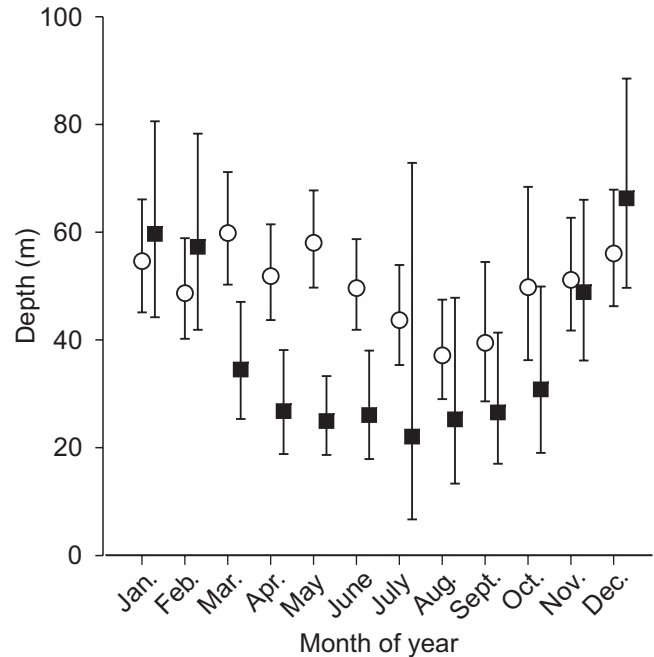
In addition to model results, we examined maximum values for each measure of diving performance. Maximum values provide more information about physiological limits than do mean values (Horning and Trillmich 1997).

Results

Dives made by young SSLs were predominately short and shallow; 82.3% of dives were <2 min and 86.9% of dives were <10 m. Long (>5 min) and deep dives (>100 m) constituted only 2.49% and 0.77%, respectively, of total dives. The maximum depth recorded for a pup was 252 m, logged by a 0.8-year-old male. The maximum depth recorded for any animal in this study was 452 m, logged by a 2.6-year-old male. The maximum mean-dive-duration for a 6-h bin was 6.43 min ($n = 41$ dives), logged by a 2.7-year-old male. Even for our oldest animal, a male estimated to be 2.9–3.2 years of age while instrumented, 80% of dives were <20 m and 81% were <2 min.

Maximum-daily-depth was affected most strongly by age (Table 2). By 0.5 years of age, young SSLs were diving to nearly 100 m, and by 1 year of age, to about 200 m; by 3 years of age, maximum depths exceeded 400 m (Fig. 2). The relationships between geometric mean maximum-daily-depth, age, sex, month, and population were complex (Table 2, Figs. 3, 4). Females appeared, on average, to dive deeper than males ($P = 0.0599$). This was particularly apparent in the east, as indicated by the significant sex \times population interaction ($P = 0.0149$) (note that the number of observations for older animals was much greater in the east-

Fig. 4. Least-squares geometric means with 95% confidence intervals for maximum-daily-depth by month for eastern and western populations. Open circles represent the eastern population and solid squares represent the western population. The graph is based on simplified analysis with some interactions omitted to illustrate relationships between maximum-daily-depth, month, and population.



ern population). The difference between males and females appeared to increase with age (age \times sex interaction, $P = 0.0482$), at least in the east (Fig. 2). Geometric mean maximum-daily-depth was greater in the east than in the west (Table 2, Fig. 3). Month-of-year had a profound effect on geometric mean maximum-daily-depth in both the eastern and western populations, with deeper diving during winter than during summer (Fig. 4). While present in both populations, the seasonal effect was more pronounced in the west (strong month \times population interaction, $P = 0.002$). On average, diving was deepest for both populations from November through February, with a more pronounced pattern for the west (Fig. 4).

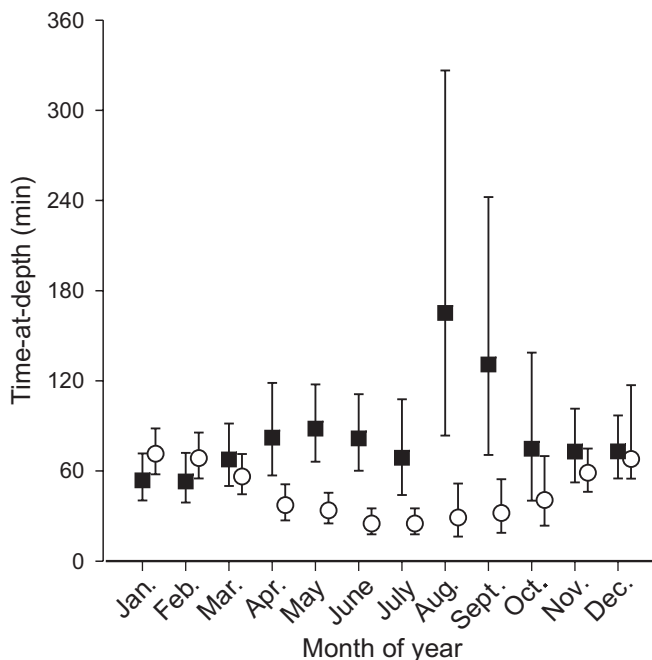
Because larger animals generally have greater aerobic dive capacity (Schreer and Kovacs 1997), we included mass-at-capture as an explanatory variable, in addition to $\ln(\text{age})$, in the analysis of maximum-daily-depth. Initially, we included mass and its interactions with sex and population. When $\ln(\text{age})$ was in the model, neither mass nor any of its interactions were important ($P > 0.14$) predictors of the geometric mean maximum-daily-depth. However, mass was significant ($P < 0.05$) when $\ln(\text{age})$ was omitted. We attribute the lack of a relationship between maximum-daily-depth and mass to the strong correlation ($r^2 = 0.62$) between mass-at-capture and $\ln(\text{age})$. For our data, $\ln(\text{age})$ and mass essentially contained the same information and we chose to retain $\ln(\text{age})$ in the analyses and omit mass. It is possible that larger animals at a given age would be able to dive deeper than smaller animals of the same age, but we were unable to detect such patterns in our data.

Table 3. Summary of linear mixed-effects model used to investigate the relationships between time-at-depth (time spent below 4 m while at sea) and age (ln-transformed), sex, population, month-of-year, time-of-day, and their interactions.

Effect	df	<i>F</i>	<i>P</i>	Partial R^2_g
Retained				
Time-of-day	3,7919	30.74	<0.0001	0.082
Month-of-year	11,238	2.48	0.0059	0.053
Population	1,71	0.03	0.8704	0.013
Sex	1,55	12.71	0.0007	0.009
Age	1,59	12.71	0.0007	0.002
Period × month-of-year	33,7669	7.89	<0.0001	
Population × time-of-day	3,7913	4.45	0.0040	
Sex × time-of-day	3,7584	2.40	0.0663	
Sex × month-of-year	11,194	1.00	0.4515	
Population × month-of-year	9,209	0.85	0.5717	
Removed				
Age × sex	1,56	2.61	0.1118	
Age × population	1,69	0.08	0.7721	
Sex × population	1,50	0.26	0.8003	

Note: Presented are main effects and two-way interactions retained and those removed from the final model. Three-way interactions are not shown. The R^2_g for the complete model was 0.089. Partial R^2_g values are for the main effect and all interactions containing that effect.

Fig. 5. Least-squares geometric means with 95% confidence intervals for time-at-depth by month during night (21:00–02:59) and the remainder of the day (03:00–20:59). Solid squares represent night and open circles represent the remainder of the day. The graph is based on simplified analysis with some interactions omitted to illustrate relationships between time-at-depth, time-of-day, and month.



Time-at-depth was affected by time-of-day, month-of-year, population, sex, and age (Table 3). Geometric mean time-at-depth was highest from November through March and lower from April through October during morning, mid-

day, and evening (Fig. 5). Time-at-depth at night was consistently high, with a geometric mean of 65.6 min per 6-h period throughout the year with no month effect ($P = 0.1110$). Geometric mean time-at-depth increased with age during all periods: evening, age ($P = 0.012$); morning, age × sex ($P = 0.014$); midday, age ($P = 0.0216$); evening, age ($P < 0.0001$). Time-at-depth seldom exceeded 250 min per 6-h period (Fig. 6), but this occurred occasionally for animals ranging from 0.5 to over 3 years of age.

Mean-dive-duration was most strongly affected by age and month-of-year (Table 4). Duration increased with age, with maximum mean durations reaching about 4 min by 1 year of age, 5 min by 2 years of age, and 6 min by 3 years of age (Fig. 7). Geometric mean-dive-duration was highest from December through March, lowest from June through August, and intermediate during the remaining months (Fig. 8). Population and sex and their interactions with age were significant (Table 5), indicating greater mean dive duration for males than for females and greater mean dive duration for SSLs from the eastern population than for those from the western population (Fig. 9). Because of the summary nature of the duration data, we cannot determine individual maximum dive durations; however, only 0.04% of recorded dives ($n = 692\,005$) were >12 min. Dives >12 min were made by 21 individuals (10 males and 11 females) between 0.5 and 3 years of age.

Dive rate decreased slightly with age (Table 5, Fig. 10). There was a pronounced seasonal pattern with a substantial increase in geometric mean dive rate from July through October, illustrated well for the eastern population, for which there was complete seasonal coverage (Fig. 11). The model (Table 5) indicated that geometric mean dive rates were different between sexes and between populations. Several interactions were significant, although the patterns were not readily apparent (perhaps lower diving rates for western ani-

Fig. 6. Time-at-depth predicted by age using a mixed-effects linear model with both sexes and populations combined. Actual data points from which predictions were computed are indicated by open circles.

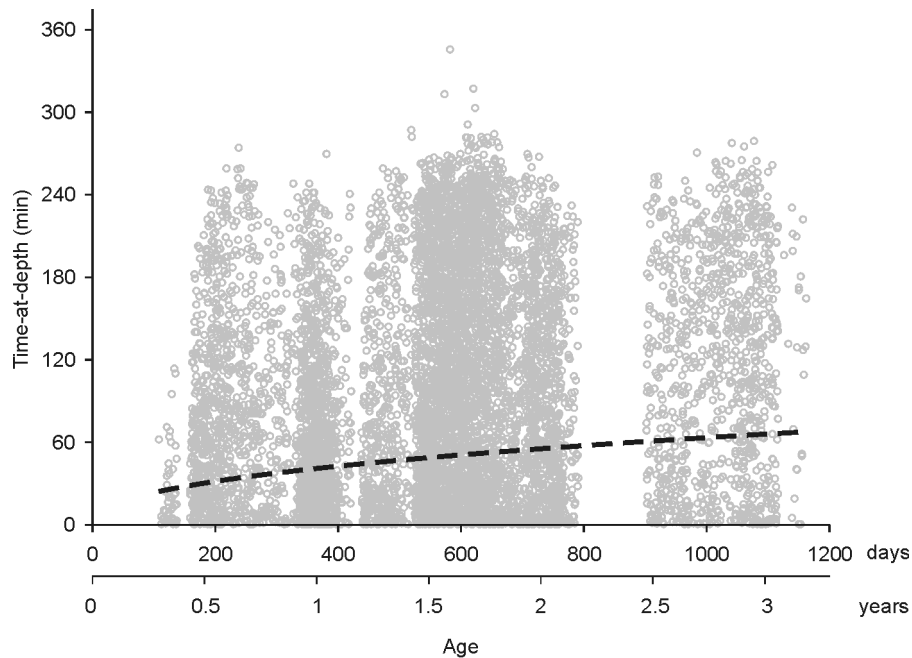


Table 4. Summary of linear mixed-effects model used to investigate the relationships between mean-dive-duration and age (ln-transformed), sex, population, month-of-year, and their interactions.

Effect	df	F	P	Partial R^2_g
Retained				
Month-of-year	11,362	3.31	0.0002	0.007
Age	1,73	22.71	<0.0001	0.005
Population	1,165	5.73	0.0303	0.001
Sex	1,73	4.45	0.0384	0.001
Age × population	1,72	4.32	0.0413	
Age × sex	1,72	4.27	0.0423	
Removed				
Population × month-of-year	9,285	1.33	0.2201	
Sex × month-of-year	11,357	0.91	0.5350	
Sex × population	1,63	0.12	0.7336	

Note: Presented are main effects and two-way interactions retained and those removed from the final model. Three-way interactions are not shown. The R^2_g for the model was 0.012. Partial R^2_g values are for the main effect and all interactions containing that effect.

mals in spring and fall), probably because of incomplete seasonal coverage in the west and a lack of older female juveniles in the east.

Time-at-sea was affected mainly by time-of-day, month-of-year, and age (Table 6). There was a highly significant interaction between time-of-day and month-of-year (Table 6), with more time-at-sea occurring at night from April to September (Fig. 12). Geometric mean time-at-sea increased with age (Table 6, Fig. 13). While sex was not a significant main effect ($P = 0.1332$), females generally spent more time at sea (Fig. 13), and this was reflected in significant interactions between sex and population, between sex and time-of-day, and between sex and month (Table 7). On average, SSLs from the west appeared to spend slightly more time at sea ($P = 0.0469$) than those from the east, although seasonal coverage in the west was incomplete (Fig. 14). Animals

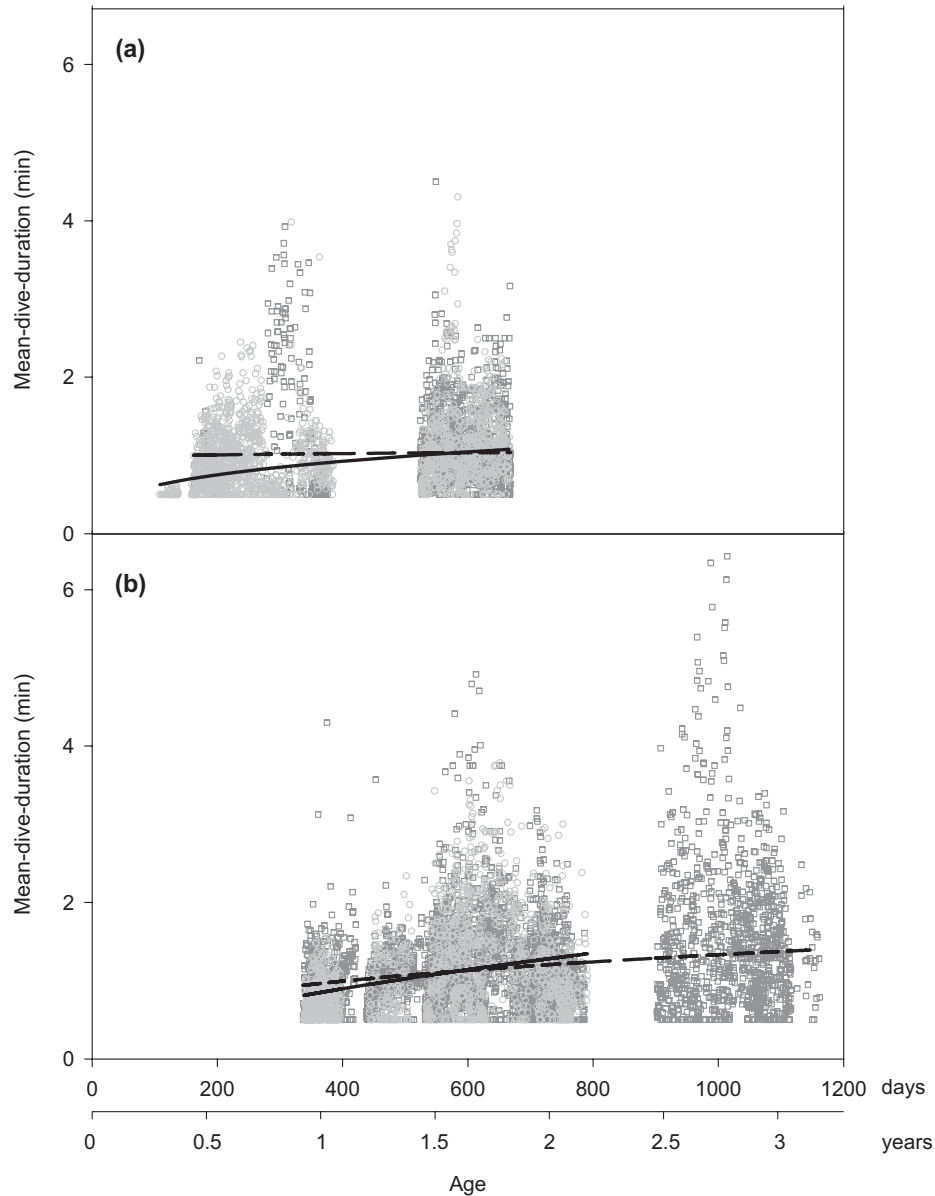
were spending up to the maximum of 6 h at sea per 6-h interval by about 0.25 years of age (Fig. 13).

Discussion

Analytical issues

Most dives by pup and juvenile SSLs were short and shallow regardless of age (0.15–3.18 years), and many were probably associated with activities such as traveling, playing, exploring, resting or sleeping, and social interactions (Burns et al. 1997), as well as foraging. Even during foraging, most dives may be well below the physiological capability of the individual (Feldkamp et al. 1989). Therefore, examination of maximum measures (Horning and Trillmich 1997), particularly of depth and duration, in conjunction with examination of relationships between mean values and

Fig. 7. Mean-dive-duration predicted by age using a mixed-effects linear model with sex (solid line, female; dashed line, male) and population (plot a, western population; plot b, eastern population) as factors. Actual data points from which predictions were computed are indicated by open circles for females and open squares for males.



age provides a more complete understanding of the ontogeny of diving performance.

The use of linear mixed-effects models for analysis of the development of diving performance is appropriate, but caution in interpretation is required. These models allow the identification and assignment of the relative importance of variables affecting diving performance, such as age, sex, and month-of-year, and elucidate their relationships. They accommodate different numbers of observations among individuals and repeated measures from different individuals with varying behavior, found to be important by Burns et al. (1997) for Weddell seals, *Leptonychotes weddellii* (Lesson, 1826). However, the combination of many dives well below physiological limits and the use of models that predict the geometric mean (i.e., ln-transformed response variables), which weight smaller values more heavily, tends to minimize div-

ing ability. Nevertheless, by combining model results with observations of maximum values for the various measures of diving performance, we obtained a relatively robust picture of the development of juvenile SSL diving ability.

The response variables we analyzed were not necessarily independent, both because of functional relationships between the responses and because they were collected simultaneously from the same animals. We examined the relationships between our response variables using linear regression between all pairs of ln-transformed responses. From the pairwise regressions, only time-at-depth and time-at-sea were strongly correlated, with an r^2 of 0.684 (Table 7). We found weaker relationships between mean-dive-duration and both time-at-depth and time-at-sea (which are themselves correlated) and between time-at-depth and dive rate (relationships that showed considerable variability). With some

Fig. 8. Least-squares geometric mean-dive-duration with 95% confidence intervals by month with sexes and populations combined. The graph is based on simplified analysis with some interactions omitted to illustrate the relationship between mean-dive-duration and month.

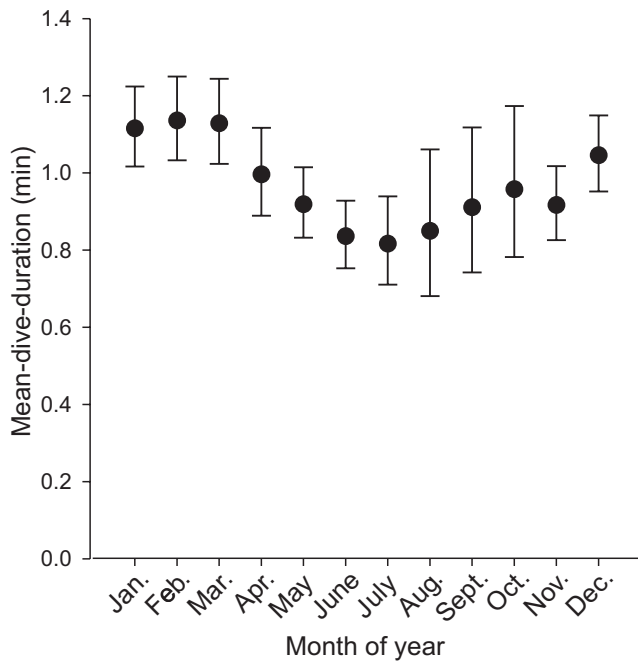


Fig. 9. Least-squares geometric means with 95% confidence intervals for mean-dive-duration by sex and population. The graph is based on simplified analysis with some interactions omitted to illustrate relationships between mean-dive-duration, gender, and population.

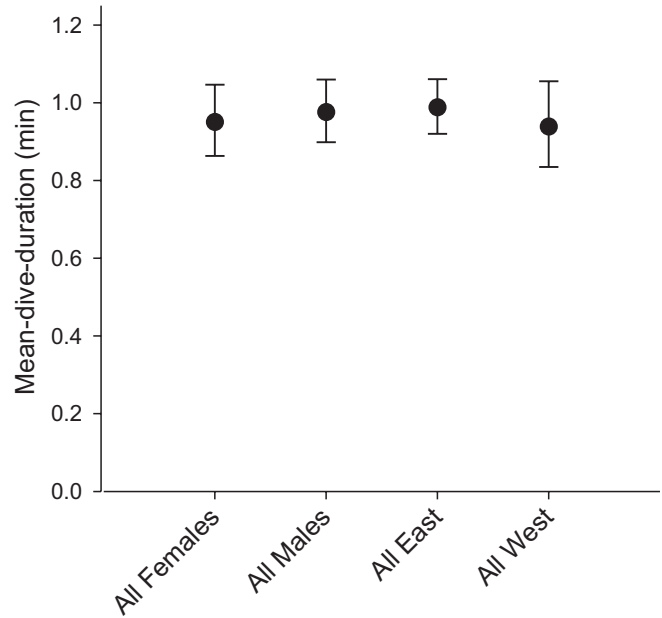


Table 5. Summary of linear-mixed effects model used to investigate the relationships between dive rate (no. of dives per hour while at sea) and age (ln-transformed), sex, population, month-of-year, and their interactions.

Effect	df	F	P	Partial R^2_g
Retained				
Month-of-year	11,891	4.12	<0.0001	0.011
Population	1,1496	15.0	0.0001	0.009
Age	1,1496	17.53	<0.0001	0.005
Sex	1,1412	7.72	0.0055	0.004
Population × month	9,748	4.46	<0.0001	
Age × population	1,1496	12.70	0.0004	
Sex × population	1,1412	7.32	0.0069	
Age × sex	1,1376	6.58	0.0104	
Removed				
Sex × month-of-year	11,931	1.49	0.1290	

Note: Presented are main effects and two-way interactions retained and those removed from the final model. Three-way interactions are not shown. The R^2_g for the model was 0.018. Partial R^2_g values are for the main effect and all interactions containing that effect.

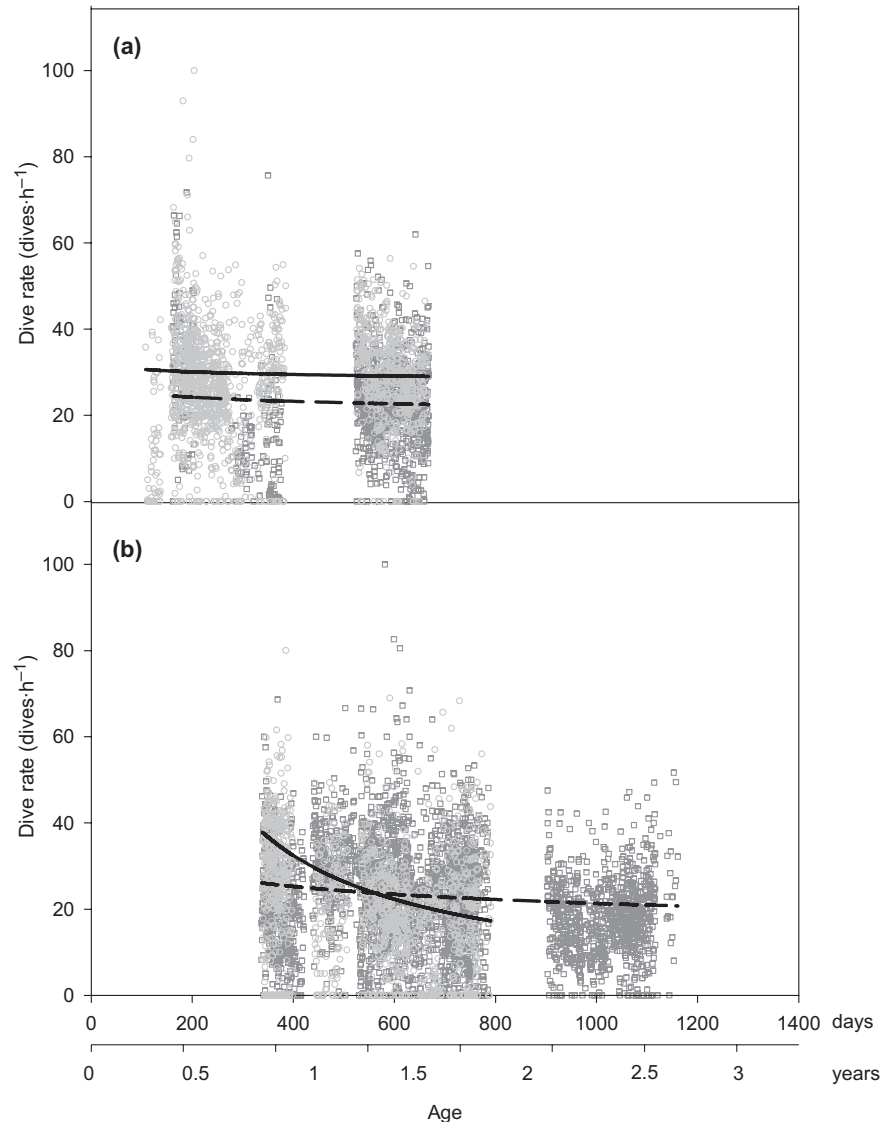
pairs of variables, the strongest pattern was an upper bound on one variable in relation to the other; for example, time-at-depth cannot exceed time-at-sea. This limiting structure often was not well represented by the pairwise correlations. Other studies have shown a high degree of correlation between depth and duration (Feldkamp et al. 1989; Horning and Trillmich 1997; Costa and Gales 2003). The r^2 between maximum-daily-depth and mean-dive-duration in this study was only 0.047 (Table 7). We suspect the reason for this low correlation was the fact that maximum-daily-depth (a single measurement for each day) was correlated with the average duration over the four 6-h periods for that day. If we had

been able to analyze depth and duration on the same scale, there would have undoubtedly been a much higher degree of correlation. Indeed, in a similar study using instruments that recorded both depth and duration for each dive, the two measures were highly correlated ($P < 0.001$), with an r^2 of 0.649 for pups and 0.826 for juvenile SSLs (Rehberg 2005).

Ontogeny of diving performance

In theory, maximum dive duration best reflects the relationship between diving ability and age (Burns et al. 1997) because the ability to stay submerged increases as body mass increases, providing both increased oxygen storage ca-

Fig. 10. Dive rate predicted by age using a linear mixed-effects model with sex (solid line, female; dashed line, male) and population (plot a, western population; plot b, eastern population) as factors. Actual data points from which predictions were computed are indicated by open circles for females and open squares for males.



pability and metabolic advantages. However, owing to the summary nature of dive duration data from SDRs, no information on the duration of individual dives was obtained. Also, as stated in the Methods, dive duration data were obtained from only 32 of 111 instrumented animals. Maximum-daily-depth was the only diving performance parameter obtained directly and is probably the most valuable for the analysis of dive ontogeny. It is the daily maximum of many dives and is most likely the closest approximation of the physiological abilities of an individual. As previously discussed, other studies have found a high correlation between depth and duration. The other measures of diving performance serve more as indices; however, their relationships with age provide insights into the ontogeny of diving performance.

As expected, age had a significant influence on all measures of diving performance (Fig. 15). Maximum-daily-depth and mean-dive-duration, in terms of both mean and

maximum measures, increased with age throughout the range of ages studied. By 0.5 years of age, young SSLs were diving to nearly 100 m and by 1 year of age, to about 200 m. By 3 years of age, maximum daily depths exceeded 400 m (Fig. 2). Maximum mean dive durations reached about 4 min by 1 year of age, 5 min by 2 years of age, and 6 min by 3 years of age (Fig. 7). By 1.5 years of age, juveniles of both sexes were capable of sustained periods of long dives. A male and a female of this age made about 50 dives in a 6-h period that averaged over 4 min. While mean time-at-depth and mean time-at-sea increased with age, near-maximum values were obtained between about 0.5 and 2 years of age (Fig. 15). Both mean and maximum dive rate declined with age (Fig. 10). This seems consistent because as the ability to dive longer develops, fewer dives would be necessary or even possible.

While significant relationships were found between age and all indicators of diving performance, only small propor-

Fig. 11. Least-squares geometric mean dive rate with 95% confidence intervals by month for Steller sea lions from the eastern population with sexes combined. The graph is based on simplified analysis with some interactions omitted to illustrate the relationship between dive rate and month.

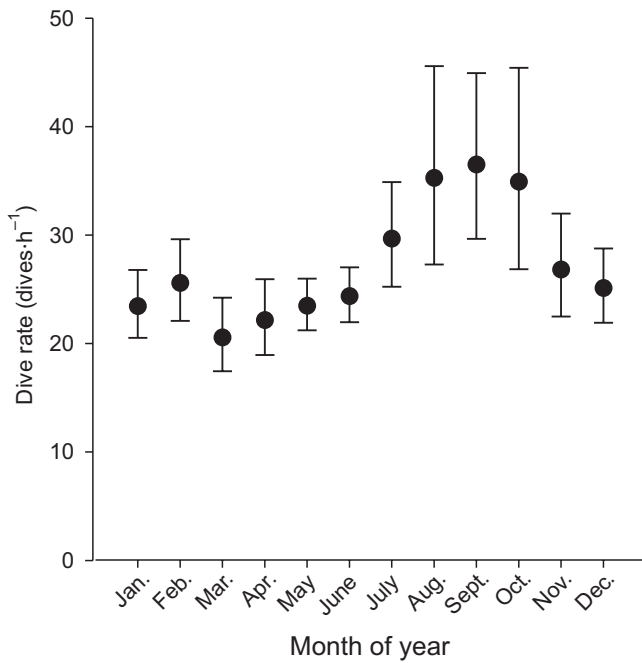


Fig. 12. Least-squares geometric means with 95% confidence intervals for time-at-sea by month during night (21:00–02:59) (solid squares) and the remainder of the day (03:00–20:59) (open circles). The graph is based on simplified analysis with some interactions omitted to illustrate relationships between time-at-sea, time-of-day, and month.

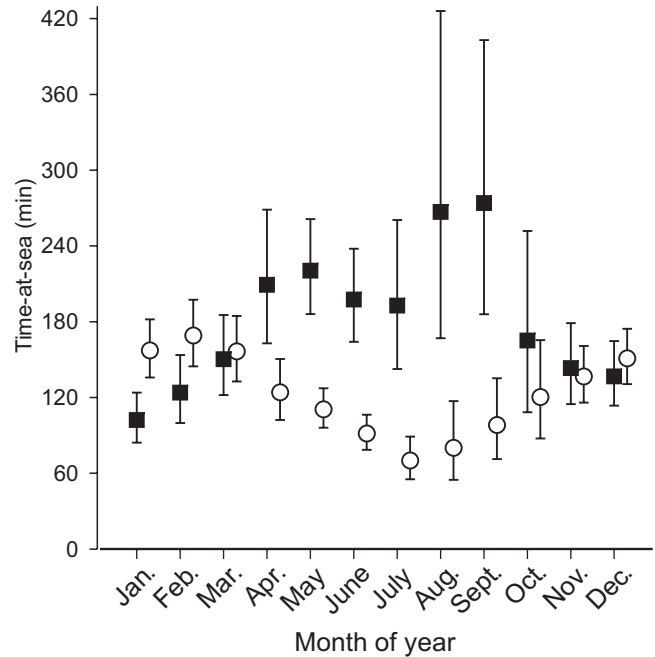


Table 6. Summary of linear mixed-effects model used to investigate the relationships between time spent at sea per 6-h period and age (ln-transformed), sex, population, month-of-year, time-of-day, and their interactions.

Effect	df	F	P	Partial R ² _g
Retained				
Month-of-year	11,596	3.26	0.0002	0.059
Time-of-day	3,7448	29.34	<0.0001	0.042
Population	1,53	4.14	0.0469	0.014
Sex	1,40	2.35	0.1332	0.008
Age	1,44	16.65	0.0002	0.004
Time-of-day × month-of-year	33,7445	8.43	<0.0001	
Sex × month-of-year	11,516	4.03	<0.0001	
Sex × population	1,40	6.05	0.0183	
Sex × time-of-day	3,7443	2.88	0.0345	
Population × time-of-day	3,7447	1.27	0.2841	
Removed				
Age × sex	1,46	2.37	0.1307	
Age × population	1,49	2.34	0.1322	

Note: Presented are main effects and two-way interactions retained and those removed from the final model. Three-way interactions are not shown. The R²_g for the model was 0.085. Partial R²_g values are for the main effect and all interactions containing that effect.

tions of the variation in these measures were attributed to age (partial R²_g between 0.002 and 0.071), and significance was determined only through large numbers of observations. This was primarily the result of many short and shallow dives that occurred regardless of age. Ontogenetic relationships were best demonstrated with the model for maximum-daily-depth (Table 2), where age explained 7% of the variation. It is important to also consider maximum values of diving

performance, which more realistically portray biological capability than do the model-generated geometric means.

Maximum dive depth and duration

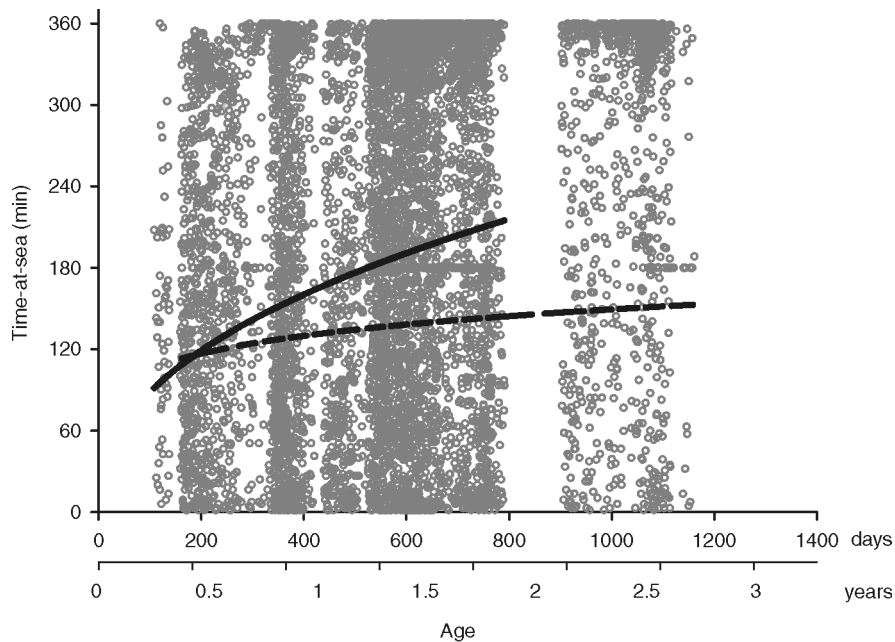
SSLs in this study dove to depths (maximum of 452 m) exceeding those previously reported for juvenile and adult female SSLs (Merrick and Loughlin 1997; Loughlin et al. 1998, 2003). The previous maximum for a juvenile was

Table 7. Correlation matrix for pup and juvenile Steller sea lion diving performance measures.

Variable	Maximum-daily-depth	Mean duration	Time-at-depth	Time-at-sea
Maximum-daily-depth				
Mean-dive-duration	0.047			
Time-at-depth	0.017	0.262		
Time-at-sea	0.009	0.175	0.684	
Dive rate	0.002	0.005	0.206	0.134

Note: Values are r^2 for linear regressions of one variable on the other (ln scale).

Fig. 13. Time-at-sea predicted by age using a linear-mixed effects model for female (solid line) and male (dashed line) Steller sea lions. Actual data points from which predictions were computed are shown as open circles. The line of values at 180 min on the y axis is an artifact of rounding.



328 m, recorded for a 1.8-year-old male (Loughlin et al. 2003). SDRs used in studies of adult females (Merrick and Loughlin 1997; Loughlin et al. 1998) did not record maximum-daily-depth, and the deepest bin included all dives >250 m; therefore, it was impossible to determine the actual depths of dives >250 m. Only about 1% of dives by adult females in these studies were >250 m; although they may have had the ability to dive deeper, they seldom did so.

Only an extremely low percentage (0.04%) of dives recorded were >12 min. The highest value for mean dive duration for any 6-h bin in this study was 4.29 min. Previous studies also found short maximum dive durations: <6 min for pups and yearlings (Loughlin et al. 2003) and about 8 min for adult females (Merrick and Loughlin 1997; Loughlin et al. 1998).

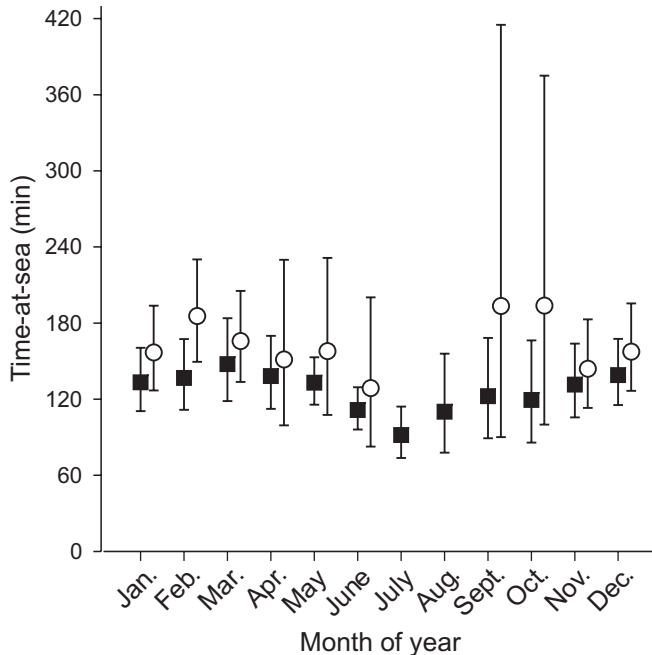
The equation for the allometric relationship between body mass and maximum dive duration for otariids (Schreer and Kovacs 1997) predicts that maximum aerobic dive duration is about 9.85 min for a 100-kg otariid (1-year-old SSL), about 10.6 min for a 200-kg animal (large juvenile), and about 10.9 min for a 273-kg animal (adult female), suggesting that few dives recorded in this study approached or exceeded the estimated aerobic dive limit. No measurements

have been made of dive duration for adult male SSLs. However, adult males exceed 900 kg (Winship et al. 2001) and the calculated aerobic dive limit is 12.3 min (Schreer and Kovacs 1997).

Richmond (2004) studied the ontogeny of body oxygen stores and aerobic dive potential in Steller sea lions, focusing on pups and juveniles. She found that blood oxygen stores reached adult levels by 0.75 years of age, while muscle oxygen stores reached adult levels at 1.75 years of age. However, aerobic dive capacity continued to increase because of gains in mass-specific metabolic efficiency. This suggests that the greatest gain in aerobic diving performance occurs during the first year, when all three factors (blood and muscle oxygen storage plus body mass) are increasing. The gain is intermediate during the second year as muscle oxygen storage and mass continue to increase. After 1.75 years, the only additional gain is through mass-specific metabolic efficiency. These findings tie nicely into the relationship we observed between age and maximum mean-dive-duration (Figs. 7, 15), where the greatest gain was during the first year of life.

Diving animals can extend dive duration beyond their aerobic dive limit by utilizing anaerobic metabolism, although

Fig. 14. Least-squares geometric means with 95% confidence intervals for time-at-sea by month for Steller sea lions from the eastern population (solid squares) and the western population (open circles). No data were available for the western stock during July or August. The graph is based on simplified analysis with some interactions omitted to illustrate relationships between time-at-sea, population, and month.



for pinnipeds this is thought to occur infrequently (Kooyman and Ponganis 1998). However, in some instances it may be advantageous despite extended recovery requirements (Schreer and Kovacs 1997). Perhaps the very small number of longer dives observed in this study were performed by SSLs utilizing anaerobic metabolism.

Gender differences in diving performance

Differences between sexes were significant for all diving performance measures, either as a main effect or as a two-way interaction. Males spent less time at sea, were, on average, shallower divers, had longer dives, and had lower dive rates. Gender differences in maximum-daily-depth and time-at-sea were apparent by 1 year of age (Figs. 3, 7). SSLs are a highly dimorphic species with differences in body mass apparent shortly after birth (Merrick et al. 1995). By 1 year of age, male mass is about 40% greater than female mass; by 10 years of age, the difference is about 270% (Winship et al. 2001). Larger animals typically dive longer, deeper, and more efficiently (Schreer and Kovacs 1997). Findings that geometric mean maximum-daily-depth was less for males were therefore counterintuitive. However, males performed the 100 (2.1%) deepest dives, suggesting that they are capable of diving deeper than females even though, on average, they dove to shallower depths. Burns et al. (1997) found that smaller yearling Weddell seals dove deeper while larger yearlings had longer dive durations, similar to the smaller female and larger male SSLs. Gender differences in foraging ecology and niche exploitation were found for gray seals,

Halichoerus grypus (Fabr., 1791) (Beck et al. 2003a, 2003b). It appears that niche separation and differences in foraging ecology may be occurring in SSLs at an early age, as we found gender differences in diving performance for our young animals. Also, fatty acid signatures were found to differ between sexes (indicating different prey utilization) in animals >1 year of age from Prince William Sound (Alaska Department of Fish and Game, unpublished data). This may be related to greater body mass, as males dove longer than females, but may also be related to differences in strategies of energy acquisition and storage. Adult males are capital breeders, as they store large quantities of energy in the form of increased fat and protein during the nonbreeding season and then fast during breeding (Olesiuk and Bigg 1990; Pitcher et al. 2000). Adult females fast for only a short period after giving birth and maintain relatively consistent energy stores throughout the year (Pitcher et al. 2000; Winship et al. 2001). Foraging and energy acquisition strategies may be inherently different by sex, even at the young ages of our study animals.

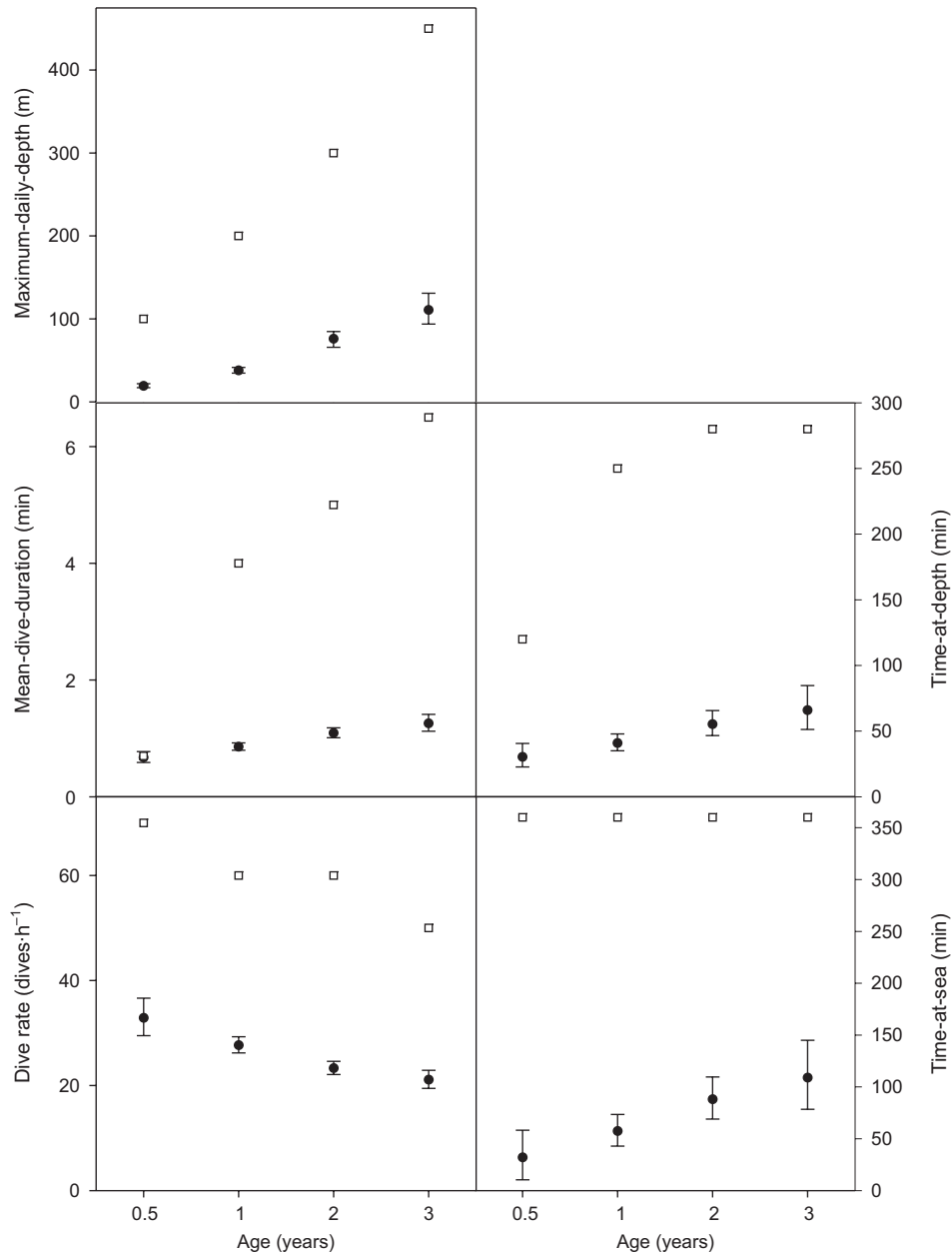
Population differences in diving performance

There were population-level differences in diving performance, with greater mean maximum-daily-depth, mean-dive-duration, and dive rate for animals from the eastern population. Sea lions from the western population spent more time at sea. All of these differences could be interpreted as “greater diving effort”, but because the results are mixed by population and we do not understand the relationship between these dive measures and foraging effort, we are hesitant to argue that either population is “working harder” at foraging than the other. In addition, the average behavioral differences between the two populations were relatively small. These differences may relate to spatial differences in bathymetry and the distribution of prey in the two areas. We also suspect that juveniles in the west were foraging independently at an earlier age than those from the east (Alaska Department of Fish and Game, unpublished data), which would likely affect diving performance. Loughlin et al. (2003) found that yearling SSLs from Washington dove deeper than those from the Gulf of Alaska and Aleutian Islands and thought this was most likely associated with differences in prey habitat. Raum-Suryan et al. (2004) found that trip duration was longer in the west and speculated that it was related to differences in prey availability and (or) age of weaning. Therefore, we can neither accept nor reject the hypothesis than juveniles from either population were expending greater effort in obtaining prey.

Diel and seasonal differences in diving performance

We found a highly significant diel effect for both time-at-sea and time-at-depth for animals from both populations. Activity was greatest at night, and this was most pronounced during the summer. This diurnal effect has been reported previously for SSLs (Merrick and Loughlin 1997; Loughlin et al. 1998, 2003) and some other otariids such as Galápagos fur seals (*Arctocephalus galapagoensis* Heller, 1904) (Horning and Trillmich 1997) and New Zealand fur seals (*Arctocephalus forsteri* (Lesson, 1828)) (Harcourt et al. 1995). Nocturnal foraging in marine mammals is assumed to occur in response to vertical migrations of prey to shallower

Fig. 15. Predicted geometric means with 95% confidence intervals (solid circles) and maximum values (open squares) by age (0.5, 1, 2, or 3 years) for maximum-daily-depth, mean-dive-duration, time-at-depth, dive rate, and time-at-sea. Geometric means were predicted from models with $\ln(\text{age})$ as the only predictor.



water, where they are more accessible (Horning and Trillmich 1997). In Alaska, a major SSL prey, Pacific herring (*Clupea harengus pallasii* Valenciennes, 1847) (Carlson 1980; Thomas and Thorne 2001), is known to migrate up in the water column during darkness, and nocturnal foraging is probably energetically efficient at that time. Another important SSL prey, juvenile walleye pollock (*Theragra chalcogramma* (Pallas, 1814)), sometimes undergoes diel vertical migration (Brodeur and Wilson 1996a). The more pronounced diurnal effect during summer was likely associated with the short period of darkness occurring in summer at the latitude of this study.

Month-of-year affected maximum-daily-depth (Fig. 4), with deeper diving during winter than during summer. Simi-

larly, mean-dive-duration (Fig. 8), time-at-depth (Fig. 5), and time-at-sea (Fig. 14) were greater in winter. Conversely, dive rate was highest during summer (Fig. 11). Deeper diving and greater dive duration during winter are likely a response to deeper prey. Two major SSL prey, Pacific herring and juvenile pollock, occurred at greater depths during winter than during summer (Carlson 1980; Brodeur and Wilson 1996b). Greater time-at-sea and time-at-depth during winter may relate to intrinsic seasonal energy requirements. Winship et al. (2001) found seasonal changes in growth rate, with greater growth during winter, and thought this was the result of inherent seasonality in food consumption associated with growth and molting. Another factor may be the availability of prey at shallower depths and in dense aggregations

during spring, summer, and fall, such as prespawning and spawning concentrations of herring, capelin (*Mallotus villosus* (Müller, 1776)), and salmon (*Oncorhynchus* spp.).

Weaning and foraging

Weaning may be an important determinant of diving performance, as young SSLs may be motivated to push the limits of diving ability when they no longer receive nourishment from their mother. Some SSLs are weaned before or on their first birthday, while others continue to suckle until their second birthday or beyond (Pitcher and Calkins 1981; Trites and Porter 2002; Alaska Department of Fish and Game, unpublished data). We had no consistent way of determining weaning status of the instrumented animals in this study and therefore could not include weaning status as a variable in our analyses of diving performance. However, the clumping of high values for maximum-daily-depth (Fig. 3) and mean-dive-duration (Fig. 7) around first and second birthdays suggests to us that newly weaned animals tend to increase diving performance. Both Loughlin et al. (2003) and Raum-Suryan et al. (2004) observed changes in diving and (or) movement patterns that coincided with presumed timing of weaning.

We were unable to directly infer much about the foraging ecology of young SSLs from the data obtained from SDRs, largely because we could not consistently determine which animals were weaned and independently foraging nor which dives were associated with actual foraging. While shallow dives may frequently be associated with traveling or social interactions, we have visually observed foraging by SSLs on capelin within 2 m of the surface. Feeding on herring near the surface during nocturnal vertical migrations (Thomas and Thorne 2001) and in shallow spawning aggregations (Womble 2003) is a common occurrence in some locations and during some seasons. Some shallow foraging would not even register as a dive on the instruments used in this study because of the 4-m dive threshold. It might be assumed that deeper dives were associated with foraging, but some of these may have been for purposes such as exploration or learning about dive capability and in this study some deep dives were made by dependent juveniles (animals with milk in their stomach when captured or observed suckling after capture).

Adaptability in diving and foraging

Young SSLs appear to have considerable plasticity in their diving performance, probably in response to the local environment and variable conditions they encounter. This is supported by findings that animals from the western population spent more time at sea, while those from the eastern population dove deeper, longer, and at a higher rate. Also, while both populations had similar basic seasonal patterns in maximum-daily-depth, with increased depth during winter, the effect was much more pronounced in the west. There were also pronounced differences in seasonal and diel patterns of time-at-depth between populations. The great majority of dives by animals in this study and in other studies of SSL diving were far below the physiological maximums of depth and duration, suggesting that if necessary and energetically cost-effective, SSLs could dive deeper and longer to effectively exploit available prey resources. SSLs appear to have the ability to function as either benthic or epipelagic

feeders (Pitcher 1981; Sinclair and Zeppelin 2002), unlike some otariids such as the Australian sea lion (*Neophoca cinerea* (Péron, 1816)), which is highly adapted to benthic foraging, and most fur seals, which are epipelagic foragers (Costa and Gales 2003). SSLs exploit different prey species throughout their range. Key species, east to west, change from Pacific hake (*Merluccius productus* (Ayres, 1855)) to walleye pollock and Pacific herring and then to Atka mackerel (*Pleurogrammus monopterygius*) (Pitcher 1981; Brown et al. 2002; Sinclair and Zeppelin 2002). The old saying “there is more than one way to get the job done” comes to mind. What is important are “cost–benefit relationships” (Feldkamp et al. 1989). In some situations it may be more efficient to dive deep and long, perhaps even exceeding the aerobic dive threshold, to access an extremely rich prey field (Boyd 1997; Costa and Gales 2003). In other instances, short, shallow dives such as those that would occur when prey migrate towards the surface during night might be an efficient strategy. This adaptability appears to be a life-history strategy that enhances species persistence in the dynamic environment characteristic of the range of the SSL in the North Pacific Ocean, and it may be necessary for the persistence of the species over the long term.

Conclusion

We found that SSLs less than 1 year of age were able to dive to depths >200 m and older juveniles dove to over 400 m, similar to most deeper dives made by adult females. Therefore, they are presumably capable of accessing the same prey resources. However, the amount of time these younger (smaller) animals could spend at depth would be less, owing to lower oxygen storage capability and higher mass-specific metabolic rates, thereby reducing their foraging efficiency. Factors such as learning to locate prey and experience capturing and handling prey are also undoubtedly significant to foraging success. In addition, the energetic requirements of young, growing juvenile sea lions are higher than those of adults (Winship et al. 2002). Therefore, the hypothesis that young animals are more vulnerable than adults to changes in prey abundance and distribution (Merrick 1995; Merrick and Loughlin 1997) appears to be well supported.

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