Abstract.–The relationship be-
tween latitude and birth timing was
assessed for captive-born California
sea lions (*Zalophus californianus*),
northern (Steller) sea lions
(*Eumetopias jubatus*), northern fur
seals (*Callorhinus ursinus*), and Pa-
cific harbor seals (*Phoca vitulina
richardsi*) from zoos and aquaria in
the United States, Canada, South
Korea, and New Zealand. The births
of 466 viable California sea lion pups
demonstrated highly significant,
negative and curvilinear latitudinal
variation in birth timing. Over the
latitudinal range of captive births,
this variation accounted for a change
of approximately –0.6 days/°latitude.
Furthermore, the variances of the
mean dates of birth for the largest
18 captive populations were signifi-
cantly dependent upon latitude;
shorter birthing periods occurred at
higher latitudes. Northern sea lions
(*n*=9) had a similar, but non-signifi-
cant latitudinal relationship in
which birthing dates occurred ap-
proximately 30 days later. No sig-
nificant relationship between lati-
tude and birthing date was found
for northern fur seals (*n*=13). The
birth dates of 110 viable Pacific har-
bor seal pups had highly significant,
positive and curvilinear latitudinal
variation, similar to that previously
described for this subspecies in the
wild between 30° and 47°N. Pupping
dates for each species in captivity
were comparable to those found for
wild populations of North Pacific pin-
nipeds. The described latitudinal
variation and the temporal consis-
tency between captive and wild
populations of California sea lions
and Pacific harbor seals support the
hypothesis that photoperiod re-
sponse maintains specific birth tim-
ing in these species.

Latitudinal variation in the birth timing of captive California sea lions and other captive North Pacific pinnipeds

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Captive pinnipeds are not only of
educational and entertainment value
to zoo and aquarium visitors, but also
offer an exceptional opportunity to
examine temporal aspects of their re-
productive biology. Zoo records usu-
ally document birth dates, outcomes,
and parental histories which are dif-
ficult, if not impossible, to obtain
in field studies. Moreover, captive
animals live in environments where
availability of food is relatively con-
stant and any movements (i.e., trans-
fers between facilities) are well
documented.

A recent census (Asper et al., 1988)
identified 924 pinnipeds in captivity
in North America. Of these, four
North Pacific species—the California
sea lion (*Zalophus californianus*), the
northern or Steller sea lion (*Eumeto-
pias jubatus*), the northern fur seal
(*Callorhinus ursinus*), and the har-
bor seal (*Phoca vitulina*)—repre-
sented 91 percent (*n*=837). These spe-
cies breed successfully in captivity
over wide latitudinal ranges.

Standard reviews of the pinnipedia
(Mate, 1979; Mate and Gentry, 1979;
Odell, 1981; Schusterman, 1981;
King, 1983) identify fixed seasons of
birth for each of the North Pacific
sea lions. Moreover, Bigg (1973)
found that captive California sea li-
ons at the London Zoo (51°N) breed
at the same time as the parent popu-
lation in California (33°N). In con-
trast, Schusterman et al. (1982) noted
that births of California sea lion pups
at Sea Life Park, Hawaii (21°N), oc-
curred significantly later than births
in California at Marineland (34°N)
and Marine World (38°N).

Regional or latitudinal variation in
birth timing, or both, has been re-
ported for the harbor seal (Bigg,
1969a; Temte et al., 1991) and the
grey seal (*Halichoerus grypus*:
Coulson, 1981). Likewise, Temte
(1985) demonstrated a 14-day shift
in the mean date of pupping for
northern fur seals between colonies
on St. George Island, Alaska (57°N),
and San Miguel Island, California
(34°N). These variations in birth tim-
ing have been interpreted as 1) se-
lection acting on discrete populations
to match reproductive efforts with
seasonal constraints (Bigg, 1973),
2) responses to latitudinally chang-
ing temporal cues, such as tempera-
ture or photoperiod (Coulson, 1981;
Temte, 1985), or 3) a combination of
the above (Temte et al., 1991; Boyd,
1991).

This study identifies and defines
the extent of latitudinal variation in
birth timing of captive California sea
lions, northern sea lions, northern fur
seals and Pacific harbor seals from
birthing records available from zoos
and aquaria scattered across a wide
latitudinal range. Comparisons of
birthing periods were made, where
applicable, between captive and wild
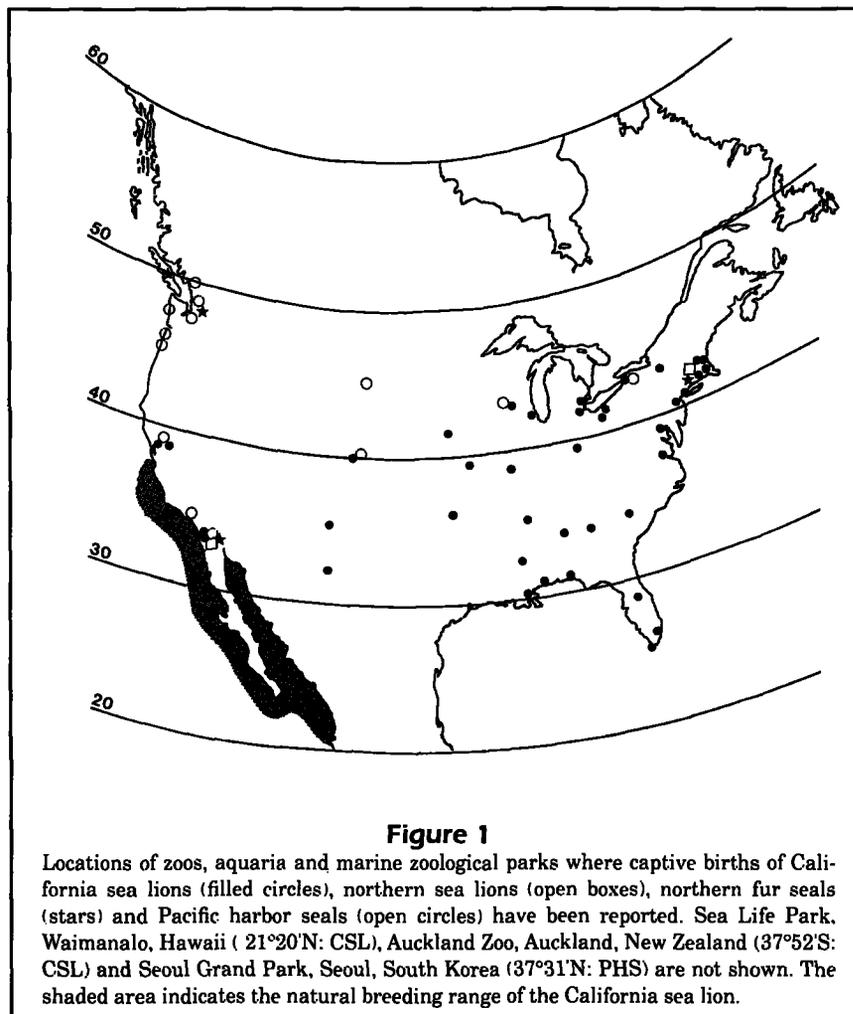populations.

Methods

The data

Data for this analysis were initially compiled from the Marine Mammal Inventory Report (MMIR), a registry of captive marine mammals maintained by the Office of Protected Resources, National Marine Fisheries Service. To comply with the Marine Mammal Protection Act, U.S. facilities that exhibit marine mammals submit yearly summaries of their captive populations, including animal identification, sex, age, date of acquisition or birth, origin, and current status. The birth dates of 527 California sea lions born in captivity at 41 locations, 9 northern sea lions born at two locations, 20 northern fur seals born at three locations, and 125 Pacific harbor seals born at 13 locations were extracted from this registry (Fig. 1). Seventy-one percent of birth date and outcome (viable pup, non-viable pup, stillborn pup) data were independently verified by contacting the appropriate facility. Of the data veri-

fied, 98.6% were accurately reported on the MMIR (Temte, 1993).

Eighty-three additional captive births of California sea lions, not reported on the MMIR, were provided by the facilities. Seven additional birth dates of captive northern fur seals were obtained from the report of Bigg (1984). Data on two births of harbor seals were obtained from the Vancouver Aquarium (Vancouver, British Columbia). To assess the effect of a major latitudinal translocation, birthing dates of 11 California sea lions born at the Auckland Zoo, New Zealand (37°S) were obtained. All cows at this facility could be traced, from zoo records, to the California Channel Islands population.

Pup identification, location, latitude, date of birth, sex, and birth outcome were entered into the database. Dates of birth were converted into numerical equivalents by using a sequential astronomical calendar (day 0 = December 21; see Temte, 1985). Birth outcomes were rated as stillbirth (pup born dead), non-viable (pup lived less than one day), or viable (pup lived at least one day).

Figure 1
Locations of zoos, aquaria and marine zoological parks where captive births of California sea lions (filled circles), northern sea lions (open boxes), northern fur seals (stars) and Pacific harbor seals (open circles) have been reported. Sea Life Park, Waimanalo, Hawaii (21°20'N: CSL), Auckland Zoo, Auckland, New Zealand (37°52'S: CSL) and Seoul Grand Park, Seoul, South Korea (37°31'N: PHS) are not shown. The shaded area indicates the natural breeding range of the California sea lion.

Statistical analysis

Data were treated separately for each species. Comparisons were made between the mean dates of birth for stillborn, non-viable, and viable pups by using the appropriate parametric or non-parametric statistic.

The birth dates of viable pups were assessed for latitudinal variation. Least squares linear regression models were fitted to the latitude-date data, and where necessary, orthogonal polynomials were used to meet statistical assumptions. Because the intra-colony variance of the mean date of birth for California sea lions was related to latitude, regressions were performed with and without weighting to correct for unequal variances. Orthogonal polynomial regression models using (latitude minus mean latitude)^2 as the quadratic term were chosen to reduce correlation between the linear and quadratic terms and to better estimate the linear coefficient (Snedecor and Cochran, 1980). To assess differences between California and northern sea lions, analysis of covariance (ANCOVA: Kleinbaum and Kupper,

1978) was utilized to control for differences in latitudinal distributions.

Results

California sea lion

The captive births of 610 California sea lions were evaluated (Table 1). Stillborn and non-viable pups accounted for 122 births (20.0%). Stillbirths occurred as early as 1 January and as late as 1 August. Whereas no significant difference was found between the timing of stillbirths and non-viable births (Kruskal-Wallace: df=1; H=0.371; NS), stillborn and non-viable pups were born an average of 28.0 days earlier than viable pups, this difference being highly significant (Kruskal-Wallace: df=1; H=70.49; P<0.001). Hence, only viable births (n=466; 22 pups with estimated birth dates were excluded) were examined for latitudinal variation.

Viable births occurred over a 21°46' latitudinal range, between 21°20'N and 43°06'N. These were normally distributed over the birthing period (Fig. 2), occurring as early as 30 April and as late as 1 September. Mean dates of pupping for individual colonies occurred from 27 May to 25 June. The mean date of birth for all viable pups was 12 June ± 13.5 days (± SD).

The variances of the mean birth dates were calculated for the 18 largest captive colonies (each with at least 6 viable births). A significant latitudinal gradient existed for this variance (Fig. 3), with a decrease of 5.6 days² for each degree of northward displacement.

A plot of pupping date versus latitude indicated that latitude variation occurred within captive California sea lions (Fig. 4). A second order orthogonal polynomial model (Table 2) was highly significant (r^2=0.206; $F_{(2,463)}$=60.23; P<0.0001) and estimated a negative latitudinal slope of approximately −0.6 days/°latitude over

Figure 2
Frequency of viable California sea lion births at all facilities during 10-day periods from 31 March (day 100) to 6 September (day 259). Dates are numbered sequentially from 21 December.

Figure 3
Intra-colony variance of the mean pupping date from the 18 largest California sea lion colonies as a function of latitude. Each colony had at least six viable births. Linear regression model: Variance (days²) = 219 − 5.58(latitude); r^2 = 0.405; t_{slope} = −3.30; P < 0.005.
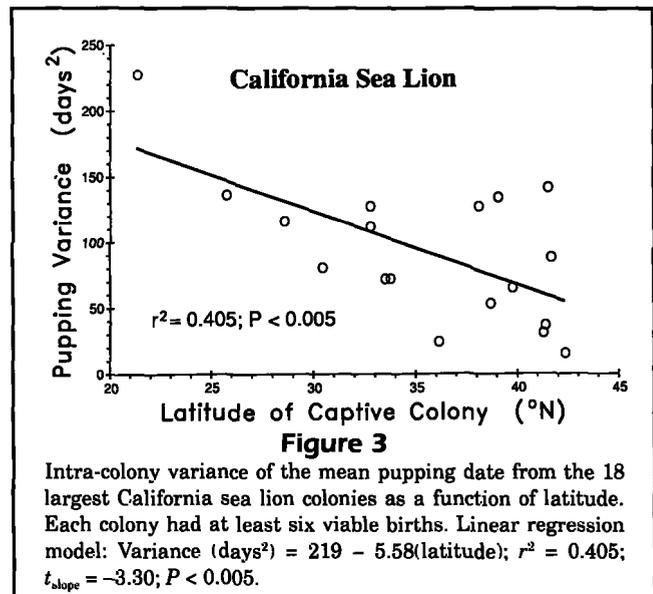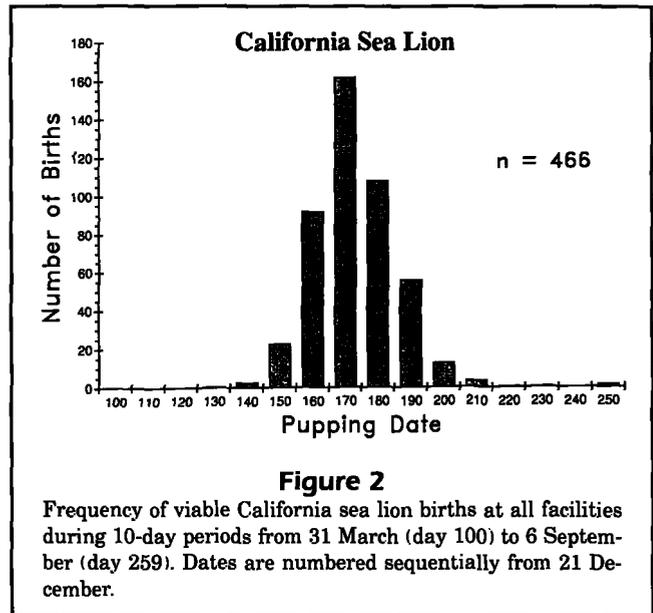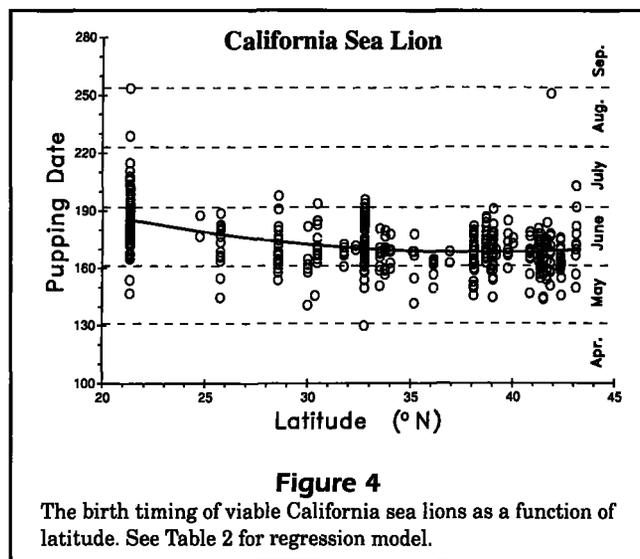
Table 1
Numbers, mean dates (month/day; sequential day number), and standard deviations of viable births, non-viable births, and stillbirths in captive North Pacific pinnipeds.

Species	Type	n	Percent	Mean date	SD (days)
California sea lion	Viable	488	80.0	6/12 (172.7)	13.5
	Non-viable	50	8.2	5/16 (145.6)	29.4
	Stillborn	72	11.8	5/14 (144.0)	46.1
Northern sea lion	Viable	9	100.0	7/09 (199.8)	16.5
Northern fur seal	Viable	13	48.1	7/10 (200.6)	14.8
	Stillborn	14	51.9	6/23 (184.2)	60.0
Pacific harbor seal	Viable	110	88.0	5/20 (150.3)	36.7
	Non-viable	5	4.0	5/11 (140.8)	47.5
	Stillborn	10	8.0	5/11 (140.8)	34.0

Figure 4
The birth timing of viable California sea lions as a function of latitude. See Table 2 for regression model.

the range of data. Weighting of the regression to correct for the unequal variances did not appreciably change the parameter estimates.

Eleven pups were born at the Auckland Zoo (Auckland, New Zealand: 37°S) from 28 November to 23 December and had a mean birth date of 11 December. The polynomial model predicted that birthing at 37°N should occur on 6 June. Therefore, California sea lions translocated to the Southern Hemisphere experienced an approximate 6-month shift in birth timing.

Climatic conditions did not appear to significantly affect the timing of birth. For example, colonies at similar latitudes (Vallejo, California: 37°47'N and Kansas City, Missouri: 39°07'N) maintained similar pupping schedules despite having vastly different seasonal temperature cycles. Following an adjustment for latitude, no significant difference was found between the birth timing of male and female pups.

Northern sea lion

The captive births of nine northern sea lions occurred at 32°45'N and 41°21'N (latitudinal range=8°36'). All births were of viable pups. The mean date of birth was 9 July ± 16.5 days (± SD; Table 1). Although the plot of pupping date vs. latitude was similar to that for the California sea lion, a simple linear regression model (Table 2) failed to demonstrate significant latitudinal effects in this species (r^2=0.271; $F_{[1,7]}$ =2.60; P=0.23); the lack of significance was possibly due to the small sample size. However, when northern sea lion data were combined with those of the California sea lion in a multiple linear regression model, no significant differences were found between the latitudinal slopes of the two species. Analysis of covariance identified significantly later birthing (P<0.001) for northern sea lions, occurring 30 days after California sea lions.

Northern fur seal

The captive births of 27 northern fur seals were reported from four locations between 32°45'N and 49°07'N (latitudinal range=16°22'). Slightly more than half of the pups were stillborn (Table 1). The mean date of birth of viable pups was 10 July ± 14.8 days (± SD). No significant latitudinal variation was detected in birth timing (Table 2: r^2=0.174; $F_{[1,11]}$=2.32; NS).

Pacific harbor seal

The birth dates of 127 captive-born Pacific harbor seals were identified from 14 locations between 32°45'N and 49°18'N (latitudinal range=16°33'). The birth outcomes of two pups were not known and they were excluded from further analysis. Of the remaining 125 births, 88.0% were of viable pups (Table 1). The mean date of birth for viable pups was 20 May ± 36.7 days (± SD). No significant differences in the annual birth timing

Table 2
Regression models for latitudinal variation in birth timing of North Pacific pinnipeds.

Species	n	Mean latitude (° North)	a	*Linear regression estimate of $PD = a + b_1(L) + b_2(L - \bar{L})^2$					r^2	Significance
				b_1(CI) ±95%		b_2(CI) ±95%				
California sea lion	466	33.21	190	−0.61	(0.17)	0.057	(0.024)		0.206	0.0001
Northern sea lion	9	35.62	271	−2.00	(2.43)	—	—		0.271	NS
Northern fur seal	13	45.03	145	1.23	(1.59)	—	—		0.174	NS
Pacific harbor seal	110	41.60	−113	5.85	(1.10)	0.681	(0.065)		0.508	0.0001

*PD = Pupping date (sequential from 21 December); L = Latitude.

were found among viable, non-viable and stillborn pups.

A simple linear regression model defined significant latitudinal variation in birth timing of viable pups with a gradient of 4.10 days/°latitude; this slope was not significantly different from that reported by Temte et al. (1991) for colonies of wild Pacific harbor seals between 30° and 47°N. A second order polynomial model (Fig. 5; Table 2), however, was more statistically appropriate based on residual analysis. This model was highly significant (r^2=0.508; $F_{(2,107)}$=55.23; $P<0.0001$), defining a positive relationship between latitude and birth date.

Data regarding sex of pup (n=102), maternal age (n=88), and the previous annual cycle of the mother (pregnant vs. non-pregnant: n=89) were available for subsets of the harbor seals. When entered, either separately or as a group, into a multiple regression model adjusting for latitude, none of these parameters was found to significantly alter birth timing.

Discussion

Use of captive birth data

Events on rookery sites or pupping beaches hamper the estimation of true pupping seasons in pinnipeds. For example, premature pupping in the California sea lion occurs with increasing frequency over a 5-month period, melting into the normal pupping season between mid-May and the end of June (Delong et al., 1973). In addition, seasonal movements of animals from breeding to feeding sites may occur (Braham, 1974; Mate, 1975), potentially obscuring latitudinal variation of birthing if seasonal entrainment occurs at latitudes other than that of the rookery site. The use of captive populations permits accurate measurement of birth dates and birth outcomes, while controlling for potential latitudinal displacement during the reproductive year.

California sea lion

This study confirms the report of Schusterman et al. (1982) and demonstrates that marked latitudinal variation occurs not only in the timing of birth, but also in the variance of the mean birth date. Furthermore, interpretations of results based on this data set representing 466 viable births from 41 locations, as compared to the three locations used by Schusterman et al. (1982), are far less sensitive to possible confounding effects induced by captivity or differences in climatic conditions. The extreme example of sea lions translocated to the Southern Hemisphere provides further evidence of strong latitudinal effect.

The birth timing of captives mirrors that of wild populations. Although a review by Mate (1979) concluded that pups, regardless of latitude, are born from mid-May to late-June over the range of California sea lion rookeries, slight latitudinal variation may exist. In Baja California, pupping occurs in late-June (Brownell et al., 1974), and Le Boeuf et al. (1983) reported a maximum pup count on 10 July at Los Islotes (28°N). Further to the north, at San Nicolas Island (33°15'N), pupping peaks during the first half of June (Peterson and Bartholomew, 1967; Odell, 1975; Heath and Francis[1,2]). Data from more northerly colonies are anecdotal in nature. For example, Braham (1974) reported a 2-week-old pup on 11 June at San Luis Obispo County, California (35°30'N).

As in captive sea lions, premature pupping in wild colonies occurred as early as January on San Nicolas and San Miguel Islands (Odell, 1970; Delong et al, 1973). Premature pups are probably represented in captivity by the stillborn and non-viable groups. The 20% rate of stillborn and non-viable pupping for captive sea lions is noteworthy considering the 5–16% rate of premature pupping reported for San Nicolas Island during years with high incidences of prematurity (Odell, 1970). Whereas pesticide exposure and disease
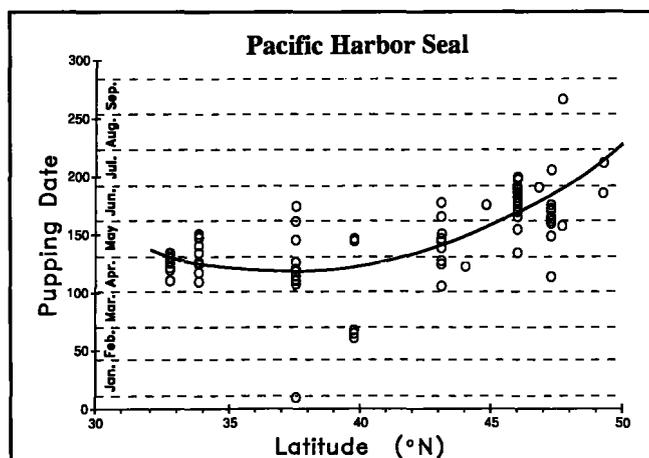

Figure 5
The birth timing of viable Pacific harbor seals as a function of latitude. See Table 2 for regression model.

[1]Heath, C., and J. Francis. 1983. California sea lion population dynamics and feeding ecology with applications for management. Results of 1981–1982 research on Santa Barbara and San Nicholas Islands. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Center, P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-83-04C.

[2]Heath, C., and J. Francis. 1984. Results of research on California sea lions, San Nicholas Island, 1983. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Sci. Center, P.O. Box 271, La Jolla, CA 92038. Admin. Rep. LJ-84-41C.

have been suggested as agents of premature pupping in wild populations (Delong et al., 1973; Odell, 1970, 1981), the high rate of stillbirth and non-viability in captivity may be influenced by the level of surveillance inherent to captive populations.

Male California sea lions were reported to be 3.37 cm longer and 1.41 kg heavier than female pups at birth (Le Boeuf et al., 1983). Year-to-year differences in mean birth lengths and weights have been related to differences in the mean birth date of harbor seals (Boulva, 1975). No such differences were found between the birth timing of male and female pups in the present study. Hence, discrepancy in birth size is likely due to greater growth velocity of fetal males.

Northern sea lion

Only limited data from two locations were available for captive northern sea lions. Although these animals appeared to have a temporal pattern of birth similar to, but 30 days later than, that of the closely related California sea lion, no significant latitudinal trend was found.

The northern sea lion has a wide distribution of breeding (see Fig. 1 in Loughlin et al., 1984), but little evidence exists for latitudinal variation in birth timing in the wild. For example, a review of median birth dates at rookeries from 37°N to 60°N by Merrick (1987) failed to demonstrate any latitudinal variation in this species.

Northern fur seal

A high rate of stillbirth was noted for the fur seal. This phenomenon was previously reported by Bigg (1984) during studies indicating that contact with substrate (e.g., arrival on shore) may stimulate parturition. Captive environments, with shallow pools and access to platforms, cannot adequately reproduce the pelagic environment which female fur seals inhabit during most of active gestation. Hence, premature parturition may be induced by enclosures.

The mean date of pupping for viable pups in captivity of 10 July was the same as that derived for St. George Island, Alaska (Temte, 1985). Unlike wild northern fur seals, however, the captives demonstrated no significant latitudinal variation. The sample set may have been too small to detect the estimated 0.6 days/°latitude trend reported by Temte (1985).

Pacific harbor seal

Captive harbor seals had a high rate of viable birthing with pups born over a pupping season comparable to that of wild counterparts (Temte et al., 1991). This species demonstrated stronger latitudinal effect than that of any other North Pacific pinniped covered in this report, with an average shift of 4.1 days/°latitude. Whereas this relationship is similar to that previously described for wild Pacific harbor seals on the North American west coast south of 47°N, the larger captive data set allows better definition of a curvilinear relationship.

Temte et al. (1991) separated the Pacific harbor seal into three subgroups based on birth timing. The northernmost group, from northern British Columbia and Alaska has no latitudinal variation in birth timing. The late-birthing group inhabits Puget Sound, Washington, and pups two months later than coastal seals at the same latitudes. The southern group, as noted above, has highly significant latitudinal variation. Morphometric analysis of skulls from each of these populations supports the hypothesis of discrete populations (Temte, unpubl. data). No individuals from populations originating in Puget Sound, northern British Columbia or Alaska were included in this study.

The sex of the pup, maternal age, and the previous maternal cycle (pregnant vs. non-pregnant) had no effect on birth timing. These findings are from captive animals with dependable food supplies. In contrast, Boyd (1984) has suggested that maternal condition affects implantation timing in grey seals.

Latitudinal variation and photoperiod

For captive California sea lions, a smooth and continual temporal change of pupping dates across latitude occurred despite wide diversity of climatic conditions. Nevertheless, as almost all the captives could be traced to a single wild population on the California Channel Islands, a strong environmental component appears to influence birth timing. This pattern is highly suggestive of a response to a predictable, latitudinally dependent seasonal cue. The 6-month shift in birth timing between hemispheres, as demonstrated by California sea lions in New Zealand, strongly supports a photoperiod hypothesis. Furthermore, the decreasing variance to the north (in the Northern Hemisphere) is as expected if photoperiodism occurs (Bronson, 1985). At higher latitudes, organisms experience a greater rate of change in photoperiod. Consequently, responses to specific cues should occur over a compressed time period.

Latitudinal variation in birth timing of the northern fur seal, a species with delayed implantation (Daniel, 1981), can be explained by a response to photoperiod occurring between ovulation and implantation (Temte, 1985). This sets the time of implantation and birth while allowing flexibility in estrus timing. For example, arrival at breeding grounds and mating occur as much

as two months earlier for parous cows than for virgin northern fur seals (Craig, 1964; Bigg, 1986); this disparity is not reflected in birth timing (Trites, 1992). Gentry (1981) noted, however, that individual parous females have fairly rigid year-to-year estrus timing, and Bigg (1984) has suggested that the breeding synchrony found in this species may be due to arrival on shore and on social factors.

The harbor seal has been shown to have delayed implantation (Fisher, 1954; Bigg, 1969b) and the California and northern sea lions are thought to have this reproductive pattern as well (Odell, 1975; Boshier, 1981; Schusterman, 1981). Hence, a similar mechanism may exist to signal implantation in these species. Temte (1985) proposed that northern fur seals responded to a photoperiod of 12.5 hours per day (prior to the autumnal equinox), thus explaining the positive slope in latitudinal variation. Likewise, the Pacific harbor seals in this study have a positive slope and may respond to long (>12.0 h/day) photoperiods. In contrast, California sea lions have a negative slope in latitudinal variation, which suggests a response to a photoperiod slightly less than 12.0 hours per day (following the autumnal equinox), and occurring prior to implantation.

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