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Population Productivity and Food Habits of Harbor Seals in the Prince William Sound - Copper River Delta Area, Alaska

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ABSTRACT

Weights, measurements and specimen materials for age determination, reproductive analysis and food habit studies were obtained from 199 harbor seals from the Prince William Sound-Copper River Delta area.

The gestation period was estimated to be 10.5 months which included a 2.5-month delay of implantation. Pupping began about 20 May, peaked during the first week in June and was completed by early July. A lactation period of 3-6 weeks was closely followed by ovulation.

By age seven all males were sexually mature. Females reached productive maturity at 3 to 5 years of age. Pregnancy rates for those age classes were: 3 years - 18 percent, 4 years - 58 percent and 5 years - 80 percent. All females 6 years old and older in the sample were pregnant. Reproductive failures were noted in five females.

Maximum skeletal size was attained by about 7 years. Adult males were significantly longer than adult females.

Body condition, as indicated by blubber reserves, followed a general pattern of good condition during winter which continued to improve until midsummer. In mid to late July, condition declined rapidly. By early October blubber reserves were again increasing.

Estimated population parameters included a 1:1 sex ratio, maximum ages of 19 years for a male and 21 years for a female, average annual mortality rate of 24 percent for ages 4-21 years and gross annual productivity of 18.8 percent.

Dominant food items for harbor seals in Prince William Sound included *Theragra chalcogramma* (pollock), *Clupea harengus* (herring) and cephalopods. On the Copper River Delta the major prey species was *Thaleicthys pacificus* (eulachon). Prey selection was characterized by primary use of abundant, schooling fishes. The majority of seals had fed on a single species.

ACKNOWLEDGEMENTS

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To all of these I express my sincere thanks.

INTRODUCTION

The land breeding harbor seal (*Phoca vitulina richardi*) is an abundant and widespread coastal resident of southern Alaska. Harbor seals occupy virtually all nearshore habitats from Dixon Entrance into the southern Bering Sea where overlap with the ice breeding form (*P. largha*) occurs. In Alaska, as in other parts of their range, harbor seals inhabit a wide variety of habitat types. They occur in both fresh and salt water, along protected and exposed coastlines and in both clear and turbid waters. They utilize a variety of hauling substrates including tidal reefs, offshore islets, mud and sand bars, sand and gravel beaches and shorefast, pan and glacial ice.

Harbor seals usually occur in close proximity to the coast. Spalding (1964) did not consider them a pelagic species and stated that they were seldom found more than 5 miles from the coast. During pelagic fur seal (*Callorhinus ursinus*) investigations, National Marine Fisheries Service biologists recorded a number of sightings off the Alaskan coast; nearly all of single animals up to 50 miles offshore (Calkins et al. 1975). Spalding (1964) reported harbor seals 30-40 miles offshore on Portlock Banks near Kodiak.

The land breeding harbor seal is not considered migratory although considerable movement occurs in response to reproductive activities, concentrations of prey species and climatic conditions.

Historically the harbor seal has been considered a nuisance and threat to fisheries. From 1927 until 1967 a bounty was paid on harbor seals in southern Alaska. However, during the 1960's a commercial industry developed utilizing harbor seal skins. Initially, high prices stimulated a peak harvest of over 50,000 animals in 1965. After this, prices dropped and the harvest stabilized at about 10,000 animals annually until passage of the Marine Mammals Protection Act of 1972 when all harvest except for native subsistence ceased.

Prince William Sound (Fig. 1), a large embayment of about 2,500 mi^2, is almost entirely enclosed by Montague, Hinchinbrook, Latouche, Elrington and Bainbridge Islands and the mainland coast. Its shoreline has numerous long, glacier-scoured bays and fiords. Many islands, offshore rocks and tidal reefs occur, making up a total coastline of about 3,000 miles. The coast is characteristically steep and rocky particularly along the fiords. Water depths within Prince William Sound are generally deep, reaching 730 meters. A minimum of 17 glaciers have tidewater terminuses and at times considerable amounts of ice are discharged into the sea. During winter months shorefast ice forms at the heads of many bays and fiords.

The Copper River Delta (Fig. 1), located about 30 miles southeast of Prince William Sound, is the terminus of a large river which drains a sizable sector of Interior Alaska. The area is a large river delta composed of deposited silt dissected by numerous river channels, intertidal sloughs, ponds, lakes and marshes. The estuary system is shallow and bounded on the seaward side by a series of small barrier islands. Much

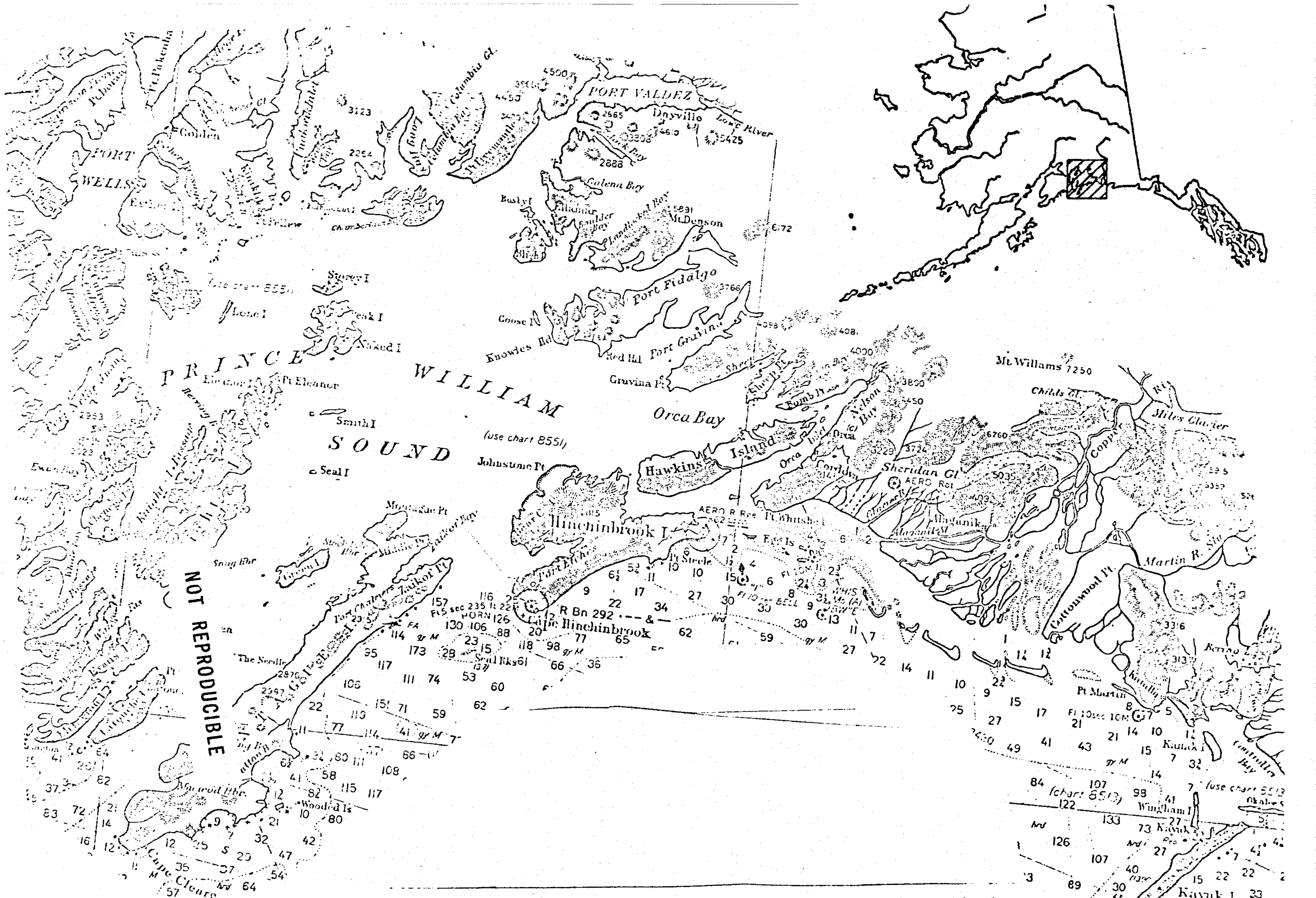

Fig. 1. Prince William Sound - Copper River Delta, Alaska

of the water in the Copper River is glacial in origin and has a very high silt content.

Harbor seals are found in Prince William Sound throughout the year. They utilize a variety of habitat types but are found most often in areas with intertidal reefs. Hauling areas include intertidal reefs, floating glacial ice, pan ice, gravel and sand beaches, rocky shores and mud bars. Harbor seals are usually found close to shore but on occasion are seen 5 or more miles offshore. Precise population figures are not available for Prince William Sound harbor seals. Reliable census techniques have not been developed. Seals are difficult to see in the water and most are undoubtedly missed during any census attempt. Even when large numbers are hauled out and can be counted it is not known what proportion of the total population this represents. During a helicopter survey of marine mammals in June 1973 about 4,000 seals were counted (Pitcher and Vania 1973). It was felt that these data did not represent population size and that the population must far exceed this figure. Calkins et al. (1975) estimated a population in excess of 13,000 animals based on past harvest data. This was not a precise estimate but was used to show the general magnitude of the population.

Unlike some areas of the state Prince William Sound did not receive continuous, intensive hunting pressure during the mid-1960's. Hunting effort was related to activity in the fishing industry. Most seal hunting was conducted by fishermen during closed fishing seasons. The peak harvest took place in 1963-64 with a take of about 2,500 animals.

Seals occupy the Copper River Delta on a seasonal basis. During most winters the Delta is ice-covered and only a few seals are present along the ocean bars. In April or May, when the ice goes out, large numbers of animals move into the river and remain until fall. By late September most seals have left the river. Again exact numbers of seals occupying the Delta are unknown. A survey flown on 25 July 1973 accounted for 1,349 seals hauled out on sand bars in the river (Pitcher and Vania 1973). On another survey flown on 15 May 1975, 1,571 were counted. From field activities conducted by skiff on the Copper River it is known that seals are abundant in the water at the same time large groups are hauled out. It appears from these observations that the survey figures are considerably below total numbers which must easily exceed 2,000 seals and may exceed 3,000. Most of the seals remain below Miles Lake which is located about 20 miles up river from salt water. However, a few move much further up river, one being seen nearly 100 air miles inland.

During 1951-1958 a dynamite bombing control program was conducted on the Copper River Delta in response to serious seal depredation problems on the salmon gillnet fishery. A reported 30,250 seals were killed during this program which reduced seal numbers to a low level (ADF&G 1958). The accuracy of these figures is questionable but undoubtedly large numbers of seals were killed. Now, nearly 18 years after cessation of control activities, fishermen are again experiencing significant depredation problems indicating considerable recovery of the population.

No information is available on where the Copper River seals spend the winter months. It is likely that they disperse, some probably moving into Prince William Sound while others may move southeast along the coast toward Icy Bay.

In order to develop and administer a rational management program, information on population dynamics is needed. Knowledge necessary for such a program includes basic reproductive biology (including age of reproductive maturity), age specific birth rates and reproductive duration. This information, when combined with knowledge of mortality rates and age and sex structure of the population, allows the manager to set harvest levels within the biological capabilities of that population.

In most cases with harbor seals, as with many animal populations, it is not feasible to directly assess population status (Summers and Mountfield 1975). Instead it is necessary to measure indirect indicators of population status. Indicators examined in this study include: age of productive maturity, pregnancy rates, growth and body condition.

Activities related to the exploration for and extraction and transportation of oil and natural gas are now taking place and are planned for Prince William Sound and the nearby Gulf of Alaska. With this development comes the potential for serious disruption of the seal's food web. It is important to identify those prey species important to the maintenance of harbor seal populations so that provisions can be made for their protection. Resolution of harbor seal conflicts with commercial fisheries, both on the Copper River and in Prince William Sound, requires accurate information on food habits.

No intensive scientific studies of harbor seals have been previously conducted in Prince William Sound. Calkins (1972) reported observations made of harbor seals in the Montague Straits area while he was studying sea otters, (*Enhydra lutris*), and Sandegren (1970) stated that harbor seals were common in the Wooded Islands where he studied Steller sea lions (*Eumetopias jubata*). General distribution and areas of high density are presented in ADF&G (1973). I mapped observations of harbor seals seen during two coastline surveys of Prince William Sound in June 1973 and March 1974 (Pitcher unpublished).

The Copper River Delta has received more attention because of the large, visible concentrations of seals and fishery depredation problems. Imler and Sarber (1947) investigated distribution, abundance, fishery depredations and food habits of seals on the Delta. Mathisen and Lopp (1963) reported on an aerial survey of seals in the Copper River area.

This paper reports the results of a 1-year study of several aspects of the biology of the land breeding harbor seal in the Prince William Sound and Copper River Delta area of Alaska. Basic objectives of the project were to investigate: (1) population productivity; (2) feeding ecology; and (3) growth and seasonal condition.

METHODS AND MEANS

During this study 199 seals were collected, 154 from Prince William Sound and 45 from the Copper River Delta (Table 1). Animals were collected periodically throughout the year in order to follow the reproductive cycle, evaluate seasonal condition and determine seasonal food habits. Seals were collected in Prince William Sound by cruising with a 16-foot outboard powered skiff until an animal was located within shooting distance of shore. One man was placed on the shore to kill the seal with a telescope sighted rifle and the animals were retrieved using the skiff. Sunken seals were recovered with a hook on the end of a bamboo pole or with scuba gear when possible. On the Copper River the seals were shot from a skiff with a shotgun. It was important to immediately retrieve each animal as they sank rapidly, probably because of the lower density of fresh water. Sunken seals could not be located because of low visibility in the silty water. Selection of animals was not entirely random, small animals were often avoided. Young animals are not nearly as wary as older ones and are much easier to collect. By taking all animals as the opportunity presented itself the sample would have been heavily biased toward the younger age classes.

Table 1. Number and dates of collected harbor seals, Prince William Sound (PWS) and the Copper River Delta (CRD).

Date	Area	Number of Animals	
		F	M
4-7 Feb 75	PWS	10	14
17-22 March 75	PWS	10	26
16-20 April 75	PWS	13	10
4-7 June 75	CRD	10	8
6 July 72	PWS	3	--
8-12 July 75	CRD	10	7
22-29 July 75	PWS	6	15
1-9 Aug 73	PWS	4	1
24-25 Sept 75	CRD	2	8
8-12 Oct 73	PWS	13	4
28 Oct-4 Nov 75	PWS	10	15
		91	108
TOTAL		199	

After each animal was collected habitat type, animal activity, group size and other pertinent information was recorded. Each animal was weighed and a series of measurements was taken including: standard length, curvilinear length, axillary girth, hind flipper length and blubber thickness (Scheffer 1967). Each seal was skinned so the blubber layer remained on the skin. Each skin was then weighed in order to determine what percentage of body weight the blubber comprised (Beck 1970).

The lower jaw or skull, reproductive organs, fetuses, stomach contents and large intestines were removed from each animal. Specimen materials were preserved in formalin or by freezing. Additional materials collected included blood and tissue samples for disease and environmental contaminant analysis.

Age determination techniques utilizing cementum annuli in the teeth have been well documented for harbor seals (Bishop 1967, Bigg 1969), and include analysis of two known-aged animals (Mansfield and Fisher 1960 and Divinyi 1971). Canine teeth were decalcified, sectioned at 40 microns on a International Equipment Company microtome cryostat and stained in a hot bath of Harris' Hematoxylin-Paragon (Johnson and Lucier 1975). Ages were determined by examining the stained sections through a binocular dissecting microscope at about 15X. Each year one opaque and one translucent layer are deposited in the cemuntum and ages were determined by counting these layers (Bigg 1969).

Both ovaries and the entire uterus were preserved from each female unless a large fetus was present. Large fetuses were removed, measured and weighed in the field. In the laboratory each uterus was opened and examined. When a fetus was found it was weighed, measured and the sex determined. Placental scars were noted and evidence of unsuccessful pregnancies was recorded. The ovaries were sliced with a scalpel into sections 1-2 mm thick and examined macroscopically for the presence of corpora lutea and corpora albicantia.

Weights, volumes and measurements were taken from the testes of each male. A smear of epididymal fluid was examined microscopically for the presence of mature sperm. Sperm abundance was subjectively classified as absent, trace, or abundant.

Stomach contents were removed in the field, wrapped in muslin and preserved in formalin. Contents of large intestines were washed through brass sieves (2.00 and 0.84 mm^2) to recover identifiable materials, primarily fish otoliths and cephalopod beaks (Smith and Gaskin 1974). These were preserved in 70 percent ethanol.

Stomach contents were weighed and their volumes determined in the laboratory. The contents were sorted and when possible the number of individual organisms counted. As digestion was often advanced, skeletal materials, particularly otoliths and cephalopod beaks were primarily used for identification (Havinga 1933, Fitch and Brownell 1968, Perrin et al. 1973, Pinkas et al. 1971).

Fish otoliths and other skeletal materials were identified when possible by comparing them with a reference collection in our laboratory. All otoliths were then sent to John Fitch of the California Dept. of Fish and Game for final identification. Cephalopod beaks were identified as either squid or octopus with the aid of Pinkas et al. (1971). Squid beaks were sent to Clifford Fiscus of National Marine Fisheries Service for identification.

RESULTS AND DISCUSSION

REPRODUCTION

Pupping

Skiff surveys conducted from 15-18, 22-25 May 1973 and 4-9 June 1973 in Prince William Sound and collecting activities from 4-7 June 1975 and 8-12 July 1975 on the Copper River Delta provided some data on the timing and progression of pupping. The first pups were observed on 23 May when two pups were seen among 74 seals. Of 68 seals observed on 24 May, two were pups. On 6 June 1973, during a skiff survey of the College Fiord area, 75 seals were observed, 26 of which were pups. Evidence of recent births included feces containing lanugo and blood stains on ice floes used as pupping platforms. From 4-7 June 1975 I collected six mature females, five were postpartum and one was pregnant with a full term fetus. During that time period many female-pup pairs were observed. Two mature females were collected on 10 and 11 July 1975, both of which were postpartum. Considerably fewer females were seen with pups than during the previous collecting trip. From these observations it appeared that pupping began about 20 May, peaked during the first week in June and was completed by early July. Others working in Alaska have documented a pupping period up to 2 months (Bishop 1967, Johnson 1976). More intensive field work in the Prince William Sound-Copper River Delta area could reveal a similar pattern.

Boulva (1975) found that variations in annual birth dates occurred and speculated that they might have been related to year to year differences in air and water temperatures. Bigg (1969A) demonstrated clinal variations in the pupping season of harbor seals in North America. In the eastern North Pacific pups are born progressively later going southeast from Alaska and then earlier from Washington to Mexico.

Lactation and Weaning

Five postpartum females collected from 4-8 June were lactating. One of two postpartum females collected on 10 and 11 July was lactating. The other female had apparently completed lactation and had recently ovulated. Two mature females which apparently had produced pups earlier in the summer were collected on 23 and 25 July. Neither was lactating and both had well developed corpora lutea (preimplantation). These data are insufficient to precisely delineate the length of lactation but are in agreement with values presented in the literature; Bishop (1967) 3 weeks, Bigg (1969) 5-6 weeks, Knudtson (1974) 5-6 weeks and Johnson (1976) 3-5 weeks. Johnson (1976) reported a gradual weaning period of about 1 week.

Ovulation

Ovulation in harbor seals apparently occurs shortly after weaning. Bishop (1967) felt it occurred about 2 weeks after weaning. Fisher (1954) said that breeding took place immediately after termination of lactation. In British Columbia ovulation was thought to occur at the end of weaning or shortly thereafter (Bigg 1969).

Ovulation had not occurred in six lactating females collected during this study (two on 4 June, one on 5 June, two on 6 July and one on 11 July). A newly formed corpus luteum was present in the ovary of a female collected on 10 July. The rupture site of the follicle was still visible. Four females taken between 10 and 28 July all had ovaries containing a recently formed corpus luteum.

Delay of Implantation

A period of delayed implantation (11 weeks) was first demonstrated in the harbor seal by Fisher (1954). Additional evidence was presented by Harrison (1960) who calculated a 2-to 3-month delay, Bishop (1967) 1.5 to 2 months and Bigg (1969) 2 months.

Five mature females taken between 22 July and 25 September had normal appearing corpora lutea. No signs of embryos or implantation sites were found. Three females collected on 11 October contained very small implanted embryos less than 3 mm in length. Another animal collected on the same date had an implanted embryo 8 mm long. Seven embryos from seals collected between 28 October and 4 November ranged from 9 mm to 95 mm in length and from 0.1 g to 12.3 g in weight indicating considerable variation in implantation dates. From these data it appears that the delay in implantation is about 2.5 months. Implantation probably occurs from late September to late October, peaking in early October.

Female Age of Sexual Maturity

Sexual maturity in the female is usually defined as the age at which ovulation first occurs (McLaren 1958, Bigg 1969). Productive maturity (McLaren 1958), or the age at which a female first produces offspring, is a more meaningful definition when population dynamics are the primary concern, so it is used in this study.

In the Prince William Sound-Copper River area (Table 2) 18 percent of the collected females were mature at 3 years, 58 percent at 4 years and 80 percent at 5 years. All females 6 years old and older were mature. The majority appeared to attain maturity during their fourth year.

In British Columbia, Bigg (1969) found that females were becoming pregnant for the first time from 3 to 5 years of age. In the Gulf of Alaska female seals were found to mature at 3 or 4 years (Bishop 1967).

Reproductive Rates

Age specific pregnancy rates were calculated after examination of 73 female reproductive tracts collected between implantation and ovulation (Table 2). Bigg (1973) demonstrated that the presence of a normal appearing corpus luteum during the period of delayed implantation could not be considered as definite evidence that a blastocyst was present. Therefore, animals collected during this period were not used in calculating productivity rates.

Table 2. Productive maturity and age specific pregnancy rates for harbor seals in the Prince William Sound-Copper River area.

Age	Total Animals	No. Pregnant	Pregnancy Rate	
2 years or less	21	0	0%	
3	11	2	18%	46%
4	12	7	58%	
5	5	4	80%	
6	4	4	100%	100%
7	5	5	100%	
8-12	15	15	100%	
All ages	73	37	51%	

In age classes 0-2 years no pregnant animals were found. Reproductive rates for the age classes in which sexual maturity was attained were: 3 years - 18 percent, 4 years - 58 percent and 5 years - 80 percent. The combined rate for these three age classes was 46 percent. All collected animals 6 years old and older were pregnant.

Reproductive Failures

Reproductive failures may be classified in three categories: (1) a missed pregnancy where either fertilization did not occur or the blastocyst failed to implant, (2) resorption of an embryo and (3) abortion in which the fetus was expelled from the uterus (Craig 1964 and Bigg 1969).

The ovaries of three females taken on 9, 12 and 28 October contained smaller than normal corpora lutea (diameters of 8 mm, 12 mm, and 14 mm versus a $\bar{x}$ of 15 mm) and no evidence of embryos or implantation sites. It appeared that either fertilization did not occur in these animals or the blastocyst failed to implant. A female collected on 18 April was not pregnant and the uterus appeared immature, however, one ovary contained a large, distinct corpus albicans. No placental scars or evidence of an implantation site were visible. It is probable that ovulation occurred and fertilization did not occur or the blastocyst did not implant. One apparent instance of resorption was found. The uterus of a seal collected on 28 October had a swelling similar to a typical implantation site. Instead of an implanted embryo and accompanying membranes a small mass of necrotic appearing tissue was found. No instances of abortion were observed.

All reproductive failures found were in 3-, 4- and 5-year-old animals and involved initial ovulations. Craig (1964) found that in the fur seal missed pregnancies (i.e., unsuccessful fertilization or failure of the blastocyst to implant) were most common in young animals. Abortions and resorptions occurred at all ages.

Age of Sexual Maturity and Seasonal Potency in the Male

Sexual maturity in males was defined by McLaren (1958) as the first appearance of sperm in the ejaculatory ducts. However, because a high concentration of sperm is necessary for fertilization (Laws 1956) and the period of adolescence may be extended, a more workable definition is presence of sperm in quantity in the epididymis (Hewer 1964 and Bigg 1969).

Males were considered sexually mature if abundant epididymal sperm was present during the period of 1 June to 1 August, when ovulation is likely to occur in females. Using these criteria male harbor seals became mature from 3 through 5 years of age (Table 3). Six-year-old males were not included in the sample taken during the breeding season. Five, 6-year-old males were collected in February and March. All had relatively large testes and three had traces of epididymal sperm suggesting most 6-year-old males are sexually mature. All males were mature by 7 years. One instance of probable reproductive senility was noted. The epididymal fluid from a 19-year-old male collected on 26 July contained only traces of sperm. Testes volume was considerably less in this animal than for potent males during the same season; 28 cc compared to $\bar{x}$ of 53.2 cc.

Growth of testes and bacula has been used as an indirect indicator of sexual maturity (Laws 1956, Hewer 1964). Fig. 2 shows testes volume and baculum weight plotted by age class. Both show similar patterns of growth, with a slow increase through age 2 and then rapid growth from 2 through 6 years. After 6 years testes volume remains constant while baculum weight continues to increase slowly.

Sexual maturity in male harbor seals, as indicated by abundance of epididymal sperm and the indirect indicators of bacula and testes size was attained by 7 years. Some individuals were apparently capable of breeding at a considerably younger age. No data are available on the relationship between physiological and behavioral maturity in harbor seals.

Table 3. Age of sexual maturity in 32 male harbor seals based on the presence of abundant epididymal sperm during the period 1 June - 1 August.

(Years) Age	No. of Males	(Epididymal Sperm) Absent	Trace	Abundant	Mature %
0-12 mos.	5	5			
2	4	4			
3	4	2	1	1	25%
4	4	2		2	50%
5	3	2		1	33%
6	0				
7	2			2	100%
8-19	8		1	7	88%

Mature males (7 years old and older) were examined by collecting period (Table 4) to determine seasonal potency patterns. Some mature males appeared to be in breeding condition from March until September. Too few animals were collected during August-December to accurately document the annual decline of potency. In British Columbia, Bigg (1969) collected data which suggested that adult males were in breeding condition from March to November. Bishop (1967) found numerous sperm in the epididymes of adult seals collected from 25 May through 15 August but few or no sperm from those collected in late October.

Table 4. Seasonal potency in male harbor seals, 7 years and older.

Time Period	Number of Animals	(Epididymal Sperm) None	Trace	Abundant	Percent Potent
4 June-29 July	10		1*	9	90%
24 Sept	1	1			0%
29 Oct-2 Nov	6	5	1		0%
5-7 Feb	3	3			0%
17-20 March	5	2		3	60%
19-20 April	4		1	3	75%

* 19-year-old male--apparently reproductively senile.

These data suggest that males are physiologically capable of breeding in advance of ovulating females and beyond their normal ovulation period.

In mature (6^+ years) and adolescent (3-5 years) males the testes showed seasonal variation in volume reflecting the period of potency. In mature males, for the period 17 March through 9 August, mean testes volume was 53.4 cc versus 34.3 cc for males collected between 24 September and 7 February. This difference was highly significant ($P < 0.01$) when tested with a t-test. Males between 3 and 5 years of age showed a similar pattern but not to the same extent; 17 March - 9 August $\bar{x}$ = 26.2 cc, 24 September - 7 February $\bar{x}$ = 13.9 cc a significant difference ($P < 0.05$). Juvenile males (0-2 years) did not show a significant seasonal variation; 17 March - 9 August $\bar{x}$ = 4.8 cc, 24 September - 7 February $\bar{x}$ = 4.4 cc ($P > 0.1$).

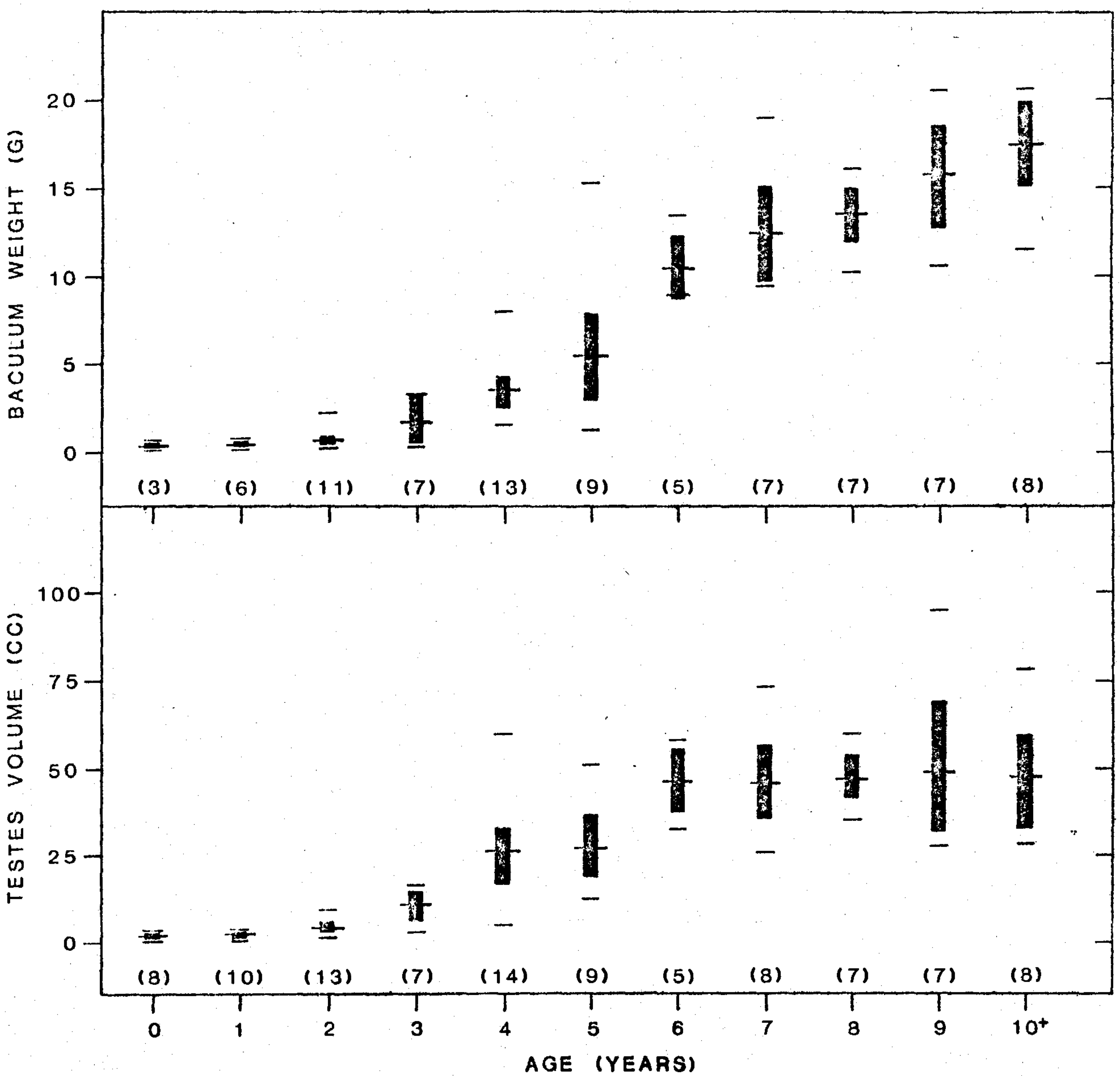

FIG. 2. TESTES VOLUME AND BACULUM WEIGHT BY AGE CLASS FOR MALE HARBOR SEALS. VERTICAL LINE, RANGE; BOX, MEAN WITH 95% CONFIDENCE LIMITS; HORIZONTAL LINE IN BOX, MEAN; NUMBER IN PARENTHESIS, SAMPLE SIZE.

Productivity and Population Status

Although causative factors are not clearly understood it is generally accepted that populations which are reduced below "carrying capacity" of their habitat respond with increased productivity. Conversely, populations maintained at high levels often display reduced productivity. Strong evidence has been presented indicating that this has occurred with several species of marine mammals. Laws (1962) related exploitation to increased pregnancy rates and decreased age of sexual maturity in several species of baleen whales. An exploited population of harp seals (*Pagophilus groenlandicus*) showed increased productivity because of reduced age of sexual maturity (Sergeant 1966, 1973).

Population productivity data collected during this study were compared to data collected in a similar study conducted by Bigg (1969) in British Columbia (Table 5). A chi-square test was used to test for differences in pregnancy rates of animals 3 years old and older in the two samples. The British Columbia sample had a significantly higher pregnancy rate than the Prince William Sound sample ($P < 0.05$). To obtain additional insight into this difference samples were separated into two groups: ages 3-5 years when sexual maturity was obtained and 6 years and older. Additional chi-square tests were performed which showed a highly significant difference in pregnancy rates for 3-5-year-old females from the two populations ($P < 0.01$), with the British Columbia animals having the higher pregnancy rates. Pregnancy rates for animals 6 years and older showed no significant difference ($P > 0.10$).

Table 5. A comparison of age specific pregnancy rates and age of sexual maturity of harbor seals in Prince William Sound and British Columbia.

	Prince William Sound			British Columbia		
Age	Total Animals	Pregnancy Rate		Total Animals	Pregnancy Rate	
2 years	12	0%		2	0%	
3	11	18%)		13	85%)	
4	12	58%)	46% *	4	100%)	86% *
5	5	80%)		5	80%)	
6	4	100%)		5	100%)	
7	5	100%)	100% **	6	67%)	93% **
8-28	15	100%)		31	97%)	

* Combined pregnancy rate for 3-, 4- and 5-year-old females.
** Combined pregnancy rate for females 6 years old and older.

Therefore, from these data we concluded that the British Columbia population had a significantly higher reproductive rate than the Prince William Sound population. The difference was in the younger age classes indicating a lower age of sexual maturity in British Columbia.

This lends insight into relative population status. It appears that the British Columbia population was exploited at a fairly high rate for many years (Bigg 1969). Copper River Delta seals were the target of an intensive control program in the 1950's but have not been heavily exploited since then. In Prince William Sound periodic hunting in the 1960's was not thought to have greatly reduced numbers. Thus, it appears likely that the higher productivity exhibited by the British Columbia population is a result of lower relative population numbers.

GROWTH

Assuming a 1 October mean implantation date and 1 June mean birth date the period of active fetal development is about eight months. Combining this with an estimated 2.5-month delay in implantation the total gestation period is approximately 10.5 months. Prenatal growth appears to be linear when measured by length, however, weight increases very rapidly during the later stages of development (Fig. 3).

One newborn seal and one full term fetus were collected. The fetus was a female which weighed 13 kg and was 82.3 cm long (standard length). The newborn pup was also female and weighed 10.9 kg and was 81 cm long. Weights and lengths at birth presented in the literature include: 81.6 cm and 10.2 kg in British Columbia (Bigg 1969), 87.5 cm and 10.9 kg for one male and 91.0 cm and 12.5 kg for one female on the Copper River Delta, Alaska (Imler and Sarber 1947), 84.5 cm and 11.6 kg for males and 76.5 cm and 11.8 kg for females, Tugidak Island, Alaska (Bishop 1967). Because of the small sample sizes and individual variation it is not possible to compare size at birth from area to area.

From examination of the limited data (Fig. 4) it appears that weight stabilized or even dropped after weaning while length continued to increase. This may reflect difficulty in attaining nutritional independence.

Examination of growth in both male and female harbor seals shows that maximal skeletal size (standard length) was attained by about 7 years (Figs. 5 and 6). Bigg (1969) combined his data from British Columbia and Bishop's (1967) data from the Gulf of Alaska, concluding that most females are fully grown by 5 years but males continue to grow until they are 9-10 years old.

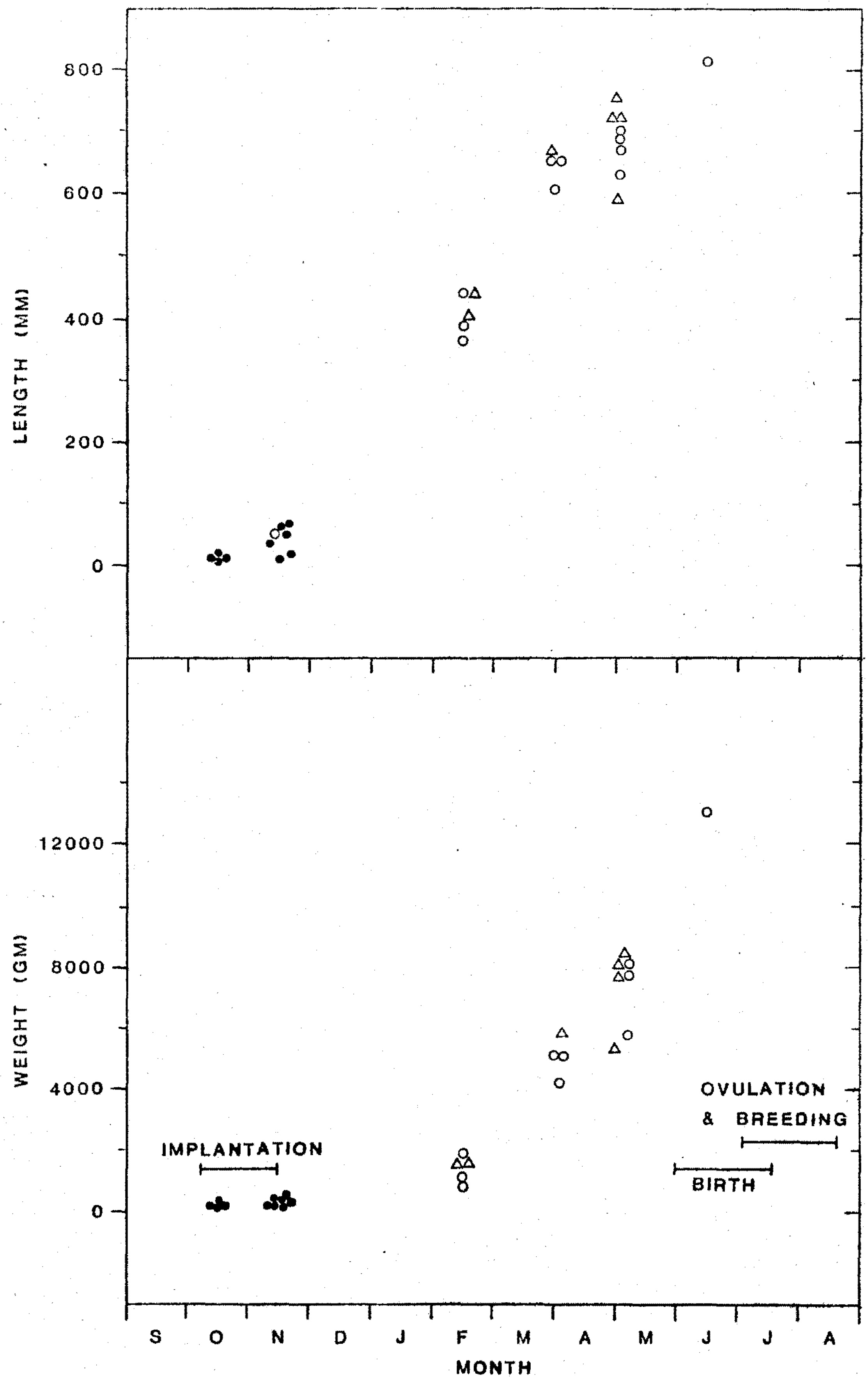

FIG. 3. PRENATAL GROWTH IN STANDARD LENGTH AND WEIGHT FOR 30 HARBOR SEALS. △, MALE; ○, FEMALE; ●; SEX UNKNOWN.

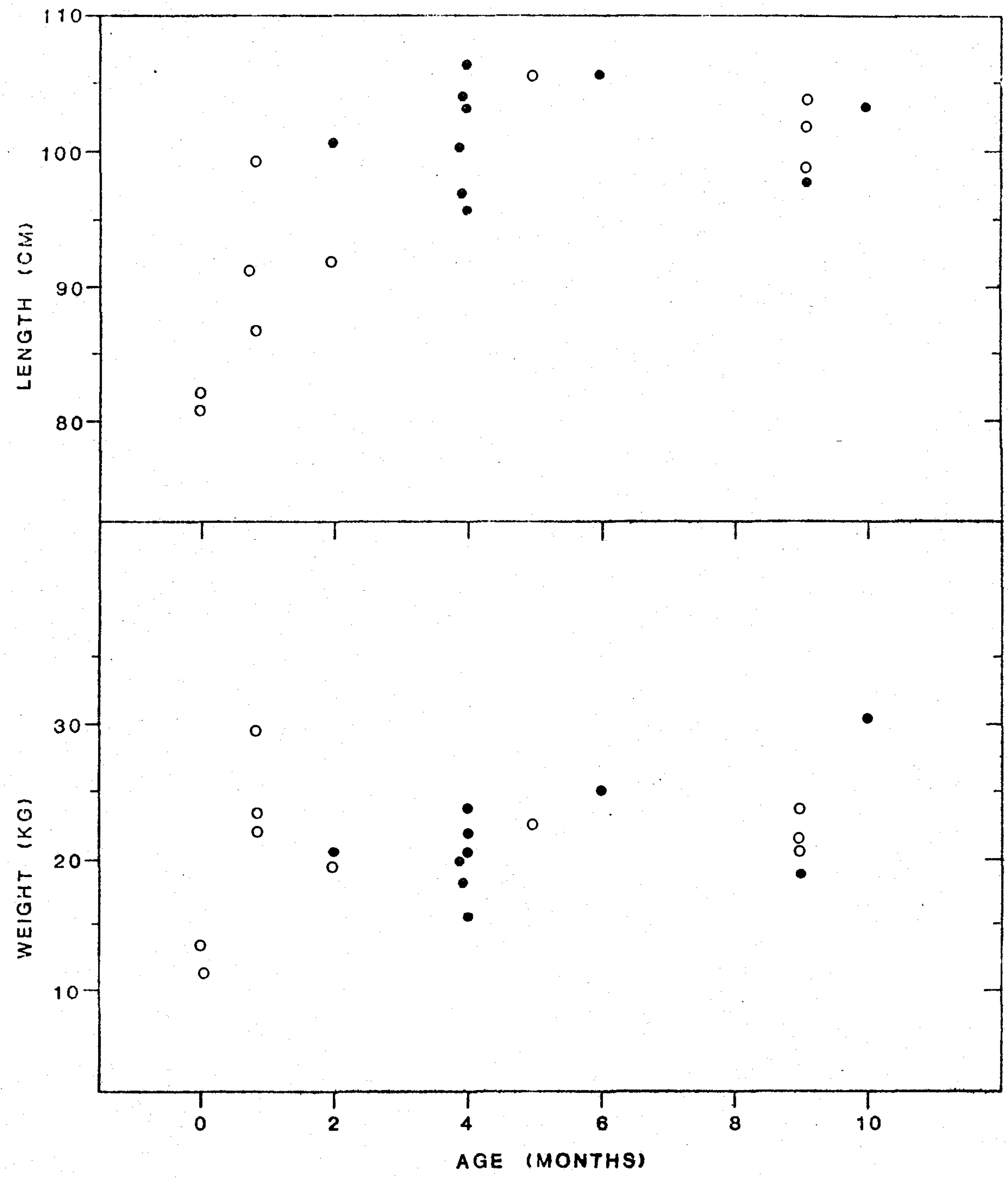

FIG. 4. FIRST YEAR BODY GROWTH IN STANDARD LENGTH AND WEIGHT FOR 21 HARBOR SEALS. ●, MALE; ○, FEMALE.

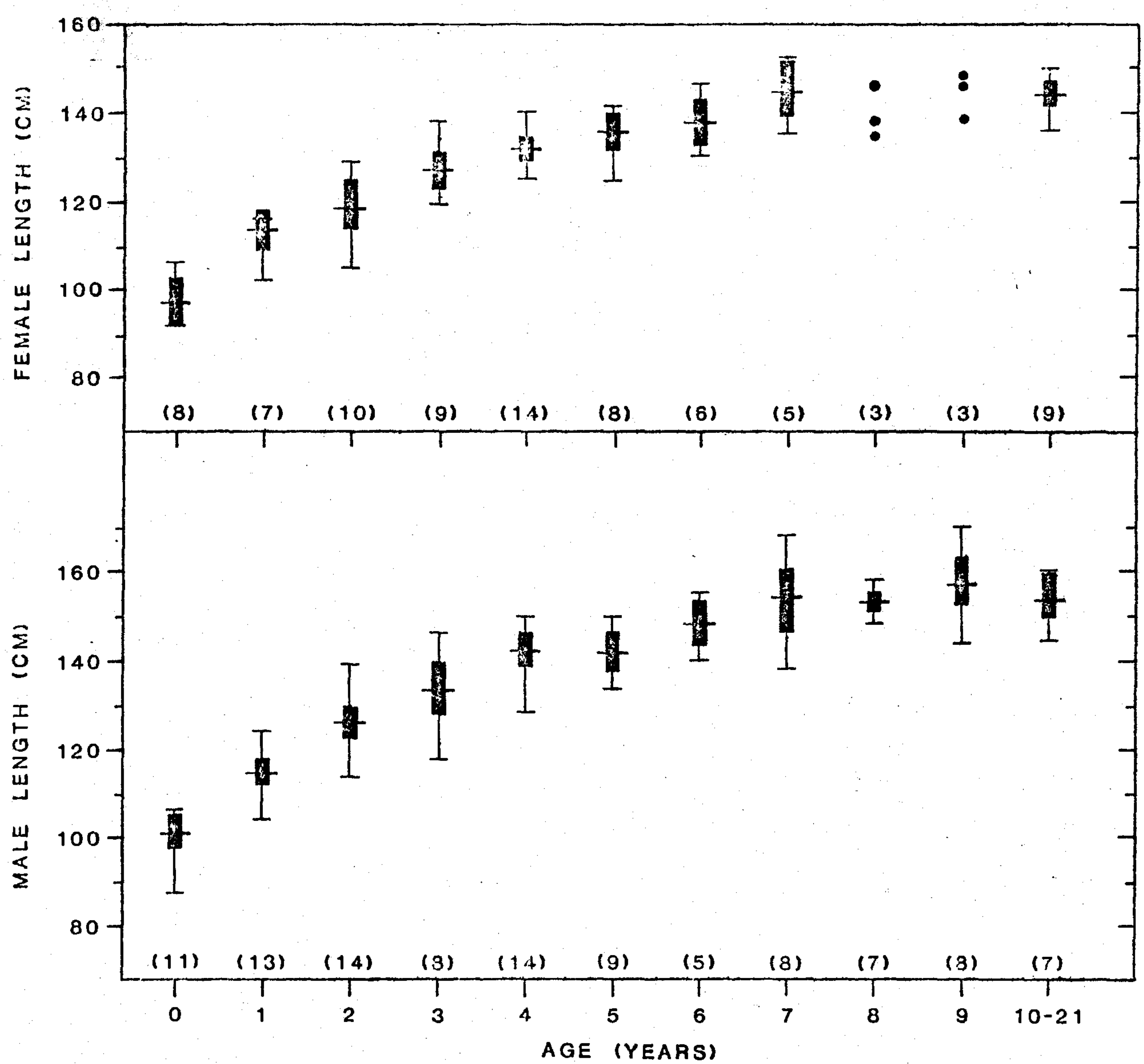

FIG. 5. STANDARD LENGTHS OF MALE AND FEMALE HARBOR SEALS BY AGE CLASS. VERTICAL LINE, RANGE; BOX, MEAN WITH 95% CONFIDENCE LIMITS; HORIZONTAL LINE IN BOX, MEAN; NUMBER IN PARENTHESIS, SAMPLE SIZE.

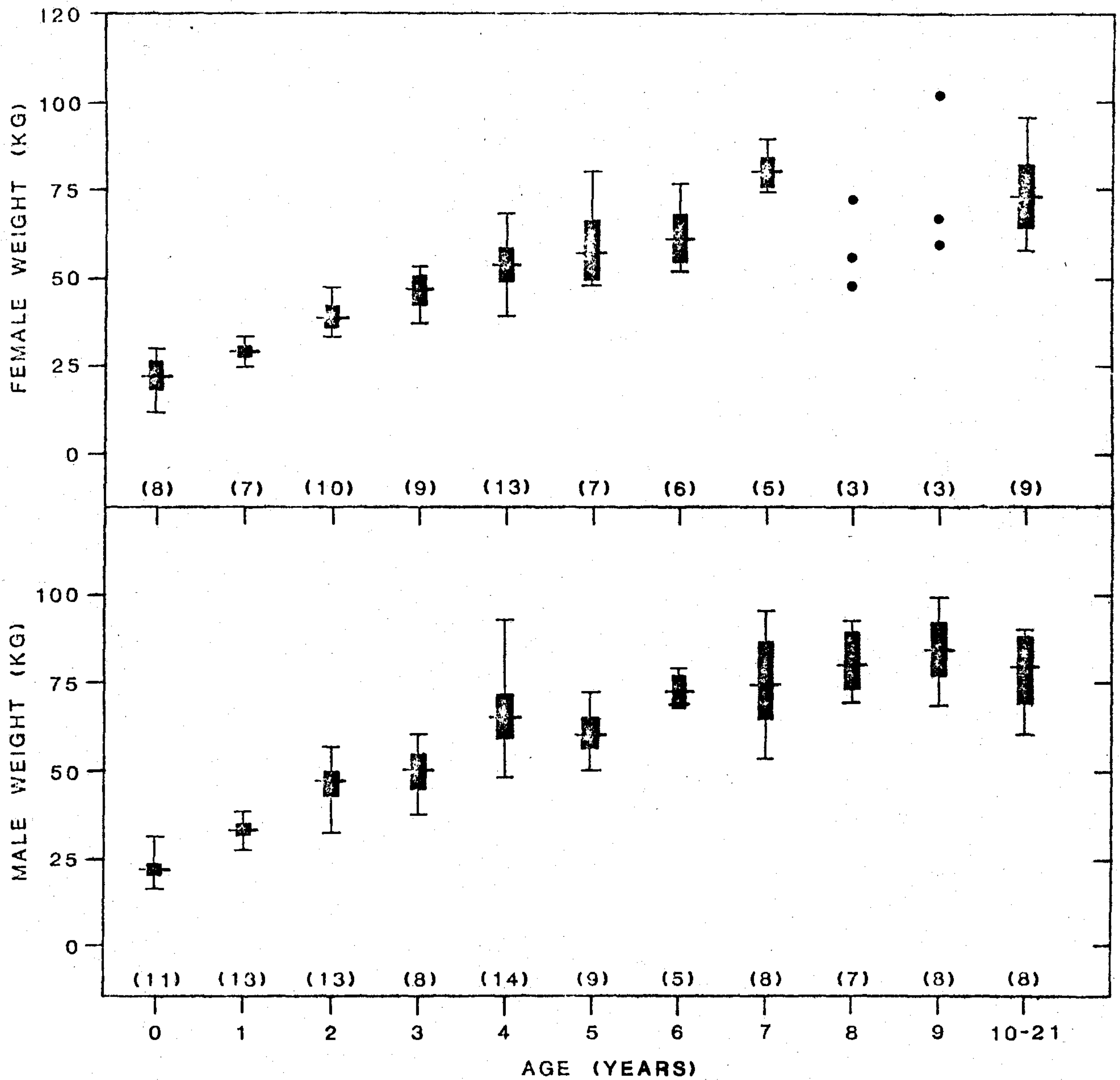

FIG. 6. WEIGHTS OF MALE AND FEMALE HARBOR SEALS BY AGE CLASS. VERTICAL LINE, RANGE; BOX, MEAN WITH 95% CONFIDENCE LIMITS; HORIZONTAL LINE IN BOX, MEAN; NUMBER IN PARENTHESIS, SAMPLE SIZE.

To examine sex specific differences in harbor seal growth the data were divided into two age categories, 0-6 years and 7 years old and older. Weights and standard lengths were then tested with a t-test. Adult males (7 years old and older) had a mean standard length of 154.4 $\pm$ 2.7 cm (95 percent confidence limits) and were 7.2 percent longer than adult females at 144.0 $\pm$ 2.4 cm. This was a highly significant difference ($P<0.01$). Adult males were 8.5 percent heavier than adult females with a mean weight of 78.8 $\pm$ 4.0 kg compared to 72.6 $\pm$ 6.3 kg. This difference was not significant ($P>0.05$).

For seals 6 years old and younger, males had a mean standard length of 127.8 $\pm$ 3.8 cm (95 percent confidence limits) and mean weight of 47.0 $\pm$ 4.1 kg compared to females at 123.2 $\pm$ 3.5 cm and 44.1 $\pm$ 3.7 kg. Males averaged 3.7 percent longer and 6.6 percent heavier than females (neither of these differences was significant [$P>0.05$]).

The heaviest animal collected was a 9-year-old female weighing 102.3 kg. This female, taken on 6 June, was pregnant with a full term fetus that weighed 13 kg. The longest seal was a 9-year-old male with a standard length of 170.4 cm.

Changes in body size and growth rates may be a reflection of the population's relationship to food resources (Scheffer 1955). Laws (1959, 1960) discussed the relationship of growth and attainment of sexual maturity. He concluded that a slow growth rate resulted in an increased age of sexual maturity which in turn reduced population productivity.

BODY CONDITION

Measurements of body fat have been used by seal researchers as indices of body condition. These include blubber thickness, a condition index (girth x 100/length) and ratio of blubber weight to total body weight. During this study two of these indices were used, blubber thickness (Scheffer 1967) and a ratio of weight of the hide and blubber layer to total body weight. A condition index was also calculated from body measurements (axillary girth x 100/standard length).

Fig. 7 shows seasonal condition patterns demonstrated by these three indices. Although all indicators do not show exactly the same pattern the basic trend is similar. Throughout the winter months condition was good and it appeared to increase slowly until midsummer. In mid to late July condition declined rapidly, probably in response to physiological drains of lactation, breeding and molting. By early October blubber reserves were again increasing. Sample sizes were too small to allow analysis of these data by sex, age, reproductive status and season.

Most animals taken during this study were weighed and then skinned with the blubber layer attached to the skin. The skin and blubber were then weighed. Five skins were completely fleshed and weighed in order to estimate the relationship of skin to total body weight. Mean value for these skins was 6.1 percent of total body weight with a range of

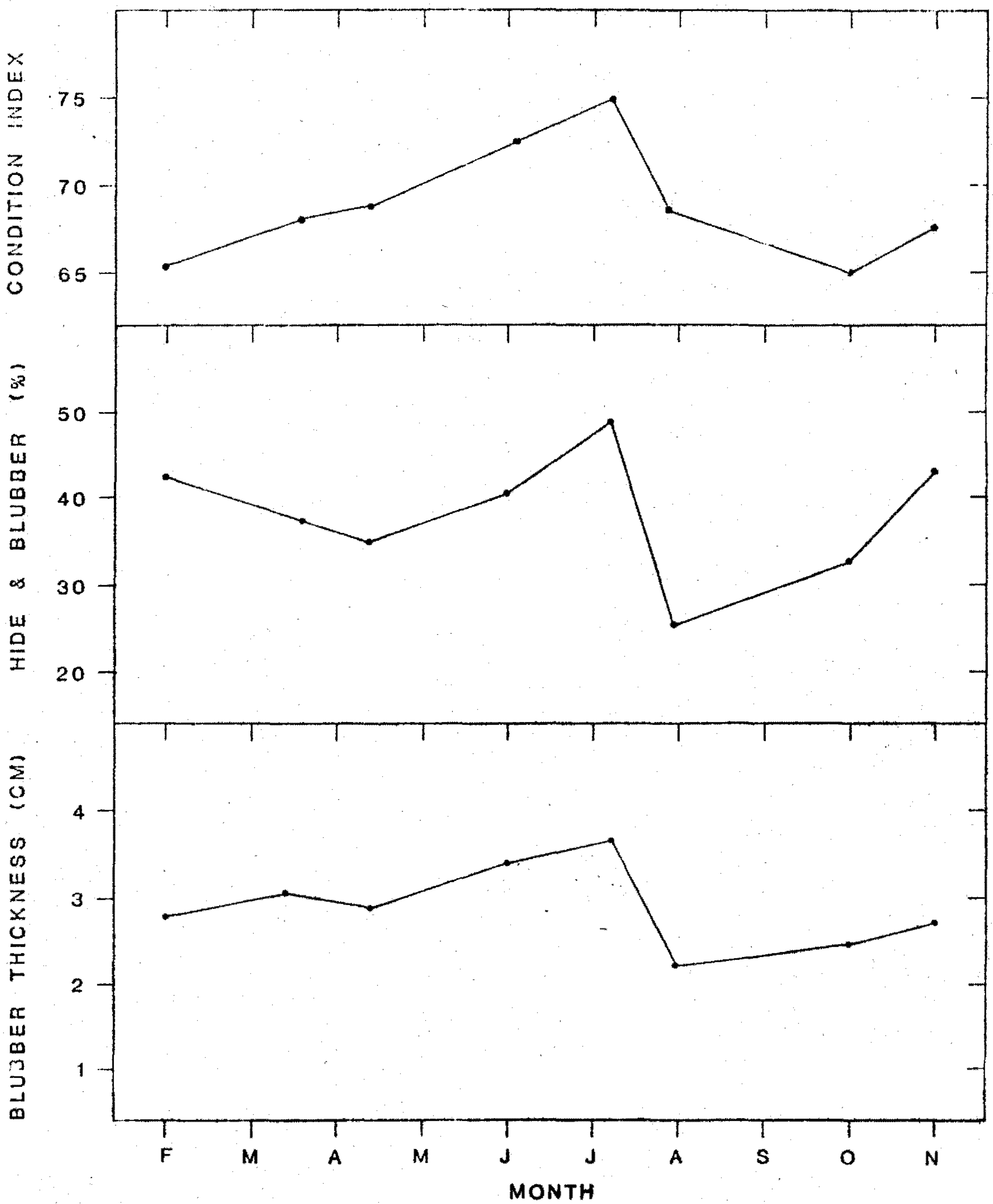

FIG. 7. HARBOR SEAL CONDITION INDICES, BLUBBER THICKNESS, WEIGHT OF HIDE AND BLUBBER AS PERCENT OF TOTAL BODY WEIGHT, AND CONDITION INDEX (AXILLARY GIRTH X 100/STANDARD LENGTH). FOR BOTH SEXES AND ALL AGES EXCEPT PUPS. POINTS ARE MEANS FOR EACH COLLECTING PERIOD. 1975.

5.3-7.4 percent. Using 6.1 percent of total body weight as an approximate weight for each skin, blubber values ranged from 49.3-14.5 percent of total body weight. The three animals with the highest blubber reserves were: a weaned pup where blubber equaled 49.3 percent, a nursing pup from which blubber was 42.8 percent and an adult female taken in July which apparently had not produced a pup that season at 43.1 percent of total body weight. Low blubber values obtained during this study were from a 3-year-old male taken on 25 July at 14.5 percent and from a 10-month-old pup with blubber equaling 20.8 percent of total weight.

Females were typically fatter than males although considerable overlap occurred. Mean blubber thickness for females of all age classes taken throughout the year was 3.17 $\pm$ 0.19 cm (95 percent confidence limits) compared to 2.71 $\pm$ 0.14 cm for males. A t-test used to test these data showed that this difference was highly significant ($P < 0.01$). T-tests were also run for the condition index and proportion of blubber and hide to body weight, both of which showed significant differences between males and females ($P < 0.05$).

Degree of fatness, like growth, has the potential for providing information on the relationship of populations to their food supply. Should food become more difficult to obtain an increased amount of energy would be expended in foraging, resulting in reduced blubber reserves. Before this information can be meaningful, however, additional baseline data must be gathered and the effects of sex, age, season and reproductive activity evaluated.

POPULATION CHARACTERISTICS

Our original proposal was for a 3-year study of harbor seals in the Prince William Sound-Copper River area. Due to the importance of marine mammal research in the Outer Continental Shelf Environmental Assessment Program in Alaska, the Prince William Sound work was not submitted for renewal. Because of this, sample sizes for estimating population statistics are small. Further complicating these analyses was the bias against small animals in collections. Younger animals, pups through about 3 years, were undoubtedly misrepresented as very small animals were selected against. The preponderance of males (57%) in the sample may be the result of differential behavior. I had the impression that males were generally bolder and more curious than females which would make them more susceptible to collecting. Oritsland and Benjaminsen (1975) mentioned that female hooded seals (*Cystophora cristata*) may be poorly represented in a sample because they avoid hunters.

Sex Ratio

The sex ratio for 18 harbor seal fetuses was 7 females:11 males which did not differ significantly from an even sex ratio ($P > 0.05$). Other studies (Bishop 1967 and Bigg 1969) found fetal and early postnatal sex ratios which approximated 1:1. In the sample of 186 postnatal seals (Table 6) 57 percent (101) were males which did not differ significantly from a 1:1 ratio ($P > 0.05$). Bigg (1969) found that 53 percent of 245 seals older than 1 year were females. Bishop (1967) noted that a randomly selected sample of 50 seals contained 46 percent females.

Table 6. Sex and age structure of 186 harbor seals collected in Prince William Sound and the Copper River Delta.

AGE	MALES #	MALES %	FEMALES #	FEMALES %
0-12 mos.	11	10.7	7	8.8
1 year	13	12.3	6	7.5
2	14	13.2	10	12.5
3	8	7.6	9	11.3
4	14	13.2	14	17.5
5	10	9.4	7	8.8
6	5	4.7	6	7.5
7	8	7.6	5	6.3
8	7	6.6	3	3.8
9	8	7.6	4	5.0
10	2	1.9	3	3.8
11	2	1.9	1	1.3
12	-	-	1	1.3
13	2	1.9	2	2.5
14	-	-	-	-
15	-	-	-	-
16	-	-	-	-
17	-	-	-	-
18	-	-	-	-
19	2	1.9	1	1.3
20	-	-	-	-
21	-	-	1	1.3
TOTAL	106	100.5	80	100.5

Longevity and Mortality

Maximum ages for harbor seals collected during this study were 19 years for males and 21 years for a female (Table 6). In British Columbia the oldest animals found were a 20-year-old male and a 29-year-old female (Bigg 1969). The oldest animals for which Bishop (1967) obtained ages were a 25-year-old male and a 28-year-old female. Klinkhart (1969) stated that harbor seals lived to over 32 years of age. This was based on a female from Tugidak Island, Alaska, which was aged at 32 years (conversation July 1976 with Edward Klinkhart, Alaska Dept. of Fish and Game, Anchorage, Alaska).

A life table was constructed to examine mortality rates (Table 7). Because of the small sample size both sexes were combined. I began the life table at age 4 because of collecting bias i.e., small seals were selected against, which probably caused the younger age classes to be misrepresented. The average annual mortality rate for ages 4-21 years was 24 percent. Bigg (1969) found average mortality rates for males 0-5 years were 21 percent and females 20 percent. The average annual mortality rate for seals 6 years and older was 29 percent for males and 15 percent for females.

Table 7. Life table for 108 harbor seals 4-21 years old (sexes combined).

Age	No. Killed	No. Killed/1000	No. Survivors/1000	% Mortality
4 years	28	259	1000	26
5	17	157	741	21
6	11	102	584	17
7	13	120	482	25
8	10	93	362	26
9	12	111	269	41
10	5	46	158	29
11	3	28	112	25
12	1	9	84	11
13	4	37	75	49
14	0	0	38	0
15	0	0	38	0
16	0	0	38	0
17	0	0	38	0
18	0	0	38	0
19	3	28	38	74
20	0	0	10	0
21	1	9	10	90
TOTAL	108	999	1	

Productivity

Gross productivity can be calculated from age specific reproductive rates if the sex and age structure of the population is known. I did not have a large enough random sample to estimate the population structure. Because of this I used my data in combination with Bigg's (1969) data to approximate a generalized harbor seal population. I assumed a 1:1 sex ratio and a life span of 21 years. Annual mortality rates of 20 percent were used for all age classes. Age specific pregnancy rates presented earlier were used i.e., 0-2 years = 0 percent, 3 years = 18 percent, 4 years = 58 percent, 5 years = 80 percent and 6 years and older = 100 percent. Using these data, gross productivity was calculated to be 18.8 percent of the prepupping population. Bigg (1969) calculated gross productivity of 25.7 percent by similar means. The major difference he found was higher pregnancy rates in the 3-5 year age classes. Composition counts of a pupping concentration on Sable Island, Novia Scotia (Boulva 1975) showed gross production of 25.7 percent. Bishop (1967) found that pups represented 32 percent of certain seal herds he observed on Tugidak Island. This figure appears high and the groups of seals he observed may not have been representative of all sex and age classes in the population.

Sex and Age Segregation

Segregation of various segments of harbor seal populations has been noted, however, the extent and mechanics are unknown. Van Bemmel (1956) found segregation of adults, juveniles and pregnant females along the coast of the Netherlands. In California, Knudtson (1974) found seals hauling out in both sexually mixed and sexually segregated herds. He found groups composed mostly or entirely of males and others consisting largely of females and pups. He suggested that this might be the result of breeding competition between males leading to the formation of bachelor herds of subordinate males. Richardson (1973) stated that pregnant females and cows with pups hauled out together at some distance from males and juveniles along the Maine coast. A professional seal hunter stated that when hunting in the Gulf of Alaska he had occasionally encountered groups of animals which appeared to be of the same sex (conversation July 1975 with F. Woelkers, Seward, Alaska).

In Prince William Sound I made several observations suggesting that at least some degree of segregation occurs. On 6 June 1973, 75 seals were seen hauled out on glacial ice flows in College Fiord. Fifty-two of these animals were female-pup pairs (26 pairs), a much higher percentage than would be present if all population segments were represented. From 17-19 March 1975 16 consecutive male seals were collected in about 16 linear miles along the western side of Knight Island. Ages ranged from 1 to 9 years with a fairly even distribution. Assuming an even sex ratio, no collecting bias and random distribution, the probability of this happening was 0.5^{16}. On 22 March 1975 I observed about 125 seals hauled out on glacial ice floes in Nassau Fiord. These animals all appeared to be small. Six were collected, all of which were either 10 months or 1 year and 10 months old. There was an even sex ratio.

Thus there is considerable circumstantial evidence that some segregation occurs in harbor seal populations. This could have important implications in a management program. Measures should be provided to insure that particular sex or age classes are not overharvested. Evaluation of a catastrophic event when large numbers of animals were killed could be undertaken properly only if the population segments involved were known.

FOOD HABITS

During this study, 151 stomachs and 105 large intestines from animals collected in Prince William Sound were examined for identification of food items. An additional 45 stomachs and large intestines were obtained from the Copper River Delta. Food items were identified from 142 of the 196 animals.

Analysis of food items was based primarily on frequency of occurrence. Volumetric measurements were made of total stomach contents. Where more than one species was present in a stomach, an attempt was made to determine volumes for each species. This was not possible in most cases as the flesh had been digested to the point where it could not be separated. Recovery of otoliths and cephalopod beaks from intestinal contents provided no quantitative information except frequency of occurrence.

In the Prince William Sound sample, fishes comprised 82.4 percent of harbor seal food items (Table 8). Cephalopods, comprised nearly equally of squid (8.6 percent) and octopus (8.0 percent), made up the remaining portion. Gadidae (the cod family) was the dominant group of fishes at 47.1 percent. *Theragra chalcogramma* (pollock) was by far the most important single species, comprising 34.2 percent of the total occurrences. *Clupea harengus* (Pacific herring), at 16.0 percent, was the other major item. Trace amounts of shrimp fragments (*Pandalus* spp. and *Crangon* spp.) were found in the stomachs of six seals. These were probably secondary food items as they always occurred in conjunction with fish remains and in very small amounts.

Table 8. Frequency of occurrence of harbor seal food items, Prince William Sound, Alaska.

Food Items	Number of Occurrences	Percentage of Occurrences
Cephalopoda		
Decapoda (squids-Gonatidae)	16	8.6%
Octopoda (*Octopus* sp.)	15	8.0%
Unidentified cephalopods	2	1.1%
Clupeidae		
Clupea harengus (herring)	30	16.0%
Salmonidae		
Oncorhynchus spp. (salmon)	4	2.1%
Osmeridae		
Mallotus villosus(capelin)	8	4.3%
Thaleicthys pacificus (eulachon)	3	1.6%
Gadidae		
Gadus macrocephalus (Pacific cod)	12	6.4%
Microgadus proximus (tomcod)	8	4.3%
Theragra chalcogramma (pollock)	64	34.2%
Eleginus gracilis (saffron cod)	4	2.1%
Zoracidae		
Unid. Zoracid	2	1.1%
Scorpaenidae		
Sebastes spp. (rockfishes)	2	1.1%
Hexagrammidae		
Hexagrammus stelleri (greenling)	1	.5%
Trichodontidae		
Trichodon trichodon (Pacific sandfish)	4	2.1%
Pleuronectidae		
Atheresthes stomias (arrowtooth flounder)	1	.5%
Glyptocephalus zachirus (Rex sole)	1	.5%
Hippoglossoides elassodon (flathead sole)	1	.5%
Lepidopsetta bileneata (rock sole)	1	.5%
Unidentified Fishes	8	4.3%
TOTAL	187	99.9%

The results of harbor seal stomach content analyses in Southeastern Alaska (Imler and Sarber 1947) were similar in some respects to those of this study. Gadids, primarily *T. chalcogramma* and herring were key species in both studies. Pleuronectids were more important in Southeastern Alaska, with a frequency of occurrence of 15 percent compared to only

2.1 percent in Prince William Sound. Shrimp were found to be important in Southeastern, particularly during June and July, while they were not considered a primary food item in this study. Cephalopods comprised nearly 18 percent of the occurrences in Prince William Sound compared to 8 percent in Southeastern.

Other reports of harbor seal food items in Alaska include *Octopus* sp., *Hexagrammus superciliosus* (greenling), *T. chalcogramma* and *Pleurogrammus monopterygius* (Atka mackerel) all from Amchitka Island (Wilke 1957 and Kenyon 1965). Bishop (1967) found shrimp and octopus remains in harbor seal stomachs on Tugidak Island and Aialik Bay.

A seasonal comparison of occurrence of major food items (Table 9) indicates that only minor seasonal variation occurs in utilization of prey species. The dominant species (*T. chalcogramma*) was heavily used at all times. Herring were heavily used in both winter and summer, but were lightly utilized during the fall. Although it is not well documented, fisheries biologists studying herring in Prince William Sound felt that many herring moved out of Prince William Sound during summer and then returned in winter (conversation 15 Feb. 1975 with Peter Fridgen, Alaska Department of Fish and Game, Cordova, Alaska). Cephalopods were eaten at consistent rates throughout the year. Salmon (*Oncorhynchus* spp.) were encountered only during summer; this was expected as very few salmon are present in the area during other portions of the year. Three relatively minor prey species; *Mallotus villosus*, *Eleginus gracilis*, and *Trichodon trichodon* appeared to occur only during certain periods. Little is known about seasonal distribution of these fishes. These were relatively rare food items and the seasonal aspects of their occurrence may be the result of sampling biases.

Table 9. Seasonal occurrence of selected harbor seal food items, Prince William Sound, Alaska.

	Percent of total occurrences for each seasonal period		
Food Item	Oct.-Nov.	Feb.-April	July-August
Cephalopods	18%	17%	17%
Clupea harengus	4%	24%	25%
Oncorhynchus spp.	0%	0%	14%
Mallotus villosus	0%	7%	4%
Theragra chalcogramma	40%	35%	25%
Eleginus gracilis	8%	0%	0%
Trichodon trichodon	0%	4%	0%

As previously mentioned, seals are present on the Copper River Delta only on a seasonal basis from about May through September. *Thaleicthys pacificus* (eulachon) was the dominant food item for these seals (Table 10). This was the only species encountered in the June sample and, with the exception of a single red salmon (*Oncorhynchus nerka*), was the sole prey species encountered in July. In contrast, the September sample contained four different species; *C. harengus, T. chalcogramma, Leptocottus armatus* (sculpin) and an unidentified flat fish (Pleuronectidae). This drastic shift in prey utilization is likely a reflection of availability of *T. pacificus* which move into the Copper River in the spring and are gone by late summer (conversation 13 Feb. 1975 with Ralph Pirtle, Alaska Department of Fish and Game, Cordova, Alaska). Some salmon are in the river from May through September. The four species found in the September sample were all marine or estuarine species and indicate at that time seals are probably moving down at least as far as the river mouth to feed and then moving back up river.

Table 10. Frequency of occurrence of harbor seal food items, Copper River Delta, Alaska.

Food Items	Number of Occurrences	Percentage of Occurrences
Clupeidae		
Clupea harengus (herring)	1	3.6%
Salmonidae		
Oncorhynchus nerka (red salmon)	1	3.6%
Osmeridae		
Thaleicthys pacificus (eulachon)	22	78.6%
Gadidae		
Theragra chalcogramma (pollock)	2	7.1%
Cottidae		
Leptocottus armatus (sculpin)	1	3.6%
Pleuronectidae		
Unidentified pleuronectid	1	3.6%
TOTAL	28	100.1%

Imler and Sarber (1947) reported on the contents of 67 harbor seal stomachs taken on the Copper River. Sixty-four of the seals had been feeding on *T. pacificus*, two on *Oncorhynchus* spp. and one on a gadid. Their collections took place from late May through June.

Additional sampling should be conducted in late July, August and early September on the Copper River in order to obtain a more complete picture of food habits of harbor seals. Weather and time limitations prevented additional collections during this study.

Evidence has been presented indicating that feeding activity is reduced during portions of the annual cycle of seals i.e., pupping, lactation, breeding, and molting (Spalding 1964, Sergeant 1973 and Richardson 1973). To examine this, mean volumes of stomach contents for each of the major collecting periods were compared (Table 11). No discernible correlation between pupping and lactation (June) or breeding (July) and mean volume of stomach contents was noted. No animals were collected during the general molting period of August and September (Stutz 1967). Six lactating females were collected, none of which had food in their stomachs. The intestinal contents of three of these seals contained fish otoliths indicating some feeding had taken place, although possibly on a reduced level. Ten adult males were taken from 9-29 July, all in breeding condition. No evidence of reduced feeding was found. Mean stomach content volume was 347 cc and evidence of recent feeding was found in all but one animal.

Table 11. Mean volume of stomach contents for each collecting period.

Collecting Period	Mean Volume Stomach Contents
4-7 February	110.8cc
17-22 March	238.9cc
16-20 March	107.6cc
4-7 June-Pupping and lactation	223.1cc
9-12 July-Lactation	240.6cc
22-29 July-Breeding	234.3cc
28 October - 4 November	327.2cc

Specialized feeding of newly weaned harbor seal pups on shrimp has been reported by Havinga (1933), Fisher (1952) and Bigg (1973). During this study nine seal pups (0-12 mos.) were collected from which food items were identified. The stomach of a weaned pup approximately 2 months old contained a single shrimp. Another 2-month-old pup had been feeding on small *Microgadus proximus* 5 - 10 cm in length. Two 4-month-old and one 5-month-old pups had been feeding on 7-10 cm *T. chalcogramma*. Five pups taken at 10 months were feeding on *Mallotus villosus*, a smelt less than 13 cm in length. It appears that harbor seals, at least in the Prince William Sound area, prey mostly on small fishes during their first year. Spalding (1964) demonstrated an increase in prey size with increasing age (and size) in the northern fur seal. The stomachs of two pups which were taken at approximately 5 weeks of age were empty except for sand. This may be another indication that the transition from weaning to nutritional independence is somewhat difficult.

It does not appear feasible to accurately calculate feeding rates from data collected in this type of study. Limited insight can be gained by examining the relationship of stomach content weights to body weights. The highest value for stomach contents as percent of total body weight was 3.7 percent from a 4-year-old male. Other high values were 3.3 percent, 3.2 percent, and 3.0 percent. These figures are low compared to literature values for daily food consumption for pinnipeds; 5 percent (Havinga 1933), up to 10 percent (Ronald et al. 1970), 16-18 percent for captive juveniles (Dieterich 1970), 7.6 percent (Geraci 1971) and 10 percent for young animals and 5 percent for adults (Sergeant 1973). Most of these rates were derived from captive animals where food is often unlimited and activity patterns are modified. Detailed information will have to come from specifically designed research on nutrition and energetics of pinnipeds.

The majority of seals (61 percent) had fed on a single prey species. Twenty-eight percent had been feeding on two species, 9 percent on three and 3 percent on four. Prey selection was characterized by primary use of abundant schooling species, particularly *T. chalcogramma, T. pacificus* and *C. harengus*. The selection of this type prey over more solitary species is logical as an energy conservation measure. *Octopus* sp. was the only solitary prey item which was selected on a regular basis (8 percent).

Frequency of occurrence food habit analysis used in this study has the potential for distorting the relative importance of various prey species. Perrin et al. (1973) pointed out that frequency of occurrence or direct numerical analysis tends to exaggerate any unimportant, small but numerous organisms. Otoliths and characteristic bones from larger fish tend to persist longer than those from smaller fish which would bias the data toward larger prey (Fiscus and Baines 1966). For comparative purposes, percent occurrence was compared to percent volume in instances where volumes could be calculated (Table 12). In most instances, agreement was relatively close. A number of uncommon species occurred only as skeletal components, such as otoliths, and are not represented in the volumetric presentation. Cephalopods showed a higher percent occurrence than volume which is probably the result of their large, persistent beaks which may be retained for some period. *Onchorhynchus* spp. showed a much higher volume than frequency of occurrence. They are large fish and three of the four occurrences were recent meals resulting in large volumes.

SUMMARY

1. Specimen materials, weights and measurements were obtained from 199 seals, 154 from Prince William Sound and 45 from the Copper River Delta.

2. Pupping appeared to begin about 20 May, peaked during the first week in June and was completed by early July.

3. The duration of the lactation period was not precisely determined, however, data collected were compatible with those presented in the literature indicating a lactation period of 3 to 6 weeks.

Table 12. Harbor seal food items, a comparison of frequency of occurrence with percent of volume.

Prince William Sound

Food Items	Percent Occurrence	Percent Volume
Cephalopods	17.6%	12.3%
Decapoda	8.6%	7.4%
Octopoda	8.0%	4.8%
Fishes	82.4%	87.7%
Clupea	16.0%	12.8%
Oncorhynchus spp.	2.1%	11.8%
Mallotus	4.3%	4.6%
Thaleicthys	1.6%	2.8%
Gadus	6.4%	0.2%
Microgadus	4.3%	0.0%
Theragra	34.2%	44.4%
Eleginus	2.1%	0.4%
Zoracidae	1.1%	0.0%
Sebastes spp.	1.1%	0.7%
Hexagrammus	0.5%	0.0%
Trichodon	2.1%	0.0%
Artheresthes	0.5%	0.0%
Glyptocephalus	0.5%	0.6%
Hippoglossoides	0.5%	0.0%
Lepidopsetta	0.5%	0.0%
Unidentified Fishes	4.3%	9.5%

4. Ovulation appeared to take place shortly after cessation of lactation during the month of July.

5. The period of delayed implantation was estimated at 2.5 months from approximately mid-July to early October.

6. Females reached productive maturity at 3 to 5 years of age. Pregnancy rates for those age classes were: 3 years - 18 percent, 4 years - 58 percent and 5 years - 80 percent. All females 6 years and older (24) in the sample were pregnant.

7. Reproductive failures were noted in five females. In four instances either the blastocyst failed to implant or fertilization did not occur. One instance of resorption was found. All reproductive failures were in 3-, 4- and 5-year-old animals and appeared to involve initial ovulations.

8. Sexual maturation in males occurred from 3 to 5 years of age. By age seven all males were mature. A 19-year-old male collected on 26 July was suspected of being reproductively senile as only trace amounts of epididymal sperm were found and testis size was very small.

9. Most mature males appeared to be physiologically capable of breeding considerably in advance of ovulating females and somewhat beyond their normal ovulation period.

10. Reproductive rates for females collected in Prince William Sound and the Copper River Delta were significantly lower than those found in British Columbia (Bigg 1969). The higher rates in British Columbia resulted from earlier attainment of productive maturity which may have been related to a higher degree of exploitation.

11. Total gestation period was about 10.5 months including a 2.5 month delay of implantation. Birth weights for two female pups were 13.0 kg and 10.9 kg.

12. Maximum skeletal growth was reached by about age 7 years. Adult males (7 years old and older) were significantly (P 0.01) longer than adult females; standard length of 154.4± 2.7 cm (95% confidence limits) for males compared to 144.0± 2.4 cm for females. Adult males were also heavier than females; 78.8± 4.0 kg and 72.6± 6.3 kg, however, the difference was not significant (P 0.05).

13. Body condition as measured by blubber reserves showed a general pattern of good condition during winter which slowly increased until midsummer. In mid to late July condition dropped rapidly. By early October blubber reserves were again increasing.

14. Fetal and postnatal sex ratios from this sample and from the literature approximated 1:1.

15. Maximum ages for harbor seals collected during this study were 19 years for a male and 21 years for a female. Maximum recorded age for a wild harbor seal is 32 years.

16. An average annual mortality rate of 24 percent was calculated from a life table which combined both sexes and used age classes 4-21 years.

17. Gross annual productivity of 18.8 percent was calculated using age specific pregnancy rates obtained from this study and sex and age structure data from this study and the literature.

18. Several instances of probable sex and age segregation were noted including a concentration of females with pups, an area which appeared to contain nearly all males and a group of predominately pups and yearlings.

19. The dominant food item in Prince William Sound was *Theragra chalcogramma* (pollock) comprising 32.4 percent of the total occurrences. The other major species was *C. harengus* (herring) which accounted for 16.0 percent of the occurrences. Cephalopods (divided nearly equally between squids and octopus) comprised 17.6 percent of the occurrences.

20. On the Copper River Delta *Thaleicthys pacificus* (eulachon) was the most important item accounting for 78.6 percent of the occurrences. In the fall, after *T. pacificus* was no longer available, seals were feeding on marine species indicating probable movement out of the river to feed.

21. During their first year of life seals appeared to utilize small fishes less than 15 cm in length.

22. The highest value for stomach contents as percent of total body weight was 3.7 percent.

23. Prey selection was characterized by primary use of abundant schooling fishes particularly *T. chalcogramma, C. harengus* and *T. pacificus*. The majority (61 percent) of seals had fed on a single species.

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