REPRODUCTION, AGE DETERMINATION, AND BEHAVIOR

OF THE

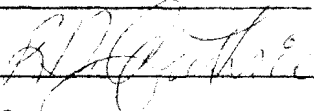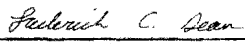# HARBOR SEAL, PHOCA VITULINA L., IN THE GULF OF ALASKA
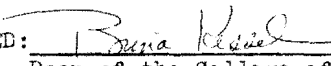
RICHARD H. BISHOP, B. S.

REPRODUCTION, AGE DETERMINATION, AND BEHAVIOR

OF THE

HARBOR SEAL, PHOCA VITULINA L., IN THE GULF OF ALASKA

APPROVED:

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Vice President for Research and
Advanced Study

REPRODUCTION, AGE DETERMINATION, AND BEHAVIOR

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HARBOR SEAL, PHOCA VITULINA L., IN THE GULF OF ALASKA

A

THESIS

Presented to the Faculty of the

University of Alaska in Partial Fulfillment

of the Requirements

for the Degree of

MASTER OF SCIENCE

By

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College, Alaska

ABSTRACT

Reproduction, age determination, behavior and growth of the harbor seal, Phoca vitulina, were studied in the Gulf of Alaska during 1963 and 1964.

Females are sexually mature at 3 to 4 years of age and bear one pup per year. Gestation is calculated to be 271 days. Pupping begins by 5 May and ends in late June. Lactation lasts about 3 weeks, and ovulation occurs about 2 weeks later. Implantation occurs from late August to late September. The male matures at 5 to 6 years of age and produces sperm from late May to early August. Mating depends on the female being in estrus.

Age determination was based on cementum and dentine layers found in the canine tooth.

Tide and wind conditions normally determined timing and duration of haul-out. Mild intraspecific strife promoted a spatially stable group on shore. Desertion of pups was common in early May but declined as pupping progressed. Male mating behavior is characterized by aggressiveness of similar form toward females and other males.

Pups gain over 75 percent of their birth weight by the time of weaning.

Females producing young composed up to 32 percent of the population on one pupping rookery.

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PREFACE

This study was made possible by funds provided under Federal Aid in Wildlife Restoration Project W-6-R-6, Work Plan L-2, through the Cooperative Wildlife Research Unit of the University of Alaska.

Among the many individuals who contributed to the completion of the study I am particularly grateful to the folowing.

Dr. Frederick C. Dean, Dr. David R. Klein, Dr. Francis H. Fay, Mr. John J. Burns, and Dr. Victor B. Scheffer all contributed ideas, discussion, and constructive criticism. In addition, Dr. Dean, Dr. Klein, and Dr. R. Dale Guthrie critically reviewed this thesis.

Mr. Grant Lortie gave valuable assistance in the field, and prepared the figures in the thesis. Mr. Oral Burch and Mr. Al Burch provided fine hospitality and assistance in the field. Mr. William Robertson provided the apparatus and technique used in making the photomicrographs.

My wife, Mary, has contributed greatly to the completion of the task.

Authorities for scientific names used herein are Scheffer (1958) for pinnipeds, Hall and Kelson (1959) for other mammals, and American Ornithologist's Union (1957) for birds.

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INTRODUCTION

The harbor seal, _Phoca vitulina_, is more abundant than any other seal in Alaska's coastal waters (Brooks, 1963), but in spite of the abundance and accessibility of harbor seal populations, the details of harbor seal life history are still incompletely known. Except as they affected commercial salmon fishing, little economic importance was formerly attached to the harbor seal; studies of more important or valuable species naturally took precedence. As a result of the dramatic rise in value of seal hides since 1963, considerable attention has been focused on the harbor seal.

The present study was designed with three chief objectives in mind; (1) to determine the annual reproductive cycle of the harbor seal and to obtain an estimate of population productivity; (2) to devise and implement a reliable and practical age determination technique; and (3) to determine the post-natal growth pattern. During the second field season observation of behavioral patterns was emphasized. Information on general life history and biology was obtained as the study proceeded.

Taxonomy and distribution: The harbor seal is known locally by several names including spotted seal, hair seal, and harbor seal, of which spotted seal is the most widely used and understood in Alaska.

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Harbor seals are found throughout Alaska's coastal
waters. Scheffer (1958) reviews the taxonomy of P. vitulina,
and gives the range of Phoca vitulina richardi (p.92) as:

> North and west coasts of North America from Herschel
> Island (69°35'N., 139°W., Dunbar 1949, p.9) to eastern
> Bering Sea, Aleutian Islands, and southward along the
> coast to northern Baja California, Mexico.

He goes on to say that the area in the Bering Sea where P.
v. richardi intergrades with the Asian subspecies, P. v.
largha, is unknown, and gives the range of P. v. largha
(p.94) as "From Bering Strait southwestward along Asiatic
shores and islands to China; northwestward into Chukchi
Sea(?)."

For some time harbor seals have been known to inhabit
Iliamna Lake, Alaska, but Scheffer (1958) did not know if a
breeding population existed there. According to Wassie
Nickoli of Iliamna, the harbor seals are year-round residents,
and pup at the lake (vive voce). To this writer's knowledge
the Iliamna seals have not been studied in any detail.

In reviewing the taxonomic work on the North Pacific
harbor seals, Scheffer points out that Doutt (1942) and Os-
good (1904) could find no skull characteristics which could
be used to separate P. v. largha and P. v. richardi; but
Schwarz (1942) stated that seals from south of the Alaska
Peninsula were distinguishable from P. v. largha.

Thus the exact taxonomic status of Alaskan harbor seals
is unsettled. The seals which are the subject of this study

are assumed to be P. v. richardi, in accordance with Schef-
fer's (1958) delineation of this subspecies' range.

Previous studies in the northeastern Pacific: Few non-
taxonomic studies have been conducted on harbor seals of the
western North American coast. Scheffer (1928) reported on
stomach contents of 35 seals in Washington State waters.
Scheffer and Sperry (1931) presented a detailed food habits
analysis based on contents of over 100 stomachs.

Scheffer and Slipp (1944) gave a comprehensive account
of the harbor seal in Washington State waters. Imler and
Sarber (1947) discussed food habits and other information
collected at the Copper River delta and in southeastern
Alaska. Fisher (1952) dealt with the life history and eco-
nomics of harbor seals in the Skeena River, British Columbia.
Murie (1959) recorded the distribution and habits of the
harbor seal in the Aleutian Islands. Wilke (1957) reported
on the stomach contents of harbor seals from Amchitka Is-
land in the Aleutians. Spalding (1964) has reported on the
food habits of the harbor seal in British Columbia.

Work was begun by the Alaska Department of Fish and Game
during the late 1950's and continued through 1960 in the
Copper River and southeastern Alaska areas, with the primary
emphasis on seal control, and research was tentatively
planned for Tugidak Island.

The University of British Columbia is currently conduct-
ing research on several aspects of harbor seal biology.

STUDY AREAS

This study was conducted during 1963 and 1964 in the Gulf of Alaska area (Fig. 1). The writer collected seals by hunting alone and with commercial hunters in Aialik and Harris Bays, west of Seward, in 1963. Seals concentrate and haul out in areas of floating glacial ice near active glaciers at the heads of bays. The glaciers at the heads of both Aialik and Harris Bays are extensions of the Harding Icefield. Through interaction of the glaciers and the sea, ice is intermittently calving from the faces of the glaciers.

Aialik and Harris Bays are deep bays throughout most of their length. Within both bays the waters are relatively clear and calm, compared to adjacent outer coastal waters. Turbidity due to glacial melt-water is limited to waters within about 1 mile of the glaciers.

Aialik Bay is 18 miles long and about 3 miles wide at the mouth, while Harris Bay is about 11 miles long and 3.5 miles wide at the mouth. The surrounding topography is characterized by steep mountains rising abruptly from the sea and by a scarcity of beaches.

Harbor seals were the most numerous marine mammals in Aialik and Harris Bays. Other marine mammals seen included unidentified large whales and killer whales, Orcinus orca. Occasionally a sea otter, Enhydra lutris, and sea lions, Eumatopias jubata, were seen.

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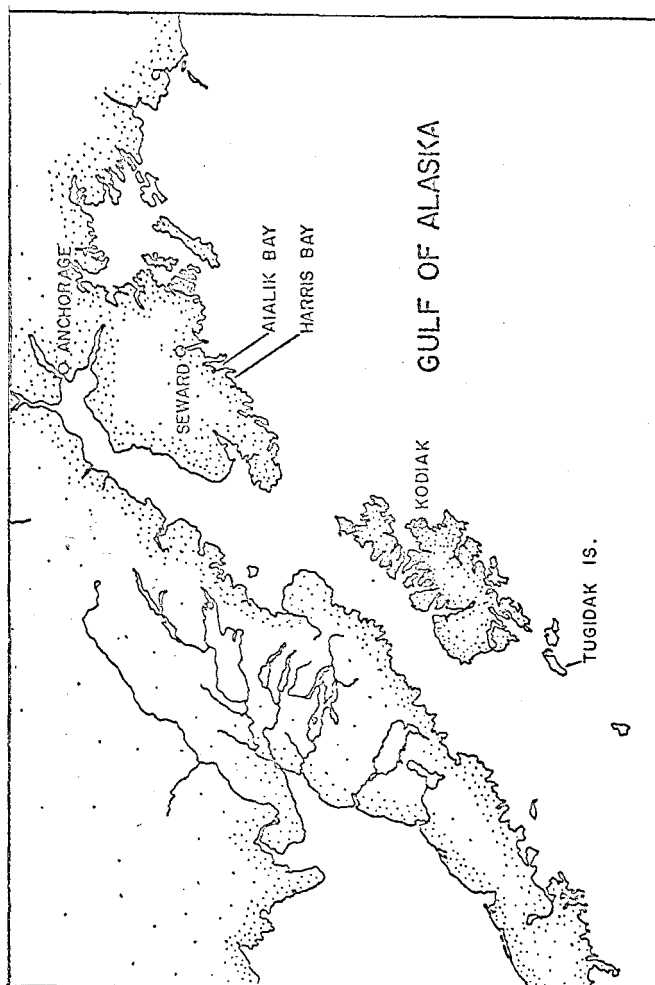
Fig. 1. Locations of Aialik Bay, Harris Bay, and Tugidak Island, study areas in southcentral Alaska.

The westerly shore of Tugidak Island was the study area
from 25 April through 31 July, 1964. Tugidak Island is
approximately 18.5 miles long, and varies in width from 3.5
to 7 miles. The maximum elevation is 161 feet. The west
beach is bordered by sheer bluffs up to 150 feet in eleva-
tion. The bluffs consist mainly of clay, which is constant-
ly eroded by a process of drying, cracking, and sloughing.
Interaction of bluff erosion, tides, and onshore winds and
swells contribute to a constantly changing beach configura-
tion. The island's main drainage patterns run easterly to
the sea, thus there are few breaks in the bluffs bordering
the west beach.

The east side of the island lacks the steep, unstable
bluffs. A series of old beach ridges has developed between
the present beach and the higher part of the island. Seals
generally do not use the east beach for hauling out, and
only occasionally was a seal seen offshore in this area.
The northerly end of the island consists of a hook of low
elevation nearly enclosing a shallow bay characterized by
extensive tidal flats. Seals commonly haul out on the out-
side border of the hook and near the mouth of the bay.

The entire island is surrounded by shoals. On the west
side, shoals extend at least 2 miles from shore. On the
east-southeast side, shoals apparently extend even further.
The water around all but the north end of the island is un-
charted. Seals apparently feed in the shoal areas off both

the east and west beaches, but little is known of the marine
life in either area.

Marine mammals observed at Tugidak Island in addition to
harbor seals included one female sea otter and her young,
occasional sea lions, and one unidentified dolphin or
porpoise.

METHODS

Field methods: Seals were usually shot with a high-powered
rifle, although some pups were taken using a club. Measure-
ments routinely collected from each seal in 1963 and 1964
consisted of the following:

1. Total weight; weight was measured to the nearest
pound with a spring scale of two hundred pounds capaci-
ty. When a very large seal was collected, the carcass
was cut in half to facilitate weighing. No correction
for blood loss was made.

2. Combined hind flipper span; the distance to the
nearest 0.5 cm from the tip of one ventral toe (hallux),
to the other when the flippers are stretched at right
angles to the long axis of the body (Fig. 2). Dr.
Victor B. Scheffer suggested this measurement as a sub-
stitute for hind flipper length and width, both of
which are difficult to obtain accurately on seals.

3. Standard length; the straight-line distance from nose
to the tip of the tail flesh, to the nearest 0.5 cm.
In a normal, relaxed position a seal's neck is only
partly extended, whether it is alive or dead. The
author attempted to keep each seal in this position dur-
ing measuring.

4. Blubber thickness; a slit to the bone just wide
enough to accomodate a steel measuring tape was made

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Fig. 2. Measuring combined hind flipper span.

mid-ventrally about half-way between the pectoral
girdle and the posterior end of the sternum. The
thickness of the blubber was measured to the nearest
millimeter. Blubber thickness is widely used as an
index to physiological condition in seals (McLaren,
1958, and others).

In addition, notes were taken on stage of molt, pelage
color, and stomach contents. In the case of females, note
was made of pregnancy, lactation, ovarian structures, and
condition of the fresh reproductive tract.

The right mandible was routinely collected, and the
canine tooth was removed and preserved in Loess' solution
(98 parts 70% ethyl alcohol plus two parts glycerine).
Gonads were collected and fixed in AFA (Guyer, 1950, p.239);
some ovaries were fixed in 10% formalin during 1963. Ovaries
from mature seals or those approaching maturity were examined
for follicles and other ovarian structures before preserva-
tion. When squeezed gently, an ovary containing a very large
follicle would feel quite spongy, even though the follicle
might not show superficially. A numbered plastic tag was
attached to each specimen collected.

Most of the data on behavior was obtained on Tugidak
Island, where from bluffs adjacent to the haul-out areas
of the seals we were able to observe the seals without
disturbing them.

Laboratory methods: Ovaries were cut by hand with a razor
blade into longitudinal sections 2 mm thick. The sections
were left joined at the base to preserve their relative
position. Each section was examined macroscopically for
corpora lutea, corpora albicantia, and follicles. A binocu-
lar dissecting microscope was used in further searches for
corpora albicantia. The greatest length and the greatest
width of corpora lutea, corpora albicantia, and the largest
follicle in each ovary were measured to the nearest 0.5 mm.
The number of corpora lutea, corpora albicantia, and the
macroscopic appearance of the various bodies was noted.

The testes were weighed to the nearest 0.5 g following
removal of accessory tissue and the epididymes. Length, and
width at the middle of the testis, were measured to the
nearest mm. Ovaries were treated similarly to the testes,
except that the width was measured at the hilus.

The presence of mature sperm in the epididymis was
taken to indicate breeding condition. The epididymis was
cut, and a small amount of the fluid from the cut surface was
squeezed onto a slide, covered with a cover glass, and
examined for sperm under the microscope at 100X and 430X.

The total length and the diameter of the pulp cavity
opening of each tooth were measured to the nearest 0.1 mm.
Teeth were then mounted on wooden blocks (5 x 2.5 x 2 cm)
with Epoxy glue. The tooth was allowed to project well be-
yond the end of the block to allow for cross-sectioning.

Teeth were sectioned on a Torrance cutting machine equipped
with a circular diamond-toothed blade and a movable chuck
which holds the material to be cut. Initially several cross-
sections were cut from each tooth before the chuck was
turned 90° and one or two longitudinal sections were taken.
With the refinement of techniques it was found that usually
one or two cross-sections and one longitudinal section were
sufficient.

Thickness of the cut sections varied. The objective was
to obtain a whole section about 0.02 mm thick. In some cases
sections were cut thin enough to require little or no grind-
ing prior to examination. Experience was the chief factor in
consistently obtaining the most desirable sections.

Tooth sections were ground only enough to remove occa-
sional saw marks which interfered with observing the deposi-
tion pattern, or to reduce the thickness of the section.
Power tools available for grinding sections included a lapi-
dary wheel, a grinding wheel, and a buffer with abrasive.
None of the power tools gave as good results as grinding
sections by hand between two fine carborundum knife sharpen-
ing stones. Hand grinding was slower, but it was felt that
the quality of sections was more easily controlled, and
grinding could be done where it was convenient to periodical-
ly examine the section under a dissecting microscope. While
sections were not perfectly smooth, the scratches and re-
maining saw marks did not affect reading of the sections. A

machine designed specifically for tooth section grinding such
as Fisher and Mackenzie (1954) describe should give compara-
ble results with a substantial saving in time.

Most of the tooth examination work was done with a
variable power binocular dissecting microscope set at 30X,
using transmitted light. A compound microscope at 150X was
frequently used for examination of cementum rings, particu-
larly when examining cross-sections. Sections were mounted
in glycerine for examination. Temporary slides were easily
prepared, and sections could be removed for further
processing if necessary.

Some sections were inadvertently ground so thin that
differentiation of layers was very difficult without stain-
ing. Staining with silver nitrate solution using a modifica-
tion of Carrick and Ingham's (1962) method aided differentia-
tion sufficiently to allow age determination of the sections,
but the specimens were not as good as unstained sections of
the proper thickness.

The technique developed to determine age of specimens
from growth layers in the tooth sections will best be under-
stood and explained in conjunction with the results.

RESULTS

Behavior

Strong gregariousness is basic to social structure and behavior among pinnipeds in general. Scheffer (1958) suggests that sociability, or gregariousness, was one major factor in the relative stabilization of evolution in pinnipeds. Scheffer and Slipp (1944) characterize the harbor seal as **loosely** gregarious when hauled out, but more or less solitary when feeding; the writer feels that this is a reasonable generalization.

Only incidental observations of behavior were obtained during 1963 in Aialik and Harris Bays, thus this account of behavior is based on observations of seals on Tugidak Island, unless otherwise stated.

Pre-pupping herd behavior: Observations of harbor seal behavior began upon our first contact with the seals on 4 May, 1964. Until mid-May the incidence of pupping was quite low, and herd behavior in early May was considered pre-pupping behavior, with infrequent localized exceptions where a pup was born.

The herd under observation contained 2,000 to 2,500 seals on 4 May, but for some time thereafter only a fraction of this number was seen ashore on a given date; however, there were no other regular haul-out areas nearer than 12 miles away, at the northern end of the island. An aerial

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reconnaisance performed on 21 April suggested that the herd
under observation composed about half of the harbor seal
population of Tugidak Island in early May. It should be
noted that estimates or counts of seals include only those
hauled out, since no accurate absolute count or estimate can
be made of seals in the water.

During the pre-pupping season, the seal herd under
observation exhibited a definite preference for a particular
section of beach within 0.5 mile from a 150 foot bluff we
called the "main bluff". Seals preferred to haul out adja-
cent to high bluffs, possibly because of the protection from
approach afforded by the bluffs. Seals also preferred a
relatively smooth beach lacking large rocks or much debris,
which may have been related to their reduced mobility and
their habit of looking about the beach when on land.

Later in the season an influx of seals and hunting
activity caused seals to haul out in many less desirable
areas of the beach.

Where no bluffs were available, as at the northerly end
of the island, seals hauled out on exposed spits and bars,
with no obstructions about.

Under normal conditions, tides are most important in de-
termining duration and timing of haul-out at Tugidak Island.
Fisher (1952) notes the importance of tides in the daily
movements of harbor seals in tide-influenced areas of the
Skeena River, British Columbia. Venables and Venables (1955)

point out that harbor seals near Fitful Head, Shetland, are
commonly seen hauling out as the tide recedes, and returning
to the sea on flood tide, but that onshore swells and human
interference frequently upset the pattern.

On Tugidak Island it became evident that seals would
haul out anytime, providing there was some exposed beach.
Events observed on 11 May illustrate the influence of tide
and wind on dispersal and, later on, haul-out. A high tide
of 7.9 feet was predicted for approximately 11:30 AM at
Tugidak. An onshore wind of 30 to 40 miles per hour, common
in May, was producing heavy surf. A small pod of seals was
ashore just north of the main bluff. At 11:40 AM the beach
and the seals were heavily awash, and at 11:50 the entire pod
made a sudden dash for the sea. In less than 5 minutes all
the seals had left the beach. Some moved as far as one-
quarter mile offshore, while others remained just beyond the
surf. At 2:00 PM the beach was still deserted, but there
were many seals milling around in the water just north of
where they were previously ashore. By then the tide had
receded enough to leave a strip of undisturbed beach, al-
though the wind had not abated. The seals swam back and
forth, "treading water" and looking at the beach. At 2:30 a
seal attempted to haul out, but, hampered by the surf, it
returned to the general congregation outside the surf. At
3:00 PM a seal successfully reached the beach, looked about
and went back to sea. At 3:05 PM nine seals landed, but two

returned to sea. Immediately as many as eight to ten seals began hauling out with each successive wave. In 3 hours 575 seals had come ashore, but more seals landed after this count. The following day, 12 May, 850 seals were ashore in nearly the same place prior to high tide. Wind and tide conditions were similar to 11 May, but the beach was only occasionally awash, and the seals made no general dispersal to the sea at high tide.

Although the sequence above was condensed in time, the same basic relationship of timing and duration of haul-out with respect to wind and tide persisted during subsequent observation. Reconnaisance by the writer and reports from hunters in the area indicated that the seals were not inclined to move around the south end of Tugidak to the lee shore, even though strong onshore winds might be of several days duration.

A seal herd undisturbed by man is quite reluctant to leave its hauling area. As the tide comes in the seals are forced to move further up the beach or to go to sea. Those seals remaining on the beach form a small crowded group, which promotes mild intraspecific strife in the form of short, sharp, open-mouthed thrusts with the head, in addition to growls, foreflipper waving, and scratching with the foreflipper. In the non-breeding period these conditions were never observed to lead to serious strife.

When seals haul out they are generally aligned facing away from the sea, i.e. toward the bluff. If they haul out on an ebbing tide, the seals gradually turn around and move nearer the water line, but there may be a considerable time lag between movement of the tide line and movement of seals. In the pre-pupping period, pregnant cows are usually first to move toward the receding tide line, with other seals gradually following. Eventually the orientation of the entire herd is reversed, with nearly all seals facing the water.

Although few observations were obtained on haul-out behavior in Aialik and Harris Bays, the contrasting conditions observed are worth mentioning. In these bays the major haul-out areas were on floating ice calved from active glaciers. Only occasional individual seals or small groups were seen hauled out on the rocky shorelines of the bays; seals were never seen on the few existing sand or gravel beaches. Tide and wind did exert an indirect influence on haul-out through their effect on the floating ice. Incoming tides and onshore winds, either alone or in combination, tended to push the ice further into the bay, compressing and stabilizing the seals' haul-out "grounds" within 1 to 2 miles of the glacier. Conversely, receding tides or an offshore wind tended to disperse the ice. Dispersion of the floating ice resulted in dispersion of seals. The usual large aggregations could not form due to discontinuous distribution of ice, but it seemed also that fewer seals in total were inclined to haul out on

scattered ice.

On Tugidak Island, when man was not a consideration, the chief biotic factor affecting harbor seal haul-out behavior was the seals themselves. Seldom was the actual initiation of haul-out observed, but related observations indicated that an important stimulus to general haul-out was the presence of seals on the beach. In the account given earlier of haul-out in relation to wind and tide, seals did not begin going ashore in earnest until a group of seven had landed and stayed on the beach. Thereafter, no hesitation to haul out was exhibited by the majority of seals, although in any group there were occasional seals which would not stay ashore after their first landing.

The caterpillar-like motion of phocids on land has been described by Bartholomew (1952) and Scheffer and Slipp (1944). The latter authors mention that when frightened the harbor seal uses its foreflippers strongly in a pulling motion, but that the belly does not leave the ground. However, I have seen many alarmed seals at close range, and in full flight the seal completely leaves the ground for a moment in each stride. In more subdued flight the seal remains largely in contact with the beach. I was able to keep pace with a seal in full flight by maintaining a fast walk, about 5 to 6 miles per hour. Normally seals shuffled along slowly, the larger, fatter seals with their foreflippers laid back against their sides. Pups and active young animals usually

used their foreflippers to aid movement on land. The new pup
is obliged to use its foreflippers as main locomotors, since
it apparently has neither the strength nor the coordination
to accomplish the caterpillar-like motion. Learning, as
opposed to instinct, may have a part in the pups' acquiring
the characteristic seal movement. On several occasions
deserted pups appeared to imitate the gait of older seals
with which they came in contact.

Within the hauled-out herd there seemed to be little
social structure. Both sexes and all sizes were intermixed.
Occasionally one might observe a group of four to six ani-
mals of about the same size resting together within the herd,
and usually these were seals which appeared to be between
yearlings and adults in size. These immature seals were
noticeably more sociable than adults and often played among
themselves. It may be that their association continues at
sea, which would tend to synchronize their activities,
including haul-out.

Within the seal herd in the pre-pupping period, domi-
nance appeared to be related to size of the seal. Large
seals were able to enter or leave the herd, change their
resting position, or move to a new resting site within the
herd more successfully than smaller seals. In addition,
large seals were usually capable of halting similar movement
by smaller seals. In a crowded herd such movement evoked
characteristic aggressive responses of varying intensity.

Foreflipper waving was a mild form of response used to warn
away another seal. Rapid waving sometimes accompanied by
scratching indicated a stronger response. Audible growls
frequently accompanied the more vigorous flipper waving. A
more aggressive action was the "head thrust" or "butt", which
was a sharp, rapid extension and retraction of the neck,
directed toward, but not necessarily contacting, another
seal. The head thrust made with the mouth open, and accom-
panied by a growl, was the strongest expression of aggression
observed in the non-breeding season. Scratching lightly with
the claws of an extended foreflipper was frequently used by a
seal to encourage its neighbor to move.

It was mentioned earlier that confined haul-out space
led to antagonism among the seals. A less confined area al-
lowed greater mobility and greater choice of spots to rest,
with a consequent decline in strife. However, while almost
constant mild strife and movement went on within the herd,
social pressure was toward a spatially static group. Rarely
was this attained, but movement was greatly restricted among
hauled-out seals. Playful immature seals confined their
activity to the herd's periphery or to the sea. Vigorous
rolling and wriggling evoked mild aggressive reactions, while
scratching, grooming, and stretching were constant but
generally tolerated activities.

Sleeping posture was quite variable. Most commonly
seals lay on their belly, with their head resting on the

beach. Some lay on their backs with flippers dangling loosely
or folded on their chests. A rock protruding from the beach
in the haul-out area was sure to have a seal resting its head
or forequarters upon it.

During the pre-pupping time there was little to upset
the activities described above. Occasionally a crab-pot
float or a low-flying eagle would alarm part of a herd. Sus-
tained alarm and subsequent flight of an entire herd was
rarely observed to occur except when caused by man. When
part of a herd is alarmed, those seals involved abruptly
raise their heads and look in the direction of the supposed
danger. In some cases a nucleus of seals, usually including
several very large animals, will stay ashore unless danger
becomes imminent, thereby inducing seals which have fled to
begin hauling out again almost immediately if the danger does
not materialize.

When frightened while in the water, harbor seals charac-
teristically dive sideways and slap the water with the flexor
surface of the extended foreflipper. The slapping action
frequently evokes a similar reaction in other seals in a
group.

By using available cover such as rocks or logs, or by
crawling along the beach, a herd could be approached quite
closely, even though some seals in the herd might be watch-
ing. Because seals were so reluctant to leave the beach,
hunters found it easy to reach the herd and kill several pups

with clubs before the pups were able to escape into the sea.
Early in the season some adult seals were also taken in this
way. After several weeks of intensive hunting, seals became
very difficult to approach during the day. Hunters then
found that with a little caution they could approach a herd
very closely at night before the seals became alarmed.
Behavior in the pupping period: Activity during the first
two weeks of May was considered "pre-pupping" behavior, al-
though a few pups were born during that time. By mid-May the
rate of pupping had increased, and new behavior patterns were
observed in addition to characteristic pre-pupping behavior.

Early in the pupping period (mid-May through 3 to 5
June) pupping activities had little effect on choice of haul-
out areas, herd behavior, or interaction between individuals,
except on a localized basis in areas of the herd where a pup
was born. Birth of a pup caused seals in the immediate area
to withdraw at once; in many cases the seals would rush to
the sea. More frequently nearby seals would only move far
enough to leave an unoccupied circle of about a 15-foot radi-
us around the new mother and pup. Some cases were observed
where a new mother would drive away nearby seals, but this
was unusual early in the season.

Desertions, the rule during the first two weeks of May,
were still very common in the latter half of May. Many de-
serted pups were observed near the herd. Seals hauling out
in the vicinity of a deserted pup would frequently retreat to

the water in apparent fear, in the same way that they re-
treated from a foreign object on the beach.

As pupping progressed, the attitude of other seals to-
ward new pups gradually changed from something close to fear,
to antagonism or occasionally tolerance. Deserted pups
searching for their mothers were not accepted by older seals,
but they no longer produced a flight reaction in older seals.
Females with pups were particularly aggressive toward de-
serted pups, butting and frequently biting the pups whenever
they approached. Many pelts taken by hunters showed bruises
apparently caused by canine teeth of older seals. Few were
badly bitten, but one was found with severe bites all over
its body. Attacks actually observed never drew blood.

There is some evidence that deserted or orphaned pups
may occasionally survive. A pup was collected on 4 July in
Aialik Bay which weighed 22 lb, about half the weight of
other pups collected at that time. It was alone and very
lethargic, but remains of several shrimp were found in its
stomach, indicating it had learned to feed. Other pups taken
about the same time were weaned or nursing, but apparently
not feeding on marine life. McLaren (1958) mentions finding
emaciated pups of the ringed seal, Pusa hispida, that were
possibly deserted before weaning by the mothers. Desertion
may have occurred with the pup in question, but loss of its
mother to hunting during the nursing period seems more
likely.

Later in the pupping season when hunters were taking numbers of pups, cows that had lost their pups often searched through a herd on the beach and in the water for their offspring. The searching cow would approach each deserted pup to smell its muzzle. Since no aggressiveness was involved, the deserted pup would respond by following the cow until she drove it off or lost it, or until it grew tired of the chase. Occasionally a tolerant cow was seen with several pups following along behind as she moved through the herd, all trying to nurse each time she stopped. Some appeared to succeed in nursing, but only briefly. Starvation was almost certainly the ultimate fate of deserted pups, and it is doubtful that such occasional feeding, if it were successful, saved many.

Newborn harbor seals are aptly described as "slim and lanky as salamanders" by Venables and Venables (1955). In spite of their lean condition, pups are able to swim and dive at birth. Pups start moving about immediately or within a few minutes after birth. Newborn pups drag themselves about by reaching forward with the foreflippers and pulling. Since newborn pups are unable to hold up their head for long, each move forward is terminated with the thump of their chin upon the beach. In the water newborn seals swim actively, but usually on the surface. Some use is made of the torso and hind flippers, but the foreflippers are used most extensively, in a vertically accentuated butterfly stroke.

Among the newborn seals, diving was observed to be very
shallow and of a few seconds duration. While no pups were
marked for individual recognition over a period of time,
general motor ability and, in the case of nursing pups, fat-
ness, allowed differentiation between very young pups and
those several days old. Pups several days old were able to
dive well and swim more nearly like adults, with the trunk
and the hind flippers providing more propulsion. Weaned
pups (3 to 5 weeks old) were occasionally observed moving
about on the beach without using their foreflippers, in the
manner of older seals.

Behavior of pups and cows--late pregnancy through weaning:
While pregnant females tend to maintain a position near the
water's edge when hauled out, some may be found throughout
the herd. Usually they may be distinguished by their out-
sized abdomen, but even this is not an infallible character-
istic. Their activities appear little different from other
seals in the herd. They may haul out on their abdomens
initially, but they usually move about for short distances
and rest on their sides, whereas other seals may move and rest
on any body surface.

Desertion has been mentioned as the rule during the
early pupping season. Behavior of a female toward a pup she
deserts consists essentially of ignoring the pup from birth.
The birth process was not observed during early pupping, but
desertion following birth was observed many times. After

giving birth the cow would normally move several feet from
the pup and lie torpidly on the beach, neither fleeing nor
approaching the pup. Should the pup in its aimless wandering
approach the cow, she would usually move further away, some-
times going to sea. On one occasion a pup was born with the
chorionic sac unruptured. The cow grabbed the pup's hind
flipper with her teeth and pulled, breaking the sac, then
moved off, and did not return. The pup struggled for several
minutes, then stopped; possibly it drowned, since it was
still half enclosed in the sac which held considerable fluid
around the head. The cow did not return to the pup. In no
case was the mother seen to return to a deserted pup.

Birth is a rapid process in harbor seals. On several
occasions births occurred in areas of the herd we had been
watching only minutes before. We observed partuition only
once. On 21 June one pregnant seal was seen in a pod of 64
seals. She began moving about rather aimlessly, circling and
apparently sniffing the beach, then she stopped. With bin-
oculars one could see that the pup was just beginning to
emerge. The cow lay on her side with head and hind flippers
raised, occasionally looking about. There was no obvious
exertion by the cow, and in 30 seconds from the time the cow
stopped, the pup was born, head first. The umbilical cord
had already broken, and the chorionic sac burst as the pup
hit the ground. Yellowish fluid and unattached lanugo (fetal
pelage) covered the pup. The pup immediately made a few

motions with its head and foreflippers. The cow moved away
slightly, returned to sniff the pup, then moved away several
feet after the fashion of a cow deserting her pup. A desert-
ed pup approached the newborn pup, and the cow immediately
moved to intercept it; after that she guarded her offspring.
The cow made no attempt to clean the pup or induce it to
nurse, which was the usual situation according to our obser-
vations. Bartholomew and Collias (1962) noted that a recent-
ly post partum northern elephant seal cow did not clean its
pup and paid no attention to the placenta. Post partum har-
bor seal cows consistently ignored the placenta, which usual-
ly was not expelled for half an hour or more following birth.

A seal hunter who had observed a birth in 1963 on Tugi-
dak Island stated that the process took "about 10 to 15
seconds". The cow turned and apparently bit the umbilical
cord, then chased the hunter down the beach a short distance.
In this case the pup was born hind flippers first, and had
partly emerged when the hunter first noticed the event.

The beach seemed preferred as a pupping site although no
comparitive quantitative data is available. Scheffer and
Slipp (1944) also suggest that harbor seals prefer to pup on
land. Births apparently did occur in the water. Placentas
were seen floating in the water under circumstances where
they would not likely have washed off the beach. Gulls rare-
ly missed seeing and eating a fresh placenta, which suggests
that those observed were expelled recently. One cow with a

new pup came ashore before she had completely expelled the placenta. She had not previously been on the beach.

Attended pups (those not deserted by their mothers) encounter few of the adverse circumstances affecting deserted pups. Little direct attention is given the pup immediately following birth, but the cow allows no animal near it.

Glaucous-winged gulls, _Larus glaucescens_, attended most births to attempt to peck the placenta or the umbilical cord. If gulls approached too closely, the cow would chase them until they flew. Gulls would peck the eyes of deserted pups, but rarely had the opportunity with attended pups. However, one blind cow was seen with her pup, and another seal with one blind eye was seen; the blind seals may have survived desertion and ensuing attacks by gulls, or they may have been blinded in some other way, such as in breeding encounters. Mansfield (1958) noted that Weddell seal pups occasionally lost an eye as the result of attacks by females with pups. A blind adult male in good condition was also observed, but blindness may have been due to genetic factors, since it was also bald except for supercilliary and mystacial vibrissae.

Pups did not usually nurse right after birth. No definite pattern was determined, but there was usually a delay of more than 30 minutes before the pup attempted to nurse.

Location of the teats does not seem instinctively known by the pup, whose initial attempts to nurse include a great deal of searching and pushing with its muzzle all over the

cow's body. The cow aids the pup, directing it caudally along her body with light scratching motions of her fore-flipper as she lies on one side. Eventually the pup learns the proper location. Upon hauling out the pup begins pushing the cow with its muzzle until she settles down, rolls on her side, and allows the pup to nurse. The cow only raises its head occasionally to look about, unless there is some disturbance in the herd. Should another seal approach too closely the cow will interrupt nursing to chase it, then return to the pup.

Venables and Venables (1955) suspected that in Shetland pups nursed only in the water until they were about 3 weeks old, but at Tugidak Island most nursing began and was carried out on shore. The contrasting environment (rough rocky shores versus smooth beach) probably contributes to the difference in nursing habit. Possible nursing in the water was seen only once at Tugidak, but the turbid water precluded adequate observation of the incident.

During the nursing period, attended pups were always accompanied by their mothers. When hauling out, cows accompanied their pups through the surf. One pup rode ashore on its mother's back. Frequently cows were forced to lead their pups ashore several times before the pups would stay. In general, cows seemed to have little control over movements of their pups on the beach. When ashore the cow followed the pup about in its aimless wandering. If other seals threatened

the pup, its mother would intervene. On only one occasion
was a cow seen to restrain her pup; the pup persisted in
attempting to return to the water, whereupon the cow would
move between pup and sea and place one foreflipper over her
pup, preventing it from moving. After two such attempts the
pup followed its mother up the beach and did not attempt to
reach the sea again.

In the water, play between the mother and pup was com-
mon, and the pup nearly always followed its mother, in con-
trast to its behavior ashore.

That deserted pups usually starve was mentioned earlier;
certainly most do, but on 21 June two separate incidents sug-
gested that adoptions may occur. In both cases a cow was
searching for her pup among hauled-out seals and, as usual,
was followed by a few deserted pups. One cow went to sea,
but was followed by a tenacious pup, which caught her and
climbed on her back to ride. She soon found another pup to
which she reacted as though it were her own. The first pup,
however, did not leave, and no intolerance had been shown by
the cow toward either pup when the group was finally lost to
view.

On another occasion, a cow came upon two pups, one of
which she chased a bit, but the second pup laid down near
her. Several times the second pup moved as though to nurse,
but the cow discouraged it. Finally the pup succeeded in
nursing, unchallenged by the cow. The adoptive cow

subsequently warned off another searching cow with head thrusts, and thereafter continued to defend the pup. The permanency of this association is unknown.

Mr. Pete Kesselring, a seal hunter of long experience, felt that adoptions occur among harbor seals. A similar belief is held by hunters from Gambell, Alaska, with respect to walrus. Considering the incidents described above and the tolerance of some seals toward deserted pups, adoption seems a possibility, but its effect on population dynamics is probably insignificant.

All normal relations between a cow and her pup were characterized by much affection and tolerance. However, when cows with pups were rushed by hunters, they became extremely agitated and rushed back and forth between the waterline and their pups. Under these conditions, two cows exhibited what seemed to have been displacement activity. Each cow bit and shook her own pup vigorously before finally retreating from the hunters, leaving her pup behind. Similar behavior in the Weddell seal female was observed by Mansfield (1958).

The process of ultimate detachment of cow and pup at weaning was not observed at Tugidak. That there is a gradual detachment is suggested by Venables and Venables (1955), who noted that near the end of the nursing period, unweaned pups were observed hauling out together, without the cows. At Tugidak, weaned pups simply began showing up in the herds under observation. A few weaned pups were evident by 28

June, but the proportion of attended pups did not appear to decline until 4 July, and a distinct decline in the proportion of attended pups became evident by 12 July.

A more exact evaluation of onset, climax, and end of weaning might have been possible had not intensive hunting earlier in the season reduced the number of pups by harvesting and probably by inducing a large number of desertions.

Breeding behavior: Onset of breeding coincided roughly with the onset of weaning. The first evidence of breeding was observed on 4 July, when a pair of seals was seen apparently copulating more canem 50 to 75 yards from shore. While details of copulation were not evident due to poor visibility, their behavior did not resemble any behavior previously observed. The larger seal grasped the smaller strongly with the foreflippers so that they moved as a unit in the water. The pair rolled languidly, submerged, surfaced, and drifted along for 10 to 15 minutes before they were lost to sight. The smaller seal made no effort to escape. Much of the time both were partly or wholly submerged, but from time to time the smaller seal raised its head to breathe, and the larger would do the same.

Indications of breeding attempts and increased male aggressiveness were more frequent as the season progressed. Male aggressiveness was directed toward other males and toward females. A typical example of aggressiveness between males follows. A bull hauled out to join the herd, and

another bull that had already hauled out moved directly to
the newcomer. They nearly touched noses, and the aggressive
bull made several short, hard bites at the head and neck
region of the newcomer. The newcomer bit back but less ag-
gressively; then both stretched out with only about 2 feet
separating them. After several wary glances at each other,
both went to sleep. On only one other occasion were both
combatants positively bulls, but other observations of male
aggression did not fit the usual pattern of behavior between
bull and cow, and the writer considers them more likely the
result of breeding-associated aggressiveness of males rather
than of direct breeding interest. For example, a large bull
abruptly reared up and grabbed a smaller seal of unknown sex
lying next to him, apparently without provocation. The
smaller seal resisted vigorously, but the bull had a very
secure hold on the small seal's back. The struggle was so
intense that all the other seals took alarm, and rushed for
the sea. The bull let go, looked about at the retreating
seals, and rushed off himself, ending the struggle. The
small seal also headed for the sea. The behavior of the
large bull and his victim is an interesting example of the
role of social facilitation in the alarm reaction of harbor
seals, as well as an example of male aggresiveness.

Aggression between males can be characterized as brief,
vigorous skirmishes, apparently with little serious injury
likely to result. However, numerous superficial cuts and

punctures were observed on bulls throughout the herd. It seems probable that some proportion of these wounds resulted from aggression between males, while some may be attributed to mating encounters with cows.

Aggressiveness of bulls toward cows was the most frequently observed aspect of breeding behavior. In form, this aggressiveness resembled aggressiveness between males. For example, the attacker normally sought to bite and hold its victim by the back of the neck. Both types of aggression were invariably accompanied by intense snarling or growling by the participants. A "breeding encounter", however, was characterized by a more formalized approach by the aggressor, the bull, and by considerably greater tenacity of purpose on the aggressor's part. Contact between a bull and a cow where mating was apparently the objective was considered a breeding encounter, whether or not copulation occurred.

It is likely that the majority of breeding encounters occur at sea, where actual mating occurs, but they also take place ashore, most frequently in smaller herds and along the loosely defined seaward edge of a larger herd. A bull seeking cows typically moved slowly along the edge of a herd, apparently without interest in other seals. When a particular cow was approached, the bull shuffled forward to within 5 or 6 feet of the cow, extended his head and neck, and seemed to be assaying the cow, but whether visually or olfactorily the writer could not determine. In a pre-breeding season

situation, a cow without a pup was not likely to react to another seal 5 feet away. During the breeding season, the bull's approach prompted the cow to react as though she or her position was being threatened. Growling, flipper waving, or head thrusts, either alone or in combination, were directed toward the bull. The bull did not visibly react to this display, but remained in his original position for a short time. Then he would rush the cow with surprising quickness and grab her by the back of the neck or head. A fierce battle followed, with the bull and cow thrashing about on the beach. Without exception the cow escaped. Sometimes the bull pursued her, but in most cases he would not. One bull recaptured a cow three times by grabbing her hind flipper as she made off. In some cases the cow escaped into the water, in other cases by moving into the herd or along the beach.

Bulls were seen to bypass what appeared to be eligible cows, going on to another seal before slowing down and beginning their characteristic approach. Cows with pups were rarely approached; those that were growled and threatened vigorously, and successfully discouraged the bull in all cases observed. Cows without pups occasionally succeeded in discouraging an approaching bull. A large cow lying near the water growled, snapped, and butted toward a bull for fully five minutes, the longest continuous sequence of seal invective observed, before the bull gave up and went to sea.

Aquatic breeding encounters were basically similar. A few bulls were seen cruising slowly about, occasionally approaching a particular seal. During the breeding season, proportionately many more seals were observed loafing offshore from a hauled-out herd than previously. Such seals were not traveling and were doing little diving. Some, especially mothers and pups, appeared to be sleeping. A very loose aggregation of perhaps 200 seals might be observed in the water on calm days near a large herd on the beach. Thus the likelihood of a bull finding a receptive cow at sea was increased considerably. Breeding encounters at sea were more vigorous due to the increased mobility of the seals. The same behavior pattern prevailed as on land; approach, rush and grab, fight, flight. Bulls were again observed to ignore some seals but to approach others.

Bulls are apparently aware of the nature of the typical breeding fights; on one occasion, while a bull was persistently grappling with a cow in the water, another bull approached rapidly. When bull #1 lost the cow momentarily, bull #2 immediately grabbed her, and the struggle continued. Bull #1 swam around the pair, biting at #2 as the opportunity arose. Finally the cow broke away and hauled out swiftly. Both bulls hauled out also, but neither approached the cow. Later the cow was collected, and found to be near ovulation.

Unfortunately, none of the breeding encounters observed were known to result in copulation. The commencement of

copulation was never observed; only pairs already copulating
were seen. However, I feel there is no doubt that events
described above were breeding encounters. The breeding at-
tempts of the bull appear to be pursued largely at random;
the bull does not seem to definitely know that a cow is
receptive. The bull's success in mating would then depend
on finding a receptive cow through continued trials. Bulls
were observed to attack several cows during their wanderings
about the beach or the water. If the cow is not receptive,
she is able to resist successfully, since she is usually
only slightly smaller than the bull, if at all.

During the course of observing a given herd, only a few
bulls were seen cruising about attacking cows. The rest of
the bulls in the herd were sleeping on the beach. At best
the incidence of encounters was quite low per unit time.

Although sexual fighting apparently is not a necessary
precursor to ovulation (Harrison, 1963, p.103), as it is
among the mustelids, fighting by the female should not be
surprising, since, as Tinbergen (1956) points out, mating
involves psychological elements of capture for the female and
"...mating behaviour therefore involves the suppression of
escape behaviour in the female." Histological evidence sup-
porting the behavioral data with respect to reproduction will
be discussed in the section on reproduction.

Play: Play in several forms occurred occasionally throughout
the period of observation (May through July). In most

instances play involved both males and females that were con-
sidered immature or possibly approaching maturity. Through-
out May and June most play observed involved one or more im-
mature seals rolling, biting, and chasing about the beach at
water's edge. Lone seals were observed on two occasions
playing with a blade of alga, tossing it about, rolling, and
snapping at it until it fell apart. On one occasion such
play was at sea, the other was ashore.

During the latter part of the pupping season, and into
the breeding season, both adult and immature seals were oc-
casionally seen playing in the water. Their play consisted
of lazily swimming and diving or submerging. Often the seal
would dive sideward instead of forward, at the same time
bringing the uppermost foreflipper around in a long arc, and
slapping the water with its flexor surface. The result was
similar to the alarm reaction of foreflipper slapping, but
the play action was much more deliberate, stronger, and
louder. When about half-way through the sideward dive, the
seal may swing its hindquarters beyond the axis of its dive,
slapping the water with its hind flippers just before sub-
merging. Such aquatic play was usually solitary, but fre-
quently was "parallel", involving more than one seal
(Bartholomew, 1952). Aquatic play involving rolling and
slapping behavior has been associated with breeding behavior
in harbor seals by Venables and Venables (1957).

On several occasions, play between two immature indi-
viduals at the water's edge consisted of chasing, playful
biting, rolling, and climbing on each other. Without having
observed normal breeding behavior, one might have interpreted
this play as preliminary breeding activity. While such play
may be a manifestation of "incipient sexual development"
(Carrick and Ingham, 1962), it would still be considered
play. It seems likely that this sort of play is analagous
to that which Venables and Venables (1955, 1957, 1959) ob-
served prior to pupping, and again in September when they
stated breeding began in Shetland. While such play may be
attributed to the approach of sexual maturity, pairs of males
or pairs of females were observed engaged in such play as
often as were mixed-sex pairs. The congeniality of this play
contrasted strongly with the aggressive encounters between
mature bulls and cows observed during the breeding season.
Vocalization: Vocalization in the harbor seal has been de-
scribed in detail by Scheffer and Slipp (1944). During this
study the most frequently used sound was some variation of a
guttural growl, most resembled in other circles by a sus-
tained, vigorous, and rather uncouth belch. A more conven-
tional growl or snarl might be used in conjunction with the
"belch". Bartholomew and Collias (1962) termed the threat
vocalization of the northern elephant seal cow a "belch-
roar". Its use by elephant seal cows was essentially the
same as that of its vocal counterpart among harbor seals,

i.e. disputes over haul-out position, defense of pup against
attack or disturbance, and toward yearlings, people, sea
lions, or other intruders. The elephant seal bull, however,
uses different threat sounds, but the harbor seal bull does
not, perhaps another indication of the less formalized social
organization of harbor seals.

When separated for some time from its mother, or de-
serted and alone, a pup's call was a hoarse "maaa-a", as
Scheffer and Slipp (1944) have noted. Deserted pups in
groups did not usually bleat unless they were removed from
the group. During the peak of pupping at Tugidak Island, and
at Aialik Bay, the bleating of pups was almost constant, and
was audible up to 2 miles on favorable days at Aialik Bay.
Attended pups were not observed bleating while with their
mothers. When approached on the beach, a pup would frequent-
ly snap at the intruder, and either growl or hiss as well.

Emission of underwater sounds by sea mammals has been
investigated in recent years. Poulter (1963) found that sea
lions, Zalophus californianus, when approaching food thrown
in the water, emitted sounds that were similar to sonar.
Schevill et al. (1963) found that Phoca vitulina concolor,
the American Atlantic subspecies, and P. v. largha emitted
low frequency impulses when nearing food used to decoy them.
The latter investigators felt that the impulses had about a
3 meter range.

Reproduction

The reproductive cycle and the corpus luteum: On the basis
of behavior and the specimens discussed below, the approxi-
mate timing of the main periods in the reproductive cycle may
be outlined as follows: Pupping,--4 May or slightly earlier
to 25 June; Nursing,--late May to mid-July; Ovulation and
mating,—late June to the end of July; Implantation,--late
August to late September. The evidence for this delay in
implantation is discussed starting on page 61.

The behavior of mature seals during the mating period
suggested that cows still nursing pups were not receptive to
mating and therefore were probably not close to being in
estrus. On comparable dates, mature cows which had no pups
were observed in breeding encounters with bulls.

No ripe follicles were found in the ovaries of ten lac-
tating cows collected from 29 May through 12 July. The larg-
est follicle found in the lactating cows measured 8.0 x 6.0
mm. The largest follicle found in a post-lactating cow meas-
ured 19 x 18 mm. From Table 1 it is apparent that follicles
were approaching ovulation in the ovary lacking a corpus
luteum of cows which had completed lactation or newly mature
cows. One newly mature cow was approaching ovulation on 9
July, and another had ovulated by 23 July, which suggests
that the timing of ovulation in mature, nulliparous cows cor-
responded roughly to the timing of ovulation in primiparous
and multiparous cows.

Table 1. Relationship of follicle development to reproductive status and the presence of the corpus luteum. N = number of ovaries; (1) number of follicles in ovaries lacking a corpus luteum; (2) number of follicles in ovaries containing a corpus luteum; (3) diameter in mm of largest follicles in ovaries lacking a corpus luteum; (4) diameter in mm of largest follicles in ovaries containing a corpus luteum.

Reproductive status of the seals	(1)			(2)			(3)			(4)		
	N	$\bar{X}$	S^2	N	$\bar{X}$	S^2	N	$\bar{X}$	S^2	N	$\bar{X}$	S^2
Late pregnancy	4	38	154.92	4	15	52.33	4	10.0	2.73	4	6.5	8.23
Lactating	10	39	168.18	10	29	49.34	10	7.0	0.82	10	5.0	2.12
Post-lactation	3	23	48.00	3	5	39.00	3	16.5	5.40	2	4.8	10.13
Post-ovulation	4	22	44.67	4	18	68.25	4	5.3	7.58	4	4.6	2.23
Early pregnancy	5	19	57.50	5	14	45.80	5	6.0	1.63	5	6.5	3.43
Immature	6	16	439.90				5	4.0	8.50			

Because some confusion of meaning may arise in terminology referring to the corpus luteum and corpus albicans, the terminology used in this study is defined as follows:

1. Pre-implantation corpus luteum; the corpus luteum from the time it is formed after ovulation to the time of implantation.

2. Corpus luteum of early pregnancy; the corpus luteum found in association with an embryo or other evidence of early pregnancy.

3. Corpus luteum of late pregnancy; the corpus luteum found in association with a term or near-term fetus.

4. Corpus luteum of lactation; the corpus luteum found in lactating females.

5. Corpus luteum of post-lactation; the corpus luteum found in females which had ceased lactating significantly. Milk occasionally could be found by making a deep incision in the mammaries. In this study, "post-lactation" also implies that ovulation has not yet taken place.

6. Corpus albicans; the corpus luteum is considered to be a corpus albicans after a new ovulation occurs, and a new corpus luteum begins to form.

The site of ovulation on the ovary's surface closes rapidly, but the follicular cavity requires some time to fill with the luteinized tissue of the membrana granulosa (Harrison, 1962). Infolding of the follicle walls after ovulation

and luteinization of the granulosa layer both aid in obliterating the follicular cavity. The pre-implantation corpus luteum appears loosely packed with luteal tissue, and may not become completely filled for some time.

The corpus luteum of early pregnancy is similar macroscopically to the pre-implantation corpus luteum, although some changes are evident. Both are a yellowish-tan color. Four of the five corpora lutea of early pregnancy found were compact appearing, but one corpus luteum was of a rather loose structure, with the remains of blood and fluid around the periphery and intruding into the body of the corpus luteum. Although the appearance of the loosely structured corpus luteum suggested a recent formation, it was associated with the largest embryo of a series collected in late October. In only one corpus luteum of early pregnancy was an unluteinized core found at the center. In the other corpora lutea of early pregnancy the characteristic white, connective tissue center (Fisher, 1954b) had formed in a position analogous to that previously occupied by the unluteinized core.

Organized vascularization was more noticeable in corpora lutea of early pregnancy than in younger corpora, but few other differences were grossly evident. The data in Table 2 show that there is some increase in the size of corpora lutea from the time of formation to early pregnancy.

A cow collected on 1 November apparently had failed to maintain pregnancy. There was no evidence of pregnancy in

Table 2. Relationship of size of the corpus luteum and reproductive status of the seal, and a summary of counts and measurements of corpora albicantia. N = number of structures; measurements in mm.

Reproductive status of the seals	Corpora lutea						Corpora albicantia					
	Length			Width			Length			Width		
	N	X̄	s^2	N	X̄	s^2	N	X̄	s^2	N	X̄	s^2
Late pregnancy	4	24.5	1.67	5	18.0	19.06	6	6.0	4.27	6	4.0	1.37
Lactating	10	16.5	14.32	10	13.0	17.29	10	7.0	2.99	10	3.0	1.60
Post-lactation	3	12.0	1.00	3	8.0	0.34	4	5.0	1.58	4	3.0	1.08
Post-ovulation	4	14.0	0.92	3	12.0	1.00	4	8.0	2.00	4	4.5	1.00
Early pregnancy	5	18.0	0.55	5	15.0	9.50	6	7.0	1.94	6	5.0	2.07
Early unsuccessful pregnancy	1	14.0		1	14.0		1	6.0		1	4.0	
Late unsuccessful pregnancy	0			0			3	6.7	0.33	3	4.5	1.75
Immature	0			0			0			0		

the uterus, and the corpus luteum was somewhat smaller than those of seals in early pregnancy, and was dark grey-brown, with a reddish cast due to extensive vascularization. McLaren (1958, p.50) illustrates a corpus luteum with the same characteristics, taken from a ringed seal which was not pregnant "...long after implantation time." Such a corpus luteum was probably regressing after the blastocyst or embryo died. It seems unlikely that the corpus would have developed to the size and compactness that it did, if it were not associated with a developing, fertilized egg (Amoroso and Finn, 1962).

Corpora lutea of seals collected in late pregnancy were very compact appearing, light yellowish-tan bodies occupying much of the volume of the ovary. The corpus luteum of specimen number 4-64 weighed 5.0 g, while the remainder of the ovary weighed 4 g. Vascularization was not so evident in corpora lutea of late pregnancy as it was in corpora lutea of early pregnancy, probably due to the increase in volume of the luteal tissue. The connective tissue elements did not appear to have developed as fully in corpora lutea of late pregnancy as they had in the corpora lutea of lactation, or in regressing corpora of later stages.

Harrison (1960, 1962) suggested that in harbor seals the corpus luteum reached its greatest size during lactation. The significance of the difference in mean lengths of corpora lutea of late pregnancy and corpora lutea of lactation was

tested, using the t test. The mean lengths as given in Table 2 were found to be significantly different at the 99 percent confidence level. The mean widths, however, were found to be significantly different at the 94 percent confidence level, although the calculated value of t (2.153) was close to the tabular value of t (2.179). On the basis of the small sample in this study, however, it seems likely that corpora lutea attain their greatest size in late pregnancy.

Fisher (1954a) has noted that the corpus luteum begins to display microscopic signs of retrogression in late pregnancy, although it appears functional macroscopically. However, Harrison (1960) states that the corpus luteum of the harbor seal shows signs of post-parturient rejuvenation, but that degeneration starts 1 week after parturition, and by 6 weeks after partuition the corpus luteum has become a corpus albicans.

The variation in appearance among corpora lutea collected from lactating cows was related to the time which had elapsed since parturition. Thus the corpus luteum of specimen number 8-64 appeared analogous to corpora lutea of late pregnancy, and the condition of the placental scar indicated that the seal had pupped quite recently. Lactating seals considered to have pupped earlier with respect to the collection date on the basis of uterine contraction and healing, had correspondingly smaller corpora lutea, and the connective tissue network in the corpora lutea was more prominent. The

trends of diminishing size of the corpora lutea and an increase in the amount of connective tissue found in the corpora continued through the post-lactation phase.

One mature seal collected during the pupping season (29 May) was not pregnant, nor did it appear to have pupped in the current season. Neither a corpus luteum nor large follicles were found in the ovary. However, a corpus albicans 7 x 6 mm in size was found, suggesting that fertilization had occurred in the previous breeding season, sometime after which the conceptus died.

Because of the protracted periods of pupping, lactating, and mating, it is difficult to give meaningful inclusive dates for the various periods of reproductive activity. Seals were known to have pupped as early as 5 May, and females in late pregnancy were collected on 25 May and 22 June. Lactating cows were collected on several dates from 29 May through 12 July. Those seals past lactation and approaching ovulation were collected from 7 July through 12 July. Seals which had ovulated and had developing corpora lutea were collected from 8 July through 6 August. The height of pupping was considered to be about 11 June, and ceased about 25 June. The proportion of attended pups was declining noticeably by 12 July, but much of the pup crop had been harvested by the time weaned pups became evident. I estimated that lactation lasted 3 to 4 weeks. Harrison (1963) estimated the lactation period of P. v. vitulina as 4 to 6 weeks, based on

observations of captive seals. He also suggested that ovulation occurs 2 to 4 weeks after lactation ends. While the information from the present study is not conclusive, it seems likely that the majority of seals had entered estrus by the end of July, which suggests that little more than 2 weeks elapsed between the end of lactation and the onset of estrus. However, I collected relatively few seals in August and a larger sample may alter this view.

On the basis of the specimens examined, I concluded that the female normally bears a pup each year, as Harrison (1963) concluded was the case in P. v. vitulina. In 92 percent of the multiparous females collected evidence was found of either two successive pregnancies, or of two successive annual ovulations. The evidence for annual ovulation or annual ovulation and pregnancy consisted of some combination of a corpus luteum, a ripe follicle, a corpus albicans, and a placental scar or a fetus. One of the two exceptions, a 13-year-old cow, had pupped in the current season and was lactating, but a corpus albicans was not found, and ovulation was not imminent since lactation was not completed. A placental scar resulting from parturition in June becomes quite indistinct as early as August, and therefore placental scars are of little value in determining the number of pregnancies an animal has experienced.

No more than one ripe follicle or one new corpus luteum was observed in the ovaries of any mature seal. On the basis

of corpora lutea and follicles observed, it was concluded
that normally only one follicle reaches ovulatory condition
each year.

The corpus albicans: The transition from a late corpus
luteum of lactation to a corpus albicans has little effect on
the macroscopic appearance of the corpus. Vascular elements
have already disappeared, and the fibrous network increases
in development as the corpus albicans grows older.

The corpus luteum continues to diminish in size through
the post-lactation period before becoming a corpus albicans
after ovulation, when it seems to regress rapidly. Three
corpora lutea of post-lactation averaged 12.0 x 8.0 mm in
cross-section, while three corpora albicantia which were con-
sidered to have been the corpora lutea of the most recently
past pregnancy averaged 8.5 x 4.5 mm.

Visible corpora albicantia all had the characteristic
white, stellate, connective tissue pattern to some degree.
The corpus albicans is a dull orange color initially, and it
may retain this color for as long as it persists. Some cor-
pora, however, fade to a pale straw color which blends with
the body of the ovary. There does not seem to be a consist-
ent relationship between estimated age of the corpus and its
color or size, except that new corpora albicantia are usually
larger than those several months or more old.

In the ovaries examined, alternate ovulation between
ovaries in successive breeding seasons was the usual

situation. The ripe follicle of the current season was not observed to develop in the ovary containing the currently active corpus luteum. However, in five mature seals where a corpus luteum and one or more corpus albicantia were found, two corpora albicantia were found in one ovary and none in the second ovary, or a corpus luteum and a corpus albicans were found in the same ovary. Thus of 25 seals in which the pattern of ovulation could be assessed, five, or 20 percent, had evidence of having ovulated twice in succession from the same ovary. Fisher (1954b) found that alternate ovulation was generally the case in the harp seal but that exceptions occurred; he also observed the same phenomenon among harbor seals.

Rapid regression of the corpora albicantia precluded obtaining an accurate estimate of past reproductive performance. Table 3 shows the number of corpora albicantia found in seals of each age group. The numbers of corpora albicantia which would be expected if maturity occurred at 4 years of age, and at 3 years of age, and assuming that pregnancy was annual, are also included. All the seals represented in Table 3 were mature. After ovulation, a new corpus luteum forms, and the previous corpus luteum is then considered a corpus albicans. Thus a 5-year-old seal which first bred at 4 years of age would not have a corpus albicans, but at about 5 years and 2 months of age, or after ovulation, a corpus albicans would be present.

Table 3. Numbers of corpora albicantia observed and numbers
          expected if corpora albicantia were persistent.
          N = number of seals.

Age[1]	N	Obs.	Exp. (2)	Exp. (3)
4	2	0	0	0
4+	3	1	0	3
5	4	1	0	3
5+	2	3	2	4
6+	1	1	2	3
7	2	2	4	6
7+	1	1	3	4
8+	2	3	8	10
11	1	1	6	7
11+	1	1	7	8
12	1	2	7	8
13	1	0	8	9
15	1	0	10	11
17	2	4	24	26
18	1	1	13	14
18+	1	1	14	15
21	1	1	16	17
22	2	4	34	36
26	1	2	22	23
28	1	4	23	24
Totals	31	33	203	231

(1) 4+, 5+, etc. indicate that both the birthday and ovula-
    tion have passed.

(2) Assuming maturity at 4 years of age and annual pregnancy.

(3) Assuming maturity at 3 years of age and annual pregnancy.

Average observed corpora albicantia per seal   = 1.06
   "   expected   "   "   "   " (2) = 6.5
   "   "   "   "   "   " (3) = 7.5

Percent of the expected corpora albicantia
          which were actually found: (2) = 16.3
                                       (3) = 14.3

All seals in their fourth year were mature at the time
of collection. Number 20-63, one of the 4-year-olds, was
nursing a pup at the time of collection, indicating that she
had mated at 3 years of age. Of the three seals just over 4
years old, one had become mature at 3 years of age. In the
5-year-old age group, one seal had matured at 3 years of age,
while the other three seals had matured at 4 years of age.
One of the seals just over 5 years old had matured at 3 years
of age, since it had two corpora albicantia, while the other
seal apparently matured at 4 years of age, or possibly one
corpus albicans had regressed completely. Of the 11 seals in
age groups 4 through 5+, five had matured at 3 years of age.
In older seals, determining the age at maturity is more dif-
ficult. The one seal in age group 6+ may have matured at 5
years of age, as the lone corpus albicans indicates. How-
ever, it is evident that in the older age groups, corpora
albicantia are not accumulating as one would expect if the
corpora were persistent for several years. An average of
about one corpus albicans is found in each adult female seal.

The data suggest that corpora albicantia most frequently
persist about 1 year, but may persist less than 1 year, or up
to 2 years. In seals over 20 years old, the proportion of
corpora albicantia that persist longer than one year rises
somewhat. Laws (1953b) felt that corpora lutea were com-
pletely resorbed within a year in most southern elephant
seals. Fisher (1954b) found that in the harp seal all the

corpora albicantia persisted up to about 10 years of age, or as much as 5 years after maturity. Thereafter one corpus albicantia was lost and one gained each year; however, corpora albicantia appeared to accumulate somewhat in seals over 20 years old.

An examination of the ovaries of eight 2-year-old seals and two 3-year-old seals showed that all were immature.

In most studies of pinnipeds the authors seem to assume that those corpora albicantia observed in the ovaries were associated with pregnancy. Laws (1953b, p.25) states that "missed" pregnancies are not represented by persistent corpora albicantia, but he does not discuss the evidence for this conclusion. Maximow and Bloom (1957, p.513) note that in the human the corpus luteum of pregnancy is larger and persists longer before becoming a corpus albicans than does a corpus luteum of menstruation. They also state that the scar resulting from a corpus luteum of pregnancy is larger and persists longer than the scar of a corpus luteum of menstruation. Amoroso and Finn (1962, p.454) noted that in most animals corpora lutea of non-pregnant cycles do not persist as long as corpora lutea of pregnancy, but that exceptions to this generalization are known.

In the present study I have assumed that corpora albicantia resulting from pregnancies persist longer than corpora albicantia of non-pregnant cycles. The evidence found in this study indicates that corpora albicantia most frequently

regress within about a year; if differential regression
occurs, it would seem that the large, well developed corpus
luteum of pregnancy would require more time to become com-
pletely resorbed than a smaller corpus luteum of non-
pregnancy. While a corpus luteum known to be associated with
a non-pregnant cycle was not found, the smaller size and ab-
normal appearance of the corpus luteum associated with early
prenatal death of the conceptus in one seal suggests that a
corpus luteum of a non-pregnant cycle would be resorbed in
much less than a year.

In Table 4 the weights of ovaries from immature seals are
grouped by age. Harrison (1960) showed that gonads of harbor
seal fetuses were precociously enlarged and these data re-
flect the same condition. After a marked decline in weight
following birth, ovary weights increase as the seal approaches
sexual maturity.

Table 4. Ovary weights of immature seals. N =
number of ovaries; (1) = term fetuses
and newborn pups; weight in g.

Age	N	$\bar{x}$	s^2	Range
0 mo [1]	6	5.0	0.17	5.5 - 4.5
1 mo	90	2.0	0.92	5.0 - 1.0
1 mo	26	1.0	0.05	1.5 - 0.5
5.5 mo	28	0.5	0.06	1.0 - 0.5
1 yr	4	1.0	0.00	1.0
1.5 yr	10	0.5	0.07	1.0 - 0.3
2 yr	9	1.5	0.97	3.5 - 1.0
3 yr	2	3.0	0.00	3.0

After sexual maturity is reached the reproductive status
of the seal strongly affects ovary weight. The data in Table
5 shows that the ovary containing a corpus luteum is consist-
ently heavier than the opposite ovary, except after lactation
has ceased. At that time the ovary containing a maturing
follicle becomes heavier, while the ovary containing a re-
gressing corpus luteum is losing weight.

Table 5. Influence of the development of corpora
lutea and follicles upon ovary weight.
N = number of ovaries; weight in g.

Reproductive status of the seals	Wt. of ovaries with a corpus luteum			Wt. of ovaries without a corpus luteum		
	N	$\bar{X}$	s^2	N	$\bar{X}$	s^2
Post-ovulation	3	4.5	2.25	3	3.5	1.00
Early pregnancy	4	5.5	2.56	4	3.5	1.00
Late pregnancy	4	10.0	9.89	4	7.5	1.23
Lactation	10	7.0	2.61	10	6.0	2.34
Post-lactation*	4	4.0	2.42	4	7.0	0.25

* Period of follicle maturation.

Although age of the seal may affect ovary weight, the
data are too limited to assess the relative influence of re-
productive status and age. I feel that the reproductive
status affects ovary weight more strongly than age. Ovary
weights appeared to be lower in animals 20 years old or more,
but a larger sample is needed to assess this possibility.

Maturity and breeding condition in the male: The presence of
numerous mature sperm in the epididymis was considered to in-
dicate that a male seal was in breeding condition. If no
sperm or very few sperm were observed, the seal was consid-
ered to be immature, or collected at a time of limited sper-
matogenic activity. Table 6 gives the testes weights of
seals considered to be immature. Sperm were not found in the
epididymes of 2-, 3-, and 5-year-old seals. No 4-year-old
males were collected. The 5-year-old male was collected on
28 October. Sperm were found in the epididymes of seals 6
years old or more that were collected from 25 May through 15
August, but few or no sperm were found in the epididymal
smears from seals 5 years old or older collected in late

Table 6. Age and testes weights of immature seals.
N = No. of testes; weight in g.

Age	N	X	s^2
Newborn or term	4	2.0	0.3
< 1 mo	105	1.5	0.1
1 mo	10	1.5	0.2
5.5 mo	21	1.0	0.1
1 yr	19	1.5	0.2
1.5 yr	8	1.5	0.1
2 yr	6	3.0	0.3
3 yr	4	3.5	0.2

October. The markedly lower testes weights of seals collect-
ed in the fall, as shown by Tables 7 and 8, probably reflect
a decline in spermatogenic activity. Backhouse and Hewer
(1964) note that testis weight and testis tubule diameter are
good indicators of spermatogenic activity. The earliest age
of maturity cannot be assessed from the data due to the lack
of 4- and 5-year-old seals collected during the breeding
season. However, it is apparent that male harbor seals are
normally capable of breeding when they are 6 years old, and
it is suggested that they may breed by 5 years of age.

The earliest date that males produce mature sperm is not
known, since no collecting was done in early May. The fact
that sperm were found in males collected in late May and in
June indicates that the males are physiologically capable of
breeding well before most females are approaching ovulation.
Observations of mating behavior support this view.

Numerous sperm were found in the epididymis of a 7-year-
old male collected on 15 August, but the testis weighed only
19 g, which suggests that the peak of spermatogenic activity
had passed. It was suggested earlier that the peak of mating
activity has passed by the end of July on the basis of mating
behavior observed, and the condition of ovaries examined.
Incidence of pregnancy: Six mature cows were taken in late
October and early November, 1963. Four of the six cows were
supporting healthy embryos. A fifth cow had been in early
pregnancy; the uterus was swollen and remnants of the

Table 7. Age and testes weights of seals in breeding condition. N = number of testes; weight in g.

Age	N	$\bar{X}$	s^2	Range of dates
6 yr	6	39.0	78.6	22 Jun - 8 Jul
7 yr	3	22.0	9.1	9 Jul - 15 Aug
9 yr	2	46.0	1.1	24 Jun
10 yr	2	31.0	1.1	25 May
11 yr	2	42.0	1.1	21 Jun
12 yr	2	37.0	10.1	24 Jun
17 yr	4	31.0	2.7	24 Jun - 23 Jul
19 yr	2	43.5	0.0	25 May
25 yr	1	27.0		9 Jul

Table 8. Age and testes weights of mature seals in non-breeding condition. N = number of testes; weight in g.

Age	N	$\bar{X}$	s^2	Range of dates
5 yr	2	6.5	0.0	28 Oct
6 yr	2	15.0	0.1	29 Oct*
9 yr	2	15.5	2.0	30 Oct*
18 yr	2	8.5	0.0	28 Oct

* One sperm found in epididymal smear.

placental membranes were present, but no embryo was found.
Over a day had elapsed between collection and examination,
and the embryo may have disintegrated in that time. It may
be that resorption was under way at the time of collection,
because a cow supporting one of the healthy embryos was not
examined until over a day after collection.

The sixth cow collected apparently was not supporting an
embryo, and the corpus luteum appeared to be regressing. It
is suggested that fertilization occurred in this seal,and the
normal development of the corpus luteum proceeded, but that
for some reason the conceptus died before or soon after
implantation.

Implantation and prenatal growth: Delayed implantation is
common and may be the rule among pinnipeds (Scheffer, 1958).
Fisher (1954a) showed that implantation occurred about 11
weeks after copulation in P. v. concolor. Harrison (1960,
1963) estimated that 2 to 3 months delay in implantation
occurred in P. v. vitulina.

In this study four embryos ranging from 11 to 44 mm in
crown-rump length were collected from 28 October through 1
November. The ages of the embryos and the time of implanta-
tion were estimated in two ways. First a curve representing
proportionate growth of human embryos was drawn using data
given by Arey (1954). The length of an embryo is represented
as a proportion of the length of the fetus at term, and the
age of the embryo is represented as a proportion of the total

gestation time. Sergeant (1962) and McLaren (1958) assumed that the prenatal growth pattern is similar among large mammals with gestation periods of similar duration. Sergeant (1962) used the curve, described above, to estimate the gestation period of the pilot whale, Globiocephala melaena. McLaren (1958) estimated the ages of ringed seal embryos on the basis of proportionate growth as expressed by a similar curve based on the human data given by Arey (1954).

The second method consisted of estimating the time of peak mating activity on Tugidak Island and adding the estimated delay in implantation given by Fisher (1954a) and Harrison (1960).

A curve representing the proportionate growth of human embryos was constructed, and part of it is reproduced in Fig. 3. The total lengths of seal embryos collected, expressed as proportions of the average total length of newborn pups and term fetuses, were found on the curve, and the proportion of gestation time elapsed was read from the time scale. June 11 was taken as the expected birthdate on the basis of observations of pupping activity at Tugidak Island. The resulting data and calculations are given in Table 9.

The crown-rump lengths of the seal embryos examined correspond closely to the crown-rump lengths of human embryos of similar development, as Table 9 shows. However, crown-rump length of the seal embryos was not used in the calculations, since it could not be expressed directly as a proportion of
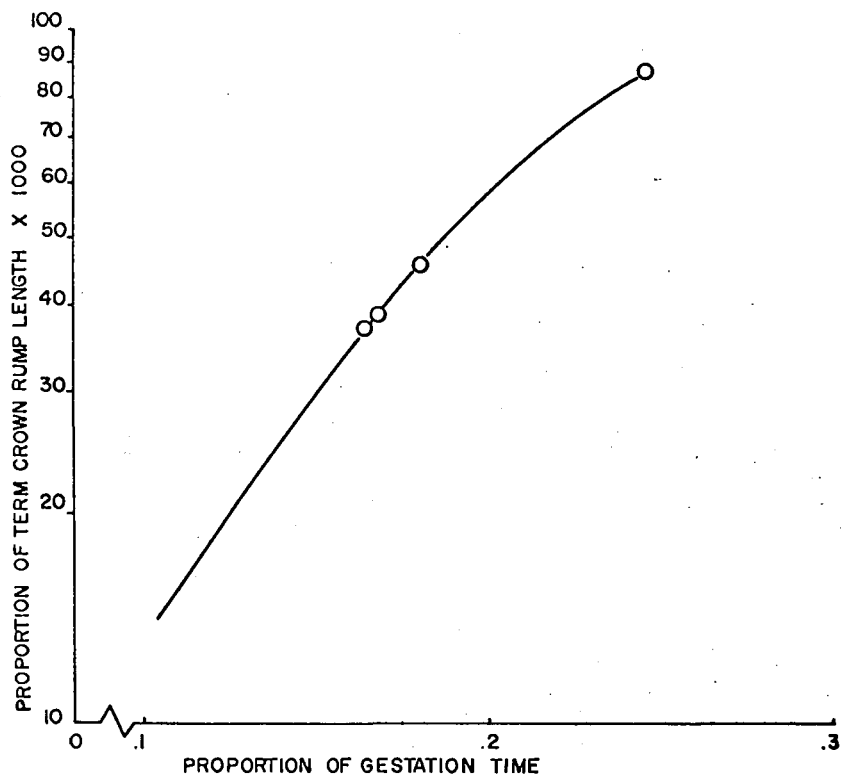
Fig. 3. Proportionate age of seal embryos.

Table 9. Calculation of embryo ages and gestation period. CRL = crown-rump length; ATL = approximate total length; PTL = proportion of term total length; PGE = proportion of gestation elapsed; PGR = proportion of gestation remaining; GR = gestation remaining; TCG = total calculated gestation; CEA = calculated embryo age; HE = age and crown-rump length of human embryos of equivalent development; AA = approximate age based on McLaren's (1958) data for ringed seal embryos.

Date Collected	CRL (mm)	ATL (mm)	PTL (x 1000)	PGE	PGR	GR* (days)	TCG (days)	CEA** (wks)	HE*** Age (wks)	HE*** Length (mm)	AA (wks)
1 Nov	11.	29.	37	.165	.835	222	266	6.5	6	12	≤6
29 Oct	12.	31.	39	.17	.83	225	271	6.5	6+	12+	6
28 Oct	17.	36.	46	.18	.82	226	276	7	7+	17+	6+
29 Oct	44.	69.	88	.25	.75	225	300	10	11+	≤56	8+
Term	785.	1000	1.								

* Average birthdate is considered to be 11 June.
   The average gestation period of the three smallest embryos (271 days) was multiplied by the proportion of gestation elapsed for each embryo.
** The morphological development of each seal embryo was compared with criteria and data from human embryos given by Arey (1954, p.106).

the average total length of newborn pups and term fetuses.
Total length of the embryo was measured along the side of the
embryo, following the vertebral column. That the calculated
ages of the seal embryos are very close to equivalent devel-
opmental ages of human embryos suggests that the early em-
bryonic development of harbor seals and humans is very simi-
lar, and that the embryonic growth curve for humans gives a
good approximation for at least early embryonic growth of
harbor seals.

The mean calculated gestation period of the three smal-
ler embryos is 271 days. The calculated gestation period of
the largest embryo was not included in calculating the mean
gestation period since it was obvious that the embryo was
notably advanced developmentally compared to the three smal-
ler embryos. If the smaller embryos are considered to be
about 6 to 7 weeks old, implantation must have occurred from
9 September through 16 September. The oldest embryo would
have implanted 3 weeks or more earlier, or near the beginning
of the fourth week of August.

A comparison of the calculated ages of harbor seal em-
bryos with the calculated age values given by McLaren (1958)
for ringed seal embryos (Table 9) suggests that harbor seals
are somewhat slower in development, and this may be related
to the longer period of gestation and larger size at birth
in the harbor seal. McLaren gives the gestation period of
ringed seals as about 240 days.

If the rate of early development of harbor seals and
humans is similar, it suggests that the rate of later pre-
natal development is dissimilar, since the harbor seal is much
larger at birth than the human. This in turn suggests that
the growth curve of human development may not be applicable
to harbor seals in later development, but without fetuses
this suggestion can not be verified.

On the basis of behavioral data, it was estimated that
the majority of pups should have been weaned by 12 July or
somewhat earlier, and that about two weeks intervened between
weaning and fertilization. If implantation is delayed for 8
to 12 weeks, then few implantations could be expected before
the end of September. Fisher (1954a) first found evidence of
implantation about 20 September in New Brunswick and Nova
Scotia harbor seals.

The progress of weaning was most difficult to observe at
Tugidak Island because of the intensive hunting, and it may
be that the normal peak of weaning occurs early in July
rather than toward the middle of the month. If so, the cal-
culated implantation times and the conclusions from behav-
ioral data and the time of delay of implantation would be
within a week or two. On the basis of the available data, I
suggest that implantation may occur from late August to the
last of September.

Age Determination

Background and assumptions: Age determination of pinnipeds
has been attempted using various criteria, including color
and appearance, body size, closing of sutures of the skull,
annuli on claws, ovarian structures, lamination of bones, and
growth layers of teeth. Examination of growth layers or in-
crements in the teeth is usually most satisfactory (Laws,
1962), and has become widely used since their correlation
with age was first established in the northern fur seal,
Callorhinus ursinus, by Scheffer (1950), and in the southern
elephant seal, Mirounga leonina, by Laws (1952). Growth
layers in teeth have been found in seven otarids, the
walrus, Odobenus rosmarus, and ten phocids (Laws, 1962).

The utility of evidence of growth increments in teeth
for age determination depends upon a regular seasonal or
annual pattern of variation in the quality and quantity of
dentine and cementum deposition, which results in contrast-
ing optical quality and width of the layers deposited. The
pattern of dentine and cementum deposition for each year is
essentially duplicated, although there is some variation
(Carrick and Ingham, 1962). Growth layers in the teeth may
thus yield discrete age data, in contrast to most other
measurable age-related characteristics.

Growth layers have previously been found in harbor seal
teeth. Laws (1953a) found growth layers in the dentine of
several phocids, including P. vitulina. Scheffer (1950)

considered the external growth ridges which he found on the canine tooth of an adult female harbor seal to be analagous to the growth ridges he found on the canine teeth of fur seals. Mansfield and Fisher (1960) estimated the age of a captive harbor seal known to be 19.5 years old at 18 to 20 years, on the basis of cementum layers, and concluded that the layers were deposited annually. However, Laws (1962) observed that the growth rings in the dentine of harbor seal teeth were indistinct, and Sergeant (1962) stated that growth rings were rarely found in the dentine of the harbor seal. In comparing the tooth structure of the harp seal, Phoca groenlandica, with that of the harbor seal, Fisher (1954b) noted that annuli of the harbor seal were faint, ill-defined and irregular.

Known-age seals were not available for this study, therefore other data were used to aid in interpreting the pattern of dentine and cementum deposition. From observation it was known that the main period of pupping was the first two weeks of June, with the greatest number of pups being seen about 13 June. The peak of pupping activity is somewhat arbitrarily considered to be 11 June. Pups were born from about 5 May through 26 June. Essentially all pups born before 15 May were deserted and ultimately died. By using 11 June as an arbitrary birth date, an error of no more than two to three weeks is introduced. For example, pups taken in late October were considered to be about 5.5 months old.

Total length of the seal, total tooth length, and diame-
ter of the pulp cavity opening at the root were considered in
interpreting the pattern of dentine and cementum deposition
with respect to age.

On the basis of Mansfield and Fisher's (1960) results,
the cementum layers were assumed to be annual depositions.
Up to two years this assumption could be verified by observ-
ing the correlation between dentine pattern, closure of the
pulp cavity opening, total tooth length, and total length of
the seal. Beyond 2 years, it was necessary to assume that
cementum layers continued to be annual in nature. During the
first year, a "double band" of cement is deposited, which
will be discussed later. The pattern of dentine deposition
found in the second year appeared the same as in two succes-
sive years and the assumption was made that these later bands
were annual in nature.

General structure of the canine tooth: In the harbor seal
the milk dentition is resorbed before birth. Laws (1962)
reports this to be the case among most phocids. In one term
fetus, I found very small bits of tooth material slightly im-
bedded in the gum tissue over the unerupted permanent carnas-
sial teeth. At birth the permanent dentition has not normal-
ly erupted although the crowns lie near the surface of the
gum tissue and seem to break through within a few days.

The enamel crown is 10 to 12 mm long, and about 0.25 mm
thick near the tip of the crown, tapering gradually to its

lower margin. The entire tooth is 17 to 20 mm long, thus the enamel covers roughly two-thirds of the tooth at birth. The fetal dentine is about 0.75 mm thick near the tip of the crown, and tapers to a thin, soft edge at the base of the tooth. The opening of the pulp cavity in the canine teeth of three newborn seals ranged from 7.6 to 8.6 mm long, and 4.6 to 5.7 mm wide. The sagittal axis of the tooth curves strongly to the labial side. As the tooth grows, the effect is accentuated as the crown is pushed outward. The axis of the root however, curves lingually. Thus a tooth approaching the limit of its length is very crooked, until cementum fills and smooths the contours as it is deposited in layers around the outside of the root of the tooth.

Dentine development: Fig. 4, a photomicrograph of the cross-section of the canine tooth of a harbor seal, illustrates the dentine with several layers labelled according to the event or time they represent. The reader may find it helpful to refer to this figure during the ensuing discussion.

Viewed using transmitted light, the fetal dentine is a uniform color which may appear white, cream colored, or gray, depending on the thickness of the section and the angle of illumination. Within this area laminations terminated by fine, dark lines are evident. Two slightly darker lines which divide the fetal dentine into three approximately equal bands are frequently evident. The significance of these dark lines in the development of fetal dentine is not known. The
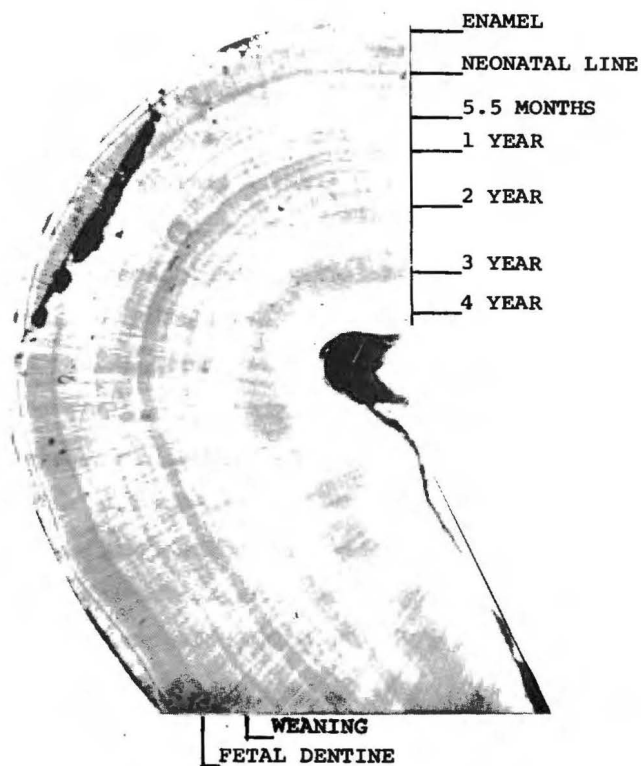
Fig. 4. Cross section of the tooth of an adult harbor seal.

fetal dentine is bounded at the pulp cavity by the neonatal line, which is considered to be the result of a discontinuity of growth at birth (Laws, 1962).

The neonatal line may be evident as a clear line with perpendicularly transmitted light, or as a dark line with oblique transmitted light. In teeth of newborn or nursing pups, the neonatal line is not always obvious, apparently due to its position at the edge of the dentine where light transmission is poor. The neonatal line also may be partially removed by grinding, which tends to affect the inner and outer edges of the section more than the area between.

During the nursing period, additional increments of dentine are laid down. In the section shown in Fig. 4 six layers are evident, each terminated by a dark border. However, the number of layers evident varied among the teeth examined. The last layer is terminated by the weaning line, a broader dark line, which is considered to be a result of a second discontinuity in growth (Laws, 1962). An analagous line has been found in the crabeater seal, Lobodon carcinophagus, by Laws (1962), the southern elephant seal (Carrick and Ingham, 1962), probably in the ringed seal (McLaren, 1958), and other seals. Observing the weaning line in a tooth collected at the time it is laid down is subject to the same difficulties as those described for the neonatal line. In older teeth the line is more obvious. Its position in the dentine of older teeth with respect to subsequent deposition corresponds to

the time of weaning.

Few pups were collected between the weaning time in
early July and the last week of October, when pup seals were
about 5.5 months old. By late October a series of five to
six bands consisting of light layers bounded by dark borders
was nearing completion. The layers deposited between weaning
and late October are thicker than previous layers, and the
dark boundaries are broader than those of earlier increments.
This series of bands is terminated by a very dark, distinct
line. In some pups this "5.5 month line" had not been de-
posited by the time they were collected in late October. In
one pup, two to three lighter bands had been deposited in
addition to the 5.5 month line. Variation in the extent of
dentine deposition may reflect differences in birth dates,
individual variation in the rate of development, or both.
The physiological significance of the dark terminal band de-
posited late in October is not known. A photograph in Laws'
(1962) paper of the tooth section from a one-year-old crab-
eater seal shows a dark line in the same relative position,
which Laws states is the limit of dentine at six months of
age.

In the harbor seal, the dentine laid down during the re-
mainder of the year consists of two light bands divided by a
dark line similar to the 5.5 month line. The first light
band consists of eight to ten laminations. The thin, dis-
tinct, dark line then occurs, followed by the second light

band, which in the section shown consists of nine layers.

The broad, dark band which follows represents the beginning of second-year deposition, and contrasts strongly with the first year dentine. A band of dark dentine consisting of three to four laminations has begun to form by the beginning of the second year. The remainder of the dentine is lighter, but with two dark lines dividing the entire second-year layer roughly into thirds. The laminations in the second-year band are wider than most of the first-year laminations.

In seven of the 11 two-year-old seals, the pulp cavity had closed at the root but was still open inside. On the basis of dentine deposition alone, it became more difficult to estimate ages in teeth of animals over two years old, since the rate of deposition after closure was unknown. The age was then estimated on the basis of cementum layers, and the pattern of dentine deposition beyond the two-year-old band was equated to cementum age. It became evident that the initial dark band found in the second-year layer was repeated in additional dentine depositions up to 4 years. The end of the fourth-year dentine is frequently hard to determine, but seems to correspond to the beginning of very translucent dentine.

Laminations in the third- and fourth-year dentine vary, and it is difficult to correlate their occurence with known seasonal physiological events. The third-year band is rather narrow, but the fourth-year band appears wider. Dentine

deposition beyond what is considered the fourth-year band is quite clear and appears more translucent than any previous deposition. This clear dentine seems to be deposited as a continuous band around the margin of the pulp cavity, but as the pulp cavity fills and becomes irregular, the dentine increments become discontinuous and simply fill the available space.

Assuming that each clear band beyond the fourth-year dentine represents a year's deposition, the total count of dentine layers in older teeth often approaches that of the cement layers, although in several cases the pulp cavity was essentially filled and "dentine age" was 12, but cementum age was much older. At best the clear dentine increments deposited beyond 4 to 5 years of age are difficult to define, and probably are not sufficiently reliable to use alone in accurately assessing age. It does appear that clear dentine increments are basically annual deposits, however.

Cementum development: Cementum is deposited in layers on the surface of the root. Cementum layers appear to consist of a light area with a dark outer border when viewed with transmitted light. A very thin band of cement was evident in the area between the end of the fetal dentine and the end of the root on teeth from larger and probably older pups in the 5.5-month-old class. However, no cementum deposition had taken place in most pups collected in late October. At 1 year of age a complete band of cementum is deposited. The first

year's band extends around the root, and up the tooth well
beyond the end of the fetal dentine. The cement layer is
very narrow in the upper part, on the order of 0.01 mm, but
near the root widens to about 0.25 mm. The narrow band de-
posited by the 5.5-month-old pup is still evident at 1 year
of age, but it seems to lose its identity in very old seals.
Since the narrow "5.5-month band" of cement does not extend
above the end of the fetal dentine, a cross-section above
this area excludes the "double band" effect, but includes the
first-year band of cementum. With experience the "double
band" can be recognized in a cross-section and evaluated pro-
perly as part of the first year's cementum. Later layers re-
semble the first layer, but no "double band" effect occurs,
and they do seem to differ structurally. In longitudinal
sections the first-year cementum is quite obvious, and is oc-
casionally set off by unusually clear borders.

It has been mentioned that in harbor seals up to two
years of age the annual nature of cementum layers can be
verified, and it seems reasonable to concur with the preva-
lent opinion that cementum layers are annual deposits.

The structure of cement varies with its position on the
tooth. On the inside curve of the tooth, the cement is
usually deposited in broader layers with darker borders and
with more large cementoblasts evident. On the outside curve
the cement is usually much more compact, with few cemento-
blasts, and narrow, dark borders. Cementum layers near the

base of the root, i.e. below a line which would include the
fetal dentine, are very broad, frequently irregular, and in-
clude many cementoblasts. As a result, cement layers in
that area sometimes are not clear. If possible it seems
preferable to examine a section that includes the fetal den-
tine, where the layers are narrower and better defined.

In Fig. 5 a longitudinal tooth section showing the
cementum is illustrated. The cementum layers are of the
broad type found on the lower part of the tooth, but in this
case the layers are well defined.

The layers of cement deposited become pregressively
narrower with age, as Hewer (1964) has noted in the grey
seal, <u>Halichoerus grypus</u>, although variations occur. In old-
er seals, cement accretion frequently has reached the edge of
the enamel cap. Hewer (1964) has found that in the grey seal
cementum layers are most accurately observed and compared in
the area just below the end of the fetal dentine, using sag-
ittal sections. In this study cementum layers were best ob-
served just above the end of the fetal dentine, using cross-
sections. By comparing cross-sections and sagittal sections,
it was found that no layers were being overlooked in the
cross-section, and the layers were usually much better
defined.

<u>Discussion</u>: The relationship of total tooth length and di-
ameter of the pulp cavity opening to age as determined from
dentine and cementum layers is shown in Tables 10a and 10b.
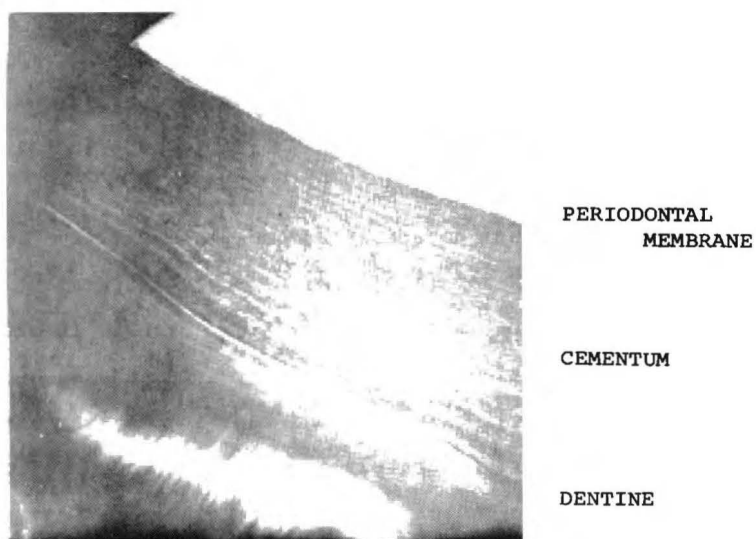
Fig. 5. Longitudinal section of the canine tooth of a 17-year-old harbor seal.

Table 10a. Measurements of the canine tooth of male harbor
seals in relation to age. Measurements in mm;
N = number of teeth measured.

Age	Total tooth length			Dia. pulp opening at the root		
	N	X̄	s^2	N	X̄	s^2
0 mo	1	18.2		1	8.6	
<1 mo	4	20.2	43.43	4	8.7	1.52
1 mo	7	24.4	4.50	5	6.7	0.84
5.5 mo	10	28.0	5.13	10	4.7	0.53
1 yr	10	31.2	1.90	9	2.6	0.35
1.5 yr	3	30.9	4.57	3	2.2	0.94
2 yr	4	30.8	9.66	(1	1.5)	
				(3	closed)	
3 yr	3	33.4	0.28	3	closed	
5 yr	1	33.0		1	closed	
6 yr	5	35.2	2.29	5	closed	
7 yr	2	34.3	0.50	2	closed	
9 yr	1	33.8		1	closed	
10 yr	1	32.9		1	closed	
11 yr	1	32.5		1	closed	
12 yr	1	29.3		1	closed	
17 yr	2	27.5	72.00	2	closed	
18 yr	1	31.2		1	closed	
19 yr	1	35.0		1	closed	
25 yr	1	33.1		1	closed	

Table 10b. Measurements of the canine tooth of female harbor
            seals in relation to age. Measurements in mm;
            N = number of teeth measured.

Age	Total tooth length			Dia. pulp opening at the root		
	N	$\overline{X}$	S^2	N	$\overline{X}$	S^2
0 mo	2	18.3	3.13	2	7.7	0.02
<1 mo	1	20.3		1	7.2	
1 mo	12	22.1	1.94	5	6.8	0.54
5.5 mo	18	26.1	3.17	17	4.2	0.43
1 yr	4	29.3	2.97	4	3.8	0.40
1.5 yr	5	30.8	5.94	5	1.7	0.50
2 yr	8	30.3	1.85	3	1.0	0.16
				4	closed	
3 yr	3	29.5	1.34	1	<1 mm	
				2	closed	
4 yr	4	31.3	1.21	4	closed	
5 yr	5	32.6	1.45	5	closed	
6 yr	1	31.0		1	closed	
7 yr	3	30.2	4.32	3	closed	
8 yr	2	30.4	3.38	2	closed	
11 yr	1	33.7		1	closed	
12 yr	1	33.0		1	closed	
13 yr	1	30.6		1	closed	
15 yr	1	30.4		1	closed	
17 yr	2	31.2	13.52	2	closed	
18 yr	2	34.6	2.00	2	closed	
21 yr	1	29.3		1	closed	
22 yr	2	26.3	31.21	2	closed	
26 yr	1	33.0		1	closed	
28 yr	1	28.3		1	closed	

It is evident that in the 1- to 3-year-old groups growth in tooth length is somewhat stabilized. Hewer (1964) has pointed out that the rapid deposition of cement in the grey seal canine tooth blocks off the dentine at the root, preventing any further elongation after the first year. A similar situation exists in the harbor seal. Variations in tooth length of older seals are due to the opposing effects of wear and cement accretion. One may also see that the pulp cavity opening closes rapidly. Of the eleven teeth in age class two, seven were closed. In the 3-year-old group, one tooth out of five was open, but the opening was less than 1 mm in diameter.

Because of the irregular deposition of dentine after 4 to 5 years of age the usefulness of dentine is limited. In seals up to 2 years old, however, it is valuable, since cementum may be lacking or difficult to observe.

The age distribution of all seals collected (Table 11) is not considered representative of the population. Younger seals were more vulnerable to the type of hunting done in 1963, and considerable selection was exercised by the writer in 1964, except with respect to pups, which were part of the commercial kill.

The physiological bases for differential deposition in teeth is poorly understood. Laws (1953a) suggested that increased irradiation resulting in increased vitamin D contributed to better calcified dentine in hauled out, fasting,

elephant seals. However, McLaren (1958) and Fisher (1954b) concluded that poorly calcified "vacuolated" dentine was deposited during the annual fasting and molt period in the ringed seal, Pusa hispida, and harp seal, respectively. Laws (1958, 1962) reached the same conclusion concerning the crab-eater seal. Sergeant (1962) and Fisher (1954b) attribute the lack of, or poor definition of, growth layers in the dentine of harbor seals to the absence of an annual fasting period. However, Spalding (1964) suggests that feeding by harbor seals is at a minimum during the summer. Mansfield and Fisher (1960) suggested that clear cementum is deposited during the spring and early summer. Although I suspect this suggestion is correct, I was unable to verify it satisfactorily.

Table 11. Age distribution of harbor seals collected. Ages of seals 5.5 months old or older determined by examination of tooth sections.

Age	N	Age	N	Age	N
Term fetus	4	6 years	6	18 years	3
Newborn	3	7 "	5	19 "	1
Nursing (1 mo)	36	8 "	2	20 "	0
Deserted (1 mo)	95	9 "	2	21 "	1
Weaned (1 mo)	22	10 "	1	22 "	2
5.5 months	30	11 "	3	23 "	0
1 year	15	12 "	2	24 "	0
1.5 years	10	13 "	1	25 "	1
2 years	12	14 "	0	26 "	1
3 "	6	15 "	1	27 "	0
4 "	4	16 "	0	28 "	1
5 "	6	17 "	4		

That an annual pattern is evident in harbor seal teeth examined in this study suggests that seasonal variation in dentine deposition is associated with factors other than nutritional extremes. Irving (1957) has pointed out the importance of endocrine secretions in tooth development. Carrick and Ingham (1962) suggest that in the southern elephant seal increases of various endocrine outputs are responsible for deposition of dense dentine during molting, periods of gonadal activity, fetal and early postnatal life, winter haul-out not associated with molting, and pregnancy.

In this study the major interest was to determine the annual pattern of deposition. The neonatal line and weaning line are usually obvious, and their occurence is well documented. The dark band considered to be the beginning of each yearly increment might well be associated with increased endocrine secretion by the gonads, since birthdates coincide with the approach of breeding season. While the darker, more dense-appearing dentine seemed to be deposited in the spring and summer, the evidence in this study is not considered conclusive.

The physiological basis for a single, annual deposit of cementum is discussed even less in the literature. Cementum is structurally and physiologically similar to bone (Irving, 1957), and one might expect some resorption and remodeling to occur. However, in seals up to 4 or 5 years old, when dentine deposition became difficult to evaluate, cementum layer

counts agreed with annual dentine layer counts. In older seals, loss of cementum may occur. Seal number 167-64 was considered to be 17 years old on the basis of cementum layers. However, the cementum around the base of the root was gone, either through attrition, resorption, or both. All the teeth were worn to the gum line, and some were missing. Although attrition was not evident in the region sectioned for age determination, considering the general condition of the jaws and teeth, it seems that resorption might have occurred, which would alter the age estimate. The seal in question appeared in good physical condition, and the writer was inclined to attribute the condition of its teeth to old age. The skull showed characteristics of old age, also. Other seals considered older on the basis of cementum layer counts did not show such extensive attrition of the teeth and jaws.

Further investigation is needed to determine the accuracy of age determination in harbor seals. Basic research in the physiology of dentine and cementum deposition, which might include vital staining, and an extensive tagging program would provide valuable information.

Growth

The study of postnatal growth was based on body measurements taken in the field, including total weight, total length, and combined hind flipper span. The data are summarized in Tables 12a and 12b, according to age as determined from tooth sections, and sex.

Table 12a. Body measurements of males. N = number of seals measured; total weight in lb, other measurements in cm.

Age	Total weight			Standard length			Combined hind flipper span			Blubber thickness		
	N	X̄	s²	N	X̄	s²	N	X̄	s²	N	X̄	s²
0 mo*	2	25.5	112.50	2	84.5	13.00	2	48.0	0.74	2	0.9	0.18
<1 mo*	50	23.5	7.07	48	81.0	2.58	48	54.5	11.64	not measured		
<1 mo**	17	30.0	9.90	16	85.0	11.02	17	55.0	7.76	not measured		
<1 mo***	6	43.5	107.46	17	93.0	23.36	7	51.0	6.37	7	2.5	0.31
5.5 mo	12	55.5	66.09	12	99.0	43.95	12	52.0	5.50	12	2.4	0.20
1 yr	9	70.0	109.75	11	109.0	14.07	11	56.0	11.43	10	2.7	0.08
1+ yr	5	71.0	109.00	11	111.5	92.75	5	57.5	9.93	4	2.3	0.06
2 yr	3	92.0	57.00	4	120.0	21.23	4	61.0	6.25	4	2.4	0.23
3 yr	2	105.5	12.95	3	126.0	5.59	2	62.5	0.50	2	3.2	0.50
5 yr	1	109.0		1	131.0		1	62.0		1	2.0	
6 yr	4	153.0	478.00	5	148.5	26.00	5	73.5	27.18	5	3.0	0.43
7 yr	2	171.0	648.00	2	152.5	24.50	2	73.0	32.00	2	2.7	0.05
9 yr	2	193.5	840.50	2	156.5	24.50	2	72.0	120.13	1	2.3	
10 yr	1	184.0		1	161.0		1	76.0		1	2.7	
11 yr	1	232.0		1	172.5		1	84.0		1	3.0	
12 yr	1	192.0		1	158.0		1	80.0		1	2.6	
17 yr	2	192.5	24.50	2	165.5	144.50	2	81.0	1.13	2	2.6	0.85
18 yr	1	160.0		1	150.0		1	67.5		not measured		
19 yr	1	193.0		1	159.0		1	75.0		1	2.8	
25 yr	1	181.0		1	163.0		1	74.0		1	2.3	

* deserted   ** nursing   *** weaned

Table 12b. Body measurements of females. N = number of seals measured; total weight in lb, other measurements in cm.

Age	Total weight			Standard length			Combined hind flipper span			Blubber thickness		
	N	X	S²	N	X	S²	N	X	S²	N	X	S²
0 mo*	4	26.0	15.25	4	76.5	4.23	4	48.0	9.16	2	1.2	0.05
<1 mo	43	21.5	25.45	38	78.5	29.85	42	53.5	13.26	not measured		
<1 mo **	19	27.5	7.45	18	81.5	20.17	19	53.0	18.75	not measured		
<1 mo ***	15	45.0	67.14	15	89.0	26.87	15	49.0	3.24	15	2.8	0.11
5.5 mo	17	47.5	47.22	17	95.5	22.38	17	51.0	7.45	16	2.1	0.14
1 yr	4	65.0	32.92	4	104.0	38.75	4	54.0	4.84	4	3.0	0.28
1+ yr	4	62.5	107.67	5	113.5	38.25	5	55.0	13.61	5	3.2	0.67
2 yr	6	86.0	279.36	6	115.5	103.92	7	61.0	14.33	5	2.7	0.22
3 yr	1	126.0		3	117.5	207.75	2	67.0	8.00	2	2.3	0.01
4 yr	3	106.5	149.50	4	132.0	14.67	3	64.5	9.75	3	2.4	0.15
5 yr	6	136.5	460.47	6	141.0	37.30	5	69.0	11.20	5	2.5	0.08
6 yr	1	141.0		1	134.0		1	65.0		1	3.8	
7 yr	2	135.5	144.50	2	146.0	12.50	2	74.0	16.82	2	2.5	0.13
8 yr	2	128.0	1,458.00	2	140.0	60.50	2	65.0	3.12	2	2.6	0.02
11 yr	1	143.0		2	148.0	0.13	2	74.0	0.50	1	2.9	
12 yr	1	240.0		1	159.0		1	75.5		1	4.5	
13 yr	1	111.0		1	145.5		1	73.0		1	1.8	
15 yr	1	121.0		1	152.0		1	78.0		1	1.9	
17 yr	2	137.5	544.50	2	150.0	4.50	2	77.0	3.13	2	2.2	0.72
18 yr	2	150.5	515.50	2	144.5	84.50	2	75.5	45.13	2	2.7	0.01
21 yr	1	226.0		1	161.5		1	77.0		not measured		
22 yr	2	143.5	180.50	2	150.5	40.50	2	74.5	72.00	2	2.6	0.08
26 yr	1	146.0		1	148.5		1	79.5		1	2.3	
28 yr	1	150.0		1	144.0		not measured			1	2.3	

* deserted   ** nursing   *** weaned

To evaluate early growth, pups were separated into five groups on the basis of age and condition, and further separated by sex. Pups were considered to be zero months old if they were term fetuses or newborn, less than 1 month old if either deserted or nursing, approximately 1 month old when weaned, and about 5.5 months old when collected in late October.

A large number of pups less than 1 month old was available due to commercial hunting on Tugidak Island in 1964. Pups were considered to be attended, or nursing, if milk was found in their stomachs, or if a cow was definitely associated with the pup, but the latter criterion could seldom be applied to pups in the commercial kill. Pups without milk in their stomachs were considered to be deserted, although some may have been nursing. The 1-month-old age class includes pups which were weaned or nearly weaned, and nearly all were collected in July. Pups included in the 5.5-months-old group were collected from 28 October through 1 November, 1963.

Although the sample is small, the available data suggest that the birth weights of males and females are similar. Most of the values given by other workers fall within the range of weights in this sample. Imler and Sarber (1947) report that a newborn male weighed 30.25 lb, and a newborn female weighed 16.5 lb. Scheffer and Slipp (1944) give the weight of a female term fetus as 27.5 lb, and a male that was

probably near-term weighed 24 lb. Fisher (1952) stated that newborn pups weighed about 23 lb, and Harrison (1960) gives the weight of newborn pups as 9 to 11 kg, or 20 to 24 lb.

The available data show that when weaned, the average weight gain in both males and females is nearly 20 lb over their birth weight. This represents a weight gain of about 71 percent in the males, and 74 percent in females. Fig. 6 shows that by the age of 5.5 months the weight is nearly twice the birth weight. Some 5.5-month-old pups are as large as the smallest 1-year-old seals. In Fig. 7 the growth in length and combined hind flipper span is illustrated.

The pattern of growth after 5.5 months of age is repre-sented graphically in Figs. 8 and 9. The curves shown are based on moving means to adjust for unequal sample sizes in the various age groups. Because many of the samples are small the curves fluctuate strongly at several points in response to a particularly large or small animal.

On the basis of the available data it seems that males grow more slowly in length after age five, but they continue to gain weight at a relatively constant rate until about age ten. Then growth seems to slow, and possibly cease. Females exhibit a pattern of growth similar to males, but they appear to have a more pronounced decline in growth rate after about age five, which may be related to earlier maturity. All the specimens included in these data were collected between late spring and early fall. Winter and spring weights might be
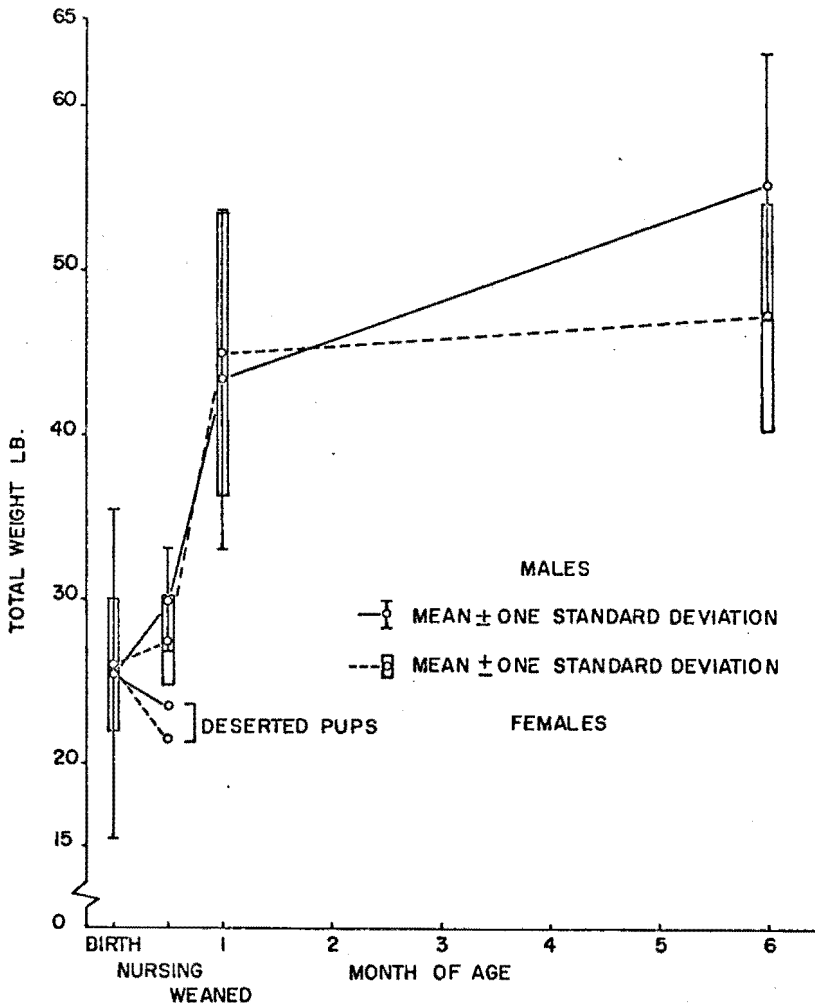
Fig. 6. Total weight of pups from birth to about 6 months of age.
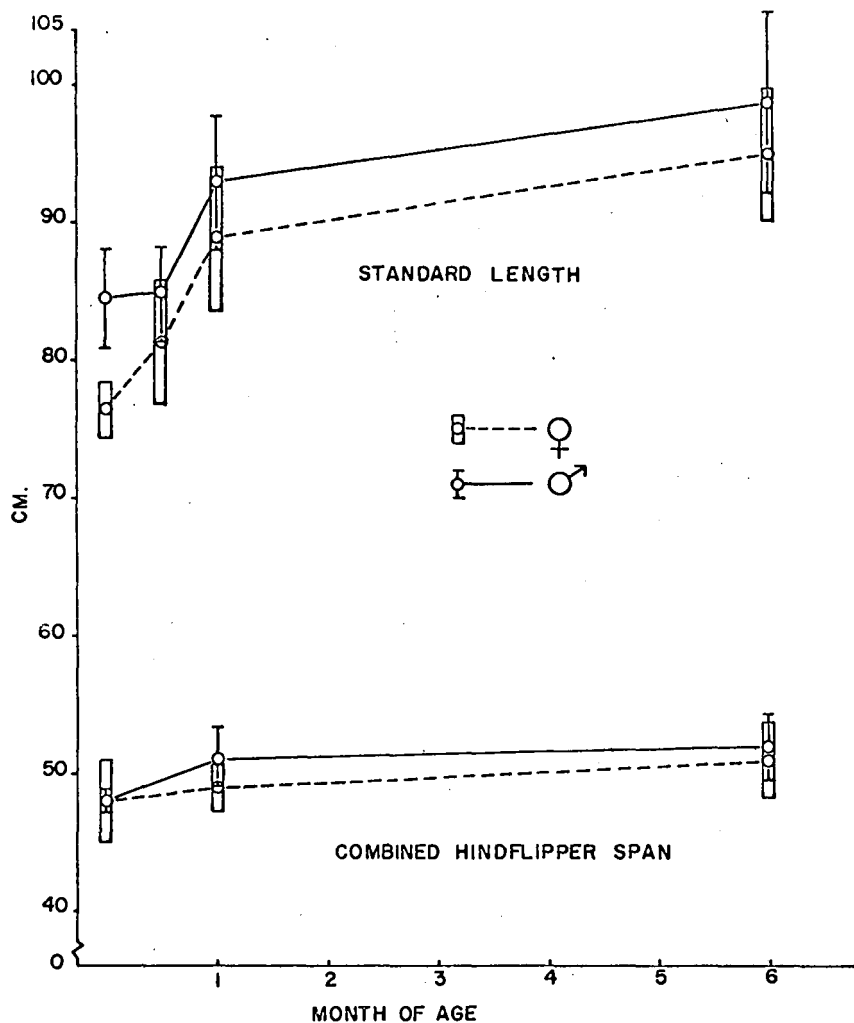
Fig. 7. Standard length and combined hind flipper span
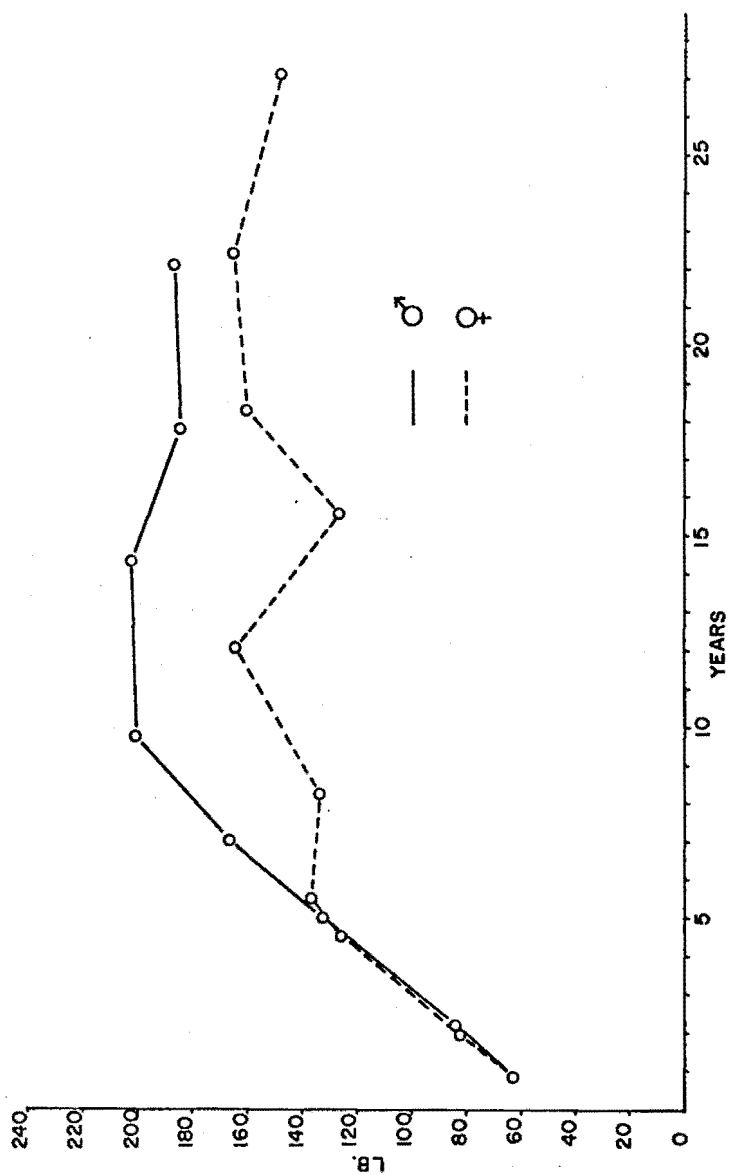of pups from birth to about 6 months of age.

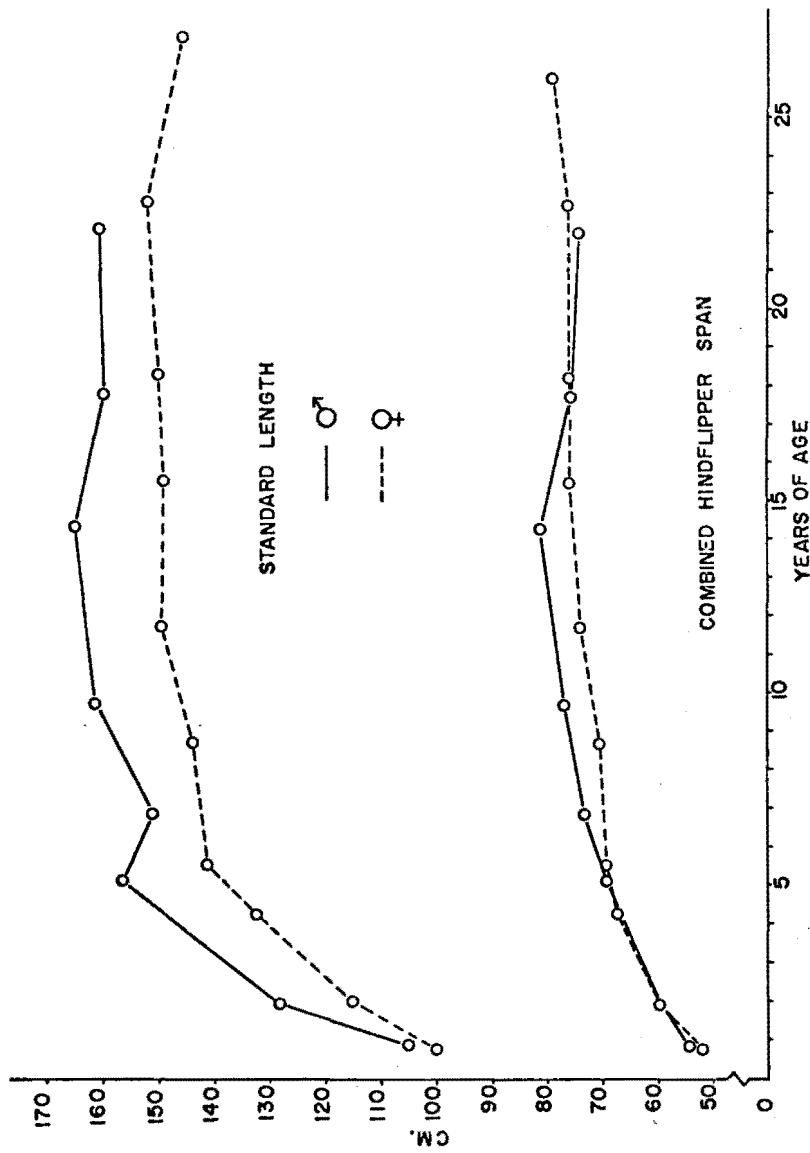Fig. 8. Total weight in relation to age, 5.5 months to 28 years.

Fig. 9. Standard length and hind flipper span in relation to age, 5.5 months to 28 years.

significantly higher according to Imler and Sarber (1947) whose observations are discussed on page 95.

The average measurements of harbor seals at developmental stages of interest are expressed as percentages of full-grown measurements in Table 13. The values which were selected to indicate full-grown size represent the assumed asymptotes of the values for each measurement, and were chosen by inspection from Figs. 8 and 9. Sexual maturity in males is considered to occur at 6 years of age, the earliest age that maturity in males could be established from the data in this study. In the female sexual maturity was found to occur at 3 to 4 years of age, and measurements from these age groups were averaged to obtain the figures used in Table 13.

The data suggest that in both males and females about 75 percent of the full-grown weight is attained by the time sexual maturity is attained. Females have attained 84 percent of their full-grown length by the time sexual maturity is reached. Laws (1956) concluded that among 12 pinnipeds the females average 86.6 percent of the full-grown length by the time sexual maturity is attained. In the harbor seal, Laws found this value to be 87.5 percent.

The form of growth in the harbor seal as shown by total length resembles that of the ringed seal as given by McLaren (1958), and that of the grey seal (Hewer, 1964).

The largest male collected in this study was 11 years old, weighed 232 lb, and was 172.5 cm in length. A 12-year-

Table 13. Body measurements at several stages of development expressed as percentages of estimated measurements of full-grown seals.

Age	% total weight		% total length		% combined hind flipper span	
	♂	♀	♂	♀	♂	♀
Newborn	13	17	50	49	56	60
Weaned	22	30	55	57	60	61
5.5 months	28	32	58	62	61	64
1 year	35	43	64	67	66	68
Sexual maturity[1,2]	77	74 (111)	87	84 (126)	86	82 (65.5)
Full-grown[3]	100 (200)	100 (150)	100 (170)	100 (155)	100 (65)	100 (80)

[1] Sexual maturity in males is assumed to occur at 6 years of age, in females at 3 to 4 years of age.

[2] Values in parentheses represent the means of values for 3- and 4-year-old females in the sample.

[3] Values in parentheses represent assumed asymptotes of the variates, derived by inspection from Figures 8 and 9.

old female weighed 240 lb and was 159 cm in length. However, she was very fat and was carrying a near-term fetus which weighed 30 lb. The largest non-pregnant female was 18 years old, weighed 168 lb, and was 151 cm in length. Fisher (1952) reported a male harbor seal from British Columbia which weighed 300 lb. The largest male examined by Scheffer and Slipp (1944) weighed 256 lb, and the largest female, which was pregnant, weighed 243 lb.

Fatness may affect the weight of seals considerably. Blubber thickness was routinely measured except on the 1964 commercial kill of pups. The increase in weight from birth to weaning is mainly attributable to an increase in blubber thickness, but among seals in other age groups and in various reproductive categories it is difficult to see a pattern of change in blubber thickness. However, seals in late pregnancy seemed to be comparatively fat; the mean blubber thickness of three cows in late pregnancy was 3.4 cm. In ten lactating cows the blubber thickness averaged 2.4 cm. In seven cows which had completed lactation, or lactation and ovulation, the blubber thickness averaged 2.3 cm.

Among the males blubber thickness varied considerably. Within the limitations of the data, a seasonal pattern of change could not be determined. However, the condition of the seals during the winter is not known, since collecting was not done from November to May. Imler and Sarber (1947) state that harbor seals in southeastern Alaska are fattest

in late winter and early spring when the blubber may reach
1.5 to 2 inches in thickness, and may weigh "up to a hundred
pounds or more in large adults."

Food Habits

With the exception of nursing pups, food was found in
the stomachs of only four seals collected in this study.
Parts of the exoskeletons of shrimp, unidentified at this
time, were found in the stomach of a very thin pup collected
on 4 July in Aialik Bay. The stomach of a fat, healthy ap-
pearing pup collected on 11 July in Aialik Bay contained de-
composed flesh that was probably fish. In the stomach of an
adult male collected on Tugidak Island on 21 June, we found
2 to 3 lb of octupus flesh, consisting mainly of sections of
the tentacles. It appeared that the seal had recently hauled
out. On 23 July the remains of at least 25 small fish, on
the basis of the vertebral columns found, plus several beaks
of octopi were found in the stomach of an adult male. The
food was well decomposed, although the seal was known to have
hauled out only moments before.

During the nursing period, milk was the only food found
in the stomachs of pups. The stomach of one deserted pup was
filled with sand. Small amounts of sand were occasionally
found in the stomachs of deserted pups. Although seal car-
casses were plentiful on the beach, deserted pups were never
observed to scavenge them.

Imler and Sarber (1947) examined 400 harbor seal stomachs from the Copper River delta, the Stikine River area, and other areas in southeastern Alaska, of which 166 contained food. Of 67 stomachs from the Copper River delta, 64 contained eulachon, Thaleichthys pacificus, exclusively, while two contained salmon, and one contained "cod". Their study in the Copper River area was coincident with the annual migration of the eulachon, and their results reflect this fact. In a more representative sample, the same authors examined 99 stomachs containing food from the Stikine River and other areas in southeastern Alaska. Fishes comprised 79.4 percent of the stomach contents by volume. The principal food was found to be gadid fishes, which comprised 22.6 percent of the stomach contents. Other fishes were found in lesser quantities. Shrimp, Caridea, were an important food in July and August in certain areas.

Pelage and Molt

Fetal pelage and molt: The fetal pelage, or lanugo, of the harbor seal is silvery-white, long, and wooly. Scheffer and Slipp (1944) describe this pelage in some detail. In their study of the harbor seal in Washington, they concluded that the lanugo is normally shed before birth. On the Skeena River in British Columbia, Fisher (1952) found one newborn pup in the fetal pelage, but the fetal hair was easily wiped off. Imler and Sarber (1947) found no evidence of pups being born in the lanugo in southeastern Alaska and the Copper

River delta area.

Mr. Pete Kesselring (vive voce) stated that pups born in the fetal pelage in Aialik Bay and adjacent areas were rare. However, Dr. Francis H. Fay (personal communication) informed me that another hunter reported seeing numbers of pups in the fetal pelage at Aialik Bay in mid-May to early June. I was unable to observe the pupping season in Aialik Bay, and the question remains in doubt.

From the beginning of our observations at Tugidak Island on 4 May, through 17 May, pups which we observed retained all or most of the lanugo at birth. We first observed a pup born without the lanugo on 18 May. Thereafter the proportion of pups which retained the lanugo at birth declined. During June they were rarely found except as deserted pups, dead or near death from days or weeks of starvation.

Only general observations were made of molting of the lanugo. The lanugo was shed first on the head, followed by the neck and foreflippers. The sequence of molting over the rest of the body was variable, but usually the back and occasionally the sides were the last areas to lose the lanugo. When the lanugo is shed, the typical short, patterned pelage is exposed. The pelage of pups resembles that of adults, but is softer and appears to be more dense.

Imler and Sarber (1947) and Fisher (1952) found that pupping starts in late May in southeastern Alaska and northern British Columbia. Scheffer and Slipp (1944) show that

pupping begins in mid-May in the coastal waters of Washington, but in Puget Sound and adjacent areas it is 1 to 2 months later. It was noted above that none of these authors found evidence of pups being born in the lanugo, or with the lanugo still fast. The harbor seals found in the Sea of Okhotsk pup in February and March, and the lanugo is retained into late April (Wilke, 1954). In the Bering Sea, most pups are probably born in April, and may retain the fetal pelage as late as 24 May, at St. Lawrence Island (Francis H. Fay, personal communication).

With respect to pupping time, the harbor seals at Tugidak Island seem to be intermediate between those found in the Bering Sea and those further south along the North American Pacific coast. Dr. Francis H. Fay (personal communication) notes that there is a progression of pupping dates among harbor seals from the Asian North Pacific, to the Bering Sea, and south along the North American continent, but that the range of dates when molt of the lanugo occurs is much more narrow. The significance of the relationship between molt of the lanugo and pupping dates, and the timing of pupping among the harbor seals of the North Pacific is a matter for speculation until more is known of the harbor seal in its various environments.

Pelage of the immature and adult: Pelage color varied widely, but it was possible to group seals as either "dark with light", where the basic color was black or nearly black,

with light spots or rings, and "light with dark", where the basic color was white, yellowish-white, or gray, with dark spots, rings, or blotches. Pelage pattern in both color groups varied from almost no spots or other markings, to a profusion of spots, rings or blotches.

Light-colored seals were more numerous than dark-colored seals. Among an estimated 1,000 seals in one herd at Tugidak Island, 102 or about 10 percent were dark seals. On 27 May we found 35 deserted pups along 4 miles of beach, of which 4, or 11.4 percent, were dark-colored. These data were obtained before commercial hunting had commenced in the study area. The proportion of dark seals in the commercial kill at Tugidak Island was not representative of the true proportion in the population, because the more valuable dark hides were selected by hunters whenever possible.

Of 53 seals collected in Harris Bay in 1963, 4 or 7.2 percent, were dark-colored. Selection for dark hides had little effect on this sample, because any seal within rifle range was shot if possible.

The molt in the immature and adult: Immature seals were beginning to molt by at least 11 July at Tugidak Island, and by 18 July some were molting heavily, although an immature female collected on 23 July was just beginning to molt. On 27 July five immature and two mature seals were collected, all of which were molting. Of the two mature seals, a nulliparous female was shedding all over the body, but a multiparous

female was just beginning to molt in a small patch dorsally and forward of the pelvis. Both had ovulated. A 1-year-old seal collected on 9 July and a 2-year-old collected on 11 July in Aialik Bay were both molting.

In mid-August two mature females which had ovulated recently, and a mature male collected in Aialik Bay were not molting, while a 1-year-old male and an immature female were molting. Among 53 seals of mixed age and sex collected in late October in Aialik and Harris Bays, none were observed to be molting. The two hunters whom I accompanied stated that the latest date they had taken a molting seal in the Aialik Bay-Kenai Peninsula area was about 15 September. However, Mr. John Vania (viva voce) informed me that hunters in the Prince William Sound, Seward, and Kenai Peninsula area had found molting seals from the first week of July through the second week in October.

Among 29 seals of various size classes collected in early August at Sitkalidak Island, north of Tugidak Island, Mr. Walter Baldwin (vive voce) found only three immature seals and two large adults that were not molting. In mid-September in the same area, Baldwin found that most immature seals had completed the molt, but that most adults were molting. During subsequent hunting, Baldwin observed that adult seals were molting as late as 15 October in the Whale Passage area, near the north end of Kodiak Island.

The evidence indicates that in the Kodiak Island and
Seward areas immature seals molt first and may begin molt-
ing by 10 July. The timing of the molt in mature females is
not entirely clear from the data, but it appears that molting
follows ovulation. As a result mature females probably do
not begin molting until mid-July or later. Although little
data is available for the adult males, it appears that they
probably start molting no earlier than the third to fourth
week in July, but that they may begin to molt as late as
mid-August.

It appears that immature seals as a group complete the
molt first, probably about 1 October. Adult seals may molt
as late as 15 October, but whether one sex completes the
molt sooner than the other is not clear.

Relatively few molting specimens were examined, and a
comprehensive study of the molt was not done. Examination
of specimens in the field suggested that molting began on the
hind flippers as a gradual thinning of the pelage with scat-
tered bare patches 2 to 3 mm in diameter subsequently appear-
ing. In the early stages of molt some seals were also molt-
ing around the eyes and muzzle. The next area to be affected
by the molt seemed to be the back, where on several specimens
the hair was very thin and could be rubbed off with the hand.
One seal collected was molting on the back, belly, and hind
flippers, with bare patches showing on the back and hind
flippers, which suggests that the belly begins molting after

the back. Beyond this stage the pattern of molt was not observed since collections were not made from mid-August to late October.

Scheffer and Slipp (1944) found that a captive 4-year-old harbor seal kept in an open air, salt water aquarium in Washington began molting toward the last of August. By mid-September new hair covered the midline of the belly, the periphery of the tail, the rump, flanks, and the top of the head and part of the muzzle. By 25 September the molt was nearly complete, with only a strip of old hair left on each side of the neck from the angle of the jaw to the throat. Upon their next observation, on 25 November, they found the new coat complete. The authors mention that the hair appeared dull and brown just prior to the molt, and most molting seals that I observed were also of a dull brownish color. However, most of them were also immature, and brown immature seals which were not molting were evident in the herds at Tugidak Island from May through July. An adult female which was just beginning to molt was the normal silver and grey color. The pelage of seals other than pups collected from May through July was rather short, coarse, and worn in appearance, even though the seals were not molting. As a result, the best potential value of prime adult or immature hides is lost if these age classes are harvested between April and October or November.

Population

The total population of Alaskan harbor seals has not been estimated. Imler and Sarber (1947) estimated that at least 6,000 seals lived in the Copper River delta area, but this figure may be a seasonal phenomenon (Mathisen and Lopp, 1963). On a 827-mile census by boat in southeastern Alaska, Imler and Sarber (1947) counted 475 seals, or .56 seals per mile.

Spalding (1964) suggested that in late winter and in spring when dispersal is at a maximum, harbor seals are distributed along the coast of British Columbia at about one seal per mile. On this basis he estimated the total number of harbor seals in British Columbia at about 17,000.

The most comprehensive census of harbor seals in Alaska was done in conjunction with sea lion investigations in the Gulf of Alaska and the Aleutian Islands (Mathisen and Lopp, 1963). Most of the areas were censused only once, but censuses were repeated in various months during 1956 and 1957 in the Kodiak Island area, including Tugidak Island. The authors pointed out the difficulties of an aerial photographic census of harbor seals, and emphasized that the figures they presented did not represent a complete survey estimate.

At Aialik Bay in August, 1963, I counted 490 to 500 seals hauled out on the ice. The largest aggregations observed earlier in the season appeared to be of about the same size. In Harris Bay a total count was not made, but the

population may have approached 500 seals in October, 1963.
The population at Tugidak Island: Although a number of areas
were censused, the only area for which Mathisen and Lopp's
(1963) data may accurately reflect the population status on a
seasonal basis is the Trinity Islands, which include Tugidak
Island and the shore of Sitkinak Island nearest Tugidak Is-
land. In 1964, few seals were observed on the near shore of
Sitkinak Island, and I feel that the population data from
Tugidak Island in 1964 may be directly compared with Mathisen
and Lopp's data for the Trinity Islands. In Table 14
Mathisen and Lopp's (1963) data for the Trinity Islands are
reproduced; the reader is referred to the original paper for
the data relating to other areas.

Table 14. Numbers of harbor seals on the Trinity Islands,
1956-1957. Data from Mathisen and Lopp (1963).

1956	Number of seals	1957	Number of seals
22-25 July	6,533	21 Mar	7,800
1-2 Sept	16,776	27-29 May	115
10-14 Dec	3,295	27-28 June	9,468
		29 Sept	13,383
		4-5 Dec	418

On the basis of the size of the herds seen from the air
when we arrived at Tugidak Island, and later counts and esti-
mates made from the bluffs overlooking the beach, I estimated
that 4,000 to 5,000 seals were using Tugidak Island as a
hauling grounds in early May. In the herd which we observed

on a regular basis during May, the maximum number of seals
seen hauled out was estimated at 2,000 to 2,500. The balance
of the population using Tugidak Island habitually hauled out
about 10 miles away at the north end of the island, and we
were unable to observe them regularly. From the reports of
hunters in the area, and observations during two flights
which I made over the north end of the island, the northern
herd or herds on Tugidak did not seem to exceed 2,500 seals
from May through July. Therefore in estimating the number of
seals using the island, 2,000 to 2,500 was added to the esti-
mate of the herds under regular observation on the west
beach.

The number of seals hauled out on the west beach varied
from as low as 67 up to 2,000 to 2,500 during May. While the
relationship was not entirely consistent, larger numbers of
seals were usually ashore on calm days when there was little
surf.

The number of seals hauled out along the west beach
varied from 45 to 570 during the first 5 days in June. On 7
June 2,321 seals were counted in 15 discontinuous groups, the
largest of which contained 425 seals. The number of seals
observed represented a marked increase over the number ashore
through most of May and in early June, and the distribution
of the seals in small groups over a distance of about 4 miles
was unique in our observations. In previous observations the
seals were normally in only one or two rather continuous

herds.

A detailed count was not made again until 13 June, but on 11 June about 300 seals were estimated to be hauled out along 2 miles of beach. On 12 June about 1,000 seals were found hauled out along a 1.5 mile section of beach. On 13 June, 4,984 seals were counted in a 5-mile section of beach, and an additional estimated 2,500 seals were occupying 2 miles of beach. Thus, on the west beach alone, about 7,500 seals were hauled out on 13 June. The estimated number of seals for the entire island was 9,500 to 10,000, since it was known from hunter reports that the herd using the northern end of the island was still there. This estimate agrees closely with Mathisen and Lopp's (1963) figure of 9,468 for the June aerial photographic census. However, their census was conducted near the end of June, and by the end of June in 1964, there seemed to be a decline in the number of seals using the west beach.

In Table 15 the most comprehensive counts and estimates for June and July, 1964, are given. It is not likely that the figures represent all the seals using the west beach on a given day, since the area was not always completely patrolled, and an unknown proportion of the herds was always in the water. We did attempt to make counts at comparable times with respect to the tides. However, the count taken on 28 June was considered to represent about half of the seals using the west beach, whereas the combined estimate and count

Table 15. Selected counts of hauled out seals, Tugidak
Island, 1964. APF = adult females producing
young; AP = attended pups; PG = pregnant fe-
males; DP = deserted pups.

Date	Total Seals	APF		AP		PG		DP	
		No.	%	No.	%	No.	%	No.	%
6 May	943	29	3.1	0	0.0	28	3.0	1	0.0
3 Jun	571	105	18.4	22	3.9	83	14.5	no count	
7 Jun	2,321	749	32.2	484	20.1	226	9.7	(24 of) 1.7 (1,372 seals)	
13 Jun	4,984 1,206 24.2 2,500* (west beach) 2,000-2,500* (north end)			844	16.9	147	2.9	215	4.3
21 Jun	831	243	29.2	120	14.4	7	0.8	116	14.0
28 Jun	1,128	306	27.1	180	16.0	0	0.0	(63 of) 11.2 (561 seals)	
30 Jun	2,328 750-1,000*	326	14.0	200	8.6	1?		126	5.4
1 Jul	2,500-3,000**								
4 Jul	1,129	193	17.0	105	9.3	0	0.0	88	7.8
7 Jul	420	40	9.5	21	5.0	0	0.0	19	4.5
12 Jul	350	30	8.5	8	2.2	0	0.0	22	6.3
23 Jul	545	0	0.0	0	0.0	0	0.0	3 (weaned)	0.6
31 Jul	3,500-4,000** (west beach) 2,000** (north end)								

* Estimated in addition to total count
** Estimated total

taken on 30 June probably represents most of the seals using
the west beach at that time. On 1 July, I made a circuit of
the south end and part of the west beach of Tugidak Island
and estimated that there were 2,500 to 3,000 seals hauled
out, mainly on the southwest corner of the island. Thus it
appeared that the seal population using the west beach had
diminished from about 7,500 to about 3,000. It also became
evident that during June the major concentration of seals
shifted southward 2 to 3 miles, probably due to the intensive
hunting activity carried on further north during the first 3
weeks of June. Much of the reduction in the number of seals
can be attributed to hunting losses, but in view of Mathisen
and Lopp's (1963) figures for late June, and my observations,
it also seems likely that the hunting harassment contributed
to a premature egress from Tugidak Island by the seals.

During July comprehensive counts were not made, but on
31 July, after most of the hunting activity had subsided, an
aerial reconnaissance of the island was made, and I estimated
that no more than 3,500 to 4,000 seals were hauled out on the
west beach. Virtually no pups were observed on the west
beach. No more than 2,000 seals were hauled out on the north
end of the island. Thus about 6,000 seals were estimated to
be on Tugidak Island at the end of July when I departed.
Mathisen and Lopp's (1963) figures for July tend to confirm
these estimates.

The influx of seals in June and the increasing number of pups suggested that Tugidak Island was a traditional pupping location. Prior to 1964, seals were not hunted heavily on Tugidak Island. Only one hunter, Darell Farmen of Kodiak Island, hunted the island somewhat regularly prior to 1963. Farmen suspected that seals moved into the Tugidak Island area during the pupping season, and that subsequently many left. Fisher (1954b) noted that females of the Atlantic harbor seal tend to congregate in certain areas during the pupping season and disperse at other times. On Tugidak Island the herds observed were of mixed sex and age.

The significance of the markedly higher number of seals recorded on Tugidak in September by Mathisen and Lopp (Table 14) is not definitely known. It may be that the difference of about 4,000 seals between their June count and their September counts represents some proportion of the annual recruitment. The apparent decline in the population during July may represent a dispersal of the seals after the pupping and mating season. By late July most pups are quite independent, and it may be that they spend more time at sea, perhaps learning to feed. The factors which may prompt the return to Tugidak Island in September by much of the population as suggested by Mathisen and Lopp's (1963) data, are unknown. The reason for the low number of seals observed by Mathisen and Lopp (1963) in December is not definitely known; Mathisen and Lopp suggest that a feeding dispersal may occur in the

winter. Sergeant (1951) suggested that harbor seals in the Wash, East Anglia, may move from the hauling grounds to the outer coast during the winter as the result of a known winter migration of bottom fish and invertebrates in that direction. Mathisen and Lopp (1963, p.19) suggest that harbor seal migrations are "frequent and extensive". A long-range program of marking animals is needed to obtain significant information on harbor seal movements.

Population structure: When a total count of the hauled out seals was made, attended pups, deserted pups, pregnant females, and immature seals were also counted. Immature seals were classified as those larger than pups but smaller than adults. The classification of adults and immatures was the result of a subjective judgement of the seals' size and proportions. Results of attempts to obtain age and sex ratios from counts of seals were considered unsatisfactory; unless the external genitalia were in view, males and females could not be distinguished reliably. During the pupping season, a bias favoring higher counts of females was introduced by the presence of pups with the females. Therefore the age-sex counts are not included here.

The sex ratio of all pups examined in the term fetus to weaned categories was 76 males: 82 females, which was not significantly different from an even sex ratio at the .99 confidence level. The cumulative sex ratio of all pups in the term fetus to 5.5-month-old category was 98 males: 99

females. In 1963 when hunting was not known to be selective with respect to sex, the sex ratio of the kill of seals 1 year old or older was 27 males: 23 females, which was not significantly different from an even sex ratio at the .99 confidence level.

From the counts given in Table 15, the percentage of adult females producing young in the population at the time of the count may be estimated by adding the number of attended pups, the number of deserted pups, and the number of pregnant females. Several sources of error arise in this method. Deserted pups may be overlooked, or if they die on the beach, they may be eaten by eagles and gulls, buried in the sand, or washed away. As the pupping season declines, the usefulness of this technique decreases, since pups become weaned or die and pregnant females are no longer found. The removal of pups by hunting also affects the accuracy of the data; on Tugidak the pup crop was heavily harvested and pups of any description became scarce in July.

The estimated percentage of adult females in each count is also given in Table 15. On 7 June the producing females were estimated to compose 32.2 percent of the observed population. Thereafter the intensity of hunting increased. On 13 June, the percentage declined, probably due to the combined effects of dying, deserted pups, hunting mortality, egress of the seals, and the natural termination of the pupping and weaning processes. The proportion of females

observed on 7 June is probably the most representative figure, as it was least affected by those factors.

The harvest of pups for bounty and hides at Tugidak Island in 1964 was estimated to be 4,000 on the basis of information obtained from the hunters, in addition to a harvest of about 1,500 seals of other ages. I observed few pups in the herds in late July, and two hunters found the same situation. On a circuit of the southern and western part of the island on 1 July I saw no more than 100 pups that were alive among 2,500 to 3,000 seals, and most of these pups were deserted. Nearly all the dead pups I observed were either skinned or the scalp had been removed for bounty purposes. The thoroughness of the hunters may be judged by the example of two hunters who collected 1,060 "scalps" for bounty, mostly from deserted pups, during an 18-hour walk along the west beach.

The number of pups which survived in 1964 is unknown but small. Because of the few surviving pups observed, I felt that perhaps all but a few hundred had been harvested or had died of starvation. However, considering Mathisen and Lopp's (1963) counts for September, and assuming that the proportion of producing females in the population may reach 32 percent, the pup crop may approach 5,500.

The 1965 harvest of pups at Tugidak Island was 4,000 (Ed Klinkhart, personal communication), essentially the same as in 1964. On the basis of the data discussed above, the total

population at Tugidak Island could range between 12,000 and
17,000 animals including the annual production.

Although little is known of other factors affecting har-
bor seal population dynamics, an annual harvest of 4,000 pups
from Tugidak Island seems excessive if the population is to
be maintained.

RECOMMENDATIONS

On the basis of results obtained in this study, and in view of the demand for harbor seal pelts with the resulting hunting pressure on seal populations in southern and western Alaska, certain recommendations seem appropriate.

More knowledge is needed concerning movements, population dynamics, and age determination of the harbor seal. An extensive tagging program would help to provide the necessary information. Tagging of pups could be readily accomplished at Tugidak Island and similar pupping areas which are supposed to exist along the Alaska Peninsula. Tagging in areas where seals haul out on floating ice, such as Aialik Bay, might be prohibitively difficult. In areas where large numbers of pups are available for tagging, hunting would need to be restricted to prevent premature loss of the tagged animals.

Although Mathisen and Lopp (1963) found that aerial census of harbor seals presented many difficulties, it is probably the most efficient means of obtaining an estimate of at least the larger harbor seal populations. A rapid assessment of major harbor seal populations seems necessary as a basis for future management, in combination with information on population dynamics.

Information on productivity, age distribution, and other aspects of population dynamics might be obtained by making

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extensive collections of specimens by accompanying commercial seal hunters. The present study is no more than a starting point in this respect.

In areas such as Tugidak Island, where pups are extremely vulnerable for a short time, restriction should be placed on the total harvest to assure adequate recruitment for a maximum sustained yield. At this time adequate data is not available to determine what the harvest level should be at Tugidak Island, but if the pup crop equals 5,500 or less as I have estimated, then an annual harvest of 4,000 seems excessive if the population is to be maintained near the current level. A decline in the populations of such areas would eventually affect the seal hide industry itself.

Where seals are more inaccessible to the biologist and the hunter, the proper balance of production and harvest will be more difficult to ascertain, but concentrations of harbor seals throughout the Gulf of Alaska, the Alaska Peninsula, and southeastern Alaska are being hunted more intensively than ever before, and some knowledge of the status of the various populations is needed.

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