

AN ABSTRACT OF THE THESIS OF

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Title: Photoperiod and the Timing of Pupping in the Pacific Harbor Seal (*Phoca vitulina richardsi*) with Notes on Reproduction in Northern Fur Seals and Dall Porpoises

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Birth and pupping season records of Pacific harbor seals (*Phoca vitulina richardsi*) were used in an analysis of photoperiod effect on the timing of birth in this species. Dates and latitudes of births were converted into photoperiods using a photoperiod equation. Sequential dates from parturition were converted into photoperiods and plotted as a function of latitude. The resulting functions of latitude vs. photoperiod were regressed to determine the point during the reproductive cycle at which latitude did not have an effect on photoperiod. The Pacific harbor seal can be divided into two geographic subgroups by their respective pupping seasons. Seals inhabiting the Puget Sound / Strait of Georgia (PS/SG) System give birth to pups an average of 88 days ($P < 0.01$) later than do seals of the North American west coast. The cline in the pupping season of coastal harbor seals can be defined by a 13.8 h/day photoperiod occurring at 68 days post partum. PS/SG harbor seals experience a significantly different photoperiod ($P < 0.001$) of 10.8 h/day at 68 days post partum. Progesterone and testosterone levels support an hypothesis that these two populations may be reproductively isolated, as coastal male seals show low testosterone levels during the breeding season for PS/SG seals. A proposed photoresponse at 68 days post partum occurs at the midpoint between estrus and implantation. This period is characterized by secondary follicular activity in the ipsilateral

ovary and other changes occurring in the uterus and corpus luteum. A response to a specific photoperiod terminating the follicular activity and leading to a specific implantation date is suggested.

Photoperiod and the Timing of Pupping
in the Pacific Harbor Seal (Phoca vitulina richardsi)
with Notes on Reproduction in Northern Fur Seals
and Dall Porpoises

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TABLE OF CONTENTS

CHAPTER 1.	GENERAL INTRODUCTION TO REPRODUCTIVE BIOLOGY OF MARINE MAMMALS	1
CHAPTER 2.	PHOTOPERIOD AND THE TIMING OF PUPPING IN THE PACIFIC HARBOR SEAL	3
	INTRODUCTION	3
	METHODS	13
	RESULTS	17
	DISCUSSION	41
CHAPTER 3.	SEXUAL SEGREGATION IN THE PACIFIC HARBOR SEAL	61
CHAPTER 4.	FOOD LIMITATION IN THE PACIFIC HARBOR SEAL: COMPUTER SIMULATION OF A METABOLIC MODEL	64
	INTRODUCTION	64
	METHODS	65
	RESULTS	73
	DISCUSSION	89
CHAPTER 5.	PHOTOPERIOD AND DELAYED IMPLANTATION IN THE NORTHERN FUR SEAL (<u>CALLORHINUS URSINUS</u>)	91
	SUMMARY	91
	INTRODUCTION	91
	MATERIALS AND METHODS	92
	RESULTS	93
	DISCUSSION	96
CHAPTER 6.	SERUM PROGESTERONE LEVELS AND REPRODUCTIVE STATUS OF INCIDENTALLY KILLED FEMALE DALL PORPOISES	101
	INTRODUCTION	101
	METHODS	102
	RESULTS	104
	DISCUSSION	107
CHAPTER 7.	GENERAL CONCLUSIONS	108
	BIBLIOGRAPHY	116
	APPENDIX I	127
	APPENDIX II	132
	APPENDIX III	137

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Range of the Pacific harbor seal (<u>Phoca vitulina richardsi</u>).	5
2. Diagrammatical representation of the female harbor seal reproductive cycle showing timing of reproductive events relative to parturition. Status: P = parturition, lac = lactation, E = estrus, pip = preimplantation period, I = implantation.	7
3. Methods of photoperiod analysis.	15
4. Mean dates of pupping with standard error bars and ranges for North Pacific harbor seals (Genus <u>Phoca</u>). Solid lines are MDPC data; dashed lines are SDPI data. Means with differing subscripts are significantly different.	20
5. Mean dates of pupping for colonies of harbor seals along the North American west coast (●), within PS/SG (○), at Hokkaido, Japan (□), and for larcha seals (★). Dates are numbered sequentially from 21 December. Regression for coastal seals only.	21
6. Individual dates of birth for harbor seals along the North American west coast (●) and within PS/SG (○). Regression for coastal seals only.	22
7. Dates reported for onset (■) and conclusion (□) of harbor seal pupping seasons along the west coast of North America.	24
8a. Contour plot of photoperiod as determined by photoperiod equation between the winter (day 0) and summer (day 182) solstices and 30°N and 60°N latitude.	25
8b. As above but between the summer (day 182) and winter (day 365) solstices. Stippled areas depict photoperiods that cannot explain a cline over the entire range.	

9. Correlation coefficient of photoperiod vs. latitude for the year starting at parturition (day 0) using MDPC data (solid line) and SDPI (dashed line). Stippled areas indicate relative occurrences of estrus and implantation. Cline in photoperiod disappears when $r = 0$. 28
10. Coefficient of determination of photoperiod vs. latitude for the year starting at parturition (day 0) using MDPC data (solid line) and SDPI data (dashed line). Stippled areas indicate relative occurrences of estrus and implantation. Cline in photoperiod disappears when $r^2 = 0$. 29
11. Slope of the regression equation of photoperiod vs. latitude for the year starting at parturition (day 0) using MDPC data (solid line) and SDPI data (dashed line). Stippled areas indicate the relative occurrences of estrus and implantation. Cline in photoperiod disappears when slope = 0. 30
12. Photoperiod at 68 days post partum in the Pacific harbor seal (MDPC data) as a function of latitude. 32
13. Frequency of observations from MDPC data of photoperiods at 68 days post partum for harbor seals in PS/SG (shaded) and along the North American west coast (unshaded). 34
14. Frequency of observations from SDPI data of photoperiods at 68 days post partum for harbor seals in PS/SG (shaded) and along the North American west coast (unshaded). 35
15. Levels of serum progesterone in pregnant (●), non-pregnant (○), and subadult (□) female harbor seals from the Columbia River and Point Defiance Zoo. Lines connect values from a single animal. 38
16. Levels of serum testosterone in adult (●) and subadult (○) male harbor seals from the Columbia River and Point Defiance Zoo. Line connects values from a single animal. 40
17. Proposed mechanisms of speciation for North Pacific harbor seals (genus Phoca). 60

- 18a. Annual survivorship of (a) subadult and adult male, (b) juvenile male and female, (c) 6-12 month-old pup, and (d) 1-6 month-old pup harbor seals as a function of food availability. 74
- 18b. As above but for (a) non-pregnant and early-pregnancy, (e) mid-pregnancy, and (f) late-pregnancy and lactating adult female harbor seals.
19. Population growth in metabolic models: (1) no density dependence, (2) density dependent survivorship, (4) density dependent survivorship and reproduction. Subscript (a) designates 1000×10^6 kcal food per quarter; (b) 400×10^6 kcal food per quarter. 76
20. Population growth in metabolic models: (3) density dependent survivorship with fixed reproductive rate and (4) density dependent survivorship and reproductive rate. Subscript (a) designates 1000×10^6 kcal food per quarter; (b) designates 400×10^6 kcal food per quarter. 77
- 21a. Net rate of change (dN/dt) of modeled population as a function of population size. Food availability is set at three levels. 78
- 21b. Specific rate of change (dN/Ndt) of modeled population as a function of population size with food availability as above.
- 22a. Survivorship of pups as a function of population size with food availability set at three levels. 80
- 22b. Survivorship of reproductive females as a function of population size with food availability as above.
23. Reproductive rate as a function of population size at three levels of food availability. 81
24. Female reproductive advantage as a function of sex ratio at birth in a stable population. Dashed line represents an evolutionary stable strategy. 88
25. Number of northern fur seal pups born per 4-day period at Adams Cove, San Miguel Island (unshaded) and East Reef Rookery, Pribilof Islands (shaded) in 1979. 94

26. The annual cycles of photoperiod as referenced to the mean dates of parturition for northern fur seals at San Miguel Island, California, 33°N (broken line) and St. George Island, Alaska, 57°N (solid line). Also shown are the approximate times of estrus and implantation. 97
27. Mean concentrations with standard error bars of serum progesterone for immature (IMM.), pregnant, and lactating (LAC.) female Dall porpoises. Pregnant females are grouped by standard length in cm of fetuses. Number of samples are shown in parentheses. 105
28. Concentrations of serum progesterone as a function of corpus luteum mean diameter. Solid circles are samples from pregnant females; open circles are from lactating females. Relationship is given by:
 $y = 0.01 \exp(0.27x); r^2=0.74.$ 106

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Approximate timing of estrus and blastocyst implantation in days after parturition in the Pacific harbor seal.	8
2a. Pupping dates of individual harbor seals.	10
2b. Year to year mean pupping dates from a single colony of harbor seals at Sable Island, Nova Scotia (Boulva, 1975).	
3. Mean pupping dates from two colonies of harbor seals.	11
4. Mean dates of events associated with pupping for Pacific harbor seals on the coast of North America.	19
5. Means and ranges of photoperiod and dP and regressions of photoperiod vs. latitude and dP vs. latitude at the dates of pupping, estrus, and implantation in coastal Pacific harbor seals.	26
6. Means and ranges of photoperiod and dP and regressions of photoperiod vs. latitude and dP vs. latitude at the date of the proposed photoresponse in coastal Pacific harbor seals.	31
7. Slopes of the regression equations for photoperiod vs. latitude, with significance levels, at intervals after estrus and before implantation in the Pacific harbor seal.	33
8. Data on female harbor seals sampled for progesterone.	37
9. Data on male harbor seals sampled for testosterone.	39
10. Length of the pupping season, with the relative timing of the mean date of pupping, for the Pacific harbor seal and the northern fur seal.	44
11. Number of female and male harbor seals at Netarts Bay and Yaquina Head, Oregon.	62
12. Age, weight, metabolic, and feeding parameters of classes of the Pacific harbor seal for computer simulation.	66
13. Seasonal parameters: water temperature and food availability in four regimens.	82

14.	Stable population size at 100 years: effects of seasonal pupping and food availability.	84
15.	A comparison of mean vital statistics of two sets of modeled populations: 100 year populations with seasonally varying pupping and food availability.	85
16.	Timing of births of northern fur seals on San Miguel Island and St. George Island.	95
17.	Photoperiod at 62 days post partum based on births of northern fur seals at San Miguel Island and St. George Island.	98
18.	Relative timing in days of pupping (P), estrus (E), photoresponse (X), and implantation (I) in the Pacific harbor seal and the northern fur seal.	110

PHOTOPERIOD AND THE TIMING OF PUPPING IN THE PACIFIC HARBOR SEAL
(PHOCA VITULINA RICHARDSI) WITH NOTES ON REPRODUCTION IN NORTHERN
FUR SEALS AND DALL PORPOISES

CHAPTER 1

GENERAL INTRODUCTION TO REPRODUCTIVE BIOLOGY OF MARINE MAMMALS

Reproduction in marine mammals has received much attention, especially with regard to the ecology and management of once commercially important, and now endangered species. The study of reproduction in these animals has typically been limited by three factors. First, because of their marine habitat, pinnipeds and cetaceans are not readily accessible, and this necessitates capture or killing of animals for sampling, if they can be found. Second, the feasibility of keeping marine mammals in captive settings is greatly restricted, yielding few locations and opportunities to obtain samples. Third, due both to public opposition and decimation of some stocks, it is sometimes difficult to obtain marine mammals in the field. As a result, marine mammal reproductive biologists are, on occasion, required to take the role of opportunists.

This assemblage of papers represents the efforts of an opportunist, and has a unifying theme of seasonality in the reproduction of three species of marine mammals: the Pacific harbor seal (Phoca vitulina richardsi), the northern fur seal (Callorhinus ursinus), and the Dall porpoise (Phocoenoides dalli dalli).

The cline in the pupping season of the harbor seal (Bigg, 1969a) serves as a point of departure for Chapter 2. The cline is refined and analyzed using photoperiod analysis. Pupping data is converted into photoperiod information at intervals throughout the reproductive cycle. The role of photoperiod in defining such a cline is discussed.

The constraints of environment on a reproducing population may influence many of the attributes of a population, and of a species. Female harbor seals have different metabolic demands than males, largely due to the energetic cost of pregnancy and lactation. Hence, some different haul-out patterns may exist between sexes to balance these costs. Chapter 3 investigates the seasonal usage of haul-out sites by harbor seals, and the possibility of sexual segregation. Chapter 4 reviews existing data on metabolism in the harbor seal and uses these values in a population model based upon metabolism, reproductive cycles, food availability, and temperature. Ultimately, this model is used to determine the best combination of seasonal food availabilities and temperature for pupping.

The northern fur seal provides a special case of the problem approached in Chapter 2. Fur seals of the same genetic line but breeding 25° of latitude apart are investigated in terms of timing of birth. The role of photoperiod in setting the reproductive cycle constitutes Chapter 5. This allows an interesting comparison: fur seals are of the Otariidae while harbor seals are of the Phocidae.

Chapter 6 reports the reproductive status and serum progesterone levels in the third seasonal breeder, the Dall porpoise. The feasibility of using samples from incidentally killed marine mammals is discussed here.

The last chapter serves as a short, general conclusion to this thesis. In it, the use of the photoperiod equation and the roles of photoperiod, delayed implantation, and seasonality in the birthing season of marine mammals are briefly discussed.

CHAPTER 2

PHOTOPERIOD AND THE TIMING OF PUPPING IN THE PACIFIC HARBOR SEAL

INTRODUCTION

The Pacific harbor seal, Phoca vitulina richardsi (Shaughnessy and Fay, 1977), inhabits a 16,000 kilometer arc along the North American west coast. At any given locality within this range, harbor seals experience wide seasonal fluctuations in photoperiod, food availability, air and water temperature, and other climatic and oceanic conditions. Despite these regimens of seasonally changing parameters, harbor seals maintain a rigid and precisely timed reproductive cycle, presumably regulated by one or more of these environmental factors. Seals in one area give birth to pups during a very short period, but this period varies from place to place (Bigg, 1969a). In addition, there is an obligate delay of implantation in this species (Fisher, 1954). Considering the narrow range of birthing dates and the presence of delayed implantation, photoperiod is viewed as the probable exogenous cue used for the initiation of blastocyst implantation, and hence may regulate the timing of the reproductive cycle.

EVOLUTION McLaren (1966) has suggested that the ice-breeding harbor seal, Phoca largha, evolved from a ringed seal ancestor (genus Pusa) in the western North Pacific, and gave rise to the land-breeding harbor seal, Phoca vitulina. This land-breeding form subsequently invaded the North Atlantic via the Arctic Ocean. Currently, two species are recognised in the genus Phoca: the largha or spotted seal (Phoca largha), and the harbor or common seal (Phoca vitulina). There are five subspecific groups of Phoca vitulina, each associated with a distinct geographical feature: P. v. vitulina in the eastern North Atlantic; P. v. concolor in the western North Atlantic; P. v. mellonae in the

land-locked Seal Lakes region of Quebec; P. v. richardsi in the eastern North Pacific; and P. v. stejnegeri of the western North Pacific (Bonner, 1979; Shaughnessy and Fay, 1977).

RANGE The Pacific harbor seal is found in the coastal waters of North America from Isla San Martin, Baja California to the Pribilof Islands and the Aleutian Chain of Alaska (Scheffer, 1967; Scheffer, 1974; Shaughnessy and Fay, 1977). The approximate latitudinal range of this subspecies encompasses 31 degrees of latitude, and extends from 30°N to 61°N (figure 1). This very wide breeding range provides an excellent opportunity to study possible photoperiodic effects involved with reproductive timing in these seals.

NATURAL HISTORY Early descriptions of Pacific harbor seals were made by Allen (1802) and Scammon (1874).

"It never exceeds six feet in length; and its thick body, with short limbs, gives the animals a bloated appearance, which seems ill adapted to much activity. Its head is short, broad, and rounded; the eyes are large, full, and expressive... The color of the animal varies but little from a light gray, thickly mottled with dull black on the back and half-way down its sides, then changing to a dingy white underneath, with here and there distinct spots of darker shades" (Scammon, 1874).

Throughout its range the Pacific harbor seal appears to be a highly opportunistic predator, with an ability to change from one food type to another (Bonner, 1979). Prey identification studies have shown a wide variety of fishes and cephalopods in the diet (Wilke, 1957; Spalding, 1964; Scheffer and Sperry, 1931; Pitcher, 1980; Graybill, 1981; Jones, 1981; and Brown and Mate, 1983). Harbor seals are generally found in small, loosely structured aggregations occupying bays, estuaries, and nearshore rocks.



Figure 1. Range of the Pacific harbor seal (*Phoca vitulina richardsi*).

REPRODUCTION Physiological estrus occurs at the cessation of lactation in the harbor seal (Bishop, 1968; Bigg, 1969b; Fisher, 1954). Approximately 5 to 6 weeks after parturition, mating occurs. Despite the fertilization of the ovum, development of the blastocyst is arrested during a period of embryonic diapause, also referred to as delayed implantation (figure 2). Implantation and reactivation of the blastocyst occur approximately two and one-half months after estrus, or about three and one half months after parturition in multiparous females (Table 1).

Prenatal growth appears to be linear for both males and females (Bigg, 1969b) and occurs over the 36 to 39 week gestation period (Bishop, 1968; Bigg, 1969b). Females give birth to their pups on isolated haul-outs or in water (Lawson and Renouf, 1985; Newby, 1973; Knutson, 1977). Bigg (1984) has discussed the role of coming ashore in parturition in the northern fur seal, however this does not appear to be a factor in harbor seals. Boulva (1975) suggested that air and water temperature may influence the timing of parturition, although the timing of implantation appeared to be fixed.

The delay of implantation forms a very intriguing sequence in the reproductive cycle of the harbor seal. This "delay" in reproductive events is widespread in mammals and has been reported in 16 families and 86 species (Renfree and Calaby, 1981). An obligate delay of implantation has been found in 9 of 10 genera of the family Phocidae, and in all six genera of the family Otariidae, but not in the walrus (family Odobenidae) (Boshier, 1981). Fries (1880) first suggested that embryonic diapause provides a mechanism to allow young to be born when conditions were "optimal." In general, this mechanism is manifested in the timing of parturition in the pinnipeds.

Harbor seals display very precise timing of parturition. This is reflected not only in annual timing of parturition in individual seals, but in the year to year timing of parturition within a single, specific population (Table 2). However, populations in different locations may display widely varying

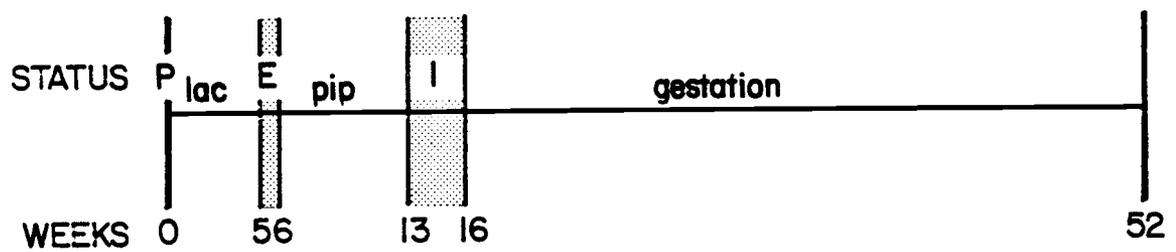


Figure 2. Diagrammatical representation of the female harbor seal reproductive cycle showing timing of reproductive events relative to parturition. Status: P = parturition, lac = lactation, E = estrus, pip = preimplantation period, I = implantation.

Table 1. Approximate timing of estrus and blastocyst implantation in days after parturition in the Pacific harbor seal.

<u>Estrus</u>	<u>Implantation</u>	<u>Reference</u>
35	95	Bishop, 1968
43	110	Bigg, 1969b
	105	Fisher, 1954
42		Bigg and Fisher, 1975

mean dates of parturition. Pupping dates of individual captive animals are similar from year to year. For example, Janet, a harbor seal at the Denver Zoological Gardens, produced four pups in five years with a range in birth dates of only three days (Schmidt, pers. comm., 1982). Extensive records from the Seaside aquarium (Johnson, 1969) show ranges in parturition dates of individual seals of no more than 7 weeks (Table 2a). Year to year comparisons of the timing of parturition in a specific population were made by Boulva (1975). A colony of harbor seals (P. v. concolor) at Sable Island, Nova Scotia (Table 2b) displayed a mean date of parturition (+/- S.E.M.) of 24 May +/- 1.45 days. The standard deviation in year to year mean date of parturition was 2.5 days, with an average duration of the pupping season of 31 days. The mean dates of parturition for seals living on southeast Vancouver Island, British Columbia (Bigg, 1969b), and captive animals at the Seaside Aquarium, Oregon (Johnson, 1969), are significantly different ($P < 0.001$; Student's t-test). However, the variances about the means are not significantly different. Standard deviations of 16.10 and 16.60 days, respectively, were obtained for the two populations (Table 3).

Scammon (1874) first recorded a major difference in the pupping seasons between harbor seals in California (June and July) and in Puget Sound (July and August). A cline in the pupping season of the Pacific harbor seal was described by Bigg (1969a). The pupping season was reported to occur later southeast from Alaska to Washington, and earlier south from Washington to Mexico.

Suggestions of a relationship between photoperiod and reproductive timing in the pinnipedia have been offered by Elden et al. (1971), Daniel (1981), and Temte (1985; Chapter 5) for the northern fur seal (Callorhinus ursinus), by Schusterman et al. (1981) for California sea lions (Zalophus californianus), and by Bigg and Fisher (1975) in the Pacific harbor seal. Bigg and Fisher (1975) proposed that

Table 2a. Pupping dates of individual harbor seals.

Location	Denver Zoo		Seaside Aquarium*		
	Janet	Flipper	Susie	Clara	
Pupping dates	2/27/75	6/17/52	5/05/51	5/25/59	
	2/24/77	6/10/54	6/19/54	6/05/60	
	2/24/78		6/11/54	5/05/61	
	2/27/79		6/16/55		
			6/28/56		

* data from Johnson (1969).

Table 2b. Year to year mean pupping dates from a single colony of harbor seals at Sable Island, Nova Scotia (Boulva, 1975).

<u>Year</u>	<u>Onset</u>	<u>Conclusion</u>	<u>Total Days</u>	<u>Mean Date</u>
1970	8 May	8 June	32	24 May
1971	11 May	7 June	28	21 May
1972	7 May	10 June	35	26 May
MEAN	9 May	8 June	31	24 May +/- 1.45 days

Table 3. Mean pupping dates from two colonies of harbor seals.

Location	S. E. Vancouver Island	Seaside Aquarium
Duration	1 year	17 years
Number of births	39	19
Reference	Bigg, 1969b	Johnson, 1969
<hr/>		
Mean date of birth	24 July (d=215)	6 June (d=167) *
Variance	259.21	275.56 **
Standard deviation	16.10 days	16.60 days
Standard error	2.60 days	3.81 days

* $P < 0.001$; ** N.S.

a type-I photoperiod effect (Wolfson, 1964) probably occurred in harbor seals: photoperiod is used to seasonally entrain an endogenous rhythm in the reproductive cycle.

ENDOCRINOLOGY There is little information on the endocrinology of delayed implantation in the pinnipeds. Furthermore, few studies have been made of general endocrinology of pinnipeds. Corticosteroids have been investigated in Weddell seals (Leptonychotes weddelli: Borrueal et al, 1974; Liggins et al, 1979), in gray seals (Halichoerus grypus: Sangalang and Freeman, 1976), and with thyroxine in a study of moult in the harbor seal (Riviere et al, 1977). Testosterone concentration was determined in three gray seals by a double isotope derivative method by Sangalang and Freeman (1976).

The newer technique of radioimmunoassay (RIA: Abraham, 1974) has been used to determine the plasma concentration of progesterone in northern fur seals (Daniel, 1975), harbor seals (Raeside and Ronald, 1981), gray seals (Boyd, 1983) and in gray seal placentas (Hobson and Boyd, 1984). RIA has also been employed to determine the plasma concentration of estrogens in the same three species (Daniel, 1974; Raeside and Ronald, 1981; Boyd, 1983), and the levels of plasma melatonin in the southern elephant seal (Mirounga leonina) (Griffiths et al, 1979).

Recently, Hobson and Boyd (1984) utilized bioassay to measure the activity of chorionic gonadotropin in the placentae of gray seals. Cross-reactivity with hCG (human chorionic gonadotropin) and ability to neutralize anti-hCG antiserum was demonstrated.

OBJECTIVES This study was originated with the following objectives in mind:

- (1) improve the resolution of the cline in the pupping season of the Pacific harbor seal from that presented by Bigg (1969a);

(2) use the photoperiod equations to analyse the latitudinal cline in the pupping season in terms of photoperiod regimens;

(3) examine the seasonal concentrations of progesterone and testosterone in the harbor seal; and

(4) propose an hypothesis pertaining to the formation of distinct populations of North Pacific harbor seals.

METHODS

DATA SETS An extensive literature search was conducted to obtain mean, specific, and ranges of dates of parturition in the Pacific harbor seal (Phoca vitulina richardsi), the Kuril seal (P. v. stejnegeri), and the spotted or largha seal (Phoca largha) at several latitudes (Appendix I). Data were organized into the following categories:

- a) STATUS: 0 = mean date of pupping
 1 = onset of pupping season
 2 = conclusion of pupping season
 3 = specific date of pupping (individual)
 4 = fetal seal obtained
 5 = premature pup / pup born dead
 6 = pup without umbilicus
 7 = captive seal pupping date
 8 = pup born dead in captivity
 9 = premature pup in captivity
- b) LOCATION: eight letter code word
- c) LATITUDE: degrees, minutes
- d) DATE: month, day.

The data were then organized into five data sets:

- 1) PDATA1 - Coastal Phoca vitulina richardsi (P. r. v.)
- 2) PDATA2 - Puget Sound / Strait of Georgia P. v. r.
- 3) PDATA3 - all P. v. r.
- 4) PDATA4 - Phoca vitulina stejnegeri
- 5) PDATA5 - Phoca largha.

When data for the mean date of pupping for a colony was reported as a general period of a month, a date was generated as follows: 7 for early-month; 14 for mid-month; and 21 for late-month. The biases introduced by this conversion should be minimal due to the size of the sample.

COMPUTER PROGRAMS A FORTRAN 77 program, PUPPIN (Appendix II), was written to allow the conversion of latitude and date information on pupping to photoperiod values. For each record of birth the photoperiod (equation 33; Appendix III) and the instantaneous rate of change of photoperiod (equation 34; Appendix III) were calculated on the day of parturition (day 0), and on the approximate dates of estrus (day 35 post partum) and blastocyst implantation (day 105 post partum). The Statistical Interactive Package System (SIPS) (Rowe and Brenne, 1982) was utilized for statistical analysis of the resulting sets of photoperiod values.

Records of the mean dates of pupping for colonies of harbor seals (MDPC: status code 0) and of specific dates of pupping for individual seals (SDPI: status code 3) were each used as separate data sets in a relative time series analysis of photoperiod effect on reproductive timing. A second FORTRAN 77 program, PROBE, was modified from PUPPIN and used to determine the photoperiod and the instantaneous rate of change of photoperiod at each recorded mean date of pupping or individual pupping, and at intervals of 10 days starting on the day of each pupping for a duration of 360 days. This provided a set of photoperiod cycles for individuals and colonies of harbor seals set relative to the parturition event. SIPS was used to perform regressions of photoperiod (P) and instantaneous rate of change of photoperiod (P') to latitude for each 10 day interval, and for each data set. The correlation coefficient, coefficient of determination, and the slope of the regression line were determined at each 10 day interval. The method of analysis is summarized diagrammatically in figure 3. The objective of this analysis was to find a point

PUPPING DATE DATA

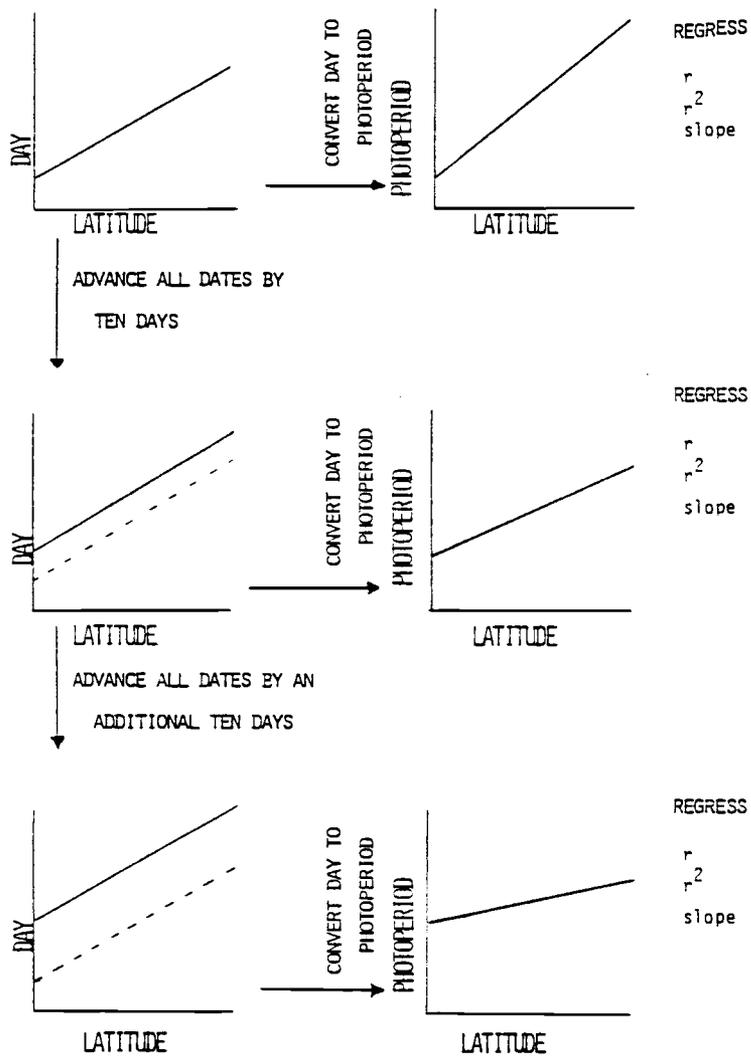


Figure 3. Methods of photoperiod analysis.

in the reproductive cycle, relative to the time of parturition, when the effect of photoperiod over the latitudinal range is negligible (ie. slope of regression of P or P' on latitude is zero).

BLOOD SAMPLES Samples of harbor seal blood were collected from Columbia River animals on an opportunistic basis during radio-tagging studies. Animals were captured by Washington Game Department personnel during July, 1981 and in March and April, 1982. Samples were also collected from captive animals at the Point Defiance Zoo and Aquarium, Tacoma, Washington, during September, October, and November, 1982. The harbor seals in captivity at the Point Defiance Zoo were obtained as pups on the Washington coast (Jim Short, pers. comm., 1985). Due to reconstruction of the zoo facilities, only limited blood samples were obtained.

A total of 21 and 11 blood samples were drawn from female and male harbor seals, respectively: July, 1981 (7 ♀, 2 ♂); March-April, 1982 (7 ♀, 3 ♂); September-November, 1982 (7 ♀, 6 ♂). Blood was collected from the intervertebral, subdural sinus using a 3-1/2 inch, 18-gauge spinal tap needle with a 30-50 cc syringe, or from the plantar aspect of the hind flipper with a 1-1/2 inch, 18-gauge needle with a 10 cc syringe (Geraci and Sweeney, 1978). Each blood sample was immediately transferred to a 10 ml heparinized (green top) Vacutainer tube and placed on ice until centrifugation. The sample was centrifuged for 8 minutes using an International Clinical Centrifuge (model CL). The serum (harbor seal blood tended to coagulate even with the heparin) was then decanted into 1.5 ml, plastic micro-centrifuge tubes and frozen at -20°C until hormone assays were performed.

SERUM PROGESTERONE DETERMINATION Serum progesterone concentration was determined for female harbor seals using radioimmunoassay (RIA). The method was identical to that developed by S. Spielvogel (Oregon State University) and used by

Temte and Spielvogel (1985) for incidentally-killed female Dall porpoises. Triplicate volumes (25 μ l) were doubly extracted using a 1:2 benzene:hexane mixture. The antiserum used, anti-progesterone-11-BSA (No. 1337, Gorden D. Niswender) does not significantly bind other steroids at physiological concentrations (Koligian and Stormshak, 1977). The binding of the antiserum in the assay performed was 37.8%. The competitor was [³H] progesterone (3000 cpm in 100 μ l; New England Nuclear; 114 Ci/mole). Intraassay variability, calculated as the coefficient of variation was 9.1%. The sensitivity of the assay was found to be 0.3 ng/ml (7.8 pg/tube).

SERUM TESTOSTERONE DETERMINATION Serum testosterone concentration was determined in male harbor seals using RIA techniques. The method was similar to that for progesterone. Again, triplicate volumes (25 μ l) were doubly extracted with benzene-hexane (1:2). The antiserum was anti-testosterone (No. S-250, Gorden D. Niswender) and yielded a binding of 58% for this assay. The competitor was [³H] testosterone (NET-553, New England Nuclear). Intraassay variation had a coefficient of variation of 8.6%. The sensitivity was found to be 0.3 ng/ml (7.8 pg/tube).

RESULTS

TIMING OF PUPPING Pupping in the Pacific harbor seal occurs as early as 1 February at Isla San Martin, Baja California (30°30'N) and as late as 15 October in Puget Sound, Washington (47°22'N). These dates enclose a 257 day pupping season in this subspecies. Seals on the coast of North America (excluding those inhabiting Puget Sound and the Strait of Georgia) display a grand mean date of pupping of 16 May. The mean onset of the pupping season occurs an average of 23 days before the mean date of pupping and pupping is concluded, on the average, 25 days after the mean date of pupping, yielding a 49 day mean pupping period.

Premature pups were reported an average of 20 days prior to the mean date of pupping, and pups without umbilici 18 days after the mean date of pupping (Table 4).

Mean dates of pupping are presented for two data sets: one comprised of the mean dates of pupping of colonies of harbor seals (MDPC), and the second of the specific pupping dates of individual seals (SPDI). Also, all harbor seal data have been further subdivided into five geographical groups: all Pacific harbor seals, coastal Pacific harbor seals, Puget Sound - Strait of Georgia harbor seals, Kuril seals, and largha seals (figure 4). Coastal Pacific harbor seals and Kuril seals pup at approximately the same time, whereas the pupping of the largha seal is considerably earlier, coinciding with the Bering Sea ice break-up, and that of the Puget Sound - Strait of Georgia (PS-SG) harbor seals is delayed by an average of 88 days. The mean dates of pupping of coastal and PS-SG seal populations are significantly different ($P < 0.01$; Wilcoxon rank sum) for both data sets (figure 4). Because Pacific harbor seals within the PS-SG system pup significantly later as a group, and because their pupping occurs approximately three months later than that of coastal seals found at the same latitude, the PS-SG population has been excluded from the photoperiod analysis of the cline in the pupping season.

CLINAL NATURE OF PUPPING ON THE PACIFIC COAST The mean dates of pupping for colonies of Pacific harbor seals define a latitudinal cline (figure 5) with the best fitting linear slope significantly different from zero ($P < 0.001$; Student's t-test). The mean dates of pupping for PS-SG seals are notably later than coastal seals at similar latitudes. The mean pupping dates for Kuril seal colonies fall along the cline for the Pacific harbor seal, whereas the mean pupping dates for largha seal colonies are considerably earlier. Specific dates of pupping of individual seals also display a latitudinal cline (figure 6) with a slope significantly different from zero ($P < 0.001$; Student's t-test).

Table 4. Mean dates of events associated with pupping for Pacific harbor seals on the coast of North America. Seals from PS/SG have been excluded.

	<u>Number</u>	<u>Mean Date</u>	<u>d +/- S.E.M.</u>
Pupping for all colonies	47	16 May	146.1 +/- 4.7
Pupping for all individual seals	52	17 May	147.6 +/- 5.0
Onset of the pupping season	53	23 Apr	123.0 +/- 4.5
Conclusion of the pupping season	44	11 Jun	172.3 +/- 4.8
Occurrence of premature pups	27	27 Apr	127.7 +/- 11.7
Occurrence of pups without umbilici	45	4 Jul	164.7 +/- 7.1

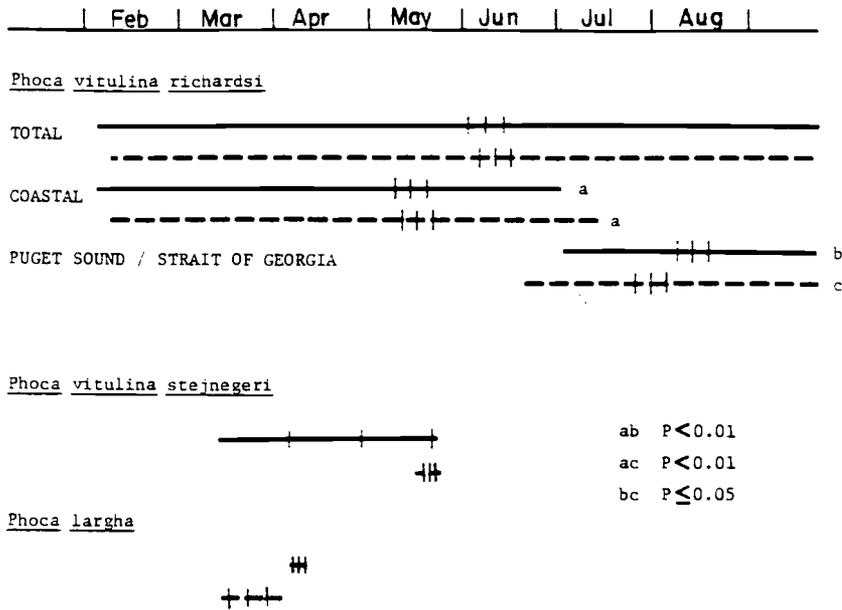


Figure 4. Mean dates of pupping with standard error bars and ranges for North Pacific harbor seals (Genus *Phoca*). Solid lines are MDPC data; dashed lines are SDPI data. Means with differing subscripts are significantly different.

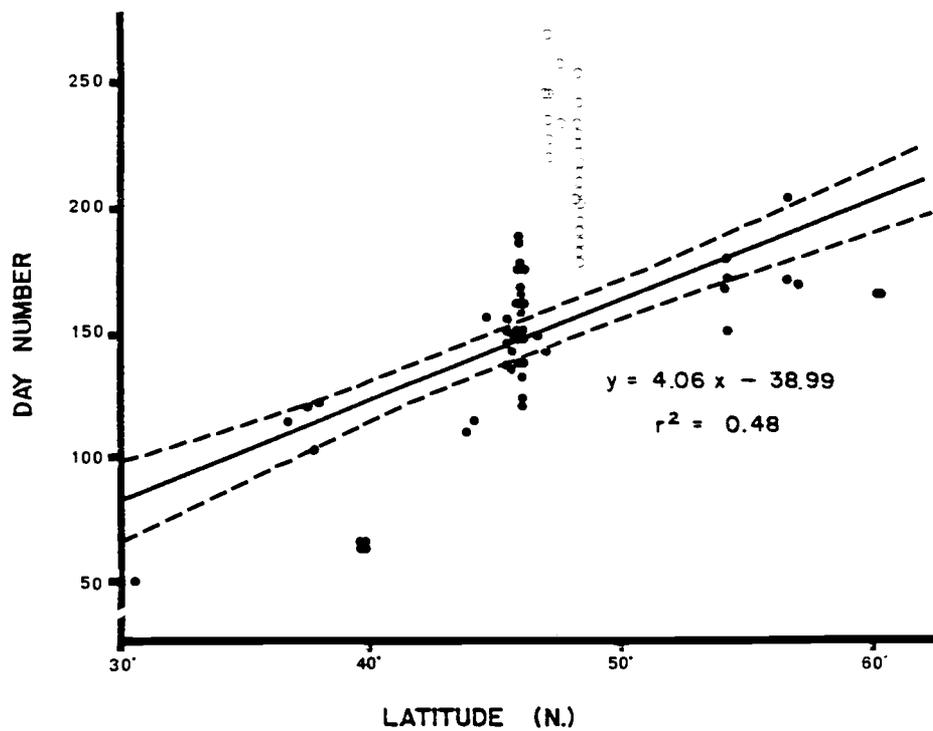


Figure 6. Individual dates of birth for harbor seals along the North American west coast (●) and within PS/SG (○). Regression for coastal seals only.

The onset and conclusion of the pupping seasons along the west coast also show similar clines (figure 7). The slope of 2.78 ± 0.31 days/degree of the cline established for the mean dates of pupping of colonies is different from that of 4.06 ± 0.46 days/degree of the cline of the specific dates of pupping at a significance level of 0.05, but not at 0.01. As points in the MDPC data set are actually composed of several actual puppings, it is more robust, and should be weighted accordingly. However, the SDPI data set serves as a good comparison set.

USE OF PHOTOPERIOD EQUATION With the photoperiod equation it is possible to map photoperiods over latitude and date (figures 8a and 8b). If the cline in the pupping season over the 31° latitudinal range of the Pacific harbor seal is defined by a single specific photoperiod, that photoperiod must be within the narrowest range of photoperiods present (unshaded areas). Furthermore, if a single specific photoperiod is responsible for the entrainment of the reproductive cycle of coastal Pacific harbor seals, it needs to be between 10 and 14 hours of daylight per day, or that available at 30°N . Also, the pupping dates would have to be clustered parallel to one of the contour lines on the photoperiod map.

PHOTOPERIOD AND THE TIMING OF PUPPING The photoperiod (P) and the instantaneous rate of change of photoperiod (P') were calculated at date of each pupping, and at the approximate dates of estrus (35 days post partum) and implantation (105 days post partum) for the MDPC and SDPI data sets. Regression of the resulting P and P' to latitude yielded slopes significantly different from zero (Table 5), indicating that neither photoperiod nor instantaneous rate of change of photoperiod at the time of pupping, estrus, or implantation define the cline.

An analysis of a time series of photoperiod throughout the annual reproductive cycle became essential to further study the possible effects of photoperiod. The correlation coefficient

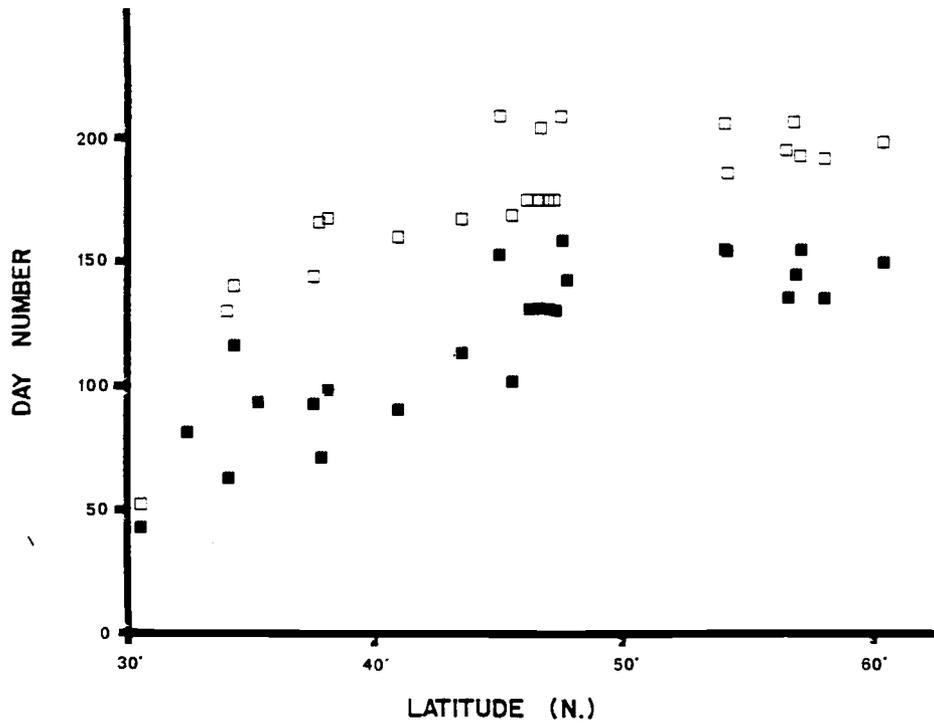


Figure 7. Dates reported for onset (■) and conclusion (□) of harbor seal pupping seasons along the west coast of North America.

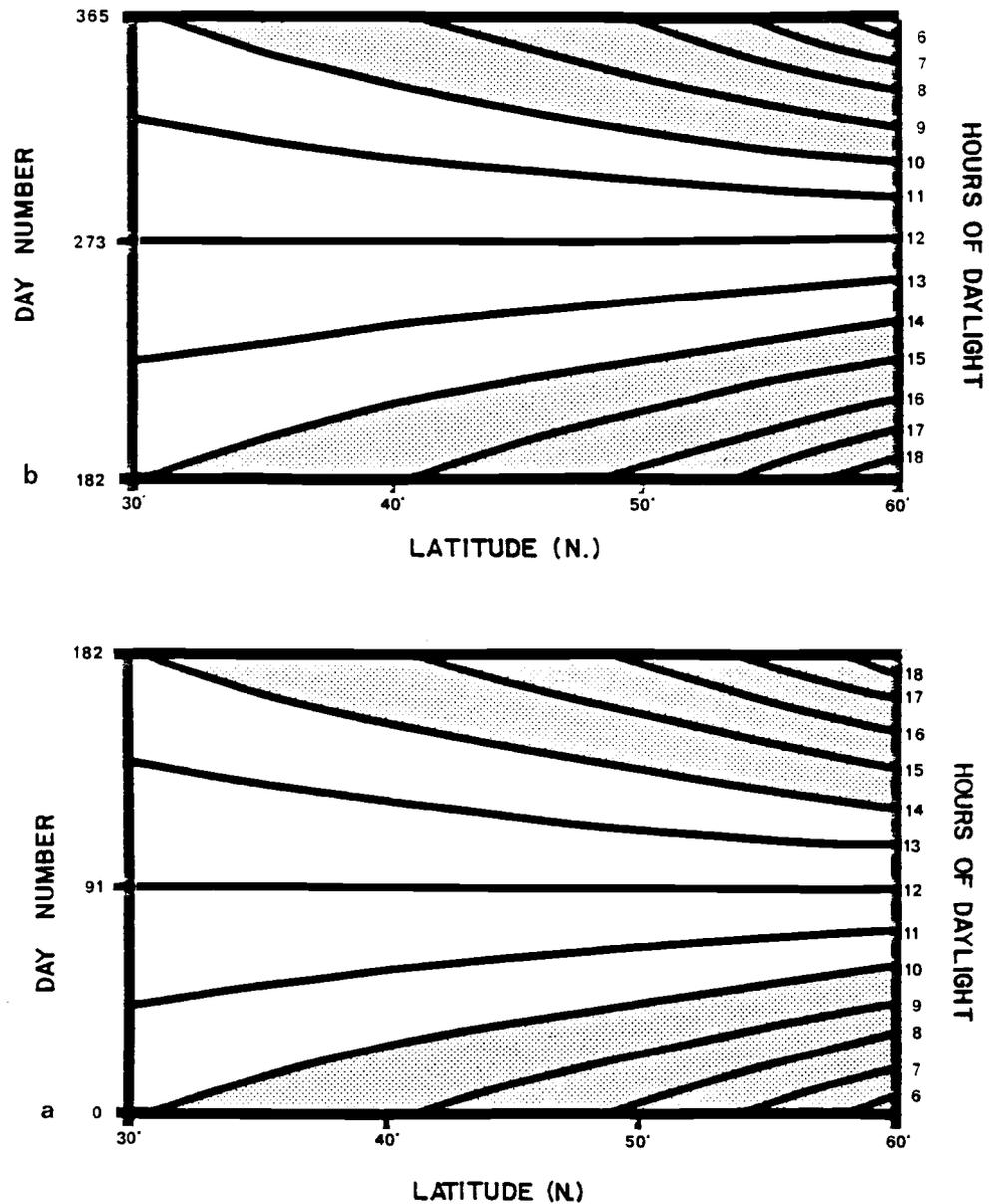


Figure 8a. Contour plot of photoperiod as determined by photoperiod equation between the winter (day 0) and summer (day 182) solstices and 30°N and 60°N latitude.

8b. As above but between the summer (day 182) and winter (day 365) solstices. Stippled areas depict photoperiods that cannot explain a cline over the entire range.

Table 5. Means and ranges of photoperiod and dP and regressions of photoperiod vs. latitude and dP vs. latitude at the dates of pupping, estrus, and implantation in coastal Pacific harbor seals. Data set is indicated by MDPC (mean date of pupping for colonies) and SDPI (specific date of pupping for individuals).

<u>Event</u>	<u>Data Set</u>	<u>Day</u>	<u>Photop.</u>	<u>S.E.M.</u>	<u>Range</u>	<u>Regression equation</u>	<u>r²</u>
Pupping	MDPC	0	14.56	0.28	11.06 / 17.88	y = 0.20x + 5.58	0.936
	SDPI	0	14.34	0.22	11.17 / 17.32	y = 0.23x + 3.79	0.773
Estrus	MDPC	35	14.70	0.18	11.79 / 16.67	y = 0.11x + 9.47	0.802
	SDPI	35	14.58	0.15	11.90 / 16.71	y = 0.13x + 8.48	0.523
Implantation	MDPC	105	12.51	0.12	10.81 / 13.97	y = -0.07x + 15.61	0.610
	SDPI	105	12.51	0.13	9.90 / 14.53	y = -0.10x + 17.61	0.405

<u>Event</u>	<u>Data Set</u>	<u>Day</u>	<u>dP</u>	<u>S.E.M.</u>	<u>Range</u>	<u>Regression equation</u>	<u>r²</u>
Pupping	MDPC	0	0.037	0.006	-0.082 / 0.098	y = 0.002x - 0.035	0.154
	SDPI	0	0.036	0.004	-0.065 / 0.090	y = 0.002x - 0.042	0.120
Estrus	MDPC	35	-0.020	0.006	-0.083 / 0.044	y = -0.004x + 0.175	0.769
	SDPI	35	-0.017	0.006	-0.083 / 0.050	y = -0.001x + 0.206	0.459
Implantation	MDPC	105	-0.032	0.002	-0.061 / 0.022	y = -0.001x + 0.028	0.821
	SDPI	105	-0.032	0.003	-0.061 / 0.035	y = -0.003x + 0.086	0.470

(figure 9) and the coefficient of determination (figure 10) indicate two times during the reproductive year, following parturition, when photoperiod can define the cline. That is, in the year relative to parturition (mean dates for colonies and specific dates for individuals) all animals in the entire latitudinal range are twice exposed to the same photoperiod. This occurs at 68 and 251 days post partum. The 68th day post partum occurs between parturition and implantation, and could be used as an exogenous cue for the initiation of blastocyst implantation, and hence regulate reproductive timing.

The slope of the regression equation of photoperiod vs. latitude is 0.00 hours per day per degree at approximately 68 days post partum (figure 11; Table 6), and attains a maximum value at 13 days post partum. Photoperiod shows no clinal nature at 68 days post partum (figure 12) for the MDPC data set and this does not appear to be an artifact (ie. the points are linear showing no upward or downward bowing). The cline disappears slightly earlier for the SDPI data set (Table 7).

PHOTOPERIOD DIFFERENCES BETWEEN COASTAL AND PS/SG SEALS

Populations of Pacific harbor seals on the west coast of North America experience a photoperiod of 13.80 ± 0.08 h/day (mean \pm S.E.M.) at 68 days post partum; populations within the PS-SG system experience a photoperiod of 10.83 ± 0.20 h/day at 68 days post partum. Individual seals from coastal populations experience a mean photoperiod (\pm S.E.M.) of 13.72 ± 0.10 h/day at 68 days post partum, whereas individual seals from the PS-SG system are exposed to 11.33 ± 0.20 h/day. A bimodal frequency distribution in the photoperiods present at 68 days post partum for all Pacific harbor seal colonies from the MDPC data set (figure 13) reflects the significant difference ($P < 0.001$; Student's t-test) between coastal and PS-SG seals. A similar distribution for SDPI data (figure 14) also demonstrates the significant difference ($P < 0.001$; Student's t-test) between the two locations.

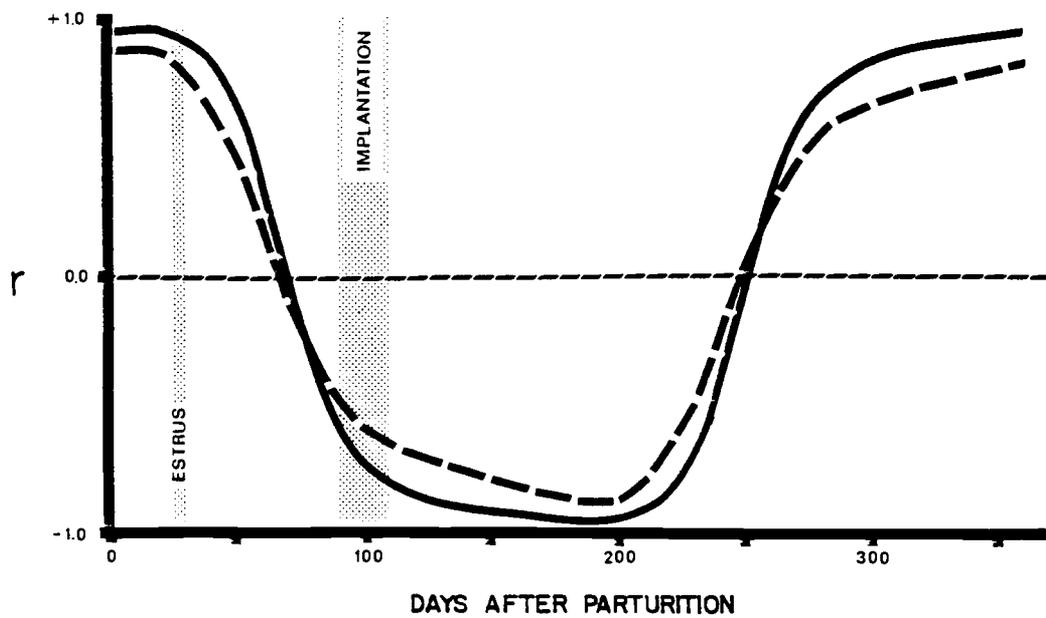


Figure 9. Correlation coefficient of photoperiod vs. latitude for the year starting at parturition (day 0) using MDPC data (solid line) and SDPI (dashed line). Stippled areas indicate relative occurrences of estrus and implantation. Cline in photoperiod disappears when $r = 0$.

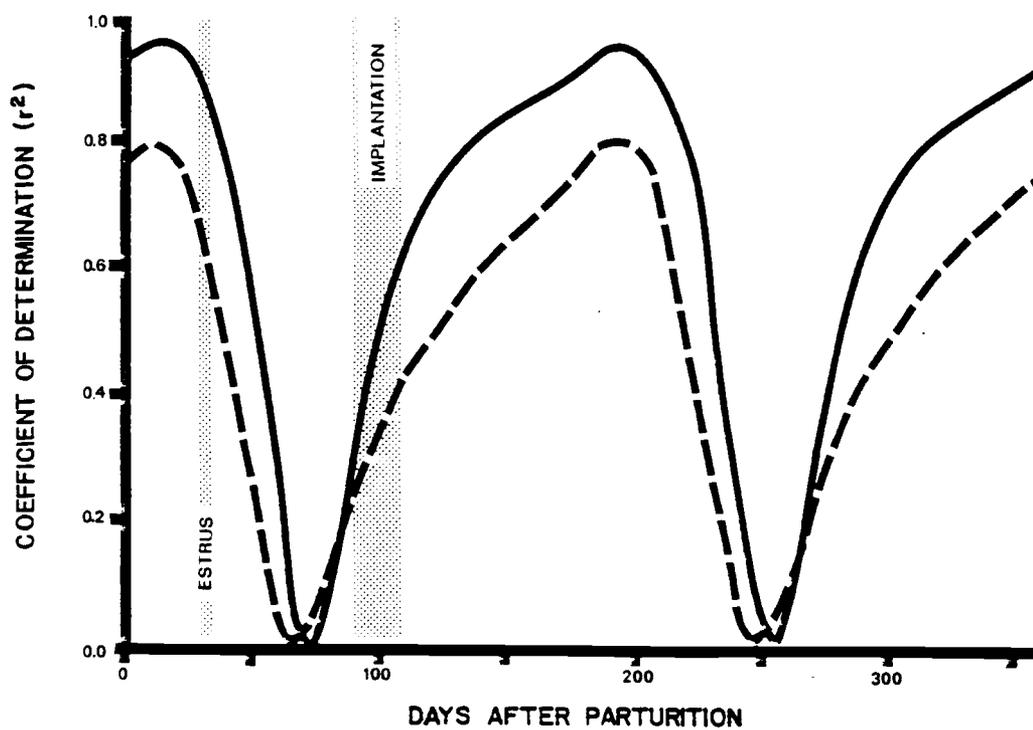


Figure 10. Coefficient of determination of photoperiod vs. latitude for the year starting at parturition (day 0) using MDPC data (solid line) and SDPI data (dashed line). Stippled areas indicate relative occurrences of estrus and implantation. Cline in photoperiod disappears when $r^2 = 0$.

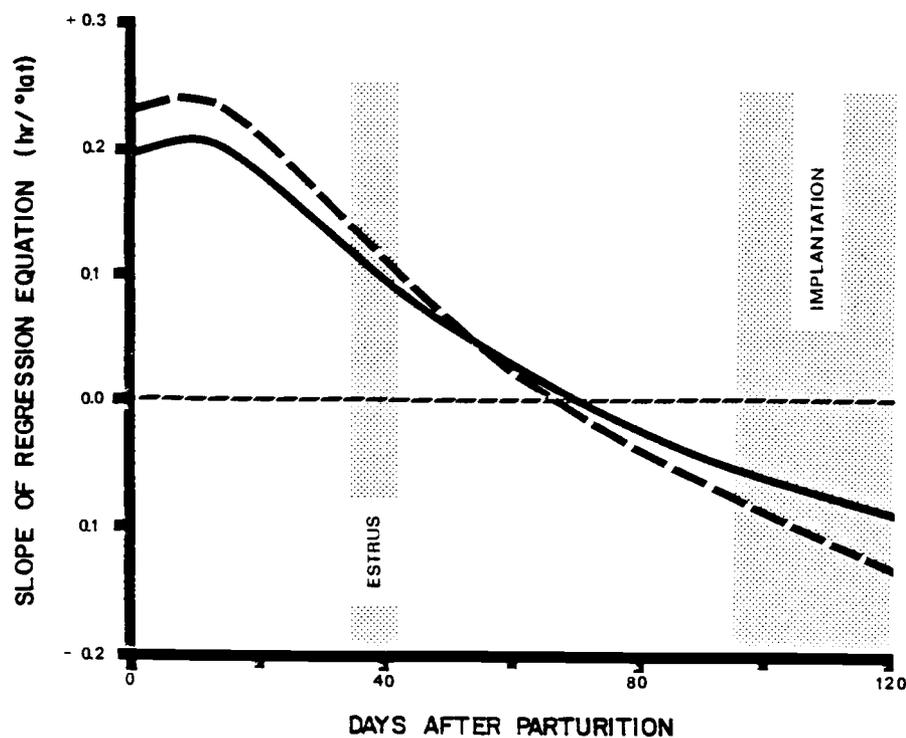


Figure 11. Slope of the regression equation of photoperiod vs. latitude for the year starting at parturition (day 0) using MDPC data (solid line) and SDPI data (dashed line). Stippled areas indicate the relative occurrences of estrus and implantation. Cline in photoperiod disappears when slope = 0.

Table 6. Means and ranges of photoperiod and dP and regressions of photoperiod vs. latitude and dP vs. latitude at the date of the proposed photoresponse in coastal Pacific harbor seals. Data set is indicated as in Table 5.

<u>Event</u>	<u>Data Set</u>	<u>Day</u>	<u>Photop.</u>	<u>S.E.M.</u>	<u>Range</u>	<u>Regression equation</u>	<u>r²</u>
Photoresp.	MDPC	68	13.80	0.08	12.32 / 14.86	y = 0.01x + 13.56	0.008
	SDPI	68	13.72	0.10	11.89 / 15.27	y = -0.01x + 14.02	0.003

<u>Event</u>	<u>Data Set</u>	<u>Day</u>	<u>dP</u>	<u>S.E.M.</u>	<u>Range</u>	<u>Regression equation</u>	<u>r²</u>
Photoresp.	MDPC	68	-0.038	0.004	-0.066 / 0.033	y = -0.003x + 0.086	0.686
	SDPI	68	-0.032	0.004	-0.066 / 0.044	y = -0.003x + 0.101	0.440

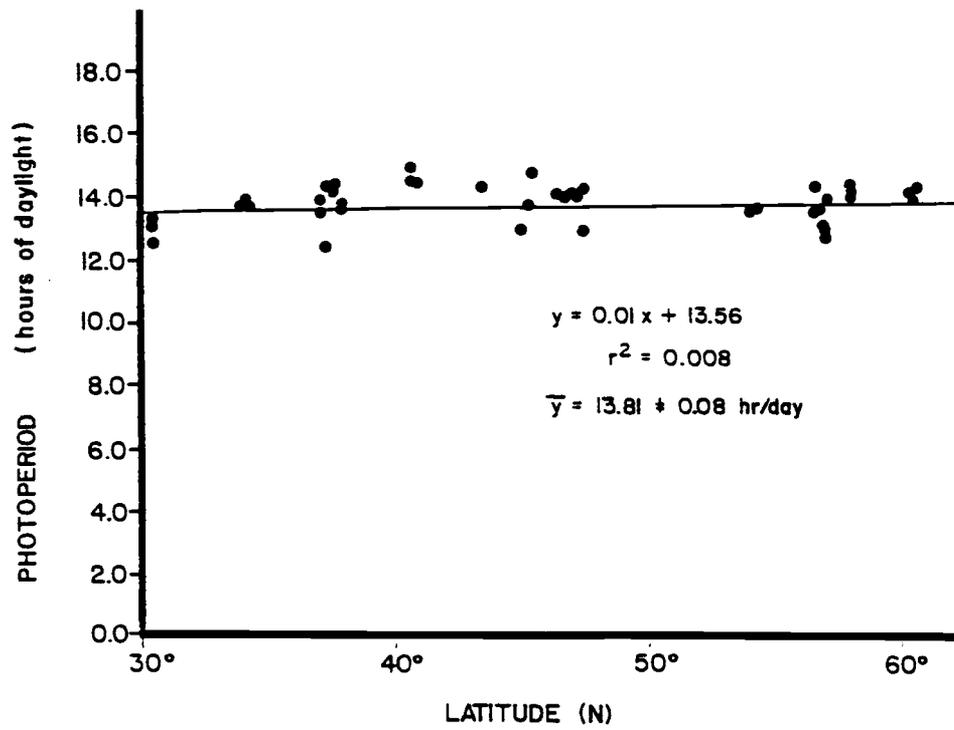


Figure 12. Photoperiod at 68 days post partum in the Pacific harbor seal (MDPC data) as a function of latitude.

Table 7. Slopes of the regression equations for photoperiod vs. latitude, with significance levels, at intervals after estrus and before implantation in the Pacific harbor seal.

<u>Days after Parturition</u>	<u>Data Set</u>	<u>Slope +/- S.E.M.</u>	<u>Significance Level* for Slope = 0.00</u>
50	MDPC	0.058 +/- 0.009	0.001
	SDPI	0.062 +/- 0.012	0.001
60	MDPC	0.027 +/- 0.009	0.01
	SDPI	0.019 +/- 0.012	0.20
70	MDPC	0.000 +/- 0.009	N.S.
	SDPI	-0.012 +/- 0.012	N.S.
80	MDPC	-0.024 +/- 0.009	0.05
	SDPI	-0.039 +/- 0.011	0.01
90	MDPC	-0.043 +/- 0.008	0.001
	SDPI	-0.063 +/- 0.011	0.001

* Student's t-test with 45 df for MDPC; 50 df for SPDI.

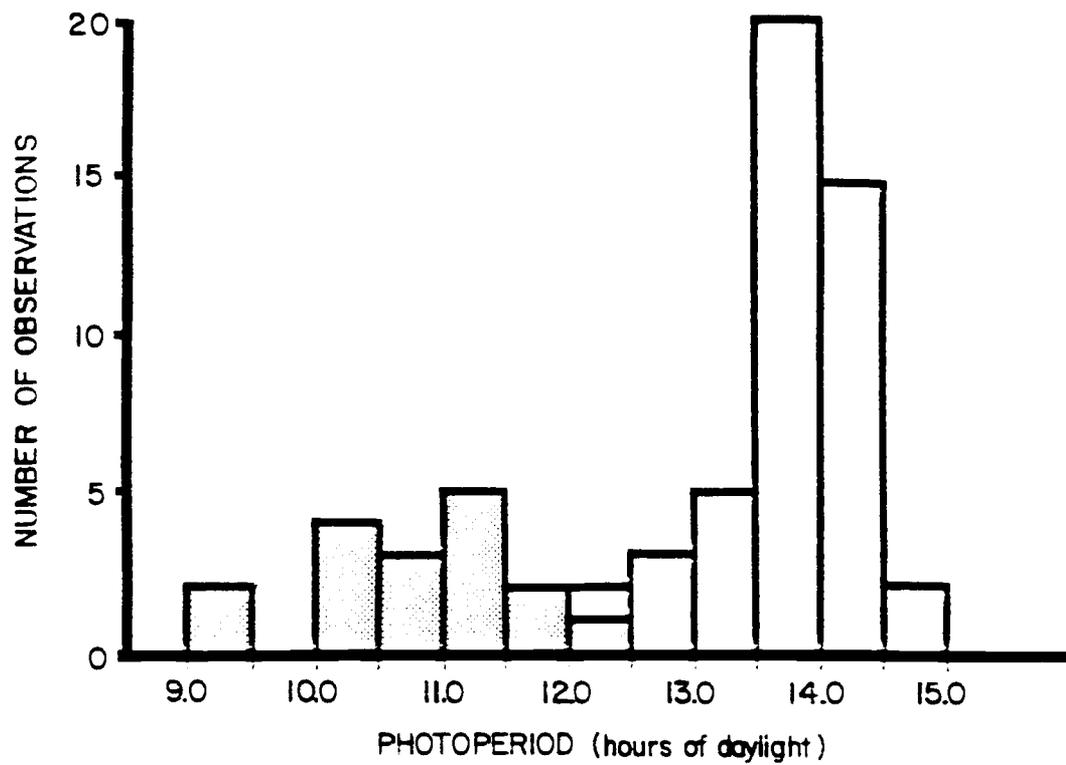


Figure 13. Frequency of observations from MDPC data of photoperiods at 68 days post partum for harbor seals in PS/SG (shaded) and along the North American west coast (unshaded).

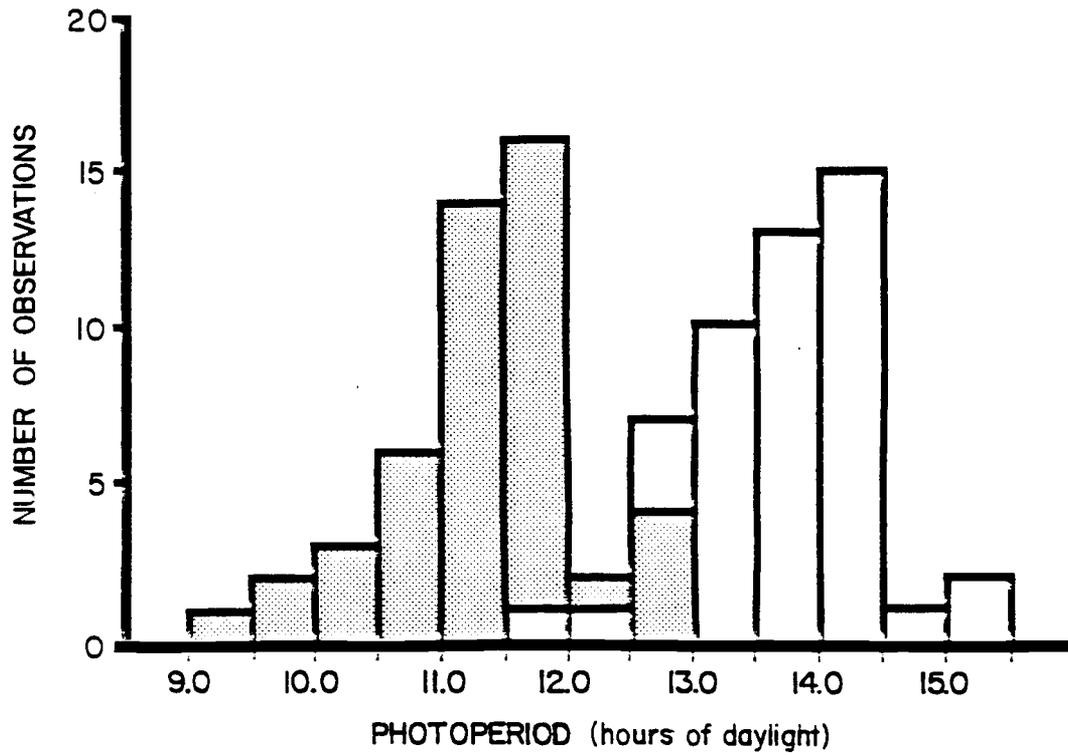


Figure 14. Frequency of observations from SDPI data of photoperiods at 68 days post partum for harbor seals in PS/SG (shaded) and along the North American west coast (unshaded).

SERUM PROGESTERONE CONCENTRATION Seven female Columbia River seals were sampled for serum progesterone during the period from 27 March to 10 April, 1982 (Table 8). Of these animals, six were determined to be pregnant by visual inspection. A mean serum progesterone concentration (\pm S.E.M.) of 33.0 \pm 4.4 ng/ml was found for the pregnant females (range: 2.4 - 74.2 ng/ml; figure 15). One adult female that was not pregnant (CF-14) had a serum progesterone concentration of 1.6 ng/ml. Seven samples were obtained from Columbia River seals during the period from 8 to 13 July, 1981, the approximate time of estrus for seals in this location (figure 15). The mean serum progesterone concentration (\pm S.E.M.) of these samples was 11.7 \pm 2.4 ng/ml (range: 0.7 - 21.5 ng/ml). An additional seven samples were taken from three captive female harbor seals at the Point Defiance Zoo on 23 September, 28 October, and 18 November, 1982. Three of these seals, PDF-1, PDF-3, and PDF-5, were pregnant (Jim Short, pers. comm., 1985) and had levels of serum progesterone between 14.4 and 18.4 ng/ml. Two other females that were not pregnant, PDF-2 and PDF-4, were each sampled twice and had between 0.4 ng/ml and 12.2 ng/ml.

SERUM TESTOSTERONE CONCENTRATION Two blood samples were obtained from adult male harbor seals on the Columbia River during the period from 28 March to 10 April, 1982 (Table 9). A third sample, CM-3, was from a subadult male which died during the tagging process. A necropsy was performed by Washington Game Department personnel and an absence of spermatogenesis was noted. A mean serum testosterone (\pm S.E.M.) of 3.6 \pm 1.6 ng/ml was found for the adult males (figure 16). Two adult males were sampled during 8-9 July, 1981 and yielded a mean serum concentration of testosterone of 2.1 \pm 0.3 ng/ml. One of the males died during the tagging process and was subsequently necropsied. No evidence of spermatogenesis was found on examination. On 23 September, 28 October, and 18 November a total of 6 blood samples were obtained from four adult and one

Table 8. Data on female harbor seals sampled for progesterone.

<u>Date</u>	<u>Location</u>	<u>Seal</u>	<u>Length</u>	<u>Weight</u>	<u>Status</u>	<u>Pregnant</u>	<u>Lactating</u>	<u>Progesterone</u>
7/08/81	Columbia River	CF-1	135 cm	56.5 kg	adult	-	-	0.7 ng/ml
7/09/81		CF-2	132	65.5	adult	-	-	11.7
		CF-3	129	65.0	adult	-	-	4.6
		CF-4	109	50.5	subadult	-	-	9.1
7/13/81		CF-5	153		adult	-	-	15.3
		CF-6	135		adult	-	-	6.1
		CF-7	145		adult	-	-	21.5
3/28/82		CF-8			adult	+	-	39.9
		CF-9			adult	+	-	21.3
		CF-10	128		adult	+	-	74.2
		CF-11	135		adult	+	-	2.4
		CF-12	133		adult	+	-	31.1
		CF-13	158		adult	+	-	2.5
		CF-14	145		adult	-	-	1.6
9/23/82	Point Defiance Zoo	PDF-1			adult	+	-	17.3
		PDF-2			adult	-	-	0.4
		PDF-3			adult	+	-	18.4
10/28/82		PDF-4			adult	-	-	12.2
		PDF-2			adult	-	-	5.3
11/18/82		PDF-4			adult	-	-	9.3
		PDF-5			adult	+	-	14.4

*Pregnancy was determined by birth or stillbirth in the nine months following sampling.
Zoo records were provided by Jim Short, Point Defiance Zoo, Tacoma, WA.

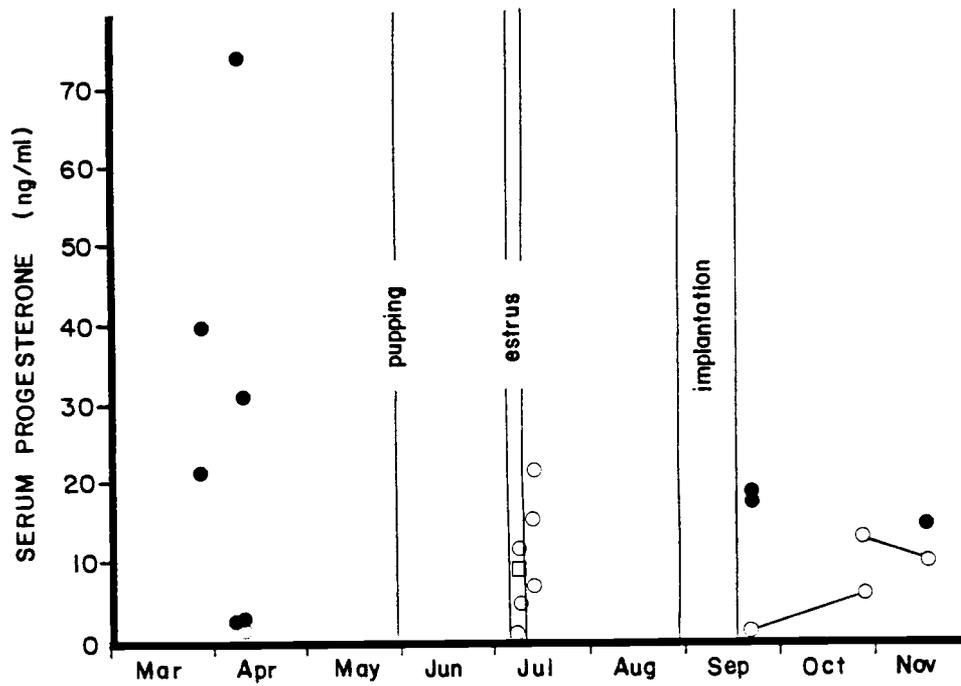


Figure 15. Levels of serum progesterone in pregnant (●), non-pregnant (○), and subadult (□) female harbor seals from the Columbia River and Point Defiance Zoo. Lines connect values from a single animal.

Table 9. Data on male harbor seals sampled for testosterone.

<u>Date</u>	<u>Location</u>	<u>Seal</u>	<u>Length</u>	<u>Weight</u>	<u>Status</u>	<u>Spermatogenesis</u>	<u>Testosterone</u>
7/08/81	Columbia River	CM-1	161 cm	104.5 kg	adult	negative*	1.8 ng/ml
7/09/81		CM-2	125		adult		2.4
3/28/82		CM-3		subadult	negative*	0.6	
4/10/82		CM-4	149	adult		5.2	
		CM-5		adult		2.0	
9/23/82	Point Defiance Zoo	PDM-1			adult		0.9
		PDM-2			adult		0.5
		PDM-3			adult		1.0
10/28/82		PDM-4			juvenile		1.1
		PDM-2			adult		0.9
11/18/82		PDM-4			juvenile		0.6

*Two of the males were sampled after death. Subsequently, the animals were necropsied and sexual state determined.

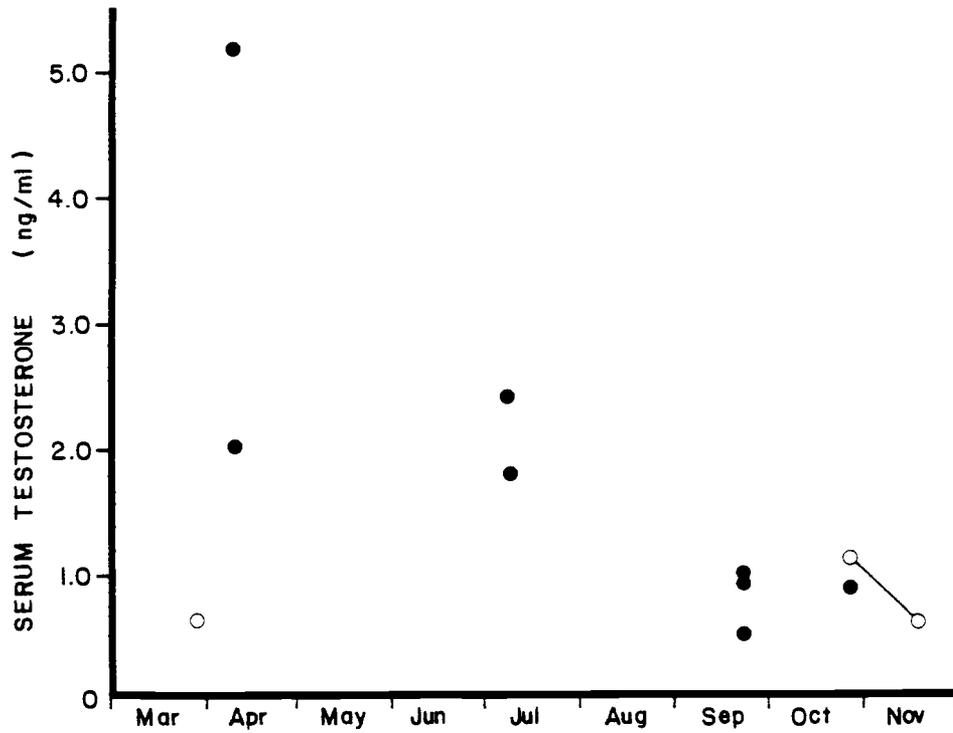


Figure 16. Levels of serum testosterone in adult (●) and subadult (○) male harbor seals from the Columbia River and Point Defiance Zoo. Line connects values from a single animal.

subadult male harbor seal at the Point Defiance Zoo. The mean serum testosterone concentration (\pm S.E.M.) for the adult males was 0.8 ± 0.1 ng/ml. Values for serum testosterone concentration of 0.6, 0.6, and 1.1 ng/ml were determined for the three samples from subadult males.

DISCUSSION

The Pacific harbor seal offers an excellent opportunity to study the effect of photoperiod on the timing of reproductive events. This species is not only found over a 31 degree latitudinal range (Shaughnessy and Fay, 1977), but has a continuous distribution over this entire range. Harbor seals are fairly conspicuous on their haul-out areas, and are readily observed during the pupping season, contributing to the wealth of data available on the onset, mean, and concluding dates of pupping for colonies and on the specific dates of parturition of individual seals. Also, as predators on commercially harvested species of fishes along the west coast, harbor seal populations have been extensively studied.

RANGE AND MOVEMENTS The range of the Pacific harbor seal is fairly unique in that it is nearly 16,000 km in length, but, with few exceptions, only 10 km in width. Recently, Stewart and Yochem (1985) have suggested that harbor seals in the Southern California Bight may be pelagic or somewhat migratory in autumn and winter. Nevertheless, strong site fidelity has been demonstrated in harbor seals on the Oregon coast and it is assumed that this occurs elsewhere. Stoel (1981) reported that 24 of 25 seals initially identified by photography were photographed three years later on the same haul-out at Strawberry Hill, Oregon. Tagging studies by Brown and Mate (1983) indicate that harbor seals will undergo regular short movements, as between Netarts and Tillamook Bays, Oregon (25 km), while remaining in the same general geographic area.

Furthermore, 45% of radio-tagged seals made at least one move from Netarts to Tillamook Bay. Pitcher and McAllister (1981) found 66% of radio-tagged harbor seals only at the haul-out tagging site in Alaska.

Longer movements have been reported in this species. Treacy and Jeffries (1983) documented movements of female harbor seals between Grays Harbor and Willapa Bay, Washington and the Columbia River Estuary during the eulachon migration. Harvey et al (1983) reported that marked seals, one pup and one 4.5 year-old male, traveled 72 and 92 km, respectively, from release sites before being resighted. Movements of a tagged female harbor seal of 225 km from Netarts Bay Oregon to the Siuslaw River, Oregon (Brown, pers. comm., 1981), and of a tagged pup from Shell Island, Oregon to Ft. Bragg, California, a distance of 400 km (Graybill, pers. comm., 1984) have been noted. Also, flipper tags from harbor seals have been recovered 550 km to the south and 75 km to the north of the Netarts Bay tagging site (Brown and Mate, 1983).

SEPARATION OF POPULATIONS Although differences in frequencies of dark pelaged seals have been reported along the range (Kelly, 1981; Shaughnessy and Fay, 1977), there is no evidence to suggest more than one continuous and interbreeding population of coastal harbor seals. However, seals inhabiting Puget Sound and the Strait of Georgia can be separated from coastal seals based upon reproductive timing. Coastal seals found at identical latitudes to PS-SG seals (Olympic Peninsula vs. Puget Sound) pup approximately three months earlier. The mean dates of pupping for both the MDPC and the SDPI data sets for coastal and PS-SG animals are significantly different ($P < 0.01$ for both data sets). This separation allows a much higher resolution of the cline in the pupping season first reported by Bigg (1969a).

CLINE IN THE PUPPING SEASON A clinal relationship in the pupping season of the Pacific harbor seal was found. A linear model for the MDPC data with a slope of 2.78 days/degree predicts

that pups are born on 3 April at 30°N and on 25 June at 60°N; the SDPI linear model, with a slope of 4.06 days/degree, predicts a 14 March birthdate at 30°N and 14 July at 60°N. As each point in the MDPC data set represents the mean date of pupping for several seals it is seen as a more rigorous representation of the cline.

These results are in agreement with those of Bigg (1969a) with the exception that pupping occurs later as one moves north from Baja California to the Pribilof Islands, Alaska. Bigg (1969a), by including points from Puget Sound, produced a two-directional cline with pupping occurring earlier both to the north and south of Washington state. This latitudinal difference in timing of reproduction is similar to that found in the northern fur seal. Fur seals breeding on San Miguel Island, California (33°N) have a 14-day advance in reproductive timing ($P < 0.001$) as compared to their "parent stock" on the Pribilof Islands, Alaska (57°N) (Temte, 1985; Chapter 5).

GENERAL TIMING OF PUPPING SEASON The analysis of data pertaining to the onset, conclusion, and mean date of pupping allows some general statements about the pupping season in this species. The grand mean date of parturition for coastal harbor seals occurred on 16 May. This is at a point 23 days into a 49 day mean pupping season. This compares well with studies of specific populations: the mean date of birth occurs approximately one-half way through the pupping season with a range of 41% to 57% (Table 10). This trend is also seen in the northern fur seal with the mean date of birth occurring 53% to 66% of the way through the pupping season.

REPRODUCTIVE CYCLE AND SOME HORMONAL CORRELATES A generalized harbor seal cycle is presented by drawing upon information from harbor seals, grey seals, harp seals, and northern fur seals. Each of these species has an obligate delay of implantation. The cycle will start with proestrus and end in lactation and proestrus for females, and with spermatogenesis in males.

Table 10. Length of the pupping season, with the relative timing of the mean date of pupping, for the Pacific harbor seal and the northern fur seal.

Harbor Seals

<u>Location</u>	<u>Length of Season (No. of Births)</u>	<u>Mean Date Relative to First Day of Birth (% of Season)</u>	<u>Reference</u>
Seaside	56 days (19)	32 (57%)	Johnson, 1969
Sable I.			Boulva, 1975
1970	32 (N.A.)	17 (53%)	
1971	28 (N.A.)	15 (54%)	
1972	35 (N.A.)	20 (57%)	
Vancouver I.	75 (39)	31 (41%)	Bigg, 1969b
West Coast	49 (N.A.)	23 (47%)	this Chapter

Northern Fur Seals

<u>Location</u>	<u>Length of Season (No. of Births)</u>	<u>Mean Date Relative to First Day of Birth (% of Season)</u>	<u>Reference</u>
San Miguel	57 days (831)	30 (53%)	Chapter 5
St. George	47 (433)	31 (66%)	Chapter 5

FEMALE REPRODUCTIVE CYCLE

PROESTRUS In a multiparous female, a single wave of follicular growth in the ovary without a corpus luteum is initiated at the time of parturition; follicles in the ipsilateral ovary remain small (Boyd, 1983). Bishop (1968) found no ripe follicles in lactating harbor seals (6x8 mm), however, there is an increase in size of follicles from early lactation to reach a size of 13-16 mm diameter by the end of lactation (Harrison, 1963). The solitary, largest follicle, destined for rupture, occurs in the contralateral ovary (from the corpus luteum) and attains a size of 14-25 mm (Harrison, 1963; Bigg, 1973). Uterine mucosa undergoes proliferation with an increase in the height of surface and glandular cells during this period (Bigg, 1973). Bigg and Fisher (1974) provide follicle diameters throughout the year. A nulliparous female was near ovulation with a single ripe follicle approximately 2 months after the mean date of parturition, leading Bishop (1968) to believe that mature nulliparous females ovulated at the same time as primiparous and multiparous females.

ESTRUS, OVULATION, AND MATING Harbor seals are usually monoestrous with an estrus duration of 3 to 5 weeks (range 1-9 weeks) in captivity, although a second estrus period has been reported occurring three to five weeks after the first in two of eleven captive seals (Bigg, 1973). Estrus in individual, non-mated, captive harbor seals occurred up to two weeks earlier and up to seven weeks later than in the previous year (Bigg 1973) and is marked by stratification and exfoliation of vaginal cells (Ouellette and Ronald, 1985; Bigg, 1973; Bigg and Fisher, 1975) and by uterine proliferation and low spinbarkeit of vaginal fluid (Bigg, 1973). Bishop (1968) reported that nursing harbor seals were not sexually receptive. Whereas there is some behavioral evidence that estrus may be inhibited by lactation in crabeater seals (Sinniff, et al, 1979), Boyd (1983) presents data which indicate that changes in lactation or pup desertion do not affect

the time of estrus in the grey seal. Although harbor seals usually ovulate and mate within two weeks after the termination of lactation (Harrison, 1963; Bishop, 1968; Bigg, 1969b; Bigg and Fisher, 1974; Boulva and McLaren, 1979), there is wide variation in the timing of ovulation. Harrison (1963) and Boulva and McLaren (1979) reported early ovulation, while Bigg and Fisher (1974) recorded a 36 day spread of first ovulations of nulliparous females. Harrison (1963) found a large (25mm) follicle at approximately 70 days after the mean date of parturition. Nulliparous northern fur seals are thought to ovulate two months after parous females (Craig, 1964). Bigg (1973) interpreted the lack of ovulation in 50% of captive harbor seals as an indication of coitus induced ovulation. However, Craig (1964) interpreted similar results from northern fur seals as an indication of spontaneous ovulation.

In experimental studies with captive harbor seals, Bigg (1973) found differences in the seasonal timing of estrus between seals from S. E. Vancouver Island, British Columbia and from Humboldt Bay, California. He suggested that the timing of estrus was under genetic control.

Mating occurs after the completion of lactation (Harrison, 1963; Boulva and McLaren, 1979). Most grey seals (82%) become pregnant after their first ovulation, but 12% show evidence of a second ovulation, and 1.2% require a third ovulation in the same season (Boyd, 1984a). Unovulated female harbor seals are anestrus for approximately 10 months, while ovulated, non-mated females may undergo a three-month pseudo-pregnancy, possibly due to vaginal stimulation during smear sampling, followed by 7 anestrus months (Bigg, 1973).

CORPUS LUTEUM FORMATION Bishop (1968) and Bigg and Fisher (1974) provide descriptions of the corpus luteum cycle within the harbor seal. The corpus luteum of pregnancy is formed from the remnants of the ruptured follicle. At formation it measures approximately 10mm in diameter, with only a slight increase in

size until after implantation (Boulva and McLaren, 1979; Fisher, 1954). Since only one follicle ruptures, there is only a single corpus luteum (Harrison, 1963), although Boyd (1984a) has found a grey seal ovary with two corpora. The ipsilateral ovary demonstrates a slight increase in weight while the contralateral ovary decreases in weight (Bishop, 1968). The uterine mucosa is characterized as secretory by as early as two weeks after ovulation (Bigg, 1973).

Bigg and Fisher (1974) consider that the luteal phase in the harbor seal lasts 10.5 months (ovulation to term) with a reduction in corpus luteum secretion during mid-delay. Fur seals demonstrate a month-long phase of luteal domination following ovulation during which the granulosa cells are luteinized. A second period is characterized by luteal regression with a reactivation of follicular activity and highly variable corpora diameters. A third period in which luteal function returns has been noted histologically and precedes implantation (Craig, 1964; Daniel, 1971). Daniel (1975) provides hormonal evidence for the second and third periods, however, progesterone remains low during the first period. Boyd (1983) demonstrated that grey seal progesterone levels remained elevated throughout the delay period.

Harbor seals from the Columbia River showed an average serum progesterone concentration of 11.7 ng/ml at or immediately after the approximate time of estrus and corpus luteum formation. Boyd (1983) suggested that the elevation of progesterone (> 4 ng/ml) and decrease in estradiol- 17β found in grey seals occurred at the time of ovulation. Six of the Columbia River seals had elevated progesterone values (> 4 ng/ml) while the seventh, an adult, had a low value (< 1 ng/ml). As none of the animals were lactating, this is interpreted as reflecting estrus and corpus luteum formation.

PERIOD OF DELAYED IMPLANTATION The harbor seal exhibits an implantation delay of about 2 months (Bigg, 1969b). During this period of embryonic diapause, changes are occurring in the uterus, corpus luteum, follicle of the ipsilateral ovary, and in steroid hormones. There is an increase in the height of uterine epithelium during early and middle delay, followed by a decrease in cell height by late delay (Bigg and Fisher, 1974). The glandular development and vascularization is similar in both uterine horns (Ouellette and Ronald, 1985). Daniel (1971) showed a quantitative change in uterine protein in mid-delay in the northern fur seal, with up to a 16-fold increase in uterine protein by late delay.

A second peak in follicular activity is noted in mid-delay in the harbor seal as indicated by an increase in the number of Graafian follicles (Bigg and Fisher, 1974). This corresponds with the time that captive females are coming into a second estrus and is paralleled by a similar increase in follicular activity in the northern fur seal (Craig, 1964). In the fur seal this second peak is coincidental with luteal regression and decreases by late delay (Craig, 1964). Also, a similar pattern is associated with the "false rut" in South American fur seals (Rand, 1955).

Mid-delay is characterized by low progesterone and low estrogen in the northern fur seal. At this point though, both begin to increase, with estradiol-17_B reaching a peak (surge) immediately before implantation (Daniel 1974, 1975).

Before reactivation, the blastocyst shows a low mitotic index (0.5%) with a long mitotic duration yielding a doubling time of approximately 50-60 days (Daniel, 1971). Daniel (1981) was unable to demonstrate the absence of a growth promoting substance, but presented some evidence that a small molecular weight serum inhibitor may control the growth of the diapausing blastocyst.

IMPLANTATION AND PLACENTATION In the harbor seal implantation occurs in a central location of the ipsilateral uterine horn approximately 105 days after parturition (Bigg and Fisher, 1974). Boshier (1977, 1981) provides ultrastructural descriptions of the grey seal corpus luteum at the time of implantation. There is a shift from type III to type II lutein secretory cells, with an increase in steroidogenesis. However, Boyd (1984a) found no increase in progesterone at the time of implantation, and injection of progesterone, estradiol-17_B, or a combination of both did not initiate implantation in the northern fur seal (Daniel, 1981). Blastocyst implantation is accompanied by a relatively standard histological pattern in the grey seal uterus, with proposed increases in progesterone exposure furthered by an estrogen surge yield a "progesteronic" cellular pattern (Boshier, 1979).

The time of implantation in grey seals was correlated to maternal body condition by Boyd (1984b), who could only conclude that "early implantation is, to some degree, dependent upon early onset of the spring increase in body condition or that the spring increase in body condition is a result of the occurrence of implantation." Coulson (1981) proposed that a cumulative temperature function set the time of implantation in grey seals and, thus, produced the variation seen in the mean dates of pupping between locations. Alternatively, the variance in mean pupping dates may have been due to temperature effects near the time of parturition (Boulva, 1975).

Histological presentation of placentation in the harp seal and grey seal is provided by Ouellette and Ronald (1985). The placenta appears to be important in the formation of chorionic gonadotropin (CG) and progesterone. Hobson and Boyd (1984) have demonstrated increasing levels of CG from about 20 days after implantation to parturition. Progesterone is also formed by the placenta. Placental content of progesterone increases until term in the grey seal (Hobson and Boyd, 1984).

PREGNANCY Bishop (1968) calculated a total gestation period for the Pacific harbor seal of 271 days (9 months). During this period the fetus grows at approximately 3.6 mm/day to 4.4 mm/day (Boulva and McLaren, 1979; Bigg, 1969b). The growth rate appears to be a linear function of the cube root of fetal weight (Boulva and McLaren, 1979).

The corpus luteum continues to grow throughout pregnancy reaching a diameter of 24 mm by parturition (Boulva and McLaren, 1979). Progesterone remains high throughout pregnancy, but starts to drop a few days before parturition in the harbor seal and between 21 and 7 days before parturition in the grey seal (Raeside and Ronald, 1981; Boyd, 1984a). Harbor seals sampled for progesterone at the Point Defiance Zoo throughout the period of early pregnancy (September - November) had variable levels of progesterone. Three separate individuals were pregnant at the time of sampling and had a mean serum progesterone of 16.7 ng/ml. Two additional individuals that were not pregnant (4 samples) had a mean serum progesterone of 6.8 ng/ml. Six pregnant Columbia River seals were sampled in late pregnancy. A mean value of 33.0 ng/ml was indicative of the large corpus luteum reported at this time, although the source, luteal or placental, cannot be determined. Two of the pregnant females had very low levels of progesterone (< 3 ng/ml) and were judged as being near-term.

PARTURITION Pupping behavior has been reported by several authors (Lawson and Renouf, 1985; Knutson, 1977; Newby, 1973). Boulva (1975) suggested that air and water temperature in late pregnancy may affect the timing of birth. The birthing event marks the initiation of a wave of follicular development and the end of the corpus luteum: at this point regression begins (Bigg and Fisher, 1974; Boyd, 1983, 1984). Boyd (1983) suggests that grey seal corpus luteum diameters follow a hyperbolic function during regression, developing into corpus albicans within 6 weeks. Fisher (1954) and Bigg and Fisher (1974) report that the corpus luteum persists throughout lactation in the harbor seal.

Ouellette and Ronald (1985) provide histological details on endometrial regression and epithelial replacement in the uterus.

LACTATION Lactation duration has been reported in the range of 30 days to 42 days for the harbor seal (Harrison, 1963; Bishop, 1968; Bigg, 1969b; Bigg and Fisher, 1974; Boulva and McLaren, 1979). A doubling of birthweight was noted at 20 days with a critical period for maternal abandonment of 10 days (Boulva and McLaren, 1979). Boyd (1984b) reported maximum decrease of blubber thickness during lactation in the grey seal, representing a period of great metabolic demand (Chapter 4).

MALE REPRODUCTIVE CYCLE The peak in spermatogenesis occurs approximately three months prior to the onset of sperm presence in the epididymis (Bigg, 1969b). Boulva and McLaren (1979) reported testicular sperm over a 10 month period (Oct-Jul), epididymal sperm during the three-month breeding season (May-Jul), maximum testicular tubule diameters over a four-month period, and maximum epididymal tubule diameters over a three-month period, each ending in July. A 9-month period when males are sexually active has been reported by Bigg (1969b), although breeding, per se, may be restricted to the estrus period of females. Bishop (1968) regarded male harbor seals as being physiologically capable of breeding well before most females enter estrus.

The data on male reproduction from Bigg (1969b) and Boulva and McLaren (1979) indicate that harbor seals in differing populations have differing times for maximum breeding potential. Male seals from eastern Canada (Boulva and McLaren, 1979) are at peak breeding condition from May through July, while western Canada male seals (Bigg, 1969b) have a peak in August through September.

A small sample of grey seal males demonstrated seasonal differences in the level of circulating testosterone, with higher levels near the breeding season (Sangalang and Freeman, 1976).

At the Columbia River where pupping occurs in late May and early June, adult harbor seal males had the highest values of testosterone in April, with intermediate levels in July. Point Defiance Zoo seals, also from coastal populations, showed low levels in September, October, and November. Juvenile males showed baseline levels in all samples.

PHOTOPERIOD Photoperiod has been isolated as an important exogenous cue regulating the seasonal timing of reproduction in mustelids (Mead, 1981). Also, photoperiod has been suggested as a proximate cue for seasonally phasing the reproductive cycle of the Pacific harbor seal (Bigg and Fisher, 1975), the northern fur seal (Callorhinus ursinus) (Elden et al, 1971; Daniel, 1981; Temte, 1985; but see: Spotte and Adams, 1982), and the California sea lion (Zalophus californianus) (Schustermann et al, 1982).

Bigg and Fisher (1975) were the first to demonstrate that female harbor seals were affected by a change in photoperiod. Long photoperiods (18 h/day) tended to advance the onset of estrus in captive female harbor seals as verified by vaginal smears; short photoperiods (6 h/day) tended to delay the onset of estrus. Due to differences in the absolute timing of estrus in seals from southeast Vancouver Island, British Columbia (PS-SG) and Humboldt Bay, California, Bigg (1973) suggested that genetic differences existed in the control mechanisms of reproductive timing between populations of harbor seals, and that a selective factor such as the availability of shrimp (Crangon spp.) may ultimately determine the absolute timing.

The analysis of photoperiod's effect for discrete populations (at a single latitude, or over a narrow latitudinal range) can only be used to demonstrate that photoperiod can affect reproductive timing. An example is provided by Canivenc and Bonnin (1981) for the European Badger (Meles meles). The analysis of photoperiod and reproductive timing for a continuous population, distributed over a wide latitudinal range,

in contrast, can be used to suggest at which point during the reproductive cycle specific photoperiodic phasing may occur. A photoperiod equation coupled with high speed computing allows the analysis of photoperiod relative to the timing of parturition for many animals throughout a latitudinal range, and further allows the identification of a specific time during the reproductive cycle when a photoperiod cue may be most likely to influence the timing of reproductive events. The use of such methods for the photoperiodic analysis of reproductive timing has been used for the northern fur seal (Temte, 1985; Chapter 5).

The photoperiod analysis reveals that Pacific harbor seals on the west coast of North America are exposed to a mean photoperiod of 13.80 ± 0.08 h/day on the 68th day post partum. At this time the slope of the linear relationship between photoperiod and latitude (figure 11) is zero, and as a consequence, the cline of the pupping season, expressed in terms of photoperiod, disappears! It is here suggested that a specific photoperiod, namely 13.80 h/day, and occurring at 68 days post partum, defines and is causative to the cline in the pupping season of the Pacific harbor seal.

The 68th day post partum lies within a 'window of reproductive timing' (Temte, 1985) for a species with an obligate delay of implantation. If photoperiod is to affect reproductive timing, it can only have its effect during this somewhat plastic period due to the deterministic nature of events from the point of implantation through ovulation. Support for such an hypothesis comes from a study of the European badger. Artificial shortening of photoperiod during this period causes implantation of the blastocyst (Canivenc and Bonnin, 1981). The normal 10 to 11 month period of embryonic diapause can be reduced to 4 to 5 months through photoperiod manipulation. This apparently is also the case with the population of harbor seals on Sable Island, Nova Scotia (Boulva, 1975). The data not only revealed high precision in the year-to-year timing of pupping, but also indicated that the timing of implantation was controlled with

"an apparently high precision." Pups born in 1971, with a mean birth date of 21 May would have required an estimated additional 4.6 days in utero to equal the mean pupping length and weight of pups born in 1972 with a mean date of birth of 26 May. Pups born in 1970, with a mean date of birth of 24 May, were of an intermediate average size. Boulva (1975) interpreted this as a strong suggestion of identical mean dates of implantation in 1970, 1971, and 1972.

Delayed implantation has been shown in several species of pinnipeds (Boshier, 1981). Seals in the family Phocidae reported to have an obligate delay of implantation include the leopard seal (Hydrurga leptonyx), the crabeater seal (Lobodon carcinophagus), the Weddell seal (Leptonychotes weddelli), the southern elephant seal (Mirounga leonina), the hooded seal (Cystophora cristata), the ringed seal (Pusa hispida hispida), the bearded seal (Erignathus barbatus), the grey seal (Halichoerus grypus), the harp seal (Pagophilus groenlandicus), and the common or harbor seal (Phoca vitulina). Members of the family Otariidae showing an obligate delay of implantation include the South American sea lion (Otaria byronia), the New Zealand fur seal (Neophoca hookeri), the southern fur seal (Arctocephalus pusillus), the Stellar sea lion (Eumetopias jubatus), the California sea lion (Zalophus californianus), and the northern fur seal (Callorhinus ursinus). It is conceivable that this widespread phenomenon allows the general trend of high precision in reproductive timing in the pinnipeds.

Changes in the timing of parturition with latitude have been reported in two other species of North Pacific pinnipeds. Daniel (1981) and Spotte and Adams (1981) addressed the possibility of photoperiodism in explaining the differences in the timing of parturition between northern fur seals resident at the Pribilof Islands, Alaska, and at San Miguel Island, California. Schusterman et al (1982) reported that latitudinal movement of California sea lions between aquaria in California and Hawaii produced changes in the timing of parturition.

Daniel (1981) placed captive female northern fur seals in different light regimens for a period of five days. However, this treatment failed to induce implantation. Three explanations exist: 1) fur seals do not respond to photoperiod, 2) the five-day duration was too short of a period for implantation to occur, or 3) the experiment was conducted at a time when the animals did not respond to a photoperiod. Spotte and Adams (1981) concluded that exposure to a photoperiod cycle different from that found at the Pribilof Islands did not affect the reproductive timing of captive fur seals at the Mystic Aquarium, Conn. However, these conclusions were based upon the estimated dates of pupping of seven aborted fetuses at the aquarium and it is doubtful that the methods used were robust enough to identify a difference in mean pupping date of less than two weeks. Also, one fur seal pup born at the Mystic Aquarium, and not reported by Spotte and Adams, had a birthdate of 30 June, 1978 (Bigg, 1984), intermediate to the mean dates in Alaska and California. The 14 day difference in the mean dates of pupping of northern fur seals at East Reef Rookery, St. George Island, Pribilof Islands, Alaska (57°N) and Adams Cove, San Miguel Island, California (33°N) can be explained by a mean photoperiod of 12.5 +/- 0.0 h/day occurring at 62 days post partum at both locations (Temte, 1985; Chapter 5). This photoperiod also occurs within the window of reproductive timing for this species, as estrus occurs at day 7 post partum, and implantation at 120 days post partum (Craig, 1964; Daniel, 1971).

It is further suggested that a specific photoperiod, occurring between estrus and implantation, acts as a trigger to initiate a sequence of physiological events leading to the implantation of the blastocyst in the harbor seal. Three lines of evidence have been used in support of this conclusion: (1) the photoperiod at 68 days post partum defines the cline in the pupping season of the Pacific harbor seal, (2) the photoperiod occurring at 62 days post partum in the northern fur seal can explain the difference in reproductive timing at colonies at 33°N

and 57°N, and (3) in both species the date of proposed photoresponse is at the approximate midpoint of the period extending from ovulation to implantation, and is coincidental with histological, functional, and hormonal changes. The most significant of these changes is the occurrence of follicular activity in the ipsilateral ovary and the strong possibility of estrus and ovulation, in at least some individuals, at this point in the reproductive cycle for both species. However, more data will be required to test this hypothesis.

EVOLUTION Phoca vitulina richardsi is thought to have emerged from the ice-breeding harbor seal Phoca largha (McLaren, 1966). Whereas the largha seal breeds on a 15 - 65 km wide ice front during the period from February through April, adjacent populations of Pacific harbor seals breed on land during June and July (Shaughnessy and Fay, 1977). This two to three month delay in reproductive timing for the Pacific harbor seal permitted breeding to occur on land rather than on ice. A seal that pups in June and July at 60°N latitude, and that is influenced by a approximate 13.80 h/day photoperiod in August or September, may be preadapted for southern dispersal as movement to the south is accompanied by an earlier pupping season, and an ability to produce pups when conditions are, perhaps, more optimal.

The identification and separation of a population of seals from Puget Sound and the Strait of Georgia (PS-SG) forms an interesting case in this approach to reproductive timing. Seals from this system pup three months later than seals on the coast at identical latitudes, even though they are exposed to identical photoperiod regimens. There is a significant difference between mean pupping dates of both areas. This difference could conceivably be due to a number of factors such as differences in water temperature or chemical composition. However, seals obtained on the coast as pups, held captive at the Point Defiance Zoo at Tacoma, Washington, and exposed to Puget Sound conditions (display tank water is pumped directly from the Sound) continue

to pup in June as do their coastal cohorts (M. Johnson, pers. comm., 1983). The genetic mechanism proposed by Bigg (1973) to explain the difference in timing of estrus in harbor seals from Humboldt Bay, California and southeast Vancouver Island, British Columbia forms an appealing explanation. Perhaps the harbor seals inhabiting Puget Sound and the Strait of Georgia are genetically different from the seals found on the coast.

As Puget Sound and the Strait of Georgia were glaciated as recently as 13,000 years ago and only opened to Pacific Ocean waters as the Vashon Glacial ice retreated (Burns, 1985), a rapid change in reproductive timing of harbor seals with strong selection is indicated. The PS-SG system is an oceanographically different environment from the coast. Water temperature tends to be slightly warmer, salinity tends to be lower, and the peak concentrations of phosphate (PO_4) appear approximately three to four months later in Puget Sound than along the Washington coast (Collias et al, 1974; Churgin and Halminski, 1974). Because pup stomach contents are often composed entirely of shrimp, Bigg (1973) speculated that the presence of shrimp (Crangon spp.) may be an important factor for weaned pup survival and that it may ultimately regulate reproductive timing. However, at this time a selective mechanism remains somewhat obscure (but see Chapter 4).

Seals radio-tagged at the Columbia River Estuary have moved as far as Gray's Harbor, Washington (S. Jeffries, pers. comm., 1982). However, there is no record of a seal moving from the coast into Puget Sound or the Strait of Georgia, although this longitudinal distance is less than the maximum latitudinal distance traveled by a harbor seal. Stutz (1967) characterized the regions of Puget Sound and the Strait of Georgia as "relative isolated centers of large breeding populations separated by stretches of narrow zones of harbour seal habitat." Although there is a possibility for allopatric reproductive isolation of harbor seals within the PS-SG system, it may be most prudent to conclude that the animals of the PS-SG system are not

geographically isolated, but experience limited interchange with individuals from coastal populations.

If differentiation of populations is to occur allochronic factors need to be invoked. Female harbor seals from the PS-SG system come into estrus during September, or about three months later than on the coast (Bigg and Fisher, 1975). As expected, male harbor seals from southeast Vancouver Island show the highest percentage of epididymal tubules with spermatazoa during August, September, and October, with the percentage dropping rapidly in November (Bigg, 1969b). It is assumed that the reproductive timing of male harbor seals on the coast is advanced by approximately three months to coincide with the breeding schedule of coastal females. This is indeed the case with harbor seals in eastern Canada (Boulva and McLaren, 1979) and probably the case for coastal Pacific harbor seals, as shown by testosterone studies performed on Columbia River harbor seals and captive harbor seals at the Point Defiance Zoo in Tacoma, Washington. Males from the Columbia River showed high levels of testosterone in early April and moderate levels in early July. Captive males obtained as pups on the Washington coast showed relatively low levels of testosterone in September, October, and November. Given high site fidelity, low rates of dispersal, and the probability that males from the nearest Pacific coast populations cannot successfully fertilize female harbor seals in the PS-SG system, conditions for isolation of populations do exist. However, there is a possibility of gene flow in the opposite direction. Tauber and Tauber (1977) discussed the seasonal timing of reproduction in a pair of sympatric lacewings. Single allelic differences at two loci resulted in gross alterations in photoperiod response and reproductive timing; the end product being reproductive isolation and speciation. A model for allochronic speciation in four steps was presented by Tauber and Tauber (1977).

It is summarized as follows:

- 1) Ancestral species is adapted to several habitats.
- 2) Stable polymorphisms are established and disruptive selection occurs.
- 3) Seasonal isolation occurs through:
 - synchronization of reproduction with favorable seasonal conditions
 - reduction of interform pairings
- 4) Differential selection increasing fitness of isolates causing divergence.

The Pacific harbor seal fits into this scheme. It is adapted to several habitats (eg. bays, estuaries, river systems, rocky coast). Variation in the photoperiod response may occur manifesting itself in the 49-day mean pupping season. Selection could conceivably operate on the ends of this distribution. If seasonal conditions were different in a given location, and if this was coupled with a reduction in interform pairings, seasonal isolation would occur. Finally, differential selection of the isolates would allow for divergence.

In the evolutionary past of the Pacific harbor seal one can find indications of allochronic isolation. A shift in reproductive timing of about three months allowed for the separation of the land-breeding harbor seal (Phoca vitulina) from the ice breeding spotted seal (Phoca largha). Allopatric isolation is seen as causative to the speciation of the harbor seal into its current five subspecific groups, with the North Pacific example being the Kuril seal (P. v. stejnegeri) and (P. v. richardsi). Further, there is an indication that a divergence in the Pacific harbor seal may be occurring in the PS-SG system due to an allochronic isolating factor (figure 17). This process, if it is occurring, provides an interesting example of sympatric speciation with a definite time scale. A differing response to photoperiod due to the synchronization of reproduction with favorable conditions is seen as the most likely cause of this reproductive isolation.

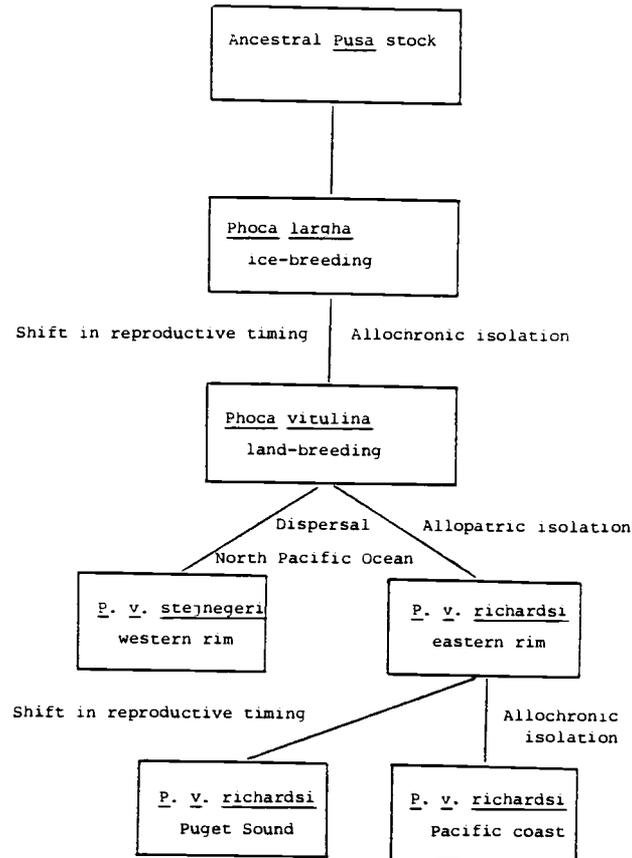


Figure 17. Proposed mechanisms of speciation for North Pacific harbor seal (genus Phoca).

CHAPTER 3

SEXUAL SEGREGATION IN THE PACIFIC HARBOR SEAL

The haul-out patterns of the Pacific harbor seal (Phoca vitulina richardsi) have been well documented on the Oregon coast (Graybill, 1981; Brown and Mate, 1983). However, there has been little attention paid to the possibility of sexual segregation in haul-out site utilization in this species. Although Bigg (1969b) has reported that the sex ratio at birth in this species is 56% female, harbor seals are thought to have a promiscuous mating system, with approximately equal representation of both sexes (Bonner, 1979). There has been no evidence to indicate segregation by sex on haul-out sites.

During 1981 and 1982 harbor seals were opportunistically observed at two locations on the Oregon coast: Netarts Bay and Yaquina Head. Numbers of seals at both locations were recorded and an attempt was made to identify the sex of as many animals as possible. A Bausch and Lomb 10-45 x 60 mm spotting scope was used to count and determine the sex of seals from the shore. Determining the sex of a seal required that the animal lie with its ventral aspect toward the observer. Males could be easily identified by the presence of a penile aperture, whereas females were identified by the presence of mammary slits and vaginal aperture. Positive sexual identification included both the observation of the penile aperture and the absence of the mammary slits and vaginal aperture or vice versa. At any given time an average of 5.0% of the seals at Netarts Bay and 15.7% of the seals at Yaquina Head could be sexually identified.

A total of 132 15-minute observations were made during 25 haul-out periods at the two locations. From November, 1981 to February, 1982, and again in November, 1982 there were significantly more female harbor seals hauled out in Netarts Bay than males (Table 11). During July, 1982 there was a significantly higher number of male than female harbor seals at the Yaquina Head haul-out ($P < 0.005$; X^2). No difference was seen

Table 11. Number of female and male harbor seals at Netarts Bay and Yaquina Head, Oregon.

Netarts Bay (protected, sandy haul-out)

<u>mo/yr</u>	<u>Number of Haul-out Periods Observed</u>	<u>Females # (%)</u>	<u>Males # (%)</u>	<u>Significance Level (X^2: 1 df)</u>
Nov/81	3	63 (68)	29 (32)	0.001
Dec/81	3	41 (72)	16 (28)	0.001
Jan/82	1	44 (69)	20 (31)	0.005
Feb/82	1	17 (77)	5 (23)	0.01
Mar/82	2	31 (58)	22 (42)	N.S.
Jun/82	1	2 (50)	2 (50)	N.S.
Nov/82	2	12 (92)	1 (8)	0.005

Total	13	210 (69)	95 (31)	0.001

Yaquina Head (exposed, rocky haul-out)

<u>mo/yr</u>	<u>Number of Haul-out Periods Observed</u>	<u>Females # (%)</u>	<u>Males # (%)</u>	<u>Significance Level (X^2: 1 df)</u>
Jul/82	7	17 (30)	39 (70)	0.005
Aug/82	2	12 (55)	10 (45)	N.S.
Sep/82	3	10 (53)	9 (47)	N.S.

Total	12	39 (40)	58 (60)	N.S.

in the number of males and females at Netarts Bay in March and June, 1982, or at Yaquina Head in August and September, 1982.

The data presented here indicate a seasonal sexual segregation of haul-out use in this species. Netarts Bay, where 69% of the all seals identified by sex were female, provides a protected, sandy haul-out area. It is also the site of harbor seal pupping (Brown, 1980). In contrast, Yaquina Head is an exposed, rocky haul-out area that is approximately 10 km from the nearest pupping area in Yaquina Bay, although pups are sometimes seen on the Yaquina Head site (Bruce Mate, pers. comm., 1985). Sixty percent of the animals identified by sex at this location were male. Whereas the data sets are far from complete and introduce bias into the comparison, there is a strong indication that females of this species tend to be found more in protected areas while males are more likely to be found in exposed areas.

CHAPTER 4

FOOD LIMITATION IN THE PACIFIC HARBOR SEAL: COMPUTER SIMULATION
OF A METABOLIC MODEL

INTRODUCTION

Emphasis has recently been placed on density dependent relationships in populations of large mammals. Evidence indicates that reproductive and mortality rates are quite often density dependent and non-linear, with most of the change in rates occurring near the carrying capacity (Fowler, 1981a, 1981b; DeMaster, 1981; Eberhardt, 1981). Fowler (1981a), in reviewing 23 published examples of large mammal populations, suggests that resources, such as food or space, predominate in the regulation of population size in large mammals, as opposed to the regulation by higher consumers in small mammal populations.

Several models have been introduced for pinniped populations including non-linear, density dependent survivorship in juvenile northern fur seals (Callorhinus ursinus; Eberhardt, 1981), and in adult and pup Weddell seals (Leptonychotes weddelli; DeMaster, 1981), and density dependent first-year mortality, age of weaning, and fertility rate in the harp seal (Pagophilus groenlandicus; Lett et al, 1981). Whereas several factors may be implicated as causative to density dependence, the availability of food is often singled out as a primary limiting resource in seals (Lett et al, 1981). Sergeant (1973) reports that thinning of male harp seals leads to an increase in the maturation rate of females. An extreme example is the effect of the EL Nino event on survivorship of Galapagos fur seals and Galapagos sea lions (Trillmich and Limberger, 1985). Despite these indications, most models tend to ignore the resource defining the carrying capacity and deal strictly with population size and arbitrary coefficients of curvilinearity to present density dependent relationships.

This model is presented with an attempt at increased realism, although some generality is sacrificed (Levins, 1966). A simple negative exponential equation, modified from those of Eberhardt (1981) and DeMaster (1981), serves to define survivorship of six classes or life history stages of Pacific harbor seals (Phoca vitulina richardsi) in terms of food availability, while incorporating values of metabolism, competitive ability, population size, and age structure. Also, the reproductive rate is dependent on survivorship, and ultimately upon food availability, again using a negative exponential equation. This model is used to investigate the timing of pupping, the sex ratio at birth, and exclusion of subadult males in a "population" of Pacific harbor seals.

METHODS

MODEL OF METABOLISM AND FOOD LIMITATION Six classes of harbor seals were chosen for this model. The classes were based on age/weight information of Bigg (1969b). These include pups, juveniles, subadult males, adult males, non-reproducing adult females, and reproducing adult females. Parametric values of age, weight, and basal metabolic rate (BMR) are listed (Table 12).

METABOLIC FACTORS Basal metabolic rates have been measured for harbor seal pups at several temperatures in air (Miller and Irving, 1975), and at several temperatures in water (Miller et al, 1976); for juvenile seals (Irving and Hart, 1957; Hart and Irving, 1959; Craig and Pasche, 1980); and for an adult female harbor seal (Matsuura and Whittow, 1973). Pup metabolism demonstrated a lower critical temperature of 20°C in water (Miller et al, 1976) and, hence, would be affected by water temperatures in the range of those off the Oregon coast. Air and water temperature in the ranges found on the Oregon coast did not affect the metabolic rates of other classes.

Table 12. Age, weight, metabolic, and feeding parameters of classes of the Pacific harbor seal for computer simulation.

Class	<u>Pups</u>	<u>Juveniles</u>	<u>Subad. ♂♂</u>	<u>Adult ♂♂</u>	<u>Adult ♀♀</u>	<u>Pregnant ♀♀</u>			
Age (years) (month of preg.)	0-1	2-3	4-6	6-9+	4-9+	1-3	4-9+	7-9	10-12
Weight (kg)	25	40	60	80	60	60	60	70	70
BMR _i (kcal/kg/h)	*	1.93	1.59	1.59	1.59	1.59	1.59	2.02	3.10
R _i (106 kcal)	*	.167	.206	.275	.206	.206	.206	.305	.469
a _i	*	1.68	2.04	2.04	2.04	2.04	2.04	1.61	1.04
k _i	.58-.79	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Based on data of Bigg (1969b), Irving and Hart (1957), Hart and Irving (1959), Matsuura and Whittow (1973), Craig and Pasche (1980), and Renouf (1980).

Metabolic rates were converted from a standard measurement of liters O_2 per kilogram per hour ($lO_2/kg/h$) to kilocalories per kilogram per hour ($kcal/kg/hr$) using the equation provided by Guyton (1976) and assuming a respiratory quotient of 0.82 (Craig and Pasche, 1980):

$$1.0 \text{ l } O_2/kg/h = 4.825 \text{ kcal/kg/h} \quad (1)$$

Pup metabolic rates were calculated as a function of quarterly sea surface temperature off Oregon (Churgin and Halminski, 1974). This relationship, based on data of Miller et al, (1976), is as follows:

$$BMR_1 = (4.825 \text{ kcal/kg/hr})(0.7 - [(0.027)(T)/2.0]) \quad (2)$$

where T = quarterly water temperature.

The metabolic rate of pregnant and lactating female harbor seals was calculated from data of Bigg (1969b). It is assumed that, due to the delay of implantation (Fisher, 1954) and minimal fetal growth in the first trimester of pregnancy, reproducing females do not exhibit elevated metabolic rates during the first half-year of the reproductive cycle (starting at the time of estrus). During the third quarter of the reproductive year, energy is required for maternal metabolism, fetal metabolism, and fetal growth. During the last quarter, energy is required as above, plus that required for 5 to 6 weeks of lactation (Bigg, 1969b). Fetal metabolism was accounted for by increasing maternal weight by 10.0 kg. Fetal growth has been measured by Bigg (1969b). For this model the following approximations of fetal growth were used: 0.0 kg in the early pregnancy; 8.0 kg/3 months (3.7 g/h) in the mid-pregnancy; and 2.2 kg/2 months (1.5 g/h) in late pregnancy. Growth weights were converted to energy equivalents (kcal) assuming a factor of 8.0 kcal/g (Knox, 1979). Lactation provides energy for pup metabolism and growth. Pups show an average increase of 13.8 kg during the month of lactation

(19.2 g/h; Bigg, 1969b). Again, an energy equivalent was calculated using a factor of 8.0 kcal/g, and an assimilation efficiency of 0.75 (Knox, 1979). Pup metabolism was added to the energy needed for growth. Hence, metabolic rates of reproductive females can be described as follows:

$$\text{1st quarter BMR} = 1.59 \text{ kcal/kg/h} \quad (3)$$

$$\text{2nd quarter BMR} = 1.59 \text{ kcal/kg/h} \quad (4)$$

$$\begin{aligned} \text{3rd quarter BMR} &= 1.59 \text{ kcal/kg/h} \\ &+ (3.7 \text{ g/h})(8.0 \text{ kcal/g})/70.0 \text{ kg} \\ &= 2.02 \text{ kcal/kg/h} \end{aligned} \quad (5)$$

$$\begin{aligned} \text{4th quarter BMR} &= 1.59 \text{ kcal/kg/h} \\ &+ (2/3)(1.5 \text{ g/h})(8.0 \text{ kcal/g})/70.0 \text{ kg} \\ &+ (1/3)(19.2 \text{ g/h})(8.0 \text{ kcal}) \\ &/ ((0.75) (70.0 \text{ kg})) \\ &= 3.01 \text{ kcal/kg/h} \end{aligned} \quad (6)$$

Minimum quarterly rations (R_i) were calculated using metabolic rates, the weight of seals in the six classes, and a time constant of 2160 hours (3 months) as follows:

$$R_i = (\text{BMR}_i)(W_i)(2160 \text{ hr}). \quad (7)$$

The ability to withstand starvation in a food limited environment is proportional to the weight of stored energy reserves, and inversely proportional to the metabolic rate. A simple form of this concept is incorporated into this model as the starvation factor (a_i). It is the value that sets the curvilinearity of the survivorship relation. The weight of the seal is converted into an energy equivalent using a factor of 7.0 kcal/g (Knox, 1979), and then divided by the quarterly metabolic demand or ration (R_i). Hence:

$$a_i = (W_i)(7000 \text{ kcal/kg}) / R_i \quad (8)$$

COMPETITIVE ABILITY A unitless intraspecific competition coefficient (k_i) is used in this model. Harbor seals display an ontogenetic acquirement of feeding ability, that is, learning is required to hunt efficiently. Data presented by Renouf (1980) was used to calculate a value of k for pups (Table 12). It is assumed that full efficiency is attained after the first year of life.

DEMAND ON THE LIMITED FOOD RESOURCE The quarterly demand on food resources of the population of harbor seals in this model is the sum of the products of the number of seals in each class (N_i) and the minimum quarterly ration of that class (R_i):

$$\text{Demand} = \sum_{i=1}^6 N_i R_i \quad (9)$$

SURVIVORSHIP BASED UPON FOOD AVAILABILITY A deterministic relationship between food availability and class-specific survivorship was formulated based on the models of Eberhart (1981) and DeMaster (1981). A non-linear, food-dependent function of a negative exponential nature was chosen as the basis of this model.

$$S_i = S_m (1 - \exp[-a_i ((k_i)(F)/\text{Demand} - 1)]) \quad (10)$$

where S_i = quarterly survivorship of i th class
 S_m = maximum quarterly survivorship
 a_i = starvation factor of i th class
 k_i = competitive ability of i th class
 F = quarterly food availability in 10^6 kcal
 N_i = number of seals in i th class
 R_i = minimum quarterly ration of seals in i th class

This equation is based upon the following set of assumptions:

- (1) food resources are divided as a function of ration among all seals. As a result all classes and all seals compete for the available food. No partitioning occurs.
- (2) competitive ability effectively changes the amount of available food for pups.
- (3) the curvature of the survivorship relationship is determined by the starvation factor (a_i).
- (4) when available food is less than or equal to demand, the survivorships are zero (ie. more than a basal level is required for survival).

This model has the advantages specified: the shape of the survivorship curves are determined by metabolic factors and food availability allowing for consistency in units. Also, interaction of all animals in a population is simulated.

REPRODUCTION BASED UPON SURVIVORSHIP The reproductive rate should produce the optimal benefit to adult females in terms of their survivorships and the production of viable, fit offspring. In more fundamental terms, a female should adopt a strategy to maximize her genetic output. Hence, if by reproducing a female ends up with more of her genes in the population than by not reproducing, she should reproduce; otherwise, she should not increase her costs and risks by becoming pregnant.

In the following year, the average non-reproducing female will have her genes (1.0) multiplied by her chance of surviving that year. Her genetic contribution to next year's population is:

$$GC_5 = (1.0)(AS_5) \quad (11)$$

where GC_5 = the genetic contribution of a
non-reproducing female

AS_5 = the annual survivorship of a
non-reproducing female

A reproducing female will, on the average, have her genes (1.0) multiplied by her chance of surviving into the next year (AS_6), plus half of her pup's genes (0.5) multiplied by the probability that her pup will survive to a given age. In this model the probability of pup survival to age four (when reproductive activity can start) is used. The reproducing female's genetic contribution to next year's population is:

$$CG_6 = (1.0)(AS_6) + (0.5)(AS_1)(AS_2)^2(AS_3) \quad (12)$$

where GC_6 = the genetic contribution of a reproducing female

AS_6 = the annual survivorship of a reproducing female

AS_1 = the annual survivorship of a pup

AS_2 = the annual survivorship of a juvenile

AS_3 = the annual survivorship of a subadult

The following equation was used in the model to determine the reproductive rate:

$$REP = REP_m (1 - \exp[-b (GC_6/GC_5)]) \quad (13)$$

where REP = reproductive rate

REP_m = maximum reproductive rate

b = curvilinearity constant

GC_5 = as above

GC_6 = as above

Like the survivorship equation, the reproductive rate relationship takes the form of a negative exponential. However, it is less deterministic than the survivorship equation in that that two parameters, REP_m and b , are empirically derived. To conform with the reproductive rate of 0.88 reported by

Bigg (1969b) for harbor seals, it was assumed that this rate came from a stable population, and that a maximum reproductive rate of 0.95 was possible. From these assumptions, a value for the constant b was calculated:

$$b = 11.94 \quad (14)$$

The reproductive rate equation makes the following ecological assumptions:

- (1) reproduction does not occur until it is advantageous, in terms of genetic contribution, to produce offspring.
- (2) the year-to-year environment is stable, allowing for predictions of survivorships. The values of annual survivorship are determined in the current year.

COMPUTER SIMULATION A FORTRAN 77 program, PHOCAV, was developed to use this metabolic/food-availability approach to population modeling. The program allows simulation of seasonal temperatures and seasonal availability of food against a background of seasonally changing parameters in seals (eg. thermal response of pup metabolism, pregnancy cycle, learning of prey capture).

At each yearly iteration an age specific, sex specific population, consisting of 18 cells, is partitioned into six classes (Table 12). These in turn are subjected to four quarterly cycles in which quarterly survivorship is determined. This survivorship is based upon quarterly parameters and the number of seals in each class at the beginning of each quarter. At the end of the year, defined as the point at which pups are weaned, the annual survivorships for the six classes are determined as is the reproductive rate. The age specific, sex specific population is subjected to the annual survival and reproductive rates. Ages are advanced by one year, and a subsequent iteration begins.

Simulations were run until stable population sizes were obtained (80-120 years). Series of simulations were made to investigate the following:

- (1) the effects on populations of unlimited population growth, food-dependent survivorship alone, and food-dependent survivorship coupled with survivorship-dependent reproductive rates.
- (2) the effects of the level of available food.
- (3) the effects of the timing of reproduction against a regimen of seasonally changing temperatures and food availabilities.
- (4) the effects of changing the sex ratio at birth.
- (5) the effects of "behavioral exclusion" of subadult males on population size.

RESULTS OF THE SIMULATIONS

SURVIVORSHIP WITH A CONSTANT POPULATION AND VARYING FOOD AVAILABILITIES Food levels were varied as a constant population was maintained to determine the shape of survivorship curves. Adult males and subadult males attained the highest survivorships at any food (figure 18a) level due to their high resistance to starvation (a_i). Juveniles are slightly less resistant and show a slightly lower survivorship. Pups cannot compete for food as well as the other classes (Renouf, 1980) and are more susceptible to starvation due to a lower body mass and higher metabolism. Pup survivorship is lowest during the 6 months post-weaning, improving as feeding skills effectively increase the available food (figure 18a).

A comparison of female survivorships (figure 18b) displays the prediction that non-pregnant and early-pregnant females have the same survivorship as subadult and adult males. However, mid-pregnancy females display a survivorship rate that is slightly lower than that of juvenile animals, and late-pregnancy females are subject to a survivorship rate only slightly better than that of a six-month old pup. The decline in female survivorship with pregnancy is due to elevated metabolic needs, and a lowered resistance to starvation.

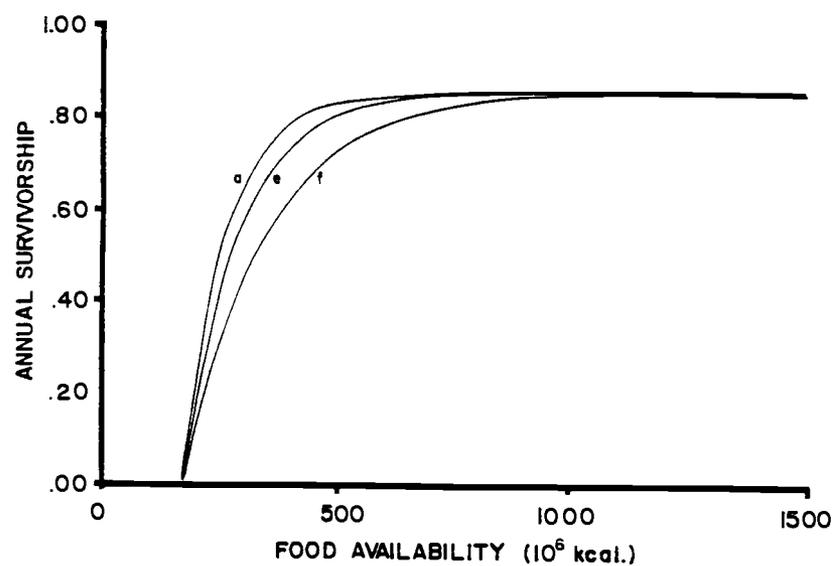
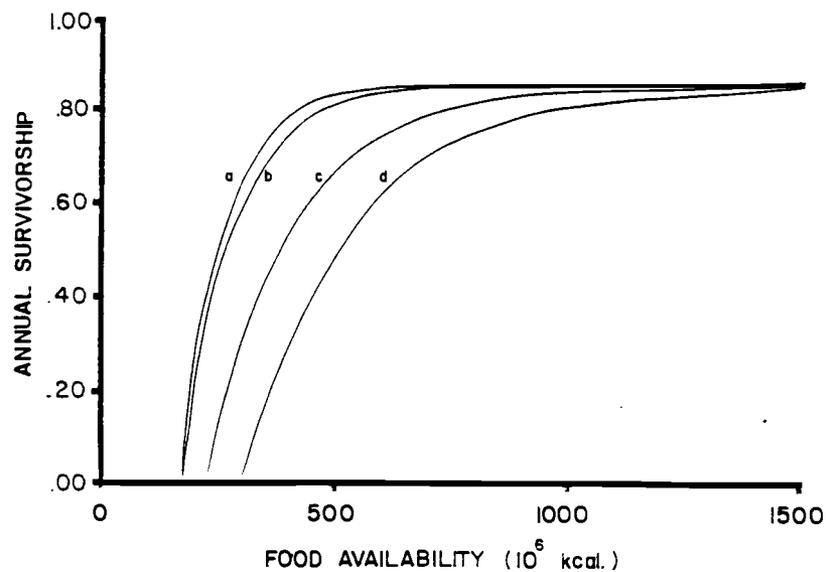


Figure 18a. Annual survivorship of (a) subadult and adult male, (b) juvenile male and female, (c) 6-12 month old pup, and (d) 1-6 month old pup harbor seals as a function of food availability.

18b. As above but for (a) non-pregnant and early-pregnancy, (e) mid-pregnancy, and (f) late-pregnancy and lactating adult female harbor seals.

POPULATION SIZE OVER TIME Four population models were compared in runs of 120 years using two different levels of food. The models were : (1) unrestricted growth, (2) density dependent survivorship with reproductive rate fixed at a maximum value, (3) density dependent survivorship with reproductive rate fixed at the level reported by Bigg (1969b), and (4) density dependent survivorship and density dependent reproductive rate. As expected, exponential growth results from limitless resources and sigmoid (logistic) curves are produced in the other models (figure 19). There is a slightly higher stable population size in the model with the maximum reproductive rate, whereas both the fixed stable reproductive rate and density dependent reproductive rate produce the same stable population size (figure 20). The stable populations in the limited models are proportional to the levels of available food (figures 19,20). Density dependent reproductive rates allow a faster increase in population size than that obtained with a fixed stable rate (figure 20).

Model (4) was used as the basis for the rest of the analysis. It permitted a high rate of population growth while reflecting measured reproductive rates at equilibrium. The net rate of change (dN/dt) for the modeled population is as expected for a population of large mammals (Fowler, 1981a). The zero-value of dN/dt is proportional to the level of available food, as is the maximum value of dN/dt (figure 21a). Most of the change (ie. the point of inflection) occurs near the carrying capacity. The specific rate of change (dN/Ndt) maintains a constant value of 0.042 after initial oscillations until the carrying capacity is approached (figure 21b). This is also similar to the generalized large mammal pattern (Fowler, 1981a). The point of inflection of the curve is proportional to the level of available food.

SURVIVORSHIPS AND REPRODUCTIVE RATE A series of simulations were conducted to determine the effects of population size on survivorship rates of the six classes of seals and the reproductive rate. The runs were made with three constant levels

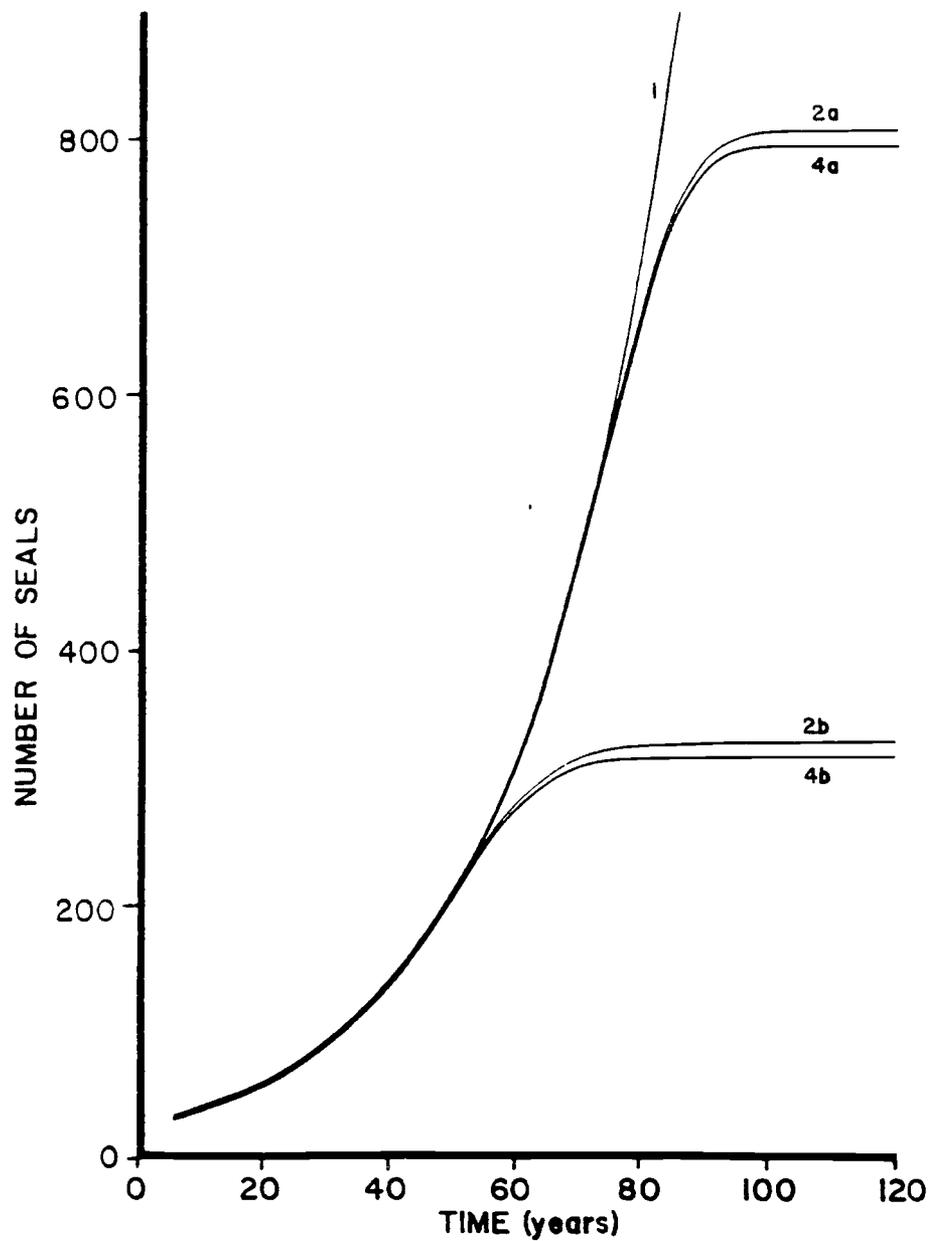


Figure 19. Population growth in metabolic models: (1) no density dependence, (2) density dependent survivorship, (4) density dependent survivorship and reproduction. Subscript (a) designates 1000×10^6 kcal food per quarter; (b) 400×10^6 kcal food per quarter.

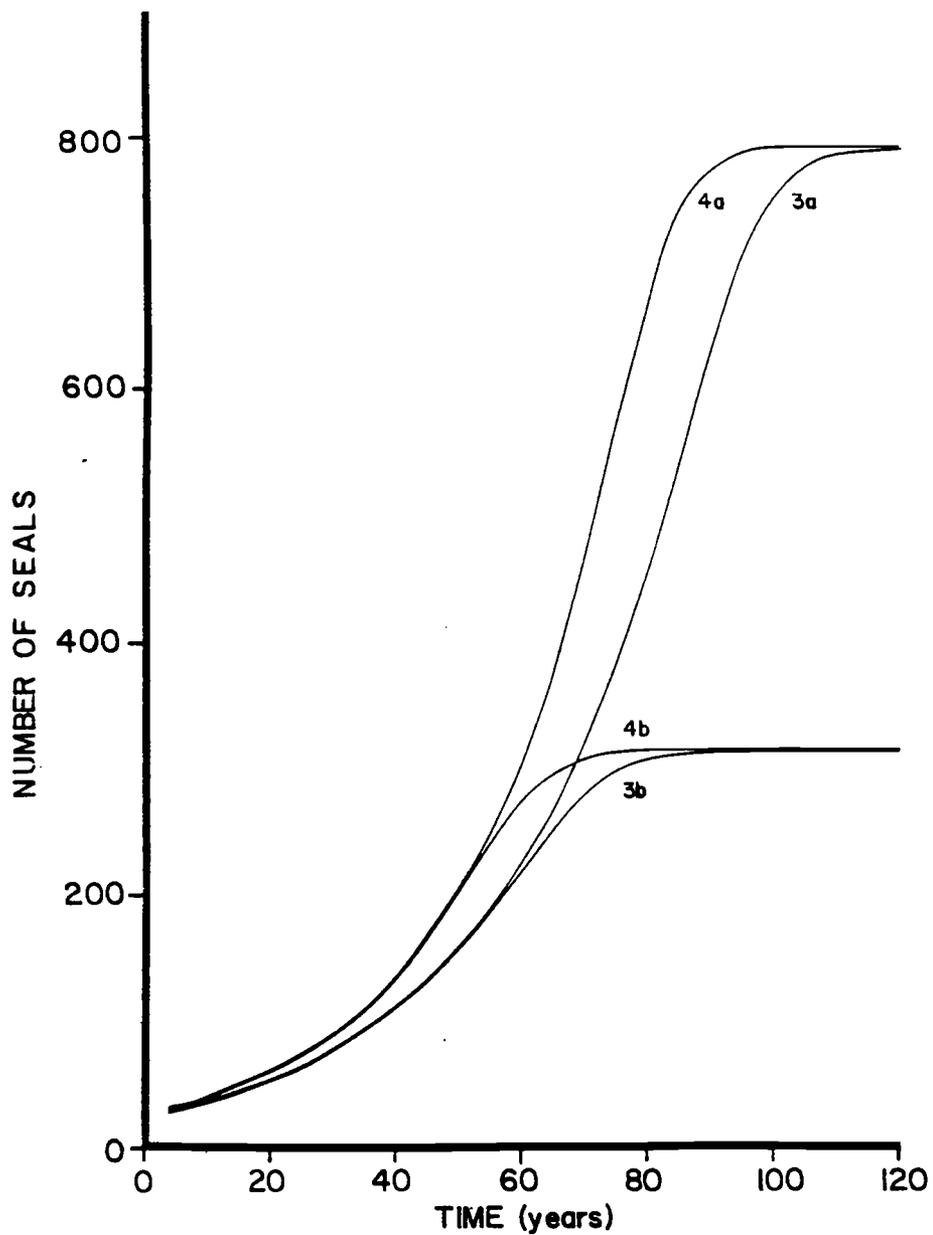


Figure 20. Population growth in metabolic models: (3) density dependent survivorship with fixed reproductive rate and (4) density dependent survivorship and reproductive rate. Subscript (a) designates 1000×10^6 kcal food per quarter; (b) designates 400×10^6 kcal food per quarter.

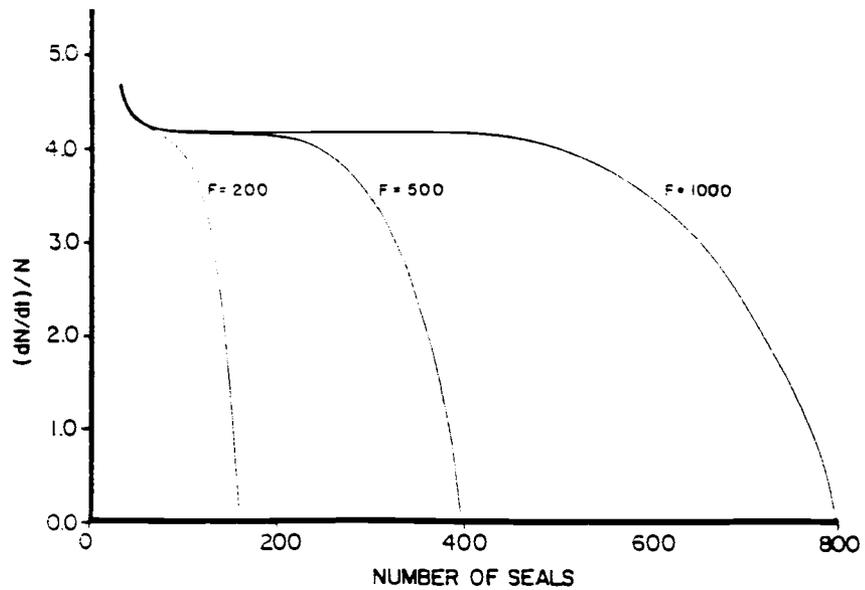
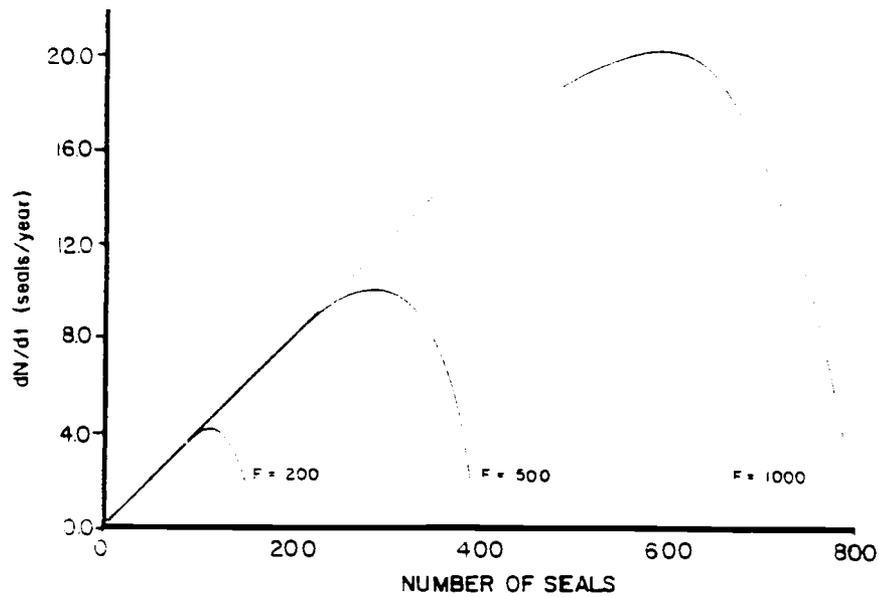


Figure 21a. Net rate of change (dN/dt) of modeled populations as a function of population size. Food availability is set at three levels.

21b. Specific rate of change (dN/Ndt) of modeled populations as a function of population size with food availability as above.

of available food (200, 500, and 1000 x 10⁶ kcal/quarter). Populations were started either above or below the carrying capacity. The analysis of the effect of the number of seals on these parameters is somewhat artificial as survivorships are based upon seal numbers and age structure, and the reproductive rate is based on survivorships.

Population growth has its greatest effect on the survivorship of pups in this model (figure 22a). Pups have the lowest resistance to starvation and the lowest competitive ability. As the number of seals in the population increases, food becomes more limiting, and the pups respond with higher mortality.

Reproducing females in this model are also subject to lowered survivorship rates as populations grow with fixed food supplies (figure 22b). Increased energetic demand during pregnancy and lactation lower this class's resistance to starvation. As with pups, survivorship is not only dependent on population size, but on the level of available food.

The reproductive rate is a non-linear, density dependent relationship (figure 23). The drop in reproduction occurs as the benefit from pregnancy decreases. This is due to higher demands on a limited supply of food, and the ensuing decrease in the survivorship of pup and reproducing female harbor seals.

EFFECTS OF ALTERING THE TIMING OF PUPPING, SEASONAL TEMPERATURE, AND SEASONAL AVAILABILITY OF FOOD A series of simulations were performed to investigate the interactive effects of seasonal temperature, seasonal availability of food, and the timing of pupping on stable population size, reproductive rate, and survivorships of the six classes of seals. The year was adjusted to allow pupping in May-June, August-September, November-December, and February-March. At each pupping date four food regimens were imposed. A total of 16 runs were made (Table 13).

The highest stable population sizes were achieved when the peak in food availability occurred either immediately before,

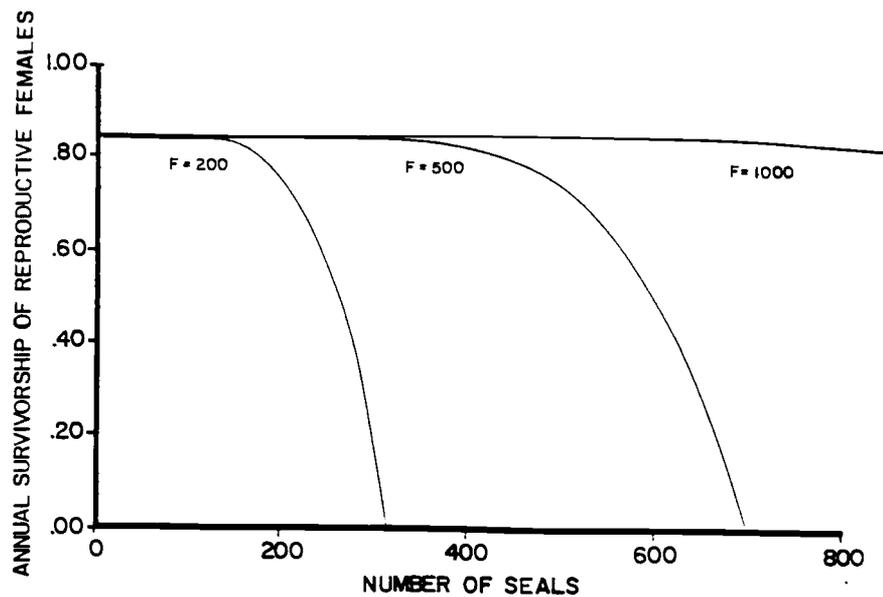
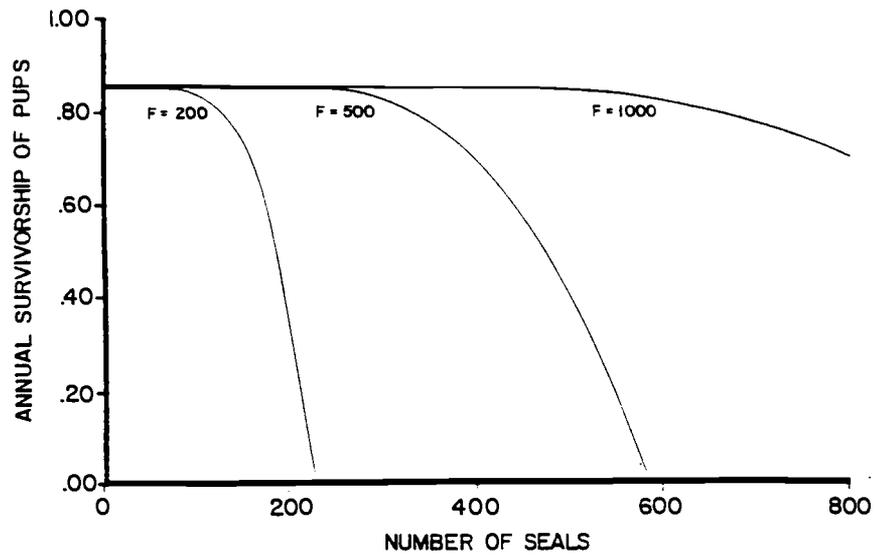


Figure 22a. Survivorship of pups as a function of population size with food availability set at three levels.

22b. Survivorship of reproductive females as a function of population size with food availability as above.

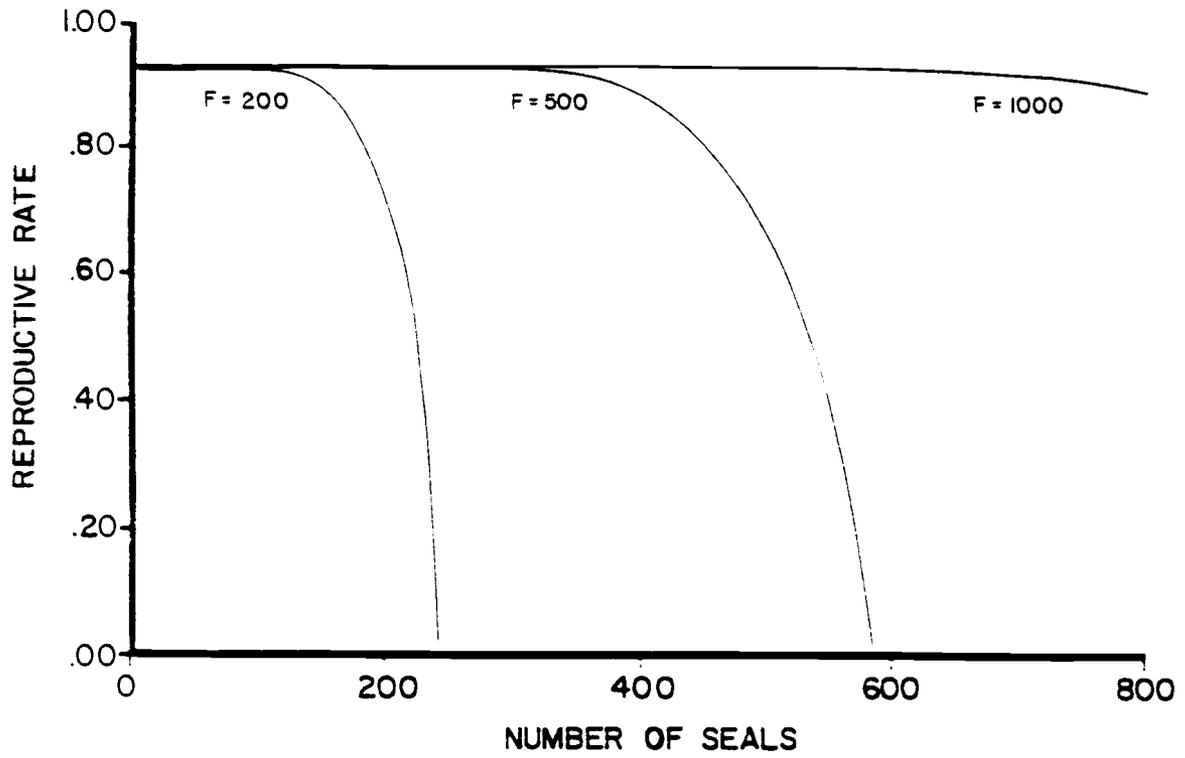


Figure 23. Reproductive rate as a function of population size at three levels of food availability.

Table 13. Seasonal parameters: water temperature and food availability in four regimens.

	<u>SPRING</u> <u>(Apr-Jun)</u>	<u>SUMMER</u> <u>(Jul-Sep)</u>	<u>AUTUMN</u> <u>(Oct-Dec)</u>	<u>WINTER</u> <u>(Jan-Mar)</u>
Water temperature*	12.26°C	14.82°C	13.04°C	9.63°C
Food availability** with peak in:				
SPRING	400	300	200	300
SUMMER	300	400	300	200
AUTUMN	200	300	400	300
WINTER	300	200	300	400

* average coastal sea surface temperature calculated from Churgin and Halminski (1974).

** food availability in 10^6 Kcal per 3 month period.

or immediately after weaning (Table 14). An increase in reproductive female survivorship resulted as food peaks occurred during late-pregnancy and lactation; pup survivorship increased as food peaks occurred after weaning.

Data was grouped into two sets for statistical purposes: one consisting of runs with food peaks immediately before and after weaning, and a second consisting of runs with food peaks occurring in the second and third quarter of the reproductive year. The mean stable populations of the two sets were significantly different ($P < 0.001$); mean survivorships of pups and reproducing females were different at significance levels of 0.20 (Table 15). High stable population levels were characterized by relatively greater survivorship of reproducing females and relatively lower survivorship of pups, indicating a possible greater importance of available food on reproducing female survivorship, and consequently, of reproducing female survivorship on population size in this model. However, the importance of food availability for weaned pups, though obscured by this analysis, should not be dismissed.

Temperature did not have much effect. Although results were not significantly different, the highest mean stable population size occurred with pupping in May-June. This caused a decrease in pup metabolism during the first six months of life when competitive ability is low.

EFFECTS OF ALTERING THE SEX RATIO The percentage of females at birth was varied between 50% and 92%. This was done in an attempt to find a sex ratio in this model at which the reproductive output (fitness) of males and females were equal. The concept of reproductive output needs to be defined.

In this analysis, consideration of the quantity of genetic material in the following year is made. Offspring produced will have one-half of the genes of each parent (Smith, 1978). Also, the offspring are reproductively benign for the first four years. Hence, the probability that a pup will reach maturity needs to be

Table 14. Stable population size at 100 years: effects of seasonal pupping and food availability.

Food availability peak in:	Pupping Occurs in:			
	<u>May-Jun</u>	<u>Aug-Sep</u>	<u>Nov-Dec</u>	<u>Feb-Mar</u>
SPRING	219.98	205.00	182.93	218.91
SUMMER	215.79	212.58	199.54	180.26
AUTUMN	183.64	217.72	216.08	204.23
WINTER	209.03	185.71	220.60	222.49

Table 15. A comparison of mean vital statistics of two sets of modeled populations: 100 year populations with seasonally varying pupping and food availability.

	<u>Set I</u>	<u>Set II</u>	<u>Significance Level*</u>
Population size	218.0 +/- 3.2	193.8 +/- 11.8	0.001
Reproductive rate	.886 +/- .003	.887 +/- .004	N.S.
Pup survivorship	.674 +/- .043	.713 +/- .060	0.20
Juv. survivorship	.841 +/- .002	.844 +/- .001	N.S.
Subadult and adult survivorship	.847 +/- .001	.847 +/- .000	N.S.
Reproducing female survivorship	.840 +/- .019	.826 +/- .014	0.20

* Student's t-test with pooled variance and 14 df.

considered. A parent's genetic contribution through an offspring (GC_o) is given by:

$$GC_o = (AS_1)(AS_2)^2(AS_3) / 2 \quad (15)$$

The total quantity of genetic material contributed to the following year by an individual can be measured by accounting for the probability of survival into the next year of that individual, the probability of reproduction, and the genetic contribution through offspring. The probability of reproduction (Pr) is given by the reproductive rate for females; and by the following equation for polygamous male harbor seals:

$$Pr_m = N_6 / (N_3 + N_4) \quad (16)$$

where N_6 = number of reproductive females

N_3 = number of subadult males

N_4 = number of adult males.

Assembling the terms yields the following reproductive contributions for females:

$$FRC = (1-REP)(AS_5) + REP[AS_6 + (AS_1)(AS_2)^2(AS_3)/2] \quad (17)$$

where FRC = female reproductive contribution

REP = reproductive rate

AS_i = annual survivorship of ith class

and for males:

$$MRC = AS_4 + (Pr_m)(AS_1)(AS_2)^2(AS_3) / 2 \quad (18)$$

where MRC = male reproductive contribution

Pr_m = probability of reproduction

AS_i = annual survivorship of ith class.

Female reproductive advantage (FRA) is defined as the ratio of

the female reproductive contribution to male reproductive contribution as:

$$\text{FRA} = \text{FRC} / \text{MRC} \quad (19)$$

When the value of FRA is 1.0, the reproductive outputs of males and females are equivalent. Maintaining this equivalency can be considered an evolutionary stable strategy (ESS) (Davies and Krebs, 1978). If the value of FRA becomes less than 1.0 it is advantageous to produce male offspring; above 1.0 it is advantageous to produce female offspring.

The equilibrium point for the harbor seal in this model is reached at a sex ratio at birth of 53% female (figure 24). This is similar to the empiric value of 56% female at birth reported by Bigg(1969b). This uneven sex ratio is explained by the relative lower survivorship rate of females in this model. As the number of females decreases due to mortality, the male reproductive contribution is reduced, and an increase in female reproductive advantage results.

When female reproductive advantage is viewed in a growing population it is found that females are favored early in a population's growth, and males are favored later. This change in female reproductive advantage can be explained by high female survivorship when food is not limiting and the higher resulting female reproductive contribution, and by the lessening of female reproductive contribution produced by lowered female survivorship as food becomes limiting.

EFFECT OF EXCLUSION OF SUBADULT MALES A "behavioral" exclusion of subadult males was performed by removing this portion of the population as demand for food was set. This exclusion produced a population that was 12.2% greater at stable equilibrium than a population where subadult males were not excluded.

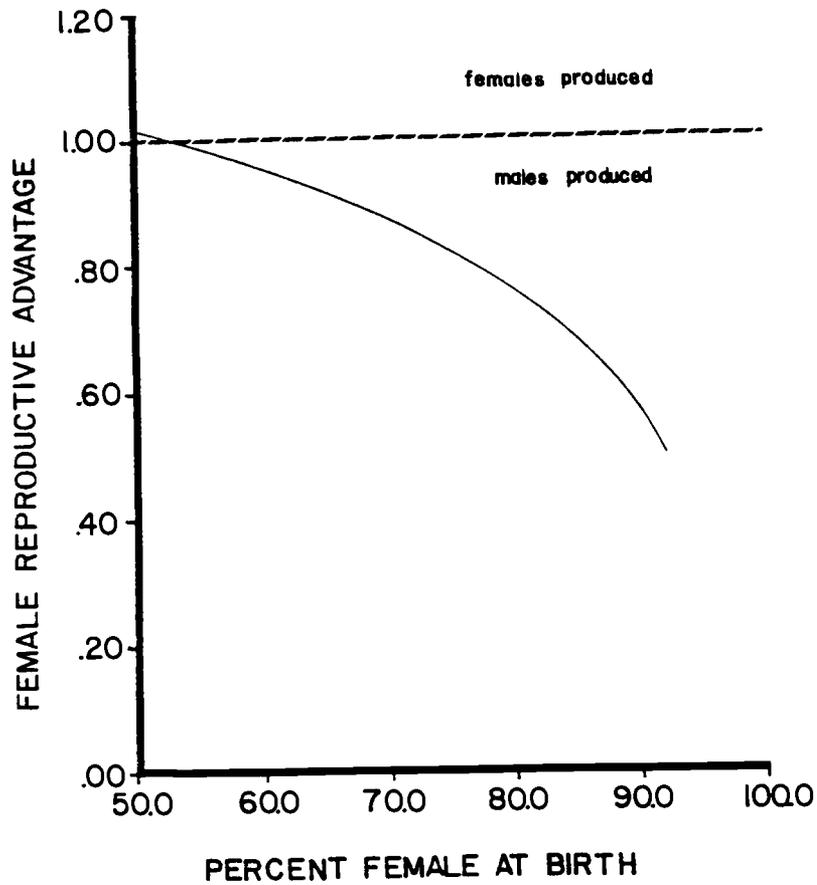


Figure 24. Female reproductive advantage as a function of sex ratio at birth in a stable population. Dashed line represents an evolutionary stable strategy.

DISCUSSION

A metabolic model was developed to form the basis of a food-limitation approach to the population dynamics of the Pacific harbor seal. This model, based upon equations for survivorship (eq. 10) and reproductive rate (eq. 13), produces similar population dynamics to those discussed by Fowler (1981a) for populations of large mammals. Also, the density dependent relationships used in other models of seal populations (eg. DeMaster, 1981; Eberhart, 1981; Lett et al, 1981) were approximated using this food-dependent model. Hanks (1981) discusses physiological condition in shaping population parameters, and suggests that demographic vigor declines in the following sequence:

- (1) juvenile mortality increases
- (2) age at first reproduction increases
- (3) fecundity decreases
- (4) adult mortality increases.

When the second and third steps are combined as the reproductive rate, the above sequence becomes that of this model based on metabolism.

One should not extrapolate to reality from the hypothetical results of a computer simulation. However, this sort of model can be used in proposing hypotheses for empirical testing. It provides possible conceptualizations for: (1) the cline in the pupping dates of harbor seals (Bigg, 1969a; Chapter 2) in that food availability may exert some ultimate control in the timing of reproduction, (2) a female biased sex ratio at birth (Bigg, 1969b), and (3) exclusion of certain elements of the population (Sergeant, 1973; Chapter 3).

This model attempts to define population size limitation as a function of available food resources. It is, in itself, limited by the numerous assumptions that are typical of any model. Also, it does not address the functional responses of prey populations

to predator density (Fowler, 1981a). It does allow, however, a basis for incorporation of functional response relationships, and through the measurement of metabolic parameters, a framework for comparative population dynamics studies as advocated by Fowler (1981b).

CHAPTER 5

PHOTOPERIOD AND DELAYED IMPLANTATION IN THE NORTHERN FUR SEAL
(CALLORHINUS URSINUS)

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SUMMARY

An equation for determination of the photoperiod at any given latitude for any given date is presented and used in an analysis of reproductive timing in the northern fur seal in which there is an obligate delay of implantation. Fur seals breeding on San Miguel Island, California (33°N) displayed a mean date of parturition that was 14 days earlier ($P < 0.001$) than that of the parent stock on the Pribilof Islands, Alaska (57°N). Previous studies have shown that changes occur in the corpus luteum, in follicles in the ovary containing the corpus luteum, in concentrations of plasma progesterone and estradiol-17_B, and in the uterine lining when there is a mean photoperiod of 12.5 h/day. This photoperiod occurs at both locations at 62 days after the mean dates of parturition, and may act as a cue for the initiation of implantation in these seals.

INTRODUCTION

In the reproductive cycle of the northern fur seal (Callorhinus ursinus) there is a 4-month delay of implantation. Viewed as obligatory in most pinniped species, delayed implantation allows about 8 months for fetal development after implantation and maintains precise reproductive timing, even though estrus occurs shortly after parturition in the otariids, and after the cessation of lactation in the phocid seals (Boshier, 1981). Female northern fur seals give birth to pups an

average of 0.8 days after returning to colony sites (Peterson, 1965; Bigg, 1984). Although estrus and copulation occur about 7 days after parturition, implantation is not expected until 120 days after copulation (Craig, 1964; DeLong, 1982). Females typically remain at the colony site and in adjacent waters until pups are weaned at 4 months before starting a pelagic migration (Peterson, 1968). Photoperiod, through an effect on pineal gland secretion, has been suggested as a possible exogenous cue for the initiation of implantation in the northern fur seal (Keyes et al, 1971; Elder et al, 1971; review by Daniel, 1981). However, an experimental study of female fur seals kept in different light regimens for up to 5 days by Daniel (1981) failed to produce any conclusive results.

Peterson et al (1968) reported that northern fur seals, initially tagged as pups in Alaska (57°N), were breeding on San Miguel Island, California (33°N). The present study examined the differences in reproductive timing and photoperiod regimens present during the period between parturition and implantation for northern fur seals breeding on San Miguel Island, California, and the Pribilof Islands, Alaska.

MATERIALS AND METHODS

Data consisting of the number of pups born per day during the 1979 pupping season at Adams Cove, San Miguel Island, California, and East Reef Rookery, St. George Island, Pribilof Islands, Alaska, were obtained from the National Marine Mammal Laboratory. These data were used to calculate the mean and variance of parturition dates at each location. Because the variances were not significantly different, the means were compared using Student's t test.

The analysis of the effect of photoperiod on reproductive timing in a wide ranging species such as the fur seal can be greatly facilitated if the photoperiod can be easily calculated from a set of latitudes and dates. Photoperiod (P) in h/day can

be described in terms of the date (D) and the latitude in degrees (L) by the following equation:

$$P = 24.00 - 7.64 (\arccos[\tan(0.01745L)\tan(0.00455D)]) \text{ h/day}$$

where the date (D) is given in terms of the sequential day number (d) from the winter solstice, 21 December, by $d - 91$, for $0 \leq d < 182$ and $273 - d$, for $182 \leq d \leq 365$. Latitudes in the southern hemisphere are considered negative. The equation is considered valid in the range of latitudes (-66.2° to 66.2°) between the Antarctic and Arctic Circles. This equation was formulated through trigonometric construct (Appendix III).

The photoperiod at parturition and for each subsequent day up to 70 days post partum was calculated for each birth. The mean and variance of photoperiods were then determined for the two locations on each day, relative to parturition, until 70 days post partum. Also, the annual photoperiod cycles at San Miguel and St. George Islands were constructed by calculating P at intervals of 10 days for 370 days.

RESULTS

The mean dates of parturition for the 1979 pupping season were calculated from 831 and 433 births on San Miguel and St. George Islands, respectively (figure 25). The mean date of parturition was 26 June at San Miguel and 10 July at St. George Island. This 14-day difference in the timing of births is significant ($P < 0.001$; Student's t test). The variances were not significantly different (Table 16). These results are similar to the 10-year mean date of parturition of 24 June for fur seals at San Miguel Island (DeLong, 1982) and the 7 July mean date of parturition on St. Paul Island in the Pribilofs (Bauer et al, 1964).

The annual cycles of photoperiod for San Miguel and St. George Islands were referenced to the mean dates of parturition

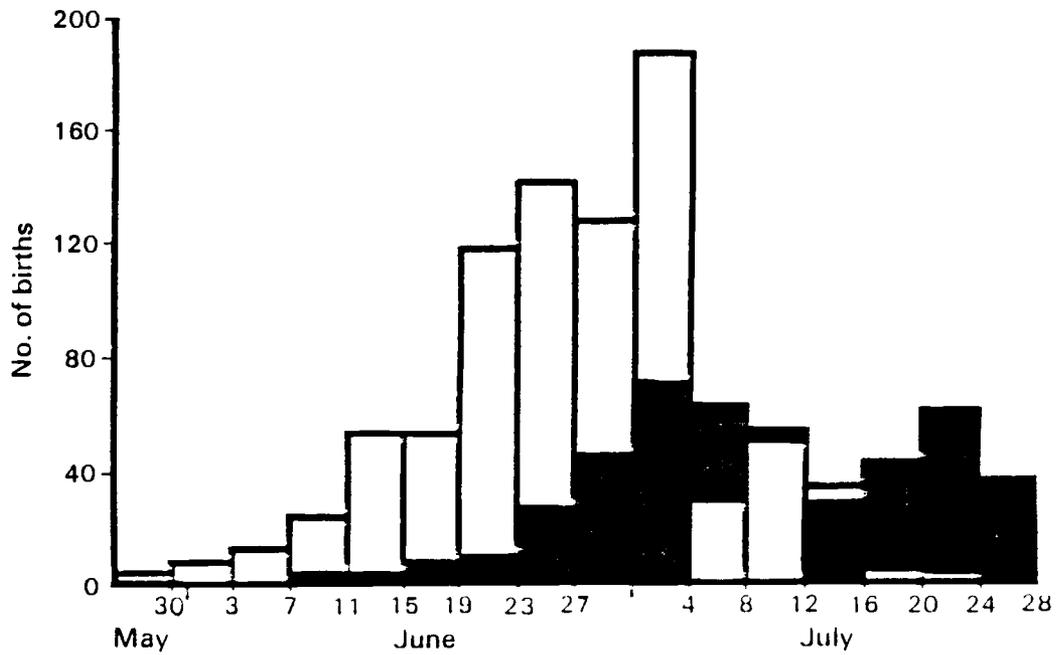


Figure 25. Number of northern fur seal pups born per 4-day period at Adams Cove, San Miguel Island (unshaded) and East Reef Rookery, Pribilof Islands (shaded) in 1979.

Table 16. Timing of births of northern fur seals on San Miguel Island and St. George Island.

	San Miguel Island (33°N)	St. George Island (57°N)
No. of births	831	433
First birth	28 May	10 June
Last birth	23 July	26 July
Mean date of birth	26 June	10 July
Variance	103.86	107.75
Standard deviation	10.19 days	10.38 days
Standard error	0.35 days	0.50 days

at each location (figure 26). At 33°N latitude photoperiod varies between 14.2 and 9.8 h/day; at 57°N latitude it varies between 17.7 and 6.2 h/day.

Comparison of the mean photoperiods at sequential days referenced to individual dates of parturition reveals that at 62 days post partum seals at both locations are exposed to a mean photoperiod of 12.5 h/day (Table 17). Photoperiods at 62 days post partum range from 11.9 to 13.2 h/day at San Miguel Island, and from 11.7 to 14.2 h/day at St. George Island.

DISCUSSION

The presence of a 2-week advance in the timing of births for San Miguel Island seals is suggestive of some latitudinal effect, perhaps similar to that reported by Schusterman et al (1982) for captive California sea lions, and by Bigg (1969a) for Pacific harbor seals along the west coast of North America. This is especially appealing in light of the Pribilof Island contribution to the original San Miguel population. Spotte and Adams (1981) reported that the timing of births in captive female northern fur seals at Mystic, Connecticut, was not affected by latitudinal conditions, specifically photoperiod, different from those of the natural range. However, their methods, based upon the estimated birth dates of only 6 aborted fetuses, may not have been robust enough to identify a difference in timing of less than 14 days.

The 12.5 h/day photoperiod lies within a 'window of reproductive timing' that exists after parturition and before implantation (unshaded area in figure 26), and while female fur seals are still at their colony site. It is during this period that an exogenous cue, such as a specific photoperiod, could regulate the reproductive timing of northern fur seals through initiation of estrus or initiation of an implantation sequence.

Studies of the reproductive physiology of female northern fur seals have been limited to the Pribilof Islands populations. At this location the 12.5 h/day photoperiod occurs on

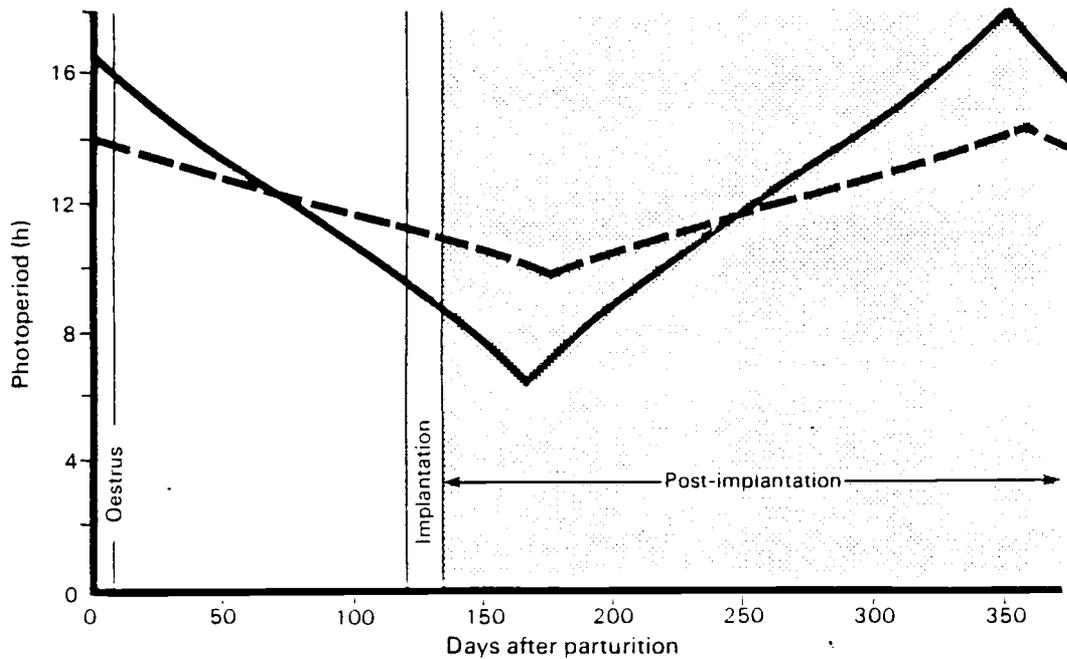


Figure 26. The annual cycles of photoperiod as referenced to the mean dates of parturition for northern fur seals at San Miguel Island, California, 33°N (broken line) and St George Island, Alaska, 57°N (solid line). Also shown are the approximate times of estrus and implantation.

Table 17. Photoperiod at 62 days post partum based on births of northern fur seals at San Miguel Island and St. George Island.

	San Miguel Island (33°N)	St. George Island (57°N)
No. of births	831	433
Photoperiod at 62 days post partum (h/day)		
Minimum	11.93	11.68
Maximum	13.22	14.19
Mean	12.53	12.54
Variance	0.04	0.31
Standard deviation (h/day)	0.21	0.56
Standard error (h/day)	0.01	0.03

11 September. Although lacking a major reproductive event, mid-September is characterized by changes in the ovary containing the recently formed corpus luteum, in the concentrations of plasma progesterone and estradiol-17_B, and in the uterine lining. Corpus luteum inactivation with a decrease in secretory function occurs in mid-August (Craig, 1964). However, Craig (1964) and Daniel (1971) report an increase in corpus luteum diameter between samples taken in early August and late September. A recurrence of follicular activity was noted by Craig (1964) following corpus luteum inactivation, and a peak of follicular activity was reported by Pearson and Enders (1951) before implantation. Also, the first ovulation of nulliparous female fur seals occurs during September (Craig, 1964). Plasma progesterone concentration increases before implantation from a low value after estrus in early September (Daniel, 1975). Estradiol-17_B concentrations are also low at this time but a surge occurs immediately before the reactivation of the blastocyst in late October (Daniel, 1974). Daniel (1971) reported that uterine protein, while showing no qualitative differences, more than doubled in concentration during the period between early August and late September. At about the same time the nuclei of uterine epithelial cells change from a granular to a vesicular appearance, and adventitial vasculature becomes more apparent within the uterine wall (Craig, 1964), as expected in preparation for implantation.

The photoperiod at the time that these changes are seen in Pribilof Island fur seals occurs 2 weeks earlier at San Miguel Island, and may explain the latitudinal difference in the timing of births between these locations. A decrease in photoperiod has been shown to affect the timing of implantation in other carnivores. Canivenc and Bonnin (1981) reported that an artificial decrease in photoperiod and temperature could trigger premature implantation in the European badger (Meles meles) by as much as 6 months. The absence of uterine protein changes and implantation in Daniel's (1981) study of northern fur seals kept

in different light regimens may have been due to the short (5-day) exposure to an altered photoperiod. It is suggested that a specific photoperiod occurring at about 62 days after parturition (or 65 days before implantation) acts to synchronize the timing of parturition in northern fur seals at a given latitude, presumably by triggering a sequence of changes that allows for the activation and implantation of the blastocyst.

CHAPTER 6

SERUM PROGESTERONE LEVELS AND REPRODUCTIVE STATUS OF INCIDENTALLY
KILLED FEMALE DALL PORPOISES

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Wildlife Management, 49(1): 51-54

INTRODUCTION

The reproductive endocrinology of odontocetes requires much elucidation. Investigations of female reproductive cycles have typically relied upon observation of the morphology and histology of the ovaries and uterus and the changes associated with ovulation, pregnancy, parturition, and lactation. The ovarian cycle has been described for Lagenorhynchus obliquidens, Stenella graffmani, Delphinus delphus (Harrison et al, 1969), Tursiops truncatus (Harrison and Ridgway, 1971), S. attenuata, S. longirostris (Benirschke et al, 1980), Phocoena phocoena (Fisher and Harrison, 1970), Phocoenoides dalli (Newby, 1982), and for two species of the the river dolphins, Inia geoffrensis and Pontoporia blainvillei (Harrison and Brownell, 1971). A review of the ovarian cycles of several species is provided by Harrison et al (1972).

Due to the difficulty, expense, and public opposition to the collection of marine mammal samples in the field, most studies of steroid hormones in these animals have been conducted on captive or zoo/aquarium animals. Exceptions include the study of the seasonal flux of testosterone in the Atlantic bottlenose dolphin by Harrison and Ridgway (1971) and the use of samples from S. attenuata and S. longirostris collected in the tuna purse seine fishery in the eastern tropical Pacific (Sawyer-Steffan and Kirby, 1980).

The Dall porpoise (Phocoenoides dalli dalli) is distributed along the eastern, northern, and western rims of the north Pacific Ocean and south of the ice front in the Bering Sea. This

small odontocete (family Phocoenidae) attains a maximum length and weight of 222 cm and 220 kg, respectively. Females are classified as type III ovulators, with most pregnancies occurring in the left horn of the uterus (Ohsumi, 1964). One offspring is produced, with the peak in parturition occurring in late June. At birth, calves average 95.3 cm in length. Pregnancy rate is reported to be 95.5% for mature females in the north Pacific Ocean (Newby, 1982).

The Japanese high seas mothership salmon gill-net fishery has a current incidental take of an estimated 2,900-13,533 Dall porpoises annually, with 71% taken within the United States Fishery Conservation Zone (Newby, 1982). As a result of this high mortality, reproductive parameters for population dynamics analysis have become essential for the management of this species.

This study was undertaken to describe the serum levels of progesterone in incidentally killed Dall porpoises and to examine the changes in these levels associated with late pregnancy and lactation. Also, the feasibility of using serum samples from incidentally killed Dall porpoises (and other marine mammals) for progesterone studies was investigated.

METHODS

BLOOD SAMPLES Blood samples were taken from 50 incidentally killed female Dall porpoises during June and July, 1980. Samples from the following groups were obtained: pregnant females (24), lactating females (8), immature females (17), and nonpregnant adult females (1). All animals were taken between 49°04' and 51°36' north latitude and 171°12' and 174°52' west longitude in the north Pacific Ocean. The porpoises were entangled and subsequently died in salmon gill nets during normal fishing operations. They were taken aboard catcherboats and transported to the motherships where biological samples were taken and necropsies performed. The elapsed time between death and the sampling of blood ranged from 2 to 16 hours (T. C. Newby, pers.

comm.). Blood samples were drawn via 10 ml, sterile Vacutainer syringe systems (red top) from the vena cava of the animal by National Marine Mammal Laboratory (NMML) personnel. The blood was centrifuged using a hand-crank centrifuge until separation of serum and formed elements was complete. The serum was decanted into a second 10-ml Vacutainer tube and frozen at -20°C until radioimmunoassays were performed.

CORPUS LUTEUM MEAN DIAMETERS Ovaries were collected at sea during necropsy and either frozen at -50°C or placed in a 10% formalin solution for further analysis at the NMML. Diameters along three axes were measured as specified by Newby (1982). From measurements provided by the NMML, the mean diameters of the corpora lutea of the sample animals were determined.

RADIOIMMUNOASSAY OF SERUM PROGESTERONE Triplicate volumes (25-50 μl) of serum were doubly extracted with a 1:2 mixture of benzene and hexane. Sawyer-Steffan and Kirby (1980) reported that hexane extraction for progesterone radioimmunoassay eliminated contamination in samples of dolphin blood. The extraction efficiency averaged $91.2 \pm 1.9\%$ (mean \pm S.E.M.). The antiserum used, anti-progesterone-11-BSA (No.1337, Gordon D. Niswender), does not bind other steroids appreciably at physiological concentrations (Koligian and Stormshak, 1977). The average binding for this antiserum in the assays performed was 54%. The competitor was [^3H]progesterone (3,000 cpm in 100 μl ; New England Nuclear, 114 Ci/mole).

The assay was validated using porpoise serum. To be certain that there was no interference by other steroids or serum constituents found in this species, we assayed a set of five serum samples with and without separation on Celite chromatography columns. No differences in progesterone concentration were found, so samples were subsequently assayed without chromatography.

Intraassay variability, calculated as the coefficient of variation, was 6.0%. Interassay variability had a coefficient of

variation of 2.9%. The assay sensitivity was found to be 0.3 ng/ml. A dilution curve using 400 μ l, 200 μ l, 100 μ l, 50 μ l, and 25 μ l was found to be parallel to that of the progesterone standards used.

RESULTS

The means and standard errors of serum progesterone levels for six groups of female Dall porpoises were calculated (figure 27). Immature females had concentrations of serum progesterone that ranged from undetectable to 31.1 ng/ml, with a mean value (+/- S.E.M.) of 0.3 +/- 0.1 ng/ml, and one mature female that was neither pregnant nor lactating had 0.5 ng/ml.

Concentrations of serum progesterone were found to range between 6.8 and 45.3 ng/ml in pregnant Dall porpoises with fetuses greater than 70 cm standard length. There were no significant differences between the mean serum progesterone concentrations of 23.2, 19.5, and 23.4 ng/ml of females with fetuses of 70-79 cm, 80-89 cm, and 90-99 cm standard length, respectively. The mean serum progesterone level of females with fetuses greater than 100 cm standard length (10.5 ng/ml) was less ($P < 0.01$) than that of females with fetuses shorter than 100 cm. No significant trends were found when maternal serum progesterone was regressed on fetal length ($r^2 = 0.03$) or fetal weight ($r^2 = 0.07$).

The concentrations of serum progesterone in lactating females ranged from undetectable levels to 11.4 ng/ml, with a mean concentration of 2.6 +/- 1.3 ng/ml. A regression of concentration of serum progesterone on corpus luteum mean diameter in pregnant and lactating Dall porpoises (figure 28) yielded a relationship best described by:

$$P = 0.01 \exp(0.27CLMD); \quad r^2 = 0.74.$$

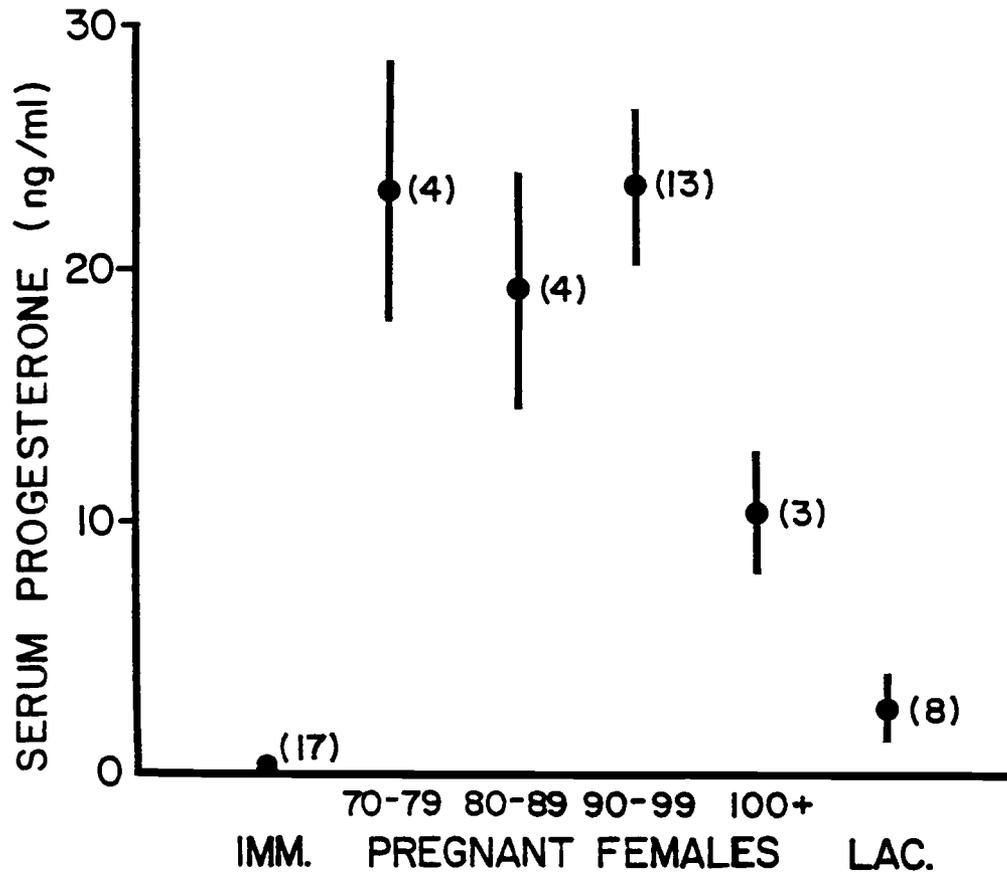


Figure 27. Mean concentrations with standard error bars of serum progesterone for immature (IMM.), pregnant, and lactating (LAC.) female Dall porpoises. Pregnant females are grouped by standard length in cm of fetuses. Number of samples are shown in parentheses.

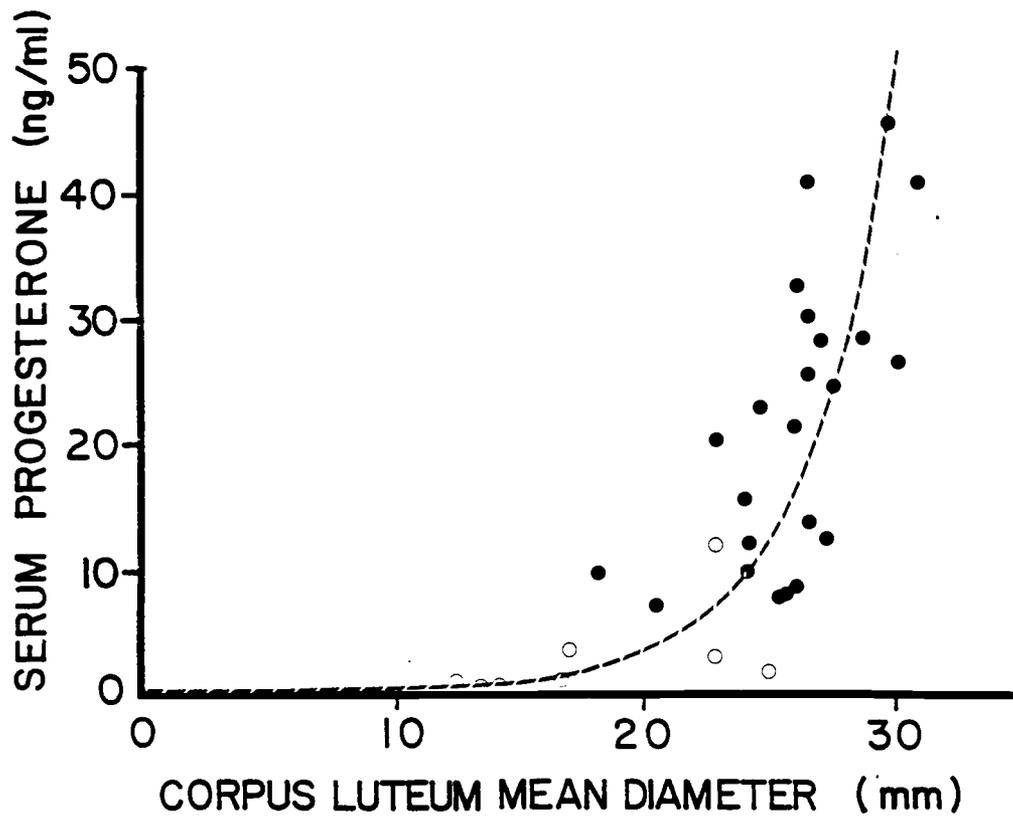


Figure 28. Concentrations of serum progesterone as a function of corpus luteum mean diameter. Solid circles are samples from pregnant females; open circles are from lactating females. Relationship is given by: $y = 0.01 \exp(0.27x)$; $r^2=0.74$.

DISCUSSION

The values presented here comprise the first report of levels of serum progesterone in Dall porpoises. Animals that were killed in salmon gill nets provided serum samples for progesterone radioimmunoassay. The mean values and ranges of serum progesterone found in pregnant females reflect those obtained for captive female Atlantic bottlenose dolphins (family Delphinidae) of 10.4 - 41.6 ng/ml (Richkind and Ridgway, 1975). The apparent time course of progesterone shows a decrease in females judged as being near term, with fetuses greater than the mean birth length of 95.3 cm. This is as expected for a large mammal and is similar to that reported for the harbor seal (*Phoca vitulina*) (Raeside and Ronald, 1981). Low values of serum progesterone in immature and nonpregnant adult Dall porpoises are also as expected.

A relationship between the corpus luteum mean diameter and serum progesterone is demonstrated. This exponential relationship ($r^2 = 0.74$) is indicative of serum progesterone levels remaining stable, at least in a relative sense, following death in these animals. We found this surprising considering the long and variable period between death and sampling of blood. Cold temperatures of approximately 6-8°C in the surface waters of the north Pacific Ocean during the sampling period (Robinson, 1976) may have helped maintain the serum progesterone levels.

Serum samples collected from incidentally killed marine mammals may prove to be a valuable source of information on the reproductive cycles of these animals. This type of sample provides a hormonal correlate to reproductive state and utilizes to a fuller extent the incidentally killed animal. Also, the examination of hormone levels in these animals can verify the results of morphological and histological studies and lend inferences to the timing of reproductive events in marine mammals.

CHAPTER 7

GENERAL CONCLUSIONS

The papers presented in this thesis are variations on a theme of seasonality in reproduction of marine mammals. Together, they allow some general conclusions regarding the use of the photoperiod equations, the role of photoperiod in phasing reproductive cycles, the role of delayed implantation in allowing specific breeding seasons, the importance of seasonality in birth, and dispersal and evolution of pinnipeds.

USE OF THE PHOTOPERIOD EQUATIONS The equations presented for the calculation of photoperiod (Appendix III) provide good approximations of the naturally available light. The use of such equations in photoperiod analysis of latitudinally variable reproductive timing provides a framework on which testable hypotheses may be built and allows comparison of natural and artificial (experimental) conditions. Bowman (1973) notes that, whereas natural changes in the photoperiod are gradual, abrupt changes of photoperiod can be equally effective in producing physiological effects, although there may be a long period of latency. Hence, the experimental condition can demonstrate that photoperiod regulates some physiological event, while the natural condition can indicate where photoresponse is likely to occur.

It has been suggested that photoperiod regulates a number of reproductive functions in mammals. Bigg and Fisher (1975) showed that photoperiod affects the timing of estrus in the harbor seal. Griffiths et al (1979) have demonstrated a seasonal flux in the concentration of plasma melatonin in the elephant seal. Further, it is likely that photoperiod controls the timing of implantation in the European badger (Canivenc and Bonnin, 1981) and regulates an endogenous reproductive rhythm in male pallid bats (Beasley and Zucker, 1984). No indication has been made as to the point in the reproductive cycle at which these photoresponses occur.

The studies reported in Chapters 2 and 5 attempt to show that photoperiod, as a sole exogenous cue, can define latitudinal variation in the pupping seasons of two North Pacific pinnipeds. Using populations that are scattered over many degrees of latitude, photoperiod analysis demonstrates that there are two points during the reproductive cycle when photoperiod could control this cycle; biological constraints, such as the specific growth rates of fetuses and the initiation of estrus with parturition, indicate that photoresponse could occur only during the period between estrus and implantation.

Photoperiod analyses can lead one to many false conclusions (D. Griffiths, pers. comm., 1984). For example, an arithmetic relationship between the total amount of illumination from the post-solstice 16-hour day and the onset of fecundity in the European red fox (Vulpes vulpes) proved to be an artifact (Lloyd and Englund, 1973). However, in both the Pacific harbor seal and the northern fur seal (similar, but unrelated species) specific photoperiods are co-occurring with the same major physiological change and this leads me to believe that photoperiod does regulate reproductive timing in these two species.

ROLE OF PHOTOPERIOD Photoperiod acts to define the cline in the pupping season of the Pacific harbor seal and can explain the 14-day advance in northern fur seals breeding in California. In both species the proposed photoresponse occurs at the approximate midpoint between estrus and implantation (Table 18). In addition, this is a period of secondary follicular activity in the ipsilateral ovary (Craig, 1964; Bigg and Fisher, 1974) and concomitant changes in the corpus luteum, uterus, and steroid hormones.

Wolfson (1964) identified five basic components of a photoresponse system. They are: (1) the role of the external factors; change in daylength, (2) the receptor which responds to light, (3) the pathway from the receptor to (4) the effector(s),

Table 18. Relative timing in days of pupping (P), estrus (E), photoresponse (X), and implantation (I) in the Pacific harbor seal and the northern fur seal.

	<u>P</u>	<u>E</u>	<u>X</u>	<u>I</u>	<u>E-X</u>	<u>X-I</u>	<u>E-X/E-I</u>
Harbor seal	0	35	68	105	33	37	0.47
Fur seal	0	7	62	127	55	65	0.46

and (5) the mechanism by which the physiological response is mediated. In most mammals the retina acts as the receptor and the anterior pituitary serves as the effector (Bowman, 1973). The pineal body may function as an intermediate. Cuello (1973) described the pineal organ of the Weddell seal as being highly organized, with capillary epithelium, cell clusters, and autonomic innervation supporting an endocrine role, but with neural architecture. Northern fur seal pineal glands were shown to have seasonal fluctuations in the concentrations of hydroxy-indole (Keyes et al, 1971), while Griffiths et al (1979) demonstrated marked circadian rhythms of elephant seal plasma melatonin in the winter, but not in the summer.

A possible mechanism of photoperiod response in seals involves the secretion of a gonadotroph (eg. FSH) or an antigonadotroph (eg. melatonin, prolactin, 5-methoxy-tryptophol) to regulate follicular development during the period of delayed implantation. Harbor seal estrus has been shown to be sensitive to photoperiod (Bigg and Fisher, 1975). European badgers experience several waves of follicular activity with ovulations in February, June, September, and October, even though implantation does not occur until December (Harrison, 1963). Again, photoperiod is involved with the cessation of follicular activity and implantation (Canivenc and Bonnin, 1981).

ROLE OF DELAYED IMPLANTATION Delayed implantation, as a reproductive feature, can take on the form of a function or an effect (King, 1984) and hence, its role is difficult to deduce. Sandell (1984) reviews several hypotheses for the existence of delayed implantation. They are: (1) phylogenetic constraint determines the presence or absence of delay, (2) delayed implantation allows for estrus to occur during lactation and may attract males to a temporary family relationship, (3) delayed implantation permits fertilization before dispersal of individuals, and (4) delayed implantation enables parturition when conditions for the young are optimal, yet permits breeding

when the adults are in better condition (Fries, 1880). To this list I add one other: (5) delayed implantation, while allowing a fixed time of birth, also allows more than one ovulatory cycle, and increases the probability of reproducing.

Pinnipeds, as a group, have delayed implantation (Boshier, 1981). Its existence as a phylogenetic constraint is probable owing to the presence of a delay in the Mustelidae (Mead, 1981) and the Ursidae (Daniel, 1981). However, Sandell (1984) and King (1984) present the case of the stoat (Mustela erminea) and the weasel (Mustela nivalis). These two closely related species have and do not have delayed implantation, respectively. Although it is present, King (1984) argues delay should contribute some advantage to the individual, or at least be of neutral value.

Temporary male-female relationships do not appear to be common in the pinnipedia, rather, promiscuous or polygynous mating systems predominate. The delay of implantation does allow female fur seals to mate while males are still on the colony site, even though males disperse before implantation. This feature, however, appears to be more of an attribute of delayed implantation than a cause. Harbor seals do not disperse, and males have access to females year-round.

Delayed implantation does permit a fixed period in which pups are born. More completely, delayed implantation allows for pregnancy, lactation, and the post-weaning periods to occur at specific times of the year. Bigg (1973) suggested that the timing of birth was ultimately dependent upon the availability of food species for newly-weaned pups. Coulson (1981) attempted to describe grey seal population birth period differences as a function of the three-month mean temperature before implantation. However, an alternative hypothesis would suggest that grey seals pup when water temperatures are optimal for pup survival.

The energy requirements for pregnant and lactating harbor seals are great. Conservative estimates (Chapter 4) of metabolic demand during this period represent an increase in the range of a 1.5 to 2.4-fold. Whereas adults are thermoneutral in water, pup

metabolism is increased by water cooler than 20°C (Miller et al, 1976). Also, since pups need to learn to catch prey (Renouf, 1980), food availability for newly-weaned pups is important. Hence, I would argue that both food availability and water temperature, and hence the season of pupping, are important factors for harbor seals.

There is mounting evidence that seals are not monoestrous. Bigg (1973) found a diestrus condition in about 18% of captive harbor seals examined. Boyd's (1984a) data on multiple ovulations and pregnancy rates support an hypothesis that seals may have up to two or three estrous cycles in a single year, and that such a system can boost pregnancy rates from 82% to 95%.

From the data reported in the literature and from the apparent association of follicular activity with a specific photoperiod prior to implantation, I conclude that delayed implantation in seals is an adaptation that provides synchrony in birthing (ie. pups are born when conditions are optimal) while permitting more than one ovulatory cycle (ie. pregnancy rates are increased).

SEASONALITY OF BIRTH There are indications that harbor seals are seasonally food limited. Haul-out attendance curves (Graybill, 1981; Brown and Mate, 1983) demonstrate that seals are absent, and presumably spending more time feeding, during the winter months. Treacy et al (1984) have documented the movement of females to take advantage of fish spawning migrations. Due to the increased expenditure of energy experienced by female harbor seals during the reproductive cycle, segregation on haul-out areas, allowing for females to be in better habitat (eg. bays and estuaries) is expected. This would allow a means to equalize reproductive energy cost between sexes. Chapter 3 presents data indicating that this haul-out segregation may be occurring. Whereas no data have been presented, it is assumed that breeding seasons in the northern fur seal and the Dall porpoise, to some extent, are shaped by food availability and temperature.

Modeled populations of harbor seals reach maximum population size when food peaks occur during late-pregnancy and lactation or during post-weaning (Chapter 4). The model indicates that both maternal and pup survival is important, but that maternal survivorships are higher and pup survivorships lower when maximum populations are attained.

Harbor seals and northern fur seals are able to maintain precise timing of birth with imprecisely timed estrus by incorporating delayed implantation. Dall porpoises (Chapter 6) maintain relatively precise birth timing without delay, but probably use a single well-timed estrus occurring immediately prior to implantation. This major difference recalls the argument regarding phylogenetic constraints.

GLOBAL DISPERSAL AND EVOLUTION OF PINNIPEDS The harbor seal evolved from the largha seal in the North Pacific basin (McLaren, 1966). Dispersal lead to the present five subspecies. I suggest (Chapter 2) that further differentiation is occurring within the Puget Sound / Strait of Georgia system. In the first disruptive event, allochronic factors are indicated: the delaying of birth by three months to allow land-breeding at high latitudes. Allopatric speciation has yielded the five subspecific groups of Phoca vitulina in the two major Northern Hemisphere basins. Allochronic speciation may be occurring in the PS/SG system with a further three-month delay in pupping.

The southern extension of the Pacific harbor seal is 30°N at Isla San Martin, Mexico (Scheffer, 1974), which is also the approximate southern extent of a 13.8 h/day photoperiod. As California sea lions extend as far south as the tip of Baja California (Mate, 1979) and the two species have some overlap in their feeding habits (Spalding, 1964; Jones, 1981), harbor seals may be limited in their southern distribution by the availability of a 13.80 h/day photoperiod.

Otariid seals are thought to have evolved in the North Pacific basin and dispersed to the Southern Hemisphere along the

North and South American west coast (McLaren, 1960). A northern fur seal ancestor with a photoresponse at a 12.5 h/day photoperiod would be preadapted for southern dispersal. Unlike the North Pacific phocids, this otariid could cross the equator.

The Guadalupe fur seal (Arctocephalus townsendi) inhabits Isla Guadalupe, Baja California (28°N). It, like the northern fur seal, has a summer breeding season (Hubbs, 1979). An indefinite breeding season has been suggested for the the Galapagos fur seal (A. galapagoensis) at 0° (Clark, 1979). However, Trillmich and Limberger (1985) report that Galapagos fur seals breed from August through November. The South American fur seal (A. australis) is found from approximately 12°S to 55°S. Vaz-Ferreira (1979) reports a November-December breeding season for this species.

Photoperiod response during the period of delayed implantation has been proposed as the mechanism that regulates the timing of birth in the Pacific harbor seal and the northern fur seal. Correlates of this photoperiod phasing may be reflected in the current distributions and breeding seasons of phocid and otariid seals.

BIBLIOGRAPHY

- Abraham, G. E. (1974) Radioimmunoassay of steroids in biological materials. ACTA ENDOCRINOL suppl. no. 183 41 pp.
- Allen, J. A. (1902) The hair seals (family Phocidae) of the North Pacific Ocean and Bering Sea. BULL AM MUS NAT HIS 16: 459-499.
- Bauer, R. D., R. S. Peterson, and V. B. Scheffer (1964) Age of northern fur seal at completion of its first molt. J MAMMAL 45: 299-300
- Beasley, L. J. and I. Zucker (1984) Photoperiod and the annual reproductive cycle of the male pallid bat (Antrozous pallidus). J REPRO FERT 79: 567-573.
- Benirschke, K., M. L. Johnson, and R. J. Benirschke (1980) Is ovulation in dolphins, Stenella longirostris and Stenella attenuata, always copulation-induced? FISH BULL 78: 507-528.
- Bigg, M. A. (1984) Stimuli for parturition in northern fur seals (Callorhinus ursinus). J MAMMAL 65(2): 333-336.
- _____ (1973) Adaptations in the breeding of the harbour seal, Phoca vitulina. J REPRO FERT suppl. no. 19: 131-142.
- _____ (1969a) Clines in the pupping season of the harbour seal, Phoca vitulina. J FISH RES BD CANADA 26: 449-455.
- _____ (1969b) The harbour seal in British Columbia. FISH RES BD CANADA BULL no. 172. 33 pp.
- _____ and H. D. Fisher (1975) Effects of photoperiod on annual reproduction in female harbour seals. Rapp. P.-v. Reun Cons int Explor Mer no. 169: 141-144.
- _____ (1974) The reproductive cycle of the female harbour seal off southeastern Vancouver Island. pp. 329-347. In: R. J. Harrison (ed.) Functional Anatomy of Marine Mammals. Vol. 2. Academic Press Inc., London. 366 pp.
- Bishop, R. H. (1968) Reproduction, age determination, and behavior of the harbor seal, Phoca vitulina l. in the Gulf of Alaska. M. S. Thesis. Univ. of Alaska. 121 pp.
- Bonner, W. N. (1979) Harbour (common) seal. pp. 58-62. In: Mammals in the Seas. Vol. II. Pinniped species summaries and report on sirenians. FAO Advisory Committee on Marine Resource Research, Working Party on Marine Mammals. FAO FISH SER (5), 152 pp.

- Borrue! , M. , P. Borrue! , M. C. Damasco, and C. P. Lantos (1974)
The in vitro investigation of four radioactive corticosteroids
in the Antarctic seal (Leptonychotes weddellii). GEN COMP
ENDOCRINOL 22: 1-12.
- Boshier, D. P. (1977) Observations on the corpus luteum of the
grey seal (Halichoerus grypus, Nilsson, 1820) at the time of
ovaimplantation. pp 333-359. In R. J. Harrison (ed.)
Functional Anatomy of Marine Mammals. Vol 3. Academic Press,
London.
- _____ (1979) Electron microscopic studies on the
endometrium of the grey seal (Halichoerus grypus) during its
preparation for nidation. J ANAT 128: 721-735.
- _____ (1981) Structural changes in the corpus luteum
and endometrium in seals before implantation. J REPRO FERT
suppl. no. 29: 143-149.
- Boulva, J. (1975) Temporal variations in birth period and
characteristics of newborn harbour seals. Rapp. P.-v. Reun
Cons int Explor Mer. 169: 405-408.
- _____ and I. A. McLaren (1979) Biology of the harbor seal,
Phoca vitulina, in eastern Canada. BULL FISH RES BD CAN no.
200. 24 pp.
- Bowman, J. C. (1973) Photoperiodicity in mammals. J REPRO FERT
suppl. no. 19: 85-88.
- Boyd, I. L. (1983) Luteal regression, follicle growth and the
concentration of some plasma steroids during lactation in grey
seals (Halichoerus grypus) J REPRO FERT 69: 157-164.
- _____ (1984a) Developmant and regression of the corpus
luteum in grey seal (Halichoerus grypus) ovaries and its use
in determining fertility rates. CAN J ZOOL 62: 1095-1100.
- _____ (1984b) The relationship between body condition and
the timing of implantation in pregnant grey seals (Halichoerus
grypus). J ZOOL LOND 203: 113-123.
- Brown, R. F. Oregon Department of Fish and Wildlife. Oregon
State University Marine Science Center. Newport, Oregon.
Personal Communication.
- _____ (1981) Abundance, movements and feeding habits of the
harbor seal Phoca vitulina, at Netarts Bay, Oregon. M. S.
Thesis. Oregon State Univ. 57 pp.
- _____ and B. R. Mate (1983) Abundance, movements and
feeding habits of harbor seals, Phoca vitulina, at Netarts and
Tillamook Bays, Oregon. FISH BULL 81(2): 291-301.

- Burns, R. E. (1985) The Shape and Form of Puget Sound. Puget Sound Books. A Washington SeaGrant Publication. Univ. Wash. Press, Seattle, Wash. 100 pp.
- Canivenc, R. and M. Bonnin (1981) Environmental control of delayed implantation in the European Badger (Meles meles). J REPRO FERT suppl. no. 29: 11-24.
- Churgin, J. and S. J. Halminski (1974) Temperature, Salinity, Oxygen, and Phosphate in Waters off the United States. Vol. III. Eastern North Pacific. U S Dept. of Commerce. NOAA publ. 260 pp.
- Clark, T. W. (1979) Galapagos fur seal. pp 31-33. In: Mammals in the Seas. Vol. II. Pinniped species summaries and report on sirenians. FAO Advisory Committee on Marine Resource Research, Working Party on Marine Mammals. FAO FISH SER (5), 152 pp.
- Collias, E. E., N. McGary, and C. A. Barnes (1974) Atlas of Chemical and Physical Properties of Puget Sound and its Approaches. Washington Sea Grant Publ. Univ. of Washington Press, Seattle and London. 235 pp.
- Coulson, J. C. (1981) A study of the factors influencing the timing of breeding in the grey seal Halichoerus grypus. J ZOO LOND 194: 553-571.
- Craig, A. B. Jr. and A. Pasche (1980) Respiratory physiology of freely diving harbor seals (Phoca vitulina). PHYSIOL ZOO 53(4): 419-432.
- Craig, A. M. (1964) Histology of reproduction and the estrus cycle in the female fur seal, Callorhinus ursinus. J FISH RES BD CANADA 21(4): 773-811.
- Cuello, A. C. (1973) Ultrastructural characteristics and innervation of the pineal organ of the Antarctic seal Leptonychote weddelli. J MORPHOL 141(2): 217-226.
- Daniel, J. C., Jr. (1971) Growth of the preimplantation embryo of the northern fur seal and its correlation with changes in uterine protein. DEVL BIOL 26: 316-328.
- _____ (1974) Circulating levels of oestradiol-17_B during early pregnancy showing an oestrogen surge preceding implantation. J REPRO FERT 37: 425-428.
- _____ (1975) Concentration of circulating progesterone during early pregnancy in the northern fur seal, Callorhinus ursinus. J FISH RES BD CAN 32: 65-66.

- _____ (1981) Delayed implantation in the northern fur seal (Callorhinus ursinus) and other pinnipeds. J REPRO FERT suppl. no. 29: 35-50.
- Davies, N. B. and J. R. Krebs (1978) Introduction: ecology, natural selection, and social behavior. In J. R. Krebs and N. B. Davies (eds.) Behavioral Ecology: an evolutionary approach. Sinauer Associates Inc., Sunderland, Mass. 494 pp.
- Delong, R. L. (1982) Population biology of northern fur seals at San Miguel Island, California. Ph.D. dissertation, University of California, Berkeley.
- DeMaster, D.P. (1981) Incorporation of density dependence and harvest into a general population model for seals, pp. 389-401. In Fowler, C. W. and T. D. Smith (eds.) Dynamics of Large Mammal Populations. John Wiley and Sons, New York. 477 pp.
- Eberhardt, L. L. (1981) Population dynamics of the Pribilof fur seals, pp. 197-220. In Fowler, C. W. and T. D. Smith (eds.) Dynamics of Large Mammal Populations. John Wiley and Sons, New York. 477 pp.
- Elden, C. A., M. C. Keyes, and C. E. Marshall (1971) Pineal body of the northern fur seal (Callorhinus ursinus): a model for studying the probable function of the mammalian pineal body. AM J VET RES 32: 639-647.
- Everitt, R. D., R. J. Beach, A. C. Geiger, S. J. Jeffries, and S. D. Treacy (1980) Marine mammal - fisheries interaction on the Columbia River and adjacent waters, 1980. Annual Report: Mar 1 1980 to Oct 31 1980. NMML/NMFS. 109 pp.
- Everitt, R. D., C. H. Fiscus, and R. L. Delong (1979) Marine mammals of northern Puget Sound and the Strait of Juan de Fuca: a report on investigations November 1, 1977 - October 31, 1978. NOAA/MEAP NOAA Tech. Mem. ERLMESA - 41. 191 pp.
- Fisher, H. D. (1954) Delayed implantation in the harbour seal, Phoca vitulina L. NATURE 173(4410): 879-880.
- _____ and R. J. Harrison (1970) Reproduction in the common porpoise (Phocoena phocoena) of the North Atlantic. J Zool., London 161: 471-486.
- Fowler, C. W. (1981a) Density dependence as related to life history strategy. ECOLOGY 62(3): 602-610.
- _____ (1981b) Comparative population dynamics in large mammal populations, pp. 437-455. In Fowler, C. W. and T. D. Smith (eds.) Dynamics of large mammal populations. John Wiley and Sons, New York. 477 pp.

- Fries, S. (1880) Über die fortpflanzung von *Meles taxus*. ZOOLOG ANZ 3: 486-492.
- Geraci, J. R. and J. Sweeney (1978) Clinical techniques. pp. 580-587. In: M. E. Fowler (ed.) Zoo and Wild Animal Medicine. W. B. Saunders Co. Philadelphia, Pa. 951 pp.
- Graybill, M. R. Oregon Institute of Marine Biology. Charleston, Oregon. Personal Communication.
- _____ (1981) Haul out patterns and diet of harbor seals, *Phoca vitulina*, in Coos County, Oregon. M. S. Thesis. Univ. of Oregon. 56 pp.
- Griffiths, D. University of Oslo, Oslo, Norway. Personal Comm.
- _____, R. F. Seamark, and M. M. Bryden (1979) Summer and winter cycles in plasma melatonin levels in the elephant seal (*Mirounga leonina*) AUST J BIOL SCI 32: 581-586.
- Guyton, A. C. (1976) Textbook of Medical Physiology. W. B. Saunders Co. Philadelphia. 1194 pp.
- Hanks, J. (1981) Characterization of population condition, pp. 47-73. In: Fowler, C. W. and T. D. Smith (eds.) Dynamics of Large Mammal Populations. John Wiley and Sons, New York. 477 pp.
- Harrison, R. J. (1963) A comparison of factors involved in delayed implantation in badgers and seals in Great Britain. pp 99-114. In: A. C. Enders (ed.) Delayed Implantation. Univ. Chicago Press, Chicago. 318 pp.
- _____, R. C. Boice, and R. L. Brownell, Jr. (1969) Reproduction in wild and captive dolphins. NATURE 222: 1143-1147.
- _____ and R. L. Brownell, Jr. (1971) The gonads of the South American dolphins, *Inia geoffrensis*, *Pontoporia blainvillei*, and *Sotalia fluviatilis*. J MAMMAL 52: 413-419.
- _____, _____, and R. C. Boice (1972) Reproduction and gonadal appearances in some odontocetes. pp. 361-419. In: R. J. Harrison (ed.) Functional Anatomy of Marine Mammals. Vol. 1. Academic Press, New York, N. Y.
- _____ and S. H. Ridgway (1971) Gonadal activity in some bottlenose dolphins (*Tursiops truncatus*). J ZOOLOG., Lond. 165: 355-366.
- Hart, J. S. and L. Irving (1959) The energetics of harbor seals in air and in water with special considerations of seasonal changes. CAN J ZOOLOG 37: 447-457.

- Harvey, J., R. Brown, and B. R. Mate (1983) Two sightings following release of rehabilitated harbor seals. MURRELET 64(1): 18.
- Hobson, B. M. and I. L. Boyd (1984) Gonadotrophin and progesterone concentrations in placentae of grey seals (Halichoerus grypus). J REPRO FERT 72: 521-528.
- Hubbs, C. L. (1979) Guadalupe fur seal. pp 31-33. In: Mammals in the Seas. Vol. II. Pinniped species summaries and report on sirenians. FAO Advisory Committee on Marine Resource Research, Working Party on Marine Mammals. FAO FISH SER (5), 152 pp.
- Irving, L. and J. S. Hart (1957) The metabolism and insulation of seals as bare-skinned mammals in cold water. CAN J ZOO 35(4): 497-511.
- Jeffries, S. J. Washington Game Department. Astoria, Oregon. Personal Communication.
- Johnson, M. University of Puget Sound. Tacoma, Washington. Personal Communication.
- Johnson, B. W. (1969) Maintenance of harbor seals (Phoca vitulina) in aquarium quarters. pp. 49-54. In: Proc Sixth Ann Conf Biological Sonar and Diving Mammals. Stanford Univ.
- Jones, R. E. (1981) Food habits of smaller marine mammals from northern California. PROC CAL ACAD SCI 42(16): 406-433.
- Kelly, B. P. (1981) Pelage polymorphism in Pacific harbor seals. CAN J ZOO 59: 1212-1219.
- Keyes, M. C., J. Wurtman, C. A. Elden, C. Chou, and R. McGuire (1971) Seasonal fluctuations of hydroxyindole levels in the pineal gland of the northern fur seal. J WILDLIFE DIS 7: 325, Abstr.
- King, C. M. (1984) The origin and adaptive advantages of delayed implantation in Mustela erminea. OIKOS 42(1): 126-128
- Knox, K. L. (1979) Energy metabolism. pp 1-33. In: M. Rechcigl (ed.) Comparative Animal Nutrition. Vol. 3 Nitrogen, electrolytes, water and energy metabolism. S. Karger, New York. 260 pp.
- Knutson, P. M. (1977) Observations on the breeding behavior of the harbor seal in Humboldt Bay, California. CAL FISH GAME 63(1): 66-70.

- Koligian, K. B. and F. Stormshak (1977) Nuclear and cytoplasmic estrogen receptors in ovine endometrium during the estrous cycle. *ENDOCRINOL* 101: 524-533.
- Lawson, J. W. and D. Renouf (1985) Parturition in the Atlantic harbor seal, Phoca vitulina concolor. *J MAMMAL* 66(2): 395-398.
- Lett, P. F., R. K. Mohn, and D. F. Gray (1981) Density-dependent processes and management strategy for the northwest Atlantic harp seal population, pp. 135-157. In Fowler, C. W. and T. D. Smith (eds.) Dynamics of Large Mammal Populations. John Wiley and Sons, New York. 477 pp.
- Levins, R. (1966) The strategy of model building in population biology. *AM SCI* 54: 421-431.
- Liggins, G. C., J. T. France, B. S. Knox, and W. M. Zopol (1979) High corticosteroid levels in the plasma of adult and foetal weddell seals (Leptonychotes weddelli). *ACTA ENDOCRINOL* 90: 718-726.
- List, R. J. (1971) Smithsonian Meteorological Tables, sixth revised edition. Smithsonian Miscellaneous Collections, Vol. 114. Smithsonian Institution Press. Washington D. C. 527 pp.
- Lloyd, H. G. and J. Englund (1973) The reproductive cycle of the red fox in Europe. *J REPRO FERT* suppl. no. 19: 119-130.
- McLaren, I. A. (1960) Are the pinnipeds biphyletic? *SYST ZOOL* 9: 18-20.
- _____ (1966) Taxonomy of harbour seals of the western North Pacific and evolution of certain other hair seals. *J MAMMAL* 47(3): 466-473.
- Matsuura, D. T. and C. C. Whittow (1973) Oxygen uptake of the California sea lion and harbor seal during exposure to heat. *AM J PHYSIOL* 225(3): 711-715.
- Mate, B. R. (1979) California sea lion. pp. 5-8. In: Mammals in the Seas. Vol. II. Pinniped species summaries and report on sirenians. FAO Advisory Committee on Marine Resource Research. Working Party on Marine Mammals. FAO FISH SER (5). 152 pp.
- _____ Oregon State University, Hatfield Marine Science Center. Personal Communication
- Mead, R. A. (1981) Delayed implantation in mustelids, with special emphasis on the spotted skunk. *J REPRO FERT* suppl. no. 29: 11-24.

- Miller, K. and L. Irving (1975) Metabolism and temperature regulation in young harbor seals Phoca vitulina richardsi. AM J PHYSIOL 229(2): 506-511.
- Miller, K., M. Rosenmann, and P. Morrison (1976) Oxygen uptake and temperature regulation of young harbor seals (Phoca vitulina richardsi) in water. COMP BIOCHEM PHYSIOL A COMP PHYSIOL 54: 105-107.
- Newby, T. C. (1973) Observations on the breeding behavior of the harbor seal in the state of Washington. J MAMMAL 54: 540-543.
- _____ (1982) Life history of Dall porpoises (Phocoenoides dalli, True 1885) incidentally taken by the Japanese high seas salmon mothership fishery in the northwestern North Pacific and the western Bering Sea, 1978 to 1980. Ph.D. dissertation, University of Washington, Seattle, Wash. 155 pp.
- National Oceanic and Atmospheric Administration (1985) Tide Tables 1986. High and Low Water Predictions. West Coast of North and South America Including the Hawaiian Islands. U.S. Department of Commerce, NOAA, NOS, 1985.
- Ohsumi, S. (1964) Comparison of maturity and accumulation rate of corpora albicantia between the left and right ovaries in cetacea. WHALES RES INST SCI REP 18: 123-148.
- Ouellette, J. and K. Ronald (1985) Histology of reproduction in harp and grey seals during pregnancy, postparturition, and estrus. CAN J ZOOL 63: 1778-1796.
- Pearson, A. K. and R. K. Enders (1951) Further observations on the reproduction of the Alaska fur seal. ANAT REC 111: 695-712.
- Peterson, R. S. (1965) Behavior of the northern fur seal. Ph.D. dissertation, Johns Hopkins University, Baltimore, Maryland.
- _____ (1968) Social behavior in pinnipeds with particular reference to the northern fur seal. pp. 3 - 53. In: Harrison, R. J., R. C. Hubbard, R. S. Peterson, C. E. Rice, and R. J. Schusterman (eds.) The Behavior and Physiology of Pinnipeds. Appleton, New York
- _____, B. J. LeBoeuf, and R. L. DeLong (1968) Fur seals from the Bering Sea breeding in California. NATURE, LOND. 219: 899-901.
- Pitcher, K. W. (1980) Food of the harbor seal, Phoca vitulina richardsi, in the Gulf of Alaska. FISH BULL 78(3): 797-798.

- _____ and D. C. McAllister (1981) Movements and haulout behavior of radiotagged harbor seals, Phoca vitulina. CAN FIELD NAT 95: 292-297.
- Raeside, J. I. and K. Ronald (1981) Plasma concentrations of oestrone, progesterone, and corticosteroids during late pregnancy and after parturition in the harbour seal, Phoca vitulina. J REPRO FERT 61: 135-139.
- Rand, R. W. (1955) Reproduction in the female Cape fur seal, Arctocephalus pusillus. PROC ZOOLOG SOC LOND 124(4):717-740.
- Renouf, D. (1980) Fishing in captive harbour seals (Phoca vitulina concolor): a possible role for vibrissae. NETH J ZOOLOG 30(3): 504-509.
- Renfree, M. B. and J. H. Calaby (1981) Background to delayed implantation and embryonic diapause. J REPRO FERT suppl. no. 29: 1-9.
- Richkind, M. and S. H. Ridgway (1975) Estrogen, corticosteroid and progestagen patterns in the pregnant and nonpregnant bottle-nosed dolphin Tursiops truncatus, following the intramuscular intravascular administration of NIH-FSH-ovine-S9. AQUATIC MAMMAL 3: 15-20
- Riviere, J. E., F. R. Engelhardt, and J. Solomon (1977) The relationship of thyroxine and cortisol to the moult of the harbor seal Phoca vitulina. GEN COMP ENDOCRINOL 31(4): 398-401
- Robinson, M. K. (1976) Atlas of North Pacific Ocean Mean Monthly Temperature and Mean Salinities of the Surface Layer. Naval Oceanographic Off. Reference Publ. 2. 173 pp.
- Rowe, K. and R. Brenne (1982) Statistical Interactive Programming System (SIPS). Command Reference Manual for Cyber 70/73 and Honeywell 440. Oregon State Univ. Department of Statistics, Stat. Computing Report No. 8. Corvallis, Oregon.
- Sandell, M. (1984) To have or not to have delayed implantation: the example of the weasel and the stoat. OIKOS 42(1): 123-126.
- Sangalang, G. B. and H. C. Freeman (1976) Steroids in the plasma of the grey seal, Halichoerus grypus. GEN COMP ENDOCRINOL 29: 419-422.
- Sawyer-Steffan, J. E. and V. L. Kirby (1980) A study of serum steroid hormone levels in captive female bottlenose dolphins, their correlation with reproductive status, and their application to ovulation induction in captivity. Mar. Mammals Comm. MMC-77/22. 21 pp.

- Scammon, C. M. (1874) The Marine Mammals of the Northwestern Coasts of North America, Described and Illustrated: Together with an Account of the American Whale-Fishery. John H. Carmany & Co., San Francisco. 319 pp.
- Scheffer, T. H. and C. C. Sperry (1931) Food habits of the Pacific harbor seal, Phoca richardii. J MAMMAL 12(3): 214-226.
- Scheffer, V. B. (1974) February birth of Mexican harbor seals. MURRELET 55(3): 44.
- _____ (1967) Newborn harbor seals on the Pribilof Islands, Alaska. MURRELET 48(2): 44.
- Schmidt, E. Denver Zoological Gardens. Denver, Colorado. Personal Communication.
- Schusterman, R., I. Kang, B. Andrews, C. McDonald, and D. Ballou (1982) Reproduction in captive California sea lions: photoperiod and annual timing of the birth season. (Abstract). p. 42. In B. Mate (ed.) Marine Mammal Information. Oregon State Sea Grant College Prog., Corvallis, Oregon. July, 1982.
- Selby, S. M. (1969) Standard Mathematical Tables. 17th edition The Chemical Rubber Company. Cleveland, Ohio. 724 pp.
- Sergeant, D. E. (1973) Environment and reproduction in seals. J REPRO FERT suppl. no. 19: 555-561.
- Shaughnessy, P. D. and F. H. Fay (1977) A review of the taxonomy and nomenclature of North Pacific harbour seals. J ZOOLOG LOND 182: 385-419.
- Short, J. Curator of Mammals. Point Defiance Zoo and Aquarium, Tacoma, Washington. Personal Communication.
- Siniff, D. B., I. Sterling, J. L. Bengston, and R. A. Reichle (1979) Social and reproductive behavior of crabeater seals (Lobodon carcinophagus) during the austral spring. CAN J ZOOLOG 57: 2243-2255.
- Smith, J. M. (1978) The ecology of sex, pp. 159-179. In J. R. Krebs and N. B. Davies (eds.) Behavioral Ecology: an evolutionary approach. Sinauer Associates, Inc., Sunderland, Mass. 494 pp.
- Spotte, S. and G. Adams (1981) Photoperiod and reproduction in captive female northern fur seals. MAMMAL REV 11(1): 31-35.
- Spalding, D. J. (1964) Comparative feeding habits of the fur seal, sea lion, and harbour seal on the British Columbia coast. FISH RES BD CANADA BULL no. 146. 59 pp.

- Stewart, B. S. and P. K. Yochem (1985) Radio-tagged harbor seal, Phoca vitulina richardsi, eaten by white shark, Carcharodon carcharias, in the Southern California Bight. CAL FISH GAME 71(2): 113-115.
- Stoel, P. (1981) Site fidelity and movements of harbor seals (Phoca vitulina) on the central Oregon coast (Abstract). Fourth Biennial Marine Mammal Conference. Dec 14-18, 1981. San Francisco.
- Stutz, S. S. (1967) Pelage patterns and population distribution in the Pacific harbor seal (Phoca vitulina richardi). J FISH RES BD CANADA 24(2): 451-455.
- Tauber, C. A. and M. J. Tauber (1977) A genetic model for sympatric speciation through habitat diversification and seasonal isolation. NATURE 268: 702-705.
- Temte, J. L. (1985) Photoperiod and Delayed implantation in the northern fur seal (Callorhinus ursinus). J REPRO FERT 73: 127-131.
- _____ and S. Spielvogel (1985) Serum progesterone levels and reproductive status of incidentally killed female Dall porpoises. J WILDL MANAGE 49(1): 51-54.
- Treacy, S. D. and S. J. Jeffries (1983) A seasonal migration of harbor seals in response to spawning runs of eulachon smelt (Abstract). Fifth Biennial Conference on the Biology of Marine Mammals, 27 November - 1 December, 1983. Boston, Mass.
- Trillmich, F. and D. Limberger (1985) Drastic effects of El Nino on Galapagos pinnipeds. OECOLOGIA 67: 19-22.
- Vaz-Ferreira, R. (1979) South American fur seal. pp. 34-36. In: Mammals in the Seas. Vol. II. Pinniped species summaries and report on sirenians. FAO Advisory Committee on Marine Resource Research, Working Party on Marine Mammals. FAO FISH SER (5), 152 pp.
- Wilke, F. (1957) Food of sea otters and harbor seals at Amchitka Island. J WILDL MANAGE 21(2): 241-242.
- Wolfson, A. (1964) Animal photoperiodism. pp. 1-49. In: A. C. Giese (ed.) Photophysiology. Vol. II. Action of light on animals and microorganisms; photobiological mechanisms; bioluminescence. Academic Press, New York. 441 pp.

APPENDIX

APPENDIX I

This is a listing of references and sources used in the analysis of the cline in the pupping season of the Pacific harbor seal (Phoca vitulina richardsi). Also, references dealing with the Kuril seal (P. v. stejnegeri) and the largha seal seal (Phoca largha) are included.

- Alaska Dept. Fish and Game (1973) Alaska's wildlife and habitat. ALASKA DEP FISH GAME. Van Cleve Printing, Anchorage, AK.
- Alcorn, D. J., L. E. Fancher, and J. G. Moss (1980) Harbor seal and fish populations before and after sewage spill in South San Francisco Bay. CAL FISH GAME 66(4): 238-240.
- Allen, J. A. (1902) The hair seals (family Phocidae) of the North Pacific Ocean and Bering Sea. BULL AM MUS NAT HIS 16: 459-499.
- Allen, S. (1980) Note on the births and deaths of harbor seal pups at Double Point, California. MURRELET 61(1): 41-43.
- (1978) Birth of a harbor seal. OCEANS 11(5): 12-13.
- Bailey, A. M. and R. W. Hendee (1926) Notes on mammals of northwestern Alaska. J MAMMAL 7(1): 9-28.
- Barabash, N. I. (1938) Mammals of the Commander Islands and surrounding sea. J MAMMAL 19: 423-429.
- Bartholomew, G. A. and R. A. Boolootian (1960) Numbers and population structure of the pinnipeds on the California Channel Islands. J MAMMAL 41(3): 366-375.
- Bigg, M. A. (1969a) Clines in the pupping season of the harbour seal, Phoca vitulina. J FISH RES BD CANADA 26: 229-455.
- (1969b) The harbour seal in British Columbia. FISH RES BD CANADA BULL No. 172. 33 pp.
- Bishop, R. H. (1968) Reproduction, age determination, and behavior of the harbor seal, Phoca vitulina lineas in the Gulf of Alaska. M. S. Thesis. Univ. of Alaska. 121 pp.

- Bonnet, P. (1951) The sea lions, seals, and sea otters of the California coast. CAL FISH GAME 37(4): 371-387.
- (1928) Report on the seals and sea lions of California. CAL FISH GAME BULL No. 14 62 pp.
- Brown, R. F. (1981) Abundance, movements, and feeding habits of the harbor seal, Phoca vitulina, at Netarts Bay, Oregon. M. S. Thesis. Oregon State Univ. 57 pp.
- Burns, J. J. (1970) Remarks on the distribution and natural history of pagophilic pinnipeds in the Bering and Chukchi Seas. J MAMMAL 51(3): 445-454.
- , G. C. Ray, F. H. Fay, and P. D. Shaughnessy (1972) Adoption of a strange pup by the ice inhabiting harbor seal, Phoca vitulina largha. J MAMMAL 53(3): 594-598.
- Calambokidis, J., K. Bowman, S. Carter, J. Cabbage, P. Dawson, T. Fleischner, J. Schuette-Hames, J. Skidmore, and B. Taylor. (1978) Chlorinated hydrocarbon concentrations and the ecology and behavior of harbor seals in Washington state waters. NSF-SOS, Evergreen State College. 121 pp.
- Divinyi, C. A. (1971) Growth and movement of a known-age harbor seal. J MAMMAL 52(4): 824.
- Everitt, R. D., R. J. Beach, A. C. Geiger, S. J. Jeffries, and S. D. Treacy (1980) Marine mammal - fisheries interactions on the Columbia River and adjacent waters. 1980. Annual Report; Mar 1, 1980 to Oct 31, 1980. NMML/NMFS 109 pp.
- , C. H. Fiscus, and R. L. Delong (1979) Marine mammals of northern Puget Sound and the Strait of Juan de Fuca: a report on investigations November 1, 1977 - October 31, 1978. NOAA/MEAP NOAA Tech. Mem. ERLMESA - 41 191 pp.
- Fancher, L. E. (1977) Population dynamics and behavior of the harbor seal, Phoca vitulina richardsi, in South San Francisco Bay. M. S. Thesis. California State Univ. at Hayward. 109 pp.
- , and D. J. Alcorn (1980) Harbor seal census in South San Francisco Bay, 1972-1977. CAL FISH GAME 68(2): 118-121.
- Finch, V. A. (1966) Maternal behavior in the harbor seal (abstract). Proc. Third Ann. Conf. Biological Sonar and Diving Mammals. Stanford Univ. pp. 147-150.
- Fisher, H. D. (1952) The status of the harbor seal in British Columbia, with particular reference to the Skeena River. FISH RES BD CANADA BULL No. 93. 58 pp.

- Fiscus, C. H., D. J. Rugh, and T. R. Loughlin (1981) Census of northern sea lions (Eumetopias jubatus) in central Aleutian Islands, Alaska, 17 June - 15 July 1979, with notes on other marine mammals and birds. NOAA Tech Mem. NMFS F/nwc - 17.
- Graybill, M. R. (1981) Haul out patterns and diet of harbor seals, Phoca vitulina, in Coos county, Oregon. M. S. Thesis. Univ. of Oregon. 56 pp.
- Hart, F. M., T. C. Newby, and R. A. Arnold (1965) Observations on maternal behavior in the harbor seal (abstract of motion picture). AM ZOO 5: 677.
- Hewlett, S. (1982) Staff Biologist, Stanley Park Zoo, Vancouver, B. C. Personal Communication.
- Imler, R. H. and H. R. Sarber (1947) Harbor seals and sea lions in Alaska. U S FISH WILDL SERV SPEC SCI REP No. 28. 23 pp.
- Johnson, B. W. (1969) Maintenance of harbor seals (Phoca vitulina) in aquarium quarters. Proc. Sixth Ann. Conf. Biological Sonar and Diving Mammals. Stanford Univ. pp. 49-54.
- Johnson, M. L. and S. J. Jeffries (1977) Population evaluation of the harbor seal (Phoca vitulina richardsi) in waters of the state of Washington. U.S. Marine Mammal Commission, NTIS # PB-270 376. Final Report.
- Klinkhart, E. G. (1967) Birth of a harbor seal pup. J MAMMAL 48(4): 677.
- Knutson, P. M. (1977) Observations on the breeding behavior of the harbor seal in Humboldt Bay, California. CAL FISH GAME 63(1): 66-70.
- Kodama, A. M., R. Elsner, and N. Pace (1977) Effects of diving history, and high altitude on blood oxygen capacity in harbor seals. AM J PHYSIOL: RESPIRAT ENVIRON EXERCISE PHYSIOL 42(6): 852-858.
- LeBoeuf, B. J. and M. L. Bonnell (1980) Pinnipeds of the California Islands: abundance and distribution. pp. 473-479. In: D. M. Power (ed.) The California Islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History. 787 pp.
- Loughlin, T. R. (1978) Harbor seals in and adjacent to Humboldt Bay, California. CAL FISH GAME 64(2): 127-132.
- Newby, T. C. (1973) Observations on the breeding behavior of the harbor seal in the state of Washington. J MAMMAL 54: 540-543.

- (1966) Viability of premature fetal harbor seals.
MURRELET 47(2): 46.
- Naito, Y. (1976) The occurrence of phocid seals along the coast of Japan and possible dispersal of populations. SCI REP WHALES RES INST 28: 175-185.
- (1973) Comparison in color patterns of two species of harbour seals in adjacent waters of Hokkaido. SCI REP WHALES RES INST 25: 301-310
- , and M. Nishiwaki (1975) Ecology and morphology of Phoca vitulina largha and Phoca kurilensis in the southern Sea of Okhotsk and northeast of Hokkaido. Rapp. P.-v. Reun. Cons. int. Explor. Mer. 169: 379-386.
- (1972) The growth of two species of harbour seals in the adjacent waters of Hokkaido. SCI REP WHALES RES INST 24: 127-144.
- Odell, D. K. (1971) Censuses of pinnipeds breeding on the California Channel Islands. J MAMMAL 52(1): 187-190.
- Pitcher K. W. (1976) Population productivity and food habits of harbor seals in the Prince William Sound - Copper River Delta area, Alaska, 7 February 1975 - 7 February 1976. Marine Mammal Commission / MM5AC011. Final Report 36 pp.
- , and D. G. Calkins (1979) Biology of the harbor seal, Phoca vitulina richardsi, in the Gulf of Alaska. Final Report RU-229 NOAA OCSEAP. 72 pp.
- , and D. C. McAllister (1981) Movements and haulout behavior of radio tagged harbor seals, Phoca vitulina. CAN FIELD NAT 95(3): 292-297.
- Risebrough, R. W., D. Alcorn, S. G. Allen, V. C. Anderlini, L. Bouren, R. L. DeLong, L. E. Fancher, R. E. Jones, S. M. McGinnis, and T. T. Schmidt (1980) Population biology of harbor seals in San Francisco Bay, California. Report No. MMC-76/19 U.S. Marine Mammal Commission, NOAA 67 pp.
- Rosenthal, R. J. (1968) Harbor seal census in Humboldt Bay during 1966 and 1967. CAL FISH GAME 54(4): 304-305.
- Roush, M. (1969) Harbor seal drama on Bolinas Lagoon. POINT REYES BIRD OBSERVATORY No. 47: 2.
- Scammon, C. M. (1874) The Marine Mammals of the Northwestern Coasts of North America, Described and Illustrated: Together with an Account of the American Whale-Fishery. Dover Publications, Inc. New York, N.Y. 1968. 319 pp.

- Scheffer, T. H. (1928) Precarious state of the seal and sea lion on our northwest coast. J MAMMAL 9: 10-16.
- Scheffer, V. B. (1974) February birth of Mexican harbor seals. MURRELET 55(3): 44.
- (1967) Newborn harbor seals on the Pribilof Islands, Alaska. MURRELET 48(2): 44.
- and J. W. Slipp (1944) The harbor seal in Washington state. AM MID NAT 32: 373-416.
- Schmidt, E. (1982) Denver Zoological Gardens, Denver, Colorado. Personal Communication.
- Shaughnessy, P. D. and F. H. Fay (1977) A review of the taxonomy and nomenclature of North Pacific harbor seals. J ZOO LOND. 182: 385-419.
- Stewart, B. S. (1981) Seasonal abundance, distribution, and ecology of the harbor seal, Phoca vitulina richardsi, on San Miguel Island, California. M. S. Thesis San Diego State Univ. 66 pp.
- Stutz, S. S. (1966) Foetal and postpartum whitecoat pelage in Phoca vitulina. J FISH RES BD CANADA 23(4): 607-609.
- Tikhomirov, E. A. (1968) Body growth and development of reproductive organs of North Pacific phocids. pp. 213-241. In: V. A. Arsen'ev and K. I. Panin (eds.) Pinnipeds of the North Pacific. Israel Program for Sci. Transl., Jerusalem, 1971. 274 pp.
- Townsend, W. E. Jr. (1977) A harbor seal is born. PAC DISCOVERY 30(2): 24-27.
- Wade, L. S. (1981) Census of harbor seals, Phoca vitulina, in San Luis Obispo County, California, 1972-1973. CAL FISH GAME 67(2): 126-128.
- Wilke, F. (1954) Seals of northern Hokkaido. J MAMMAL 35(2): 218-224.
- (1943) Unusual injury to young harbor seal. J MAMMAL 24(3): 401-402.
- Zenier, C. (1982) Tillamook Rehabilitation Center. Tillamook, Oregon. Personal Communication.

APPENDIX II

FORTRAN 77 program for conversion of pupping date information into photoperiod information.

```

COPY,PUPPIN
  PROGRAM PUPPIN(TAPE1,TAPE2)
  CHARACTER LOCAT*8, PUPMON*3, MATMON*3, IMPMON*3, XMON*3
  INTEGER PUPDAT, LATDEG, LATMIN, PD, MD, ID, XD
  INTEGER MATDAT, IMPDAT, XDAT, STATUS
  REAL LAT, PFOTOP, PDFOTO, MFOTOP, MDFOTO, IFOTOP, IDFOTO
  REAL XFOTOP, XDFOTO
  5 READ(1,10,END=90) STATUS,LOCAT,LATDEG,LATMIN,PUPMON,PUPDAT
  10 FORMAT (I1,1X,A8,2X,I2,1X,I2,2X,A3,1X,I2)
  LAT = REAL(LATDEG) + REAL(LATMIN)/60.0
  CALL REDATE(PUPMON,PUPDAT,PD,MD,ID,XD)
  CALL NAMDAT (MD,MATMON,MATDAT)
  CALL NAMDAT (ID,IMPMON,IMPDAT)
  CALL NAMDAT (XD,XMON,XDAT)
  CALL PHOTOP (LAT,PD,PFOTOP,PDFOTO)
  CALL PHOTOP (LAT,MD,MFOTOP,MDFOTO)
  CALL PHOTOP (LAT,ID,IFOTOP,IDFOTO)
  CALL PHOTOP (LAT,XD,XFOTOP,XDFOTO)
  WRITE(2,20) STATUS,LOCAT,LAT,PUPMON,PUPDAT,PD,PFOTOP,PDFOTO,
  $MATMON,MATDAT,MD,MFOTOP,MDFOTO,IMPMON,IMPDAT,ID,IFOTOP,
  $IDFOTO,XMON,XDAT,XD,XFOTOP,XDFOTO
  20 FORMAT(I1,1X,A8,2X,F5.2,4(3X,A3,1X,I2,2X,I3,2X,F5.2,1X,F5.3))
  GOTO 5
  90 END

```

```

SUBROUTINE NAMDAT(NUM,MON,DAY)
  CHARACTER MON*3
  INTEGER NUM,DAY
  IF(NUM .GT. 345) THEN
    MON = 'DEC'
    DAY = NUM - 345
  ELSEIF (NUM .GT. 315) THEN
    MON = 'NOV'
    DAY = NUM - 315
  ELSEIF (NUM .GT. 284) THEN
    MON = 'OCT'
    DAY = NUM - 284
  ELSEIF (NUM .GT. 254) THEN
    MON = 'SEP'
    DAY = NUM - 254
  ELSEIF (NUM .GT. 223) THEN
    MON = 'AUG'
    DAY = NUM - 223
  ELSEIF (NUM .GT. 192) THEN
    MON = 'JUL'
    DAY = NUM - 192
  ELSEIF (NUM .GT. 162) THEN

```

```

    MON = 'JUN'
    DAY = NUM - 162
ELSEIF (NUM .GT. 131) THEN
    MON = 'MAY'
    DAY = NUM - 131
ELSEIF (NUM .GT. 101) THEN
    MON = 'APR'
    DAY = NUM - 101
ELSEIF (NUM .GT. 70) THEN
    MON = 'MAR'
    DAY = NUM - 70
ELSEIF (NUM .GT. 41) THEN
    MON = 'FEB'
    DAY = NUM - 41
ELSEIF (NUM .GT. 10) THEN
    MON = 'JAN'
    DAY = NUM - 10
ELSE
    MON = 'DEC'
    DAY = NUM + 21
ENDIF
100 RETURN
END

```

```

SUBROUTINE REDATE (MONTH, DAY, PDATE, MDATE, IDATE, XDATE)
    CHARACTER MONTH*3
    INTEGER DAY, PDATE, MDATE, IDATE, XDATE
    IF (MONTH .EQ. 'JAN') THEN
        PDATE = 10
        GOTO 100
    ELSEIF (MONTH .EQ. 'FEB') THEN
        PDATE = 41
        GOTO 100
    ELSEIF (MONTH .EQ. 'MAR') THEN
        PDATE = 70
        GOTO 100
    ELSEIF (MONTH .EQ. 'APR') THEN
        PDATE = 101
        GOTO 100
    ELSEIF (MONTH .EQ. 'MAY') THEN
        PDATE = 131
        GOTO 100
    ELSEIF (MONTH .EQ. 'JUN') THEN
        PDATE = 162
        GOTO 100
    ELSEIF (PDATE .EQ. 'JUL') THEN
        PDATE = 192
        GOTO 100
    ELSEIF (PDATE .EQ. 'AUG') THEN
        PDATE = 223
        GOTO 100
    ELSEIF (PDATE .EQ. 'SEP') THEN
        PDATE = 254

```

```

      GOTO 100
    ELSEIF (PDATE .EQ. 'OCT') THEN
      PDATE = 284
      GOTO 100
    ELSEIF (PDATE .EQ. 'NOV') THEN
      PDATE = 315
      GOTO 100
    ELSE
      PDATE = 345
    ENDIF
100 PDATE = PDATE + DAY
    IF (PDATE .GT. 365) THEN
      PDATE = PDATE - 365
    ENDIF
    MDATE = PDATE + 35
    IF (MDATE .GT. 365) THEN
      MDATE = MDATE - 365
    ENDIF
    IDATE = PDATE + 105
    IF (IDATE .GT. 365) THEN
      IDATE = IDATE - 365
    ENDIF
    XDATE = PDATE + 68
    IF (XDATE .GT. 365) THEN
      XDATE = XDATE - 365
    ENDIF
    RETURN
  END

  SUBROUTINE PHOTOP(LATITU, NDATE, FOTOPR, DPHOTO)
    INTEGER NDATE, DATE
    REAL LATITU, FOTOPR, DPHOTO, LATCON, DATCON, LATDAT, EQUINO
    REAL DENOM, DATSEC, NUMER
    IF (NDATE .LT. 182) THEN
      DATE = NDATE - 91
      EQUINO = 1.0
      GOTO 10
    ELSEIF (NDATE .GT. 182) THEN
      DATE = 273 - NDATE
      EQUINO = -1.0
    ENDIF
10 IF (LATITU .GT. 66.3) GOTO 100
    LATCON = TAN (LATITU * 0.01745)
    DATCON = TAN (DATE * 0.00455)
    LATDAT = ACOS (LATCON * DATCON)
    FOTOPR = 24.00 - 7.64 * LATDAT
    DENOM = 1.0 - (LATCON**2)*(DATCON**2)
    DENOM = SQRT(DENOM)
    DATSEC = 1.0 / (COOS(0.00455 * DATE))
    NUMER = 0.0348 * LATCON * EQUINO * (DATSEC**2)
    DPHOTO = NUMER/DENOM
100 RETURN
  END

```

Glossary of abbreviations

DATCON	tangent of date conversion
DATE	corrected day number
DATSEC	secant of date conversion
DAY	day of the month
DENOM	denominator in equation for dP
DPHOTO	instantaneous rate of change of photoperiod
EQUINO	coefficient of dP equation for an increasing or decreasing photoperiod
FOTOPR	photoperiod
ID	day number of implantation
IDATE	day number of implantation
IDFOTO	dP at implantation
IFOTOP	photoperiod at implantation
IMPDAT	day of the month of implantation
IMPMON	month of implantation
LAT	decimal degree of pupping event
LATCON	tangent of converted latitude
LATDAT	arccosine of (LATCON * DATCON)
LATDEG	latitude (degrees) of pupping event
LATITU	latitude (degrees) of pupping event
LATMIN	latitude (minutes) of pupping event
LOCAT	location of pupping event
MATDAT	day of the month of mating
MATMON	month of mating
MD	day number of mating
MDATE	day number of mating
MDFOTO	dP at mating
MFOTOP	photoperiod at mating
MON	month of reproductive event
MONTH	month of pupping event
NAMDAT	subroutine for converting day number into month and day
NDATE	day number of reproductive event
NUM	day number of reproductive event
NUMER	numerator of equation for dP

PD	day number of pupping event
PDATE	day number of pupping event
PDFOTO	dP at pupping event
PFOTOP	photoperiod at pupping event
PHOTOP	subroutine for determination of photoperiod and dP
PUPDAT	day of pupping event
PUPMON	month of pupping event
PUPPIN	name of main program for photoperiod determination
REDATE	subroutine for enumerating the day numbers of the pupping event, mating, implantation, and photoactivation
STATUS	type of data (0 - 9)
XD	day number of photoactivation
XDAT	day number of photoactivation
XDATE	date of photoactivation (68 days post-partum)
XDFOTO	dP at photoactivation
XFOTOP	photoperiod at photoactivation
XMON	month of photoactivation

APPENDIX III

PHOTOPERIOD EQUATIONS To facilitate the analysis of the effect of photoperiod as a proximate cue for reproductive timing in the harbor seal it was necessary to develop a set of equations permitting the simple calculation of the approximate photoperiod (P) and the instantaneous rate of change of photoperiod (P') at any given latitude for any given day. These values can be obtained or calculated from the meteorological tables of List (1971), however, it was desirable to have a deterministic model of photoperiod to allow rapid analysis on computer. The photoperiod is expressed in hours of daylight per day (h/day); the instantaneous rate of change of photoperiod is expressed in hours of daylight per day per day (h/day/day = h/day²).

The equation for photoperiod was derived through trigonometric construct as follows:

Photoperiod (P) is dependent upon the latitude (L) and the tilt of the Earth (T) or season. Latitude in degrees (L) is converted into radian measure (Lr) as:

$$L_r = (L) (2 \pi) / 360^\circ = 0.01745 (L). \quad (20)$$

The tilt of the Earth (T) relative to the sun is dependent upon the position of the Earth in its annual orbit about the sun. The tilt ranges from approximately -23.7° during the northern hemisphere winter to 23.7° during the Northern hemisphere summer. To simplify the derivation it was assumed that the rate at which the tilt changes (between -23.7° and 23.7°) is constant over a 182 day period (from the winter to the summer solstice). Hence:

$$T = (47.4^\circ) (D) / 182 \text{ days}. \quad (21)$$

where D is the corrected day number given in terms of the

sequential day number relative to the winter solstice (d),
21 December, by:

$$D = \begin{cases} d - 91, & \text{for } 0 \leq d < 182 \\ 293 - d, & \text{for } 182 \leq d \leq 365. \end{cases} \quad (22)$$

Tilt in degrees (T) is converted to radian measure (Tr) as:

$$\begin{aligned} Tr &= (47.4^\circ) (D) (2\pi) / (182 \text{ days}) (360^\circ) \\ &= 0.00455 (D). \end{aligned} \quad (23)$$

A static model is adopted to determine the length of the arc at a given latitude (Lr) and tilt (Tr) that is illuminated by daylight. It is assumed that one hemisphere of the Earth is constantly illuminated; the other hemisphere is in darkness. The intersection of the Earth sphere and a plane M that passes through the poles of the Earth and the sun (figure A1) serves as a two-dimensional model in which the linear projection (line segment \overline{ts}) of a given latitude (Lr) is first considered (figure A2a). At the instant shown, line segment \overline{tp} is illuminated; line segment \overline{ps} is in darkness. The proportion of line segment \overline{cs} that is illuminated is given by the ratio $\overline{cp}/\overline{cs}$ (figure A2b). The value of $\overline{cp}/\overline{cs}$ can be related to Lr and Tr as follows:

$$\tan(Lr) = \overline{co} / \overline{cs}. \quad (24)$$

$$\overline{cs} = \overline{co} / \tan(Lr). \quad (25)$$

$$\tan(Tr) = \overline{cp} / \overline{co}. \quad (26)$$

$$\overline{cp} = \overline{co} (\tan(Tr)). \quad (27)$$

Hence:

$$\begin{aligned} \overline{cp} / \overline{cs} &= \overline{co} (\tan(Tr)) / (\overline{co} / \tan(Lr)) \\ &= \tan(Lr) \tan(Tr). \end{aligned} \quad (28)$$

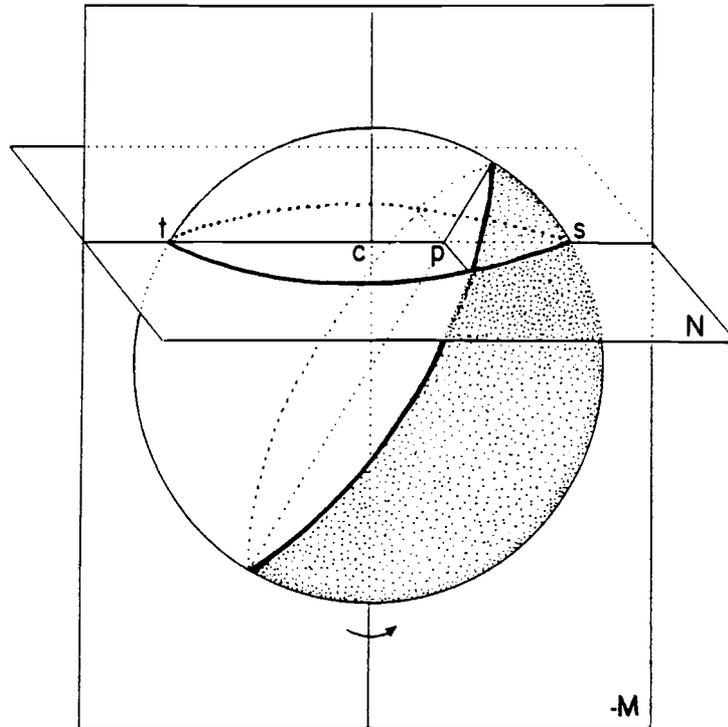


Figure A1. Diagrammatic presentation of model used in the derivation of the equation for photoperiod. Axis of rotation is vertical; stippled area indicates sphere surface in shadow.

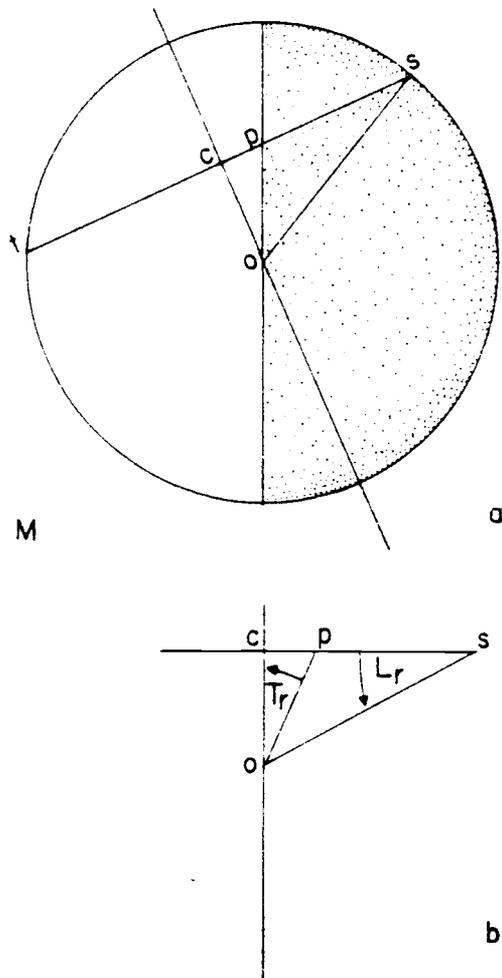


Figure A2a. Intersection of plane M with sphere E.

A2b. Detail of $\triangle OCS$ showing tilt (Tr) and latitude (Lr).

Setting \overline{cs} equal to unity yields:

$$\overline{cp} = \tan(Lr) \tan(Tr). \quad (29)$$

A polar projection of the Earth at latitude Lr (figure A3) is obtained through the intersection of a plane N and the Earth sphere (figure A1). The arclength (A) of the projected circle that is in darkness can be described as:

$$A = 2 (\arccos[\tan(Lr) \tan(Tr)]). \quad (30)$$

Converting from the arclength in radians to actual hours of darkness (Ad) is achieved as:

$$Ad = (A) (24.00 \text{ h}) / (2\pi) = (3.82 \text{ h}) (A). \quad (31)$$

Finally, the hours of darkness are subtracted from a 24 hour day to yield the photoperiod (P):

$$P = 24.00 \text{ h} - Ad. \quad (32)$$

Therefore, in final expanded form, photoperiod can be described by the following equation:

$$P = 24.00 - 7.64 [\arccos(\tan(0.01745L)\tan(0.00455D))] \text{ h/day}$$

where D is the corrected day number as in eq (3). (33)

Latitudes in the northern hemisphere are considered negative. The equation is valid in the range of latitudes between the Antarctic and Arctic Circles ($-66.2^\circ \leq L \leq 66.2^\circ$).

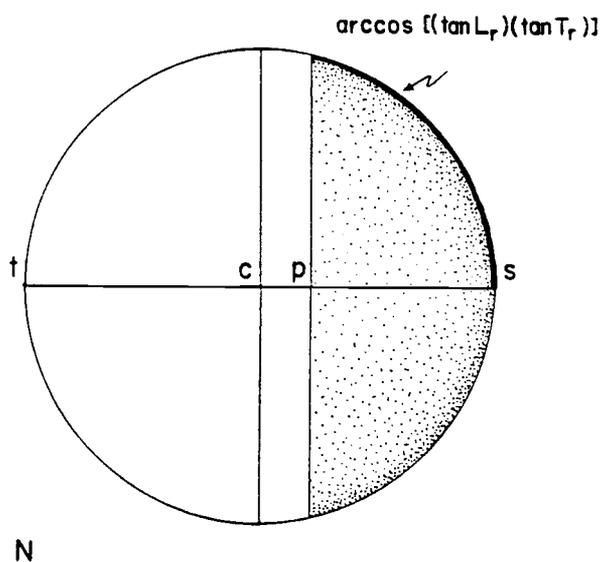


Figure A3. Intersection of plane N with sphere E. The arclength of the of the circle in shadow is given by:
 $2\arccos[(\tan T_r)(\tan L_r)]$.

The instantaneous rate of change of photoperiod was obtained as the first derivative of the equation for photoperiod (eq. 33) using Standard Mathematical Tables (Selby, 1969), and is given by:

$$P' = \frac{(S) (0.0348) (\tan(0.01745L)) (\sec^2(0.00455D))}{\sqrt{1 - (\tan^2(0.01745L) \tan^2(0.00455D))}} \quad \text{h/day}$$

where:

$$S = \begin{cases} 1, & \text{for } 0 \leq d \leq 182 \\ -1, & \text{for } 182 < d \leq 365. \end{cases} \quad (34)$$

Values of photoperiod were calculated for the 21st day of each month at 5° intervals from 0° to 60°N latitude. Comparison of these values to those in the Smithsonian Meteorological Tables (List, 1971) were made, and the accuracy of the derived values of photoperiod were calculated (Table A1).

The accuracy of the photoperiod equation (33) varied between 0.86 and 1.00 with a mean accuracy (+/- S.E.M.) of 0.972 +/- 0.002. There was a trend for accuracy to decrease with an increase in latitude from a mean accuracy of 0.99 at 0° to 0.93 at 60°N.

REVISED EQUATION FOR THE CALCULATION OF PHOTOPERIOD A second photoperiod equation was developed in April, 1983 in an attempt to remove some of the inaccuracy of equation 33. In the original version of the photoperiod equation, it was assumed that the tilt (T) of the Earth changed at a constant rate. This allowed for a very simple equation with two variables and three trigonometric functions (eq. 33).

Because the assumption that the rate of change of tilt is constant caused some error, a slightly more detailed and difficult equation for photoperiod was developed. The rate of change of tilt (T) can be modeled using the law of cosines. It is assumed that the Earth orbits the sun at a constant rate in a circular path.

Table A1. Accuracy of duration of photoperiod as calculated by equation 33 when compared to values calculated from the tables of List (1971). Accuracy calculated as $1.00 - |(T-P)/T|$ where T = the value calculated from tables and P = values calculated by equation 33.

<u>LAT</u>	<u>Date</u>												<u>MEAN</u>
	<u>DEC 21</u>	<u>JAN 21</u>	<u>FEB 21</u>	<u>MAR 21</u>	<u>APR 21</u>	<u>MAY 21</u>	<u>JUN 21</u>	<u>JUL 21</u>	<u>AUG 21</u>	<u>SEP 21</u>	<u>OCT 21</u>	<u>NOV 21</u>	
0°	.99	.99	.99	.99	.99	.99	.99	.99	.99	.99	.99	.99	.99
5°	.99	.99	.99	.99	.99	.99	.99	.99	.99	.99	.99	.99	.99
10°	.99	.99	.99	.99	.98	.98	.99	.98	.98	.99	1.00	1.00	.99
15°	.99	.99	1.00	.99	.98	.98	.99	.98	.98	.99	1.00	1.00	.99
20°	.99	.99	1.00	.99	.98	.97	.99	.97	.97	.99	1.00	.99	.99
25°	.99	.99	1.00	.99	.97	.97	.99	.97	.97	.98	1.00	.99	.98
30°	1.00	.97	.99	.99	.96	.96	.99	.96	.96	.98	.99	.98	.98
35°	.98	.98	.99	.99	.96	.96	.99	.95	.96	.98	.99	.97	.97
40°	.98	.96	.98	.98	.95	.95	.99	.95	.95	.98	.98	.97	.97
45°	.97	.95	.98	.98	.95	.95	.99	.94	.94	.98	.98	.96	.96
50°	.96	.93	.97	.98	.94	.93	.99	.93	.94	.97	.97	.94	.95
55°	.95	.90	.96	.98	.93	.92	.99	.92	.93	.97	.97	.92	.95
60°	.92	.86	.96	.97	.92	.90	.99	.90	.91	.96	.96	.88	.93
<u>MEAN</u>	.98	.96	.99	.99	.96	.96	.99	.96	.96	.98	.99	.97	.973

The equation remains in the same basic form, but the term for the calculation of the tilt of the Earth (T) has been modified and inserted. The following outlines the calculation of tilt:

$$\begin{aligned}
 T &= 90^\circ - \arccos \left[\frac{1 + (0.404/\cos D)^2 - (0.404\tan D)^2 - 0.837}{2 (0.404/\cos D)} \right] \\
 &= 90^\circ - \arccos \left[\frac{0.163 + (0.404/\cos D)^2 - (0.404\tan D)^2}{2 (0.404/\cos D)} \right] \quad (35)
 \end{aligned}$$

Converting to radian measure:

$$\begin{aligned}
 Tr &= \pi/2 - \arccos \left(\left[\frac{0.163 + (0.404/\cos(0.0172D))^2 - (0.404\tan(0.0172D))^2}{(0.808 / \cos(0.0172D))} \right] \right) \quad (36)
 \end{aligned}$$

And inserting into the photoperiod equation:

$$\begin{aligned}
 P &= 24.00 - 7.64 \arccos \left(\tan(0.01745L) \tan(\arccos[(0.163 + (0.404/\cos(0.0172D))^2 - (0.404\tan(0.0172D))^2] / (0.808 / \cos(0.0172D))) - \pi/2) \right).
 \end{aligned}$$

where L is the latitude in degrees and D is the corrected day number as follows:

$$\begin{aligned}
 D &= \begin{array}{l} d, \text{ for } 0 \leq d \leq 182 \\ 385 - d, \text{ for } 182 < d \leq 365. \end{array} \quad (37)
 \end{aligned}$$

Values for photoperiod (h/day) were calculated at 0°, 5°, 10°, 15°, 20°, 25°, 30°, 34°, 38°, 42°, 46°, 50°, 54°, 58°, and 62° North latitude on each of the following dates: 22 Dec., 21 Jan., 20 Feb., 22 Mar., 21 Apr., 21 May., and 20 Jun. These values were compared to those calculated from sunrise/sunset

tables (NOAA, 1985) and the accuracy of this revised photoperiod equation determined.

Overall, there was a mean accuracy (\pm S.E.M.) of 0.981 \pm 0.002. The equation provided a more predictable error, with most of the inaccuracy occurring in December and January at latitudes greater than 55°. In fact, only three of the calculated values were less than 95% accurate (Table A2). The mean accuracy was 95% at 62°, while the least accurate value of 88% was at 62°. This is compared to a mean accuracy of 0.972 \pm 0.002, least accurate value of 86% at 60°, and mean accuracy at 60° of 93% provided by the less sophisticated equation.

Table A2. Accuracy of duration of photoperiod as calculated by equation 37 when compared to values calculated from sunrise/sunset tables (NOAA, 1985).

<u>LAT</u>	<u>Date</u>							<u>MEAN</u>
	<u>DEC 22</u>	<u>JAN 21</u>	<u>FEB 20</u>	<u>MAR 22</u>	<u>APR 21</u>	<u>MAY 21</u>	<u>JUN 20</u>	
0°	.99	.99	.99	.99	.99	.99	.99	.99
5°	.99	.99	.99	.99	.99	.99	.99	.99
10°	.99	.99	.99	.99	.99	.99	.99	.99
15°	.99	.99	.99	.99	.99	.99	.99	.99
20°	.99	.99	.99	.99	.99	.99	.99	.99
25°	.98	.98	.99	.99	.99	.99	.99	.99
30°	.98	.98	.98	.99	.99	.99	.99	.99
34°	.98	.98	.98	.98	.98	.99	.99	.98
38°	.98	.98	.98	.98	.98	.99	.99	.98
42°	.97	.97	.98	.98	.98	.99	.99	.98
46°	.97	.97	.97	.98	.98	.99	.99	.98
50°	.96	.97	.97	.98	.98	.99	.99	.98
54°	.95	.96	.97	.98	.98	.99	.99	.97
58°	.93	.96	.96	.97	.98	.98	.99	.97
62°	.88	.92	.95	.97	.97	.98	.99	.95
MEAN	.97	.97	.98	.98	.98	.99	.99	.981

Accuracy calculated as $1.00 - |(T-P)/T|$, where T = the value calculated from tables and P = the value calculated by equation 37.