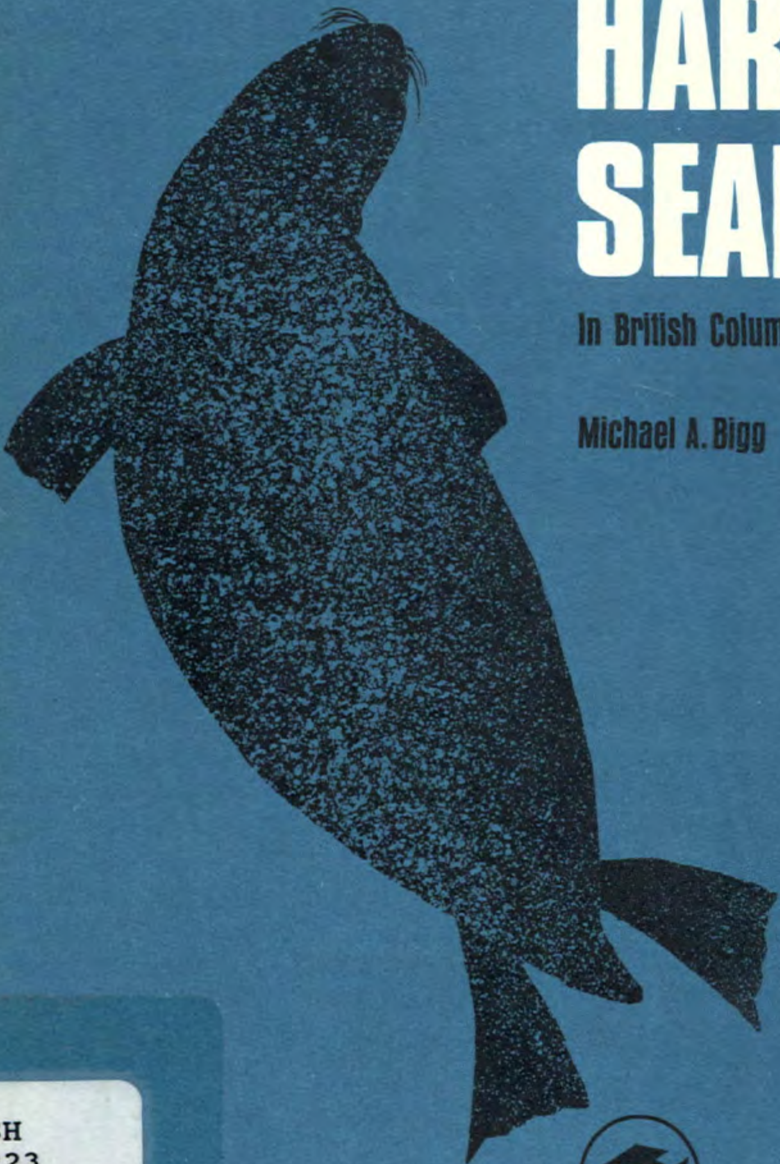
Bulletin 172

THE HARBOUR SEAL

In British Columbia

Michael A. Bigg



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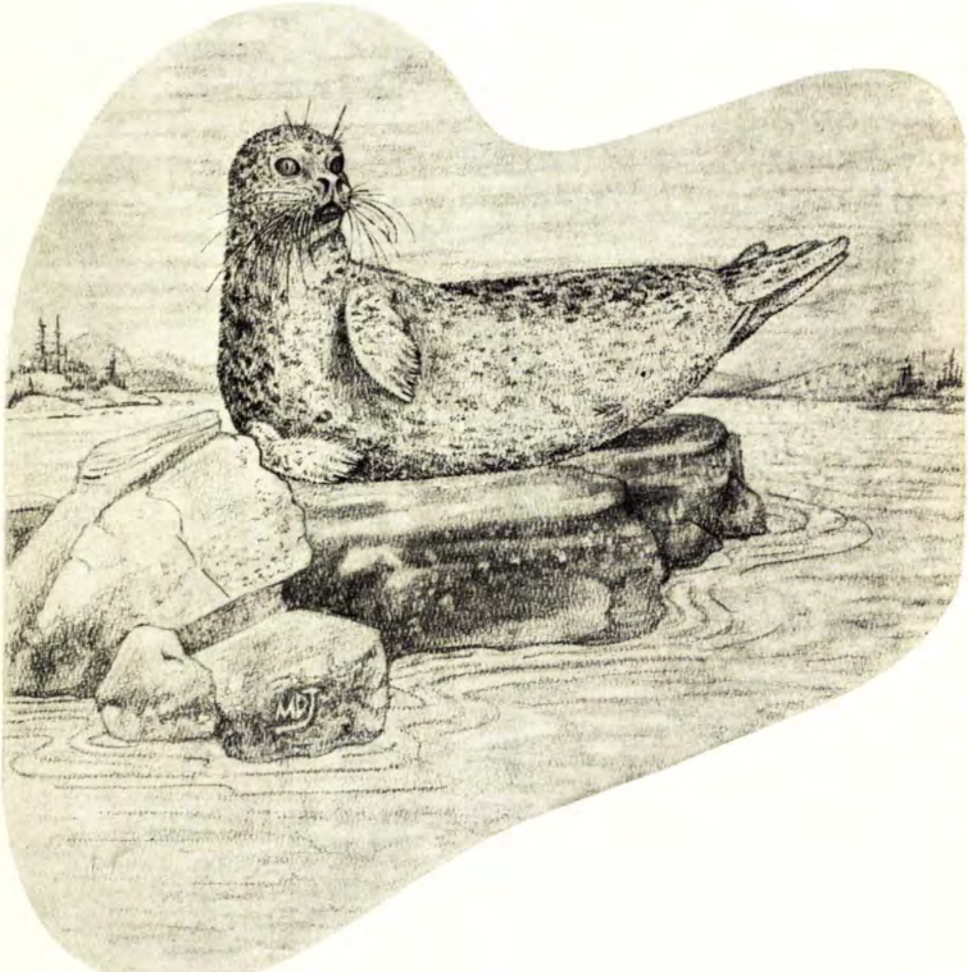

BULLETIN 172

The harbour seal in British Columbia

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ABSTRACT

The results of a field study made on the harbour seal, *Phoca vitulina richardi*, in British Columbia are reported and discussed. The study, based on field observations and a collection of 415 specimens, describes the method of determining age, the reproductive cycle and ages at sexual maturity, prenatal and postnatal growth, and population composition and dynamics.

Age was determined in postnatal seals by counting the alternating opaque and translucent annuli in the cementum of canine teeth. In pups one opaque layer of cementum is deposited during the autumn; in older seals one translucent layer, laid down from late autumn to late spring, and one opaque layer, laid down from late spring to late autumn, are deposited each year.

The main events in the reproductive cycle of the adult female in southeastern Vancouver Island are a pupping season of 2–2.5 months a year with a peak in late July; a lactation period lasting 5–6 weeks; ovulation, which occurs at the end of lactation or within a few weeks after; and a delay of implantation of about 2 months. Adult males in southeastern Vancouver Island are reproductively active (having sperm in the epididymis) from March to November and inactive (having no sperm in the epididymis) from December to February. Females mature at 2–5 years of age with most maturing at 3 and 4 years. Males mature between 3 and 6 years of age with most maturing by 5 years. On the average, 88% of mature females produce a pup each year. Reproductive failure in adult females results from an unsuccessful mating, failure of the blastocyst to implant, embryonic resorption, or abortion.

Prenatal males and females grow at similar rates from implantation to birth. At birth both sexes are about the same size averaging 81.6 cm in length and 10.2 kg in weight. By weaning time the weight averages 24.0 kg. From birth to 5 years of age males and females grow at similar rates; females are fully grown by this time and average 64.8 kg in weight and 147.7 cm in length; males continue to grow until 9–10 years of age and then average 87.0 kg in weight and 161.1 cm in length.

Females comprise 56% of prenatal seals; 50% pups; and 53% seals aged one or more years just before the pupping season. Just before the birth season 55% of all females and 42% of all males are mature. The average annual mortalities from birth to 5 years are similar, males averaging 21% and females 20%. After 5 years, mortality of the male increases to average 29%; that of the female decreases to average 15%. The number of seals in British Columbia just prior to the pupping season is estimated to be at least 11,400; a more likely estimate is calculated to be about 35,000 seals.

INTRODUCTION

This is a report on the results of a field study made on the harbour seal, *Phoca vitulina richardi* Gray, in British Columbia. The study, supported by the Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C., makes use of a recently developed method for aging the seal to describe previously unknown aspects of its general biology needed to establish a management program for its harvest in British Columbia. Field observations and a collection of 415 specimens were used to verify the method of aging and to describe the reproductive cycles and ages at sexual maturity, prenatal and postnatal growth, and population composition and dynamics. Relevant literature is also reviewed.

In British Columbia this seal is common in all coastal areas and is economically important for two reasons. First, it has gained notoriety from the fishing industry and sports fishermen as a predator on commercially valuable fish species. Fisher (1952) estimated that it damages up to 12% of the salmon caught in gillnets on the Skeena River during April and May. To reduce this predation the Department of Fisheries of Canada put a bounty on the seal from 1914 to 1964. Second, since 1962 this seal has been hunted for its commercially valued pelt. Seal hunters generally receive between $5 and $35 for a prime raw pelt and up to $50 when the demand is high. These economic considerations have resulted in three studies on its general biology including a description of its life history and status (Fisher, 1952), food habits (Spalding, 1964), and molt and pelage patterns (Stutz, 1967a, b).

The subspecies *P. v. richardi* (Fig. 1) is found on the west and north coasts of North America from Baja California to the Aleutian Islands, the eastern part of the Bering Sea, and Herschel Island (Scheffer, 1958). The species is widely distributed in the temperate coastal region of the North Atlantic and North Pacific. Other subspecies of *Phoca vitulina* include *vitulina,* found in the eastern Atlantic, *concolor,* in the western Atlantic, and *mellonae,* in the Seal Lakes, Quebec. Whether the form *P. v. largha,* found in the western Pacific, is a subspecies or a separate species is in dispute (McLaren, 1966).

Though the life cycle of the species has been studied by several workers (Havinga, 1933; Scheffer and Slipp, 1944; Fisher, 1952, 1954; Harrison, 1963; Bishop, MS, 1968), it has been generally incompletely known. The main reasons have been the difficulty in observing in the field and in collecting specimens from all months of the year, and the lack of an aging technique. Only Bishop (MS, 1968), in Alaska, has used aged specimens to describe its life cycle.

The harbour seal lives mainly along the coast, favouring tidal mud flats, sand bars, estuaries, and reefs. Though primarily marine, it is also found in accessible rivers and lakes. Generally it is wary and cannot be approached easily though it may frequent populated areas. This seal is not migratory like the northern fur seal,

FIG. 1. Two adult female *Phoca vitulina richardi* hauled out and sunning themselves.

which travels thousands of miles a year to breed, but local movements are known to be associated with tides, food, reproduction, and season. Its main foods are fish, molluscs, and crustaceans.

The species tends to form loosely gregarious herds each day, which haul out to rest in sheltered areas. When not hauled out, individuals usually disperse along the shore and become solitary. Groups are generally composed of males and females of all ages and in most areas are not larger than a few hundred seals. There is little social structure in the herd, even during the breeding season. No territory or harem is formed on land by the adult males as in the northern fur seal; instead, mating is promiscuous and takes place in the water.

Females usually have one pup a year, during a 1–2½ month period. The young may be born on land or in water and in the group or solitarily. Pups can swim and dive at birth and are closely attended by their mothers until weaning time, when they are abandoned. Mating generally occurs at weaning time or shortly after.

METHODS AND MATERIALS

In all, 324 postnatal and 79 prenatal seals were collected and studied in British Columbia between 1964 and 1968. An additional 12 postnatal seals, taken from 1958 to 1961, were examined from the pinniped collection at the Fisheries Research Board of Canada's Biological Station, Nanaimo, B.C. The lower jaw with a canine tooth (used for aging), the reproductive organs, and growth measurements were taken from most specimens. All tissues were preserved in 10% formalin.

Seals were collected from many coastal regions, the main study area being southeastern Vancouver Island and the adjacent mainland (Fig. 2). Specimens were also taken from western and northeastern Vancouver Island, southwestern Queen Charlotte Islands, the Skeena River, and Kitimat.

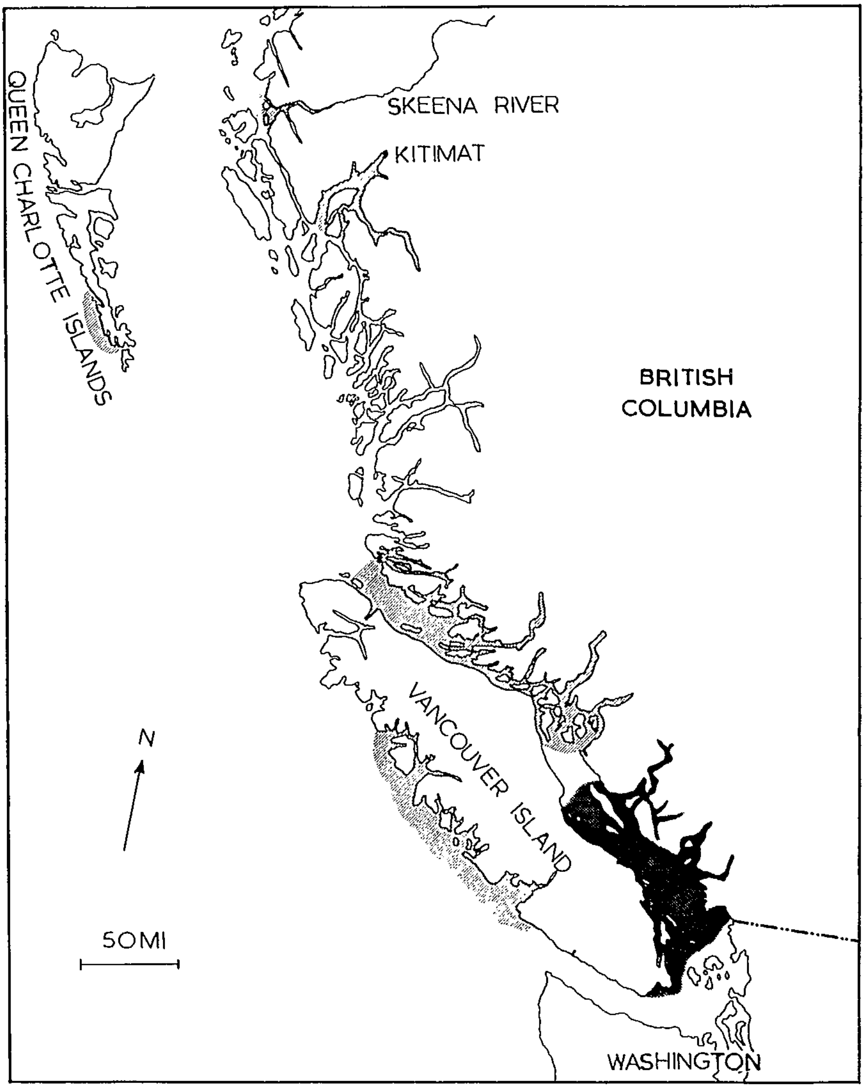

FIG. 2. Sampling areas for harbour seals in British Columbia. The main study area is crosshatched; other areas are hatched.

The seal was most effectively hunted by cruising the coast in a 12–14 ft outboard motor boat until one was spotted close to land. The animal was shot from shore with a .222 or .243 rifle with 4-power telescopic sights and was retrieved by boat. Some animals were also collected by waiting in ambush in areas they were known to frequent.

Although the seal tends to congregate in greatest numbers in large river mouths and mud flats, generally these are not the best areas to hunt as the seal cannot be approached unnoticed. Consequently, most specimens were collected as individuals from reefs, small islands, and inlets along the coast where they were more easily stalked.

For determining the age of each specimen, a canine tooth from the lower jaw was removed and sectioned to show annuli in the layer of cementum. The jaw was boiled in water for about 45 min and the tooth was extracted by working or cutting it free. Excess connective tissue was scraped off and the tooth was allowed to dry. If the opening to the pulp cavity was not yet sealed, its diameter $\left(\frac{\text{width} + \text{depth}}{2}\right)$ was noted. The teeth were stored in airtight jars to prevent cracking before they were sectioned.

Teeth were prepared for sectioning by imbedding them in Ward's Bioplastic mounting medium. Several longitudinal slices, 50–150 μ thick, were cut from the centre of each tooth with a circular diamond saw (Gillings-Hamco thin-sectioning machine). Sections were examined under a 15-power binocular dissecting microscope, in reflected light. Although annuli were usually visible in the cementum without further treatment, they were most readily seen after sections were immersed and partially cleared in benzyl-benzoate or xylene for a few days.

In calculating age, it was assumed that if a seal were collected in southern British Columbia its birth date was July 15, even though young were born from late June to early September in this region. Similarly, seals from the northern parts of British Columbia were assumed to have been born on June 15. The age given to a seal was based on the closest birthday, as is done for other species of seal (Anon., 1963; Smith, 1966). A pup, for example, is from 0.0 to 5.9 months of age; a one-year-old is 6.0 to 17.9 months; a two-year-old is 18.0 to 29.9 months and so on.

The reproductive condition of postnatal seals was determined from an examination of their reproductive organs. From each female, both ovaries and the uterus were checked for evidence of ovulation and pregnancy. The ovaries were transversely sectioned into slices 2 mm thick with a handheld razor blade and inspected for the presence and size of a corpus luteum and corpus albicans. The diameter $\left(\frac{\text{width} + \text{depth}}{2}\right)$ of each corpus was taken from the slice containing the largest view. The uterus was opened and examined for the presence and condition of an embryo.

From each male, generally both testes and epididymides were examined to determine if the seal were sexually mature and in breeding condition. The testes and epididymides were weighed separately to the nearest 0.1 g. One testis and its epididymis, usually from the right side, were examined histologically for evidence of spermatogenic activity. A transverse slice of tissue was removed from the centre of each testis and epididymis and a longitudinal section from the epididymis in the region adjacent to the vasa efferentia. Tissues were imbedded in paraffin wax, sectioned at 8 μ, and stained with Harris's haematoxylin and eosin. Sections from the testis and from the longitudinal preparation of the epididymis were examined for evidence of spermatogenic activity from a random inspection of 100 tubules. The outside diameters $\left(\frac{\text{width} + \text{depth}}{2}\right)$ of the tubules in the testis and transverse preparation of the epididymis were each taken from the first 10 tubules viewed in cross section.

Two measurements for body growth were taken from postnatal seals, standard length and weight. Standard length is body length in a straight line from the tip of the nose to the tip of the tail. Weights were recorded with a Chatillon spring scale, capacity 200 lb, without allowance for blood loss from shooting. Only length was recorded from embryos, the length from the nose across the face to the back of the head and along the side of the vertebral column to the tip of the tail being used for the standard length in small embryos.

Analyses of data involving the timing of events in the annual cycle were made on specimens collected from southeastern Vancouver Island and the adjacent mainland. Data cannot be lumped from all areas sampled because regional differences exist in the cycle. Other analyses were based on data collected from all areas.

METHOD OF AGING

As with many species of seals (Laws, 1962), age can be determined in *P. v. richardi* by counting growth zones in the cementum layer of canine teeth. These zones, or annuli, appear as alternating opaque and translucent bands in thin sections of teeth (Fig. 3A, F). It was found that between ages 1 and 29 years one opaque and one translucent zone were laid down each year (Fig. 4). Mansfield and Fisher (1960) suggested that the two zones are deposited annually, and determined that a captive seal, known to be 19.5 years old, was between 18 and 20 years old on the basis of the annuli.

Though annuli in the dentine layer of canine teeth are satisfactory for aging some species, they are not as useful as those in the cementum for aging harbour seals. Mansfield and Fisher (1960) stated that when annuli are present in the dentine they agree in number with those found in the cementum. Bishop (MS, 1968) reported that, after 4 years of age, annuli in the dentine become increasingly irregular and difficult to count.

DEVELOPMENT OF CANINE TEETH

Eruption of the canine teeth in *P. v. richardi* and deposition of dentine and cementum in them were found to occur as reported by Bishop (MS, 1968) for this subspecies in Alaska.

The canine tooth erupts through the gum within several days after birth. It consists of an enamel cap 10–13 mm long and a thin cylinder of dentine extending about 15 mm out of the cap. After birth, dentine is laid down on the inside surface of the tooth, forming a second cylinder, which gradually grows deeper into

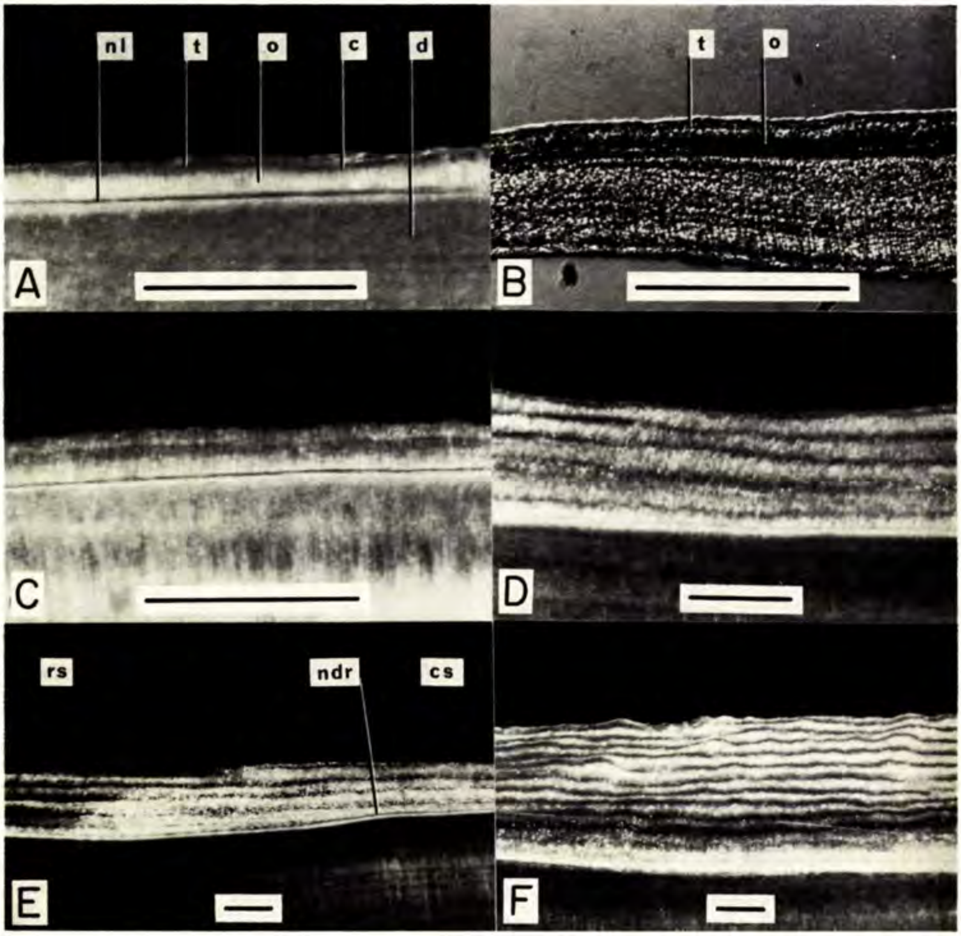

FIG. 3. Appearance of cementum layers in the canine teeth of *Phoca vitulina richardi*. Views are of longitudinal slices 50–150 μ thick; the scale represents 0.5 mm. (*A*) View in reflected light at age 7 months (specimen H5) showing dentine (*d*), cementum (*c*), and neonatal line (*nl*); the cementum contains an opaque (light) layer (*o*) and an incomplete translucent (dark) layer (*t*). (*B*) The same tooth as in *A*, viewed in transmitted light; the opaque cementum layer appears dark and the translucent layer light, though they appear light and dark respectively in reflected light (see *A*). (*C*) View in reflected light at age 1 year 0 months (B97); an opaque layer is being deposited in the cementum. (*D*) View in reflected light at 4 years 6 months (G12) showing small canals crossing each opaque layer; a translucent layer is being deposited. (*E*) View in reflected light; there are 5 opaque layers on the root side (*rs*) of the neonatal dentine ridge (*ndr*) and 4 on the crown side (*cs*) (G12, age 4 years 6 months). (*F*) View in reflected light at age 12 years 2 months (B117); an opaque layer is being deposited.

the tooth socket. The external junction of the two cylinders is marked by the neonatal dentine ridge (Fig. 5). By about 7 months of age the second cylinder of dentine extends 10–11 mm past the ridge into the jaw. After this, dentine is laid down only in the pulp cavity.

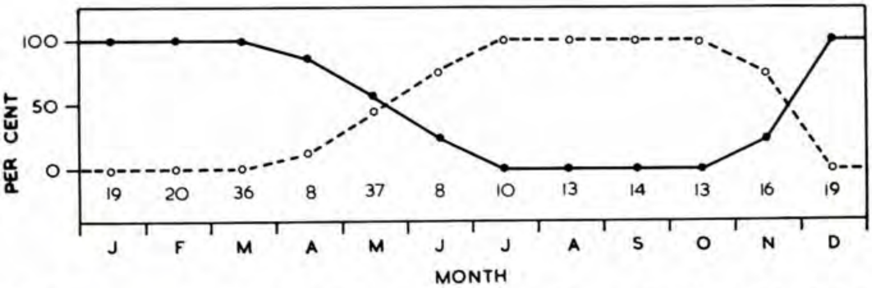

FIG. 4. Average per cents of seals collected from southeastern Vancouver Island that were depositing translucent (●) and opaque (○) cementum at the time of capture. Numerals near plotted points are numbers of seals. Ages ranged from 1 to 29 years.

The first cementum is deposited at 2–3 months of age, on the external surface of the tooth from the neonatal ridge to the opening of the pulp cavity. The cementum and dentine are separated by the neonatal line, a narrow, well-defined zone seen when thin sections of teeth are viewed microscopically (Fig. 3A). Successive layers of cementum extend almost to the enamel cap, the outer layers tending not to extend so far as the inner.

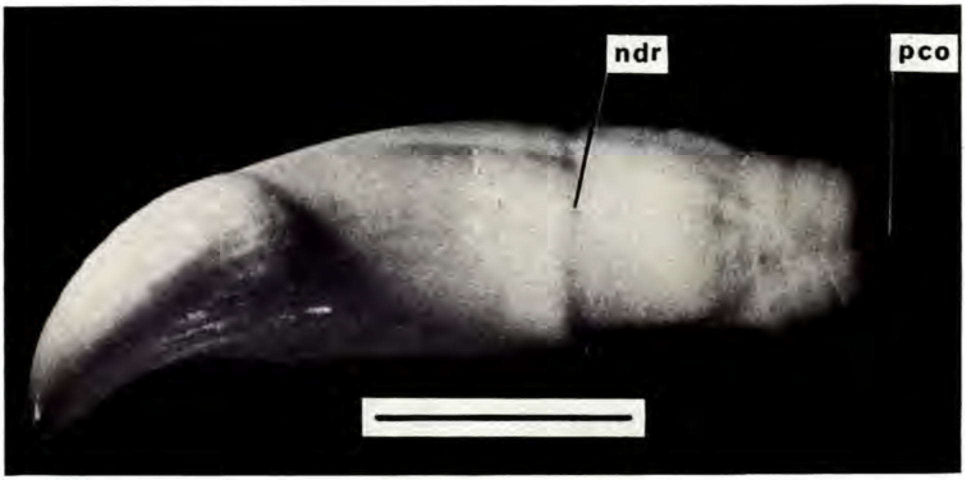

FIG. 5. Lateral view of the lower right canine tooth of a seal age 9 months (specimen B249) showing the neonatal dentine ridge (*ndr*) and pulp cavity opening (*pco*). Scale represents 10 mm.

At birth, the opening to the pulp cavity averages about 6 mm in diam (Fig. 6). By 12 months of age the opening is reduced to about 2.5 mm in diam. Seals under 12 months of age can be readily distinguished from older ones by the larger openings. The opening is sealed, except for a small canal for blood vessels and nerves, by the cementum in 2–4 years. In Alaska, the pulp cavity in this subspecies is reported to close in 2–3 years (Bishop, MS, 1968).

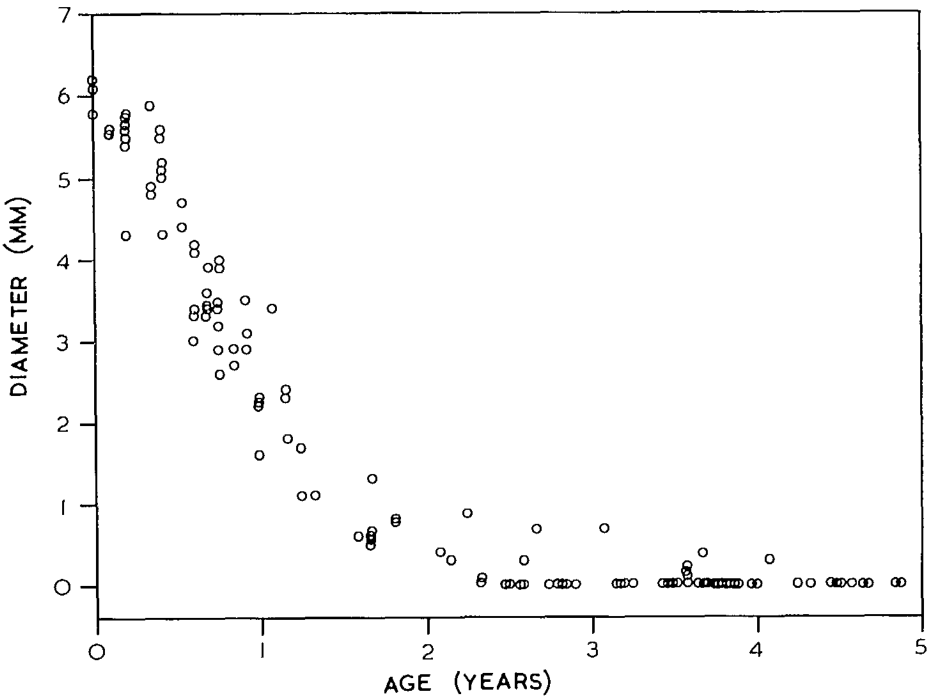

FIG. 6. Decrease in diameter of pulp cavity opening in lower canine tooth with increasing age in 117 seals.

ANNULI IN THE CEMENTUM

The alternating opaque and translucent annuli in the cementum lie parallel to the neonatal line. The opaque layers appear light in reflected light (Fig. 3A) and dark in transmitted light (Fig. 3B) because they reflect most of the light. The translucent layers appear dark in reflected light and light in transmitted light because they transmit most of the light.

The first layer, an opaque one, is deposited in 1–2 months, that is, by the end of November; only occasionally does it extend on to the crown side of the neonatal dentine ridge. Translucent layers are laid down between late autumn and late spring and later opaque layers between late spring and late autumn (Fig. 4), though Mansfield and Fisher (1960) suggested that the translucent layer is laid down during spring and early summer in the western Atlantic subspecies. At 7 months of age, for example, a seal has the first opaque layer and about half of a translucent layer (Fig. 3A); at 12 months, one and a half opaque and one translucent layer (Fig. 3C); at 4 years 6 months, five opaque and four and a half translucent layers (Fig. 3D). Because little or no cementum is formed on the crown side of the ridge until after 1 year of age in many seals (Fig. 3E), it is important to count the annuli on the root side of the ridge.

In some specimens the annuli are difficult to count because they are close together, indistinct, or appear to split. Occasionally, for example, the first opaque layer appears to be split by a narrow translucent zone. A similar extra band appears in the first year cementum of this subspecies in Alaska (Bishop, MS, 1968).

In sections that have not been completely cleared by the clearing agent (xylene or benzyl-benzoate), the opaque layers appear to contain minute, parallel, transverse canals (Fig. 3D). The canals give these layers much of their light-reflecting properties. In sections that are completely cleared, the canals are not visible and the layers are more difficult to distinguish. They can be distinguished from the translucent layers, however, as each contains several closely packed strands forming a fibrelike network. The translucent layers do not have canals or a fibre-like network and appear translucent on complete clearing. If the difference in composition between the two layers is the same as that shown by Irie (1960) for the opaque and translucent annuli in otoliths of teleost fishes, the opaque layers contain more protein and less calcium carbonate than the translucent layers.

REPRODUCTION

Observations on reproduction in *P. v. richardi* were made by others as follows: Scheffer and Slipp (1944) outlined the breeding habits in Washington State; Fisher (1952) noted dates of birth, lactation, and mating in the Skeena River; Bishop (MS, 1968) described breeding behaviour and the reproductive cycle in Alaska; and Bigg (1969) reported regional differences in the birth season.

Studies made on the subspecies in the Atlantic (*P. v. concolor* and *P. v. vitulina*) describe the reproductive organs (Harrison et al., 1952; Harrison, 1960; Amoroso et al., 1965), the annual cycle (Havinga, 1933; Fisher, 1954; Harrison, 1960, 1963), and breeding behaviour (Venables and Venables, 1955, 1957, 1959).

ANNUAL CYCLE OF ADULT FEMALE

PUPPING

In *P. v. richardi,* pupping tends to occur progressively later as one goes southeast from Alaska to southern Puget Sound, Washington, and earlier as one goes south from Willapa Bay, Washington, to Baja California (Bigg, 1969). In southeastern Vancouver Island and the adjacent mainland, births were observed from June 24 to September 6 with a peak in late July (Fig. 7). In the Skeena River pupping occurs from late May to late June (Fisher, 1952).

Though twin pregnancies have been reported in the State of Washington (Scheffer and Slipp, 1944), evidence of only single ovulations or pregnancies was found in 80 adult females collected in British Columbia.

LACTATION

The study suggests that in southeastern Vancouver Island lactation lasts from 5 to 6 weeks: the peak pupping time was late July and the peak weaning time was

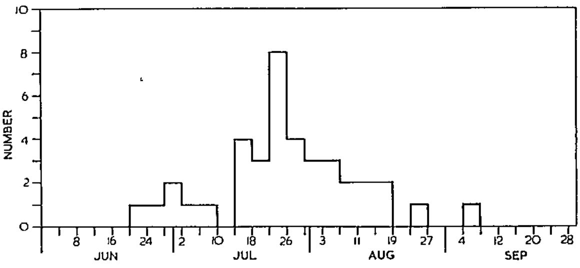

FIG. 7. Frequencies, at 4-day intervals, of newborn pups (total, 39) observed in southeastern Vancouver Island.

late August to early September. The peak weaning time was assumed to have occurred when most pups collected had no milk in their stomachs and most pups were unattended by their mothers. The lactation periods reported by other workers for *P. v. richardi* range from 3–4 weeks in Alaska (Bishop, MS, 1968) to 4–6 weeks in Washington State (Scheffer and Slipp, 1944) and about 6 weeks in the Skeena River and California (Fisher, 1952; Finch, 1966). Fisher (1952) stated that the suckling period appears to be longer for seals in fresh water than for those in salt water.

In the western Atlantic subspecies, lactation is reported to last 2–3 weeks (Fisher, 1954) and in the eastern Atlantic subspecies from 4 to 6 weeks (Havinga, 1933; Sergeant, 1951; Venables and Venables, 1955; Harrison, 1963).

OVULATION

In southeastern Vancouver Island, most ovulations probably occur during September, at the end of weaning, or shortly after. Ovulation had not taken place in any of the nine lactating females collected on July 17 (2 specimens) and 31 (1), August 7 (1), 16 (1), 22 (1), and 25 (1), and September 14 (1) and 17 (1), but had occurred in all recently pregnant nonlactating females collected on September 17 (1) and October 9 (3) and 10 (1) and a female pregnant for the first time on September 12. Therefore, as ovulation does not occur until the end of lactation or after, weaning generally being in late August to early September, and all adults taken after September had ovulated, most ovulations must occur in September.

Bishop (MS, 1968) suggested that in Alaska *P. v. richardi* ovulates about 2 weeks after weaning. In Washington State, mating is believed to take place most frequently in September (Scheffer and Slipp, 1944); in the Skeena River, during September and October (Fisher, 1952).

Ovulation in the western Atlantic subspecies is reported to occur immediately after weaning (Fisher, 1954) and in the eastern Atlantic subspecies from 2 to about 8 weeks after (Havinga, 1933; Venables and Venables, 1955, 1957; Harrison, 1963).

Though no new or imminent ovulations were observed during other months of the year in British Columbia, Harrison (1963) stated that some young females in The Wash, England, ovulated about 2 months earlier than females with suckling young. Also, Venables and Venables (1959) recorded subadult matings in Shetland, Scotland, about 4 months before adults were observed to mate.

DELAY OF IMPLANTATION

In British Columbia seals, the conceptus is not usually implanted in the uterus until mid-November, about 2 months after fertilization. No implantations were found in 8 recently ovulated females taken in southeastern Vancouver Island on September 12 (1 specimen) and 17 (1), October 9 (3) and 10 (1), and November 2 (1) and 7 (1), but all 9 collected from December 9 (1), 13 (3), 25 (1), and 31 (4) had implanted embryos. The embryos ranged from 17 to 116 mm in length, suggesting implantation about mid-November. Bishop (MS, 1968) wrote that this subspecies in Alaska has an implantation delay of about 1.5–2 months.

Fisher (1954) and Harrison (1963) reported that the two subspecies in the Atlantic had a delay of implantation of 2–3 months.

ANNUAL CYCLE OF ADULT MALE

An analysis of the size and content of the testes and epididymides of males collected in southeastern Vancouver Island (Fig. 8, 9) suggests that adult males are in breeding condition (sperm in the epididymis) from March to November and in nonbreeding condition (no sperm in the epididymis) from December to February. Males were considered adult if one or more per cent of the epididymal tubules adjacent to the vasa efferentia contained sperm or if they were 6 years of age or

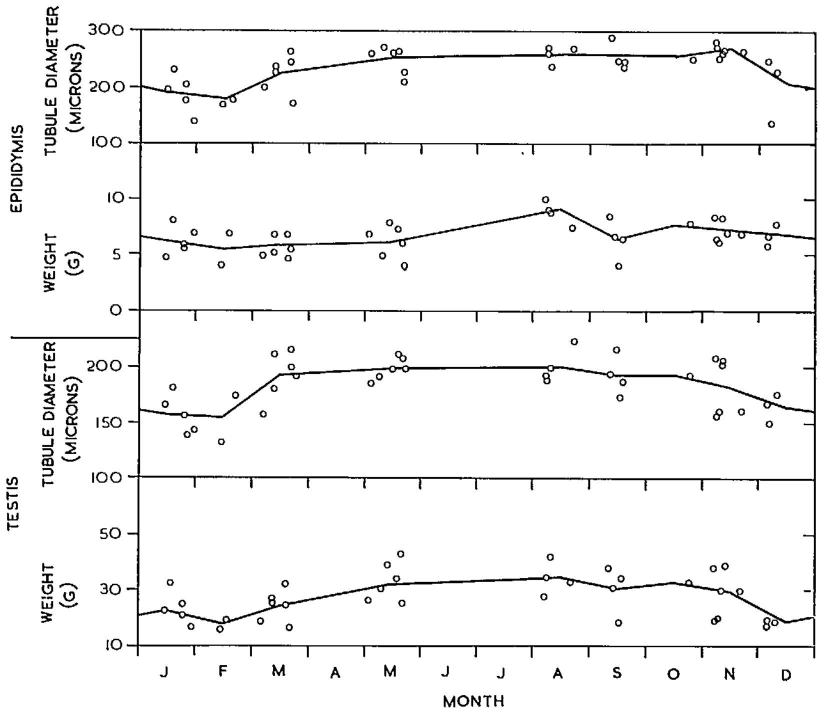

FIG. 8. Monthly variation in weights of testis and epididymis and in outside diameters of the tubules from 37 adult males collected in southeastern Vancouver Island. Lines connect average monthly values.

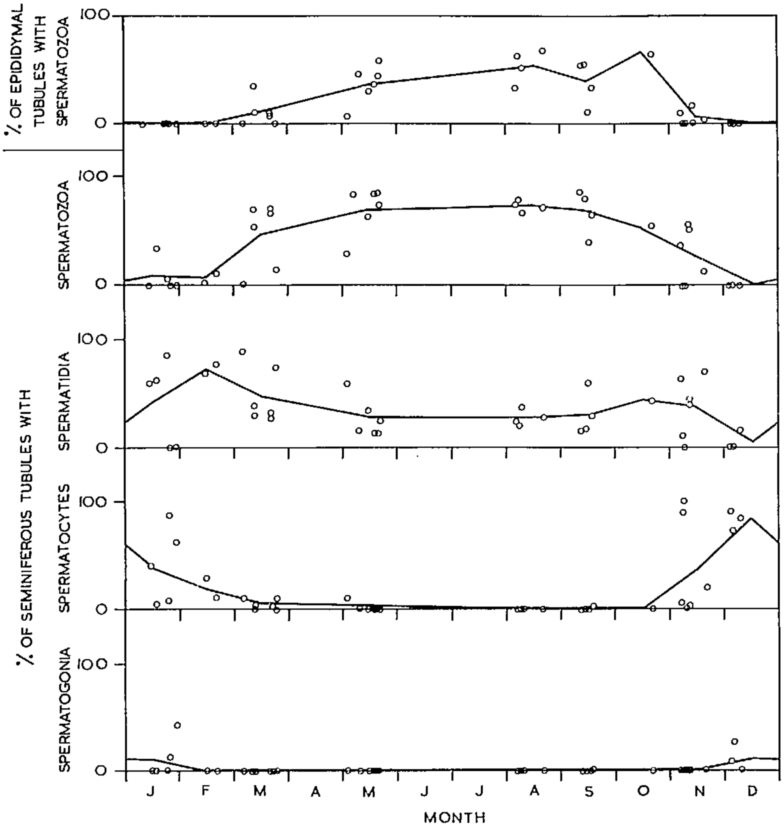

FIG. 9. Monthly development of germ cells in testis and epididymis from 37 adult males collected in southeastern Vancouver Island. Lines connect average monthly values.

older. The presence of sperm in the epididymis was chosen as a criterion of maturity rather than the presence of sperm in the testis because Bishop and Walton (1962), in reviewing patterns of mammalian spermatogenesis, stated that sperm maturation is completed in the epididymis. All males 6 years of age and older were found to have sperm in the epididymis during the breeding season (discussed later, p. 16) and were thus adult. Bishop (MS, 1968) also found that all males of this subspecies in Alaska are mature by 6 years. The age criterion permits an analysis of the reproductive condition of adults collected during the sexually inactive period.

From December to February, no sperm were found in the tubules of the epididymis (Fig. 10B). The diameters of the tubules were smallest of the year in these months (avg 194 μ) though the weight of the epididymis was smallest in February (avg 5.5 g). The weight of the testis (avg 20.6 g) and the diameters of the seminiferous tubules (avg 159 μ) were also smallest from December to February (Fig. 10A). During this time an average of 5% of the seminiferous tubules had

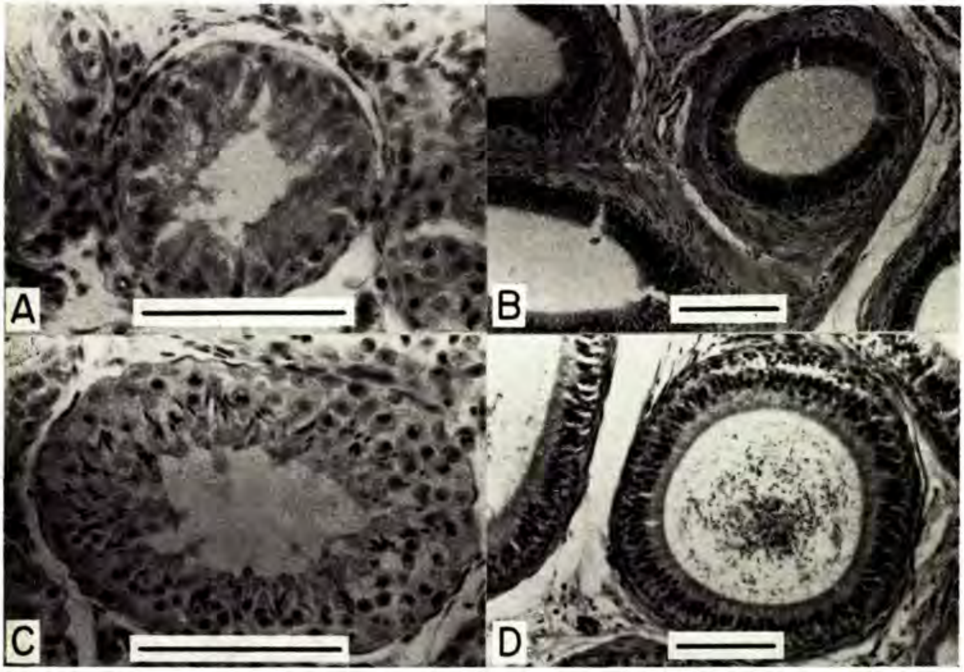

FIG. 10. Photomicrographs of seminiferous and epididymal tubules of adult males during the sexually active and inactive periods. Scale represents 100 μ. (*A*) Seminiferous tubules during the sexually inactive period (specimen B19, collected December 6) showing the small tubule diameter and germ cells at the spermatogonia stage. (*B*) Epididymal tubules from the same male as in *A*; the tubules are small and contain no sperm. (*C*) Seminiferous tubules during the sexually active period (B67, May 10) showing enlarged tubules and the development of the germ cells to sperm. (*D*) Epididymal tubules from the same male as in *C*; tubules are enlarged and contain sperm.

germ cells developed to sperm, 37% to spermatidia, 49% to spermatocytes, and 9% to spermatogonia.

From March to November, sperm were found in an average of 28% of the epididymal tubules (Fig. 10D). The diameters of the epididymal tubules were largest at this time (avg 253 μ), though the weight of the epididymis was highest in August (avg 9.1 g). Between March and November, the weight of the testis (avg 29.9 g) and the diameters of the seminiferous tubules (avg 193 μ) were highest of the year (Fig. 10C). At this time, an average of 55% of the seminiferous tubules had germ cells developed to sperm, 35% to spermatidia, 10% to spermatocytes, and 0% to spermatogonia.

The male harbour seal is, therefore, a seasonal breeder in southeastern Vancouver Island, being sexually active for 8–9 months of the year. Though most matings probably occur in September, males are capable of breeding 6 months prior to this time and 2 months afterwards.

Other studies on this subspecies suggest that in Nisqually, Washington, spermatogenesis begins in early July (Scheffer and Slipp, 1944), and in the Fraser River, British Columbia, one male collected on September 25 was in breeding condition

(Fisher, 1952). In Alaska, Bishop (MS, 1968) found epididymal sperm in males collected between May 25 and October 30 even though most matings occur from late June to late July.

Information on the subspecies from The Wash, England, suggests that adults collected in April and June have epididymal sperm and that mating occurs from mid-July to mid-September (Harrison, 1960, 1963; Amoroso et al., 1965).

AGE OF FEMALE AT SEXUAL MATURITY

Females were considered sexually mature after their first ovulation. An examination of ovaries for evidence of first ovulations (Table 1) suggests that 20% mature at 2 years of age, 38% at 3, 34% at 4, and 8% at 5 years.

Females were considered to have ovulated for the first time if their ovaries contained either one corpus luteum or one corpus albicans. This criterion was established from an analysis of the formation and regression of the corpus luteum and corpus albicans. The analysis suggests that during a reproductively successful year the corpus luteum is a large, tan-colored structure in the ovary from fertilization to parturition and then regresses to become a small, pale tan-colored corpus albicans by the next ovulation (Fig. 11, 12). Later it appears as a white knot of connective tissue. The corpus albicans is resorbed in 1–4 years, as older females, which must have ovulated many times, have only one to four corpora albicantia (Fig. 13). Bishop (MS, 1968) stated that the corpus albicans of this subspecies in Alaska generally persists for about 1 year though resorption may take less than a year or up to 2 years. Thus, females with only one corpus luteum or one corpus albicans were considered to have ovulated once; females with one corpus luteum

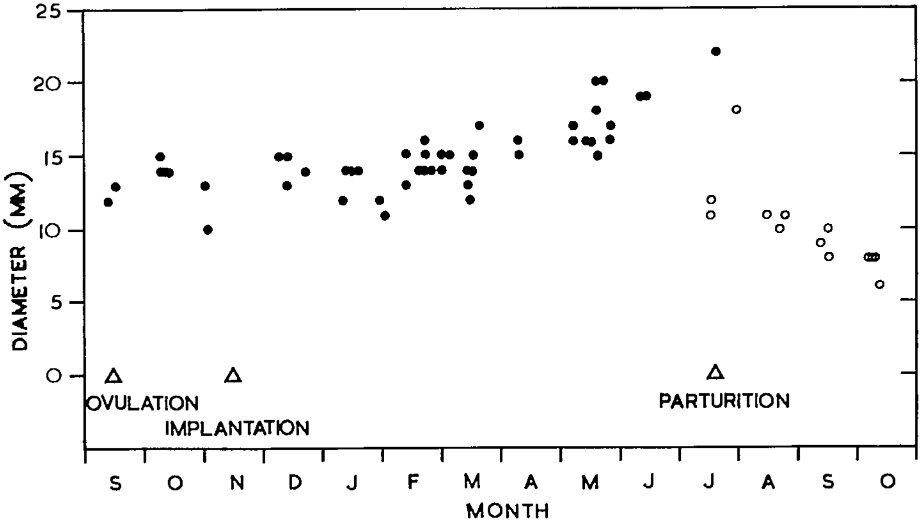

FIG. 11. Monthly variation in diameters of the corpus luteum (●) and newly formed corpus albicans (○) in 57 females during a reproductively successful year in southeastern Vancouver Island. Pregnancy was assumed during the delay of implantation.

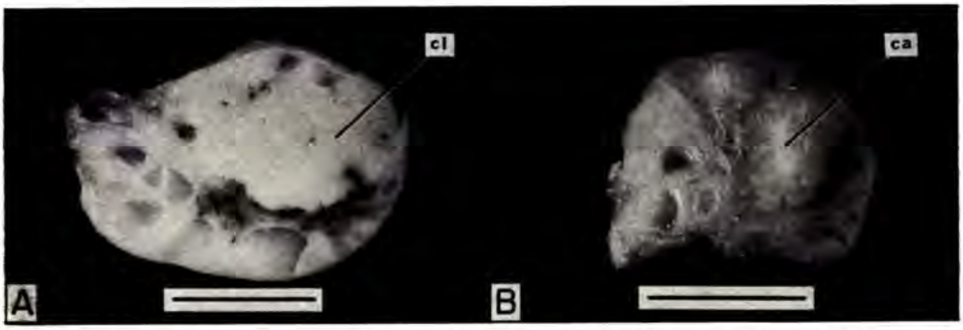

FIG. 12. Appearance of the corpus luteum (*cl*) and recently formed corpus albicans (*ca*) in a female (specimen A16, collected October 10) taken during the delay of implantation. The left ovary (*A*) contains the corpus luteum formed during the last mating season and the right (*B*) the remnants of the corpus luteum of the previous mating season. Scale represents 10 mm.

and one or more corpora albicantia or no corpus luteum and more than one corpus albicans were considered to have ovulated an indeterminable number of times due to the irregular resorption rate of the corpus albicans after 1 year.

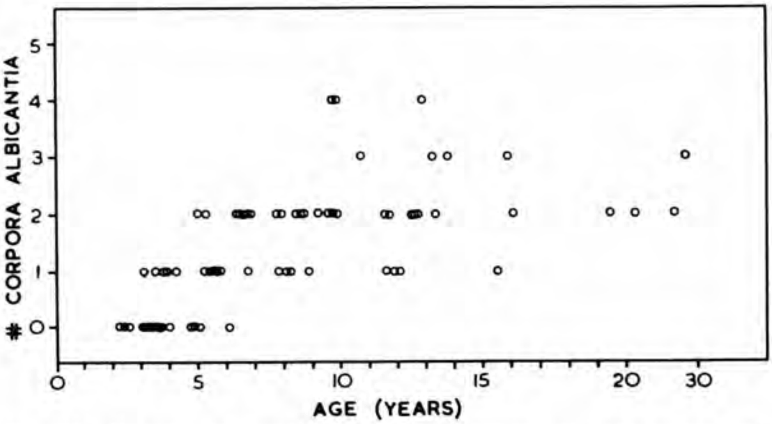

FIG. 13. Variation in number of corpora albicantia in both ovaries with increasing age in 72 females.

During a missed pregnancy, the corpus luteum and corpus albicans may regress at different rates than during a normal pregnancy. The ovulation might, therefore, go undetected. However, the corpus albicans of a missed pregnancy is not resorbed immediately; a young nonpregnant adult collected on April 19 (p. 18) had retained its corpus albicans for at least 4–5 months.

Other studies on *P. v. richardi* suggest that in Washington State females are at least 2 years of age before ovulating (Scheffer and Slipp, 1944) and in Alaska they are mature at 3–4 years of age (Bishop, MS, 1968).

Females of the eastern Atlantic subspecies are reported to mature between 3 and 6 years of age (Havinga, 1933; Laws, 1956; Harrison, 1960).

TABLE 1. Age at sexual maturity in 138 females.

Age at last mating season (*years*)	No. females in sample	1st ovulations		
		No.	Proportion (P_i)	Proportion (%) in stable sample (P_j)[a]
Pup	35	0	0/35	0
1	14	0	0/14	0
2	11	4	4/11	20
3	18	12	12/18	38
4	5	3	3/5	34
5	7	1	1/7	8
6	7	0	0/7	0
7–28	41	0	0/41	0
Total:				100

[a] Proportioning adjustment $P_j = \frac{P_i}{\Sigma P_i}$.

TABLE 2. Age at sexual maturity in 46 males collected from southeastern Vancouver Island between May 1 and September 30, the period when all adult males are thought to be in breeding condition (having sperm in the epididymis) (Fig. 9). Each male is classified on the basis of the most advanced stage of germ cell development in its testis and epididymis. The germ cell categories are as follows: 1% or more of the seminiferous tubules containing spermatogonia, spermatocytes, spermatidia, or sperm, and 1% or more of the epididymal tubules containing sperm.

Age (*years*)	No. males in sample	Immature (%)				Mature (%)
		Spermatogonia	Spermatocytes	Spermatidia	Sperm in testis	Sperm in epididymis
Pup	7	100	0	0	0	0
1	6	100	0	0	0	0
2	4	100	0	0	0	0
3	8	25	38	12	13	12
4	6	17	66	0	17	0
5	7	0	0	14	14	72
6	4	0	0	0	0	100
7–11	4	0	0	0	0	100

AGE OF MALE AT SEXUAL MATURITY

Males were considered sexually mature if one or more per cent of their epididymal tubules adjacent to the vasa efferentia contained sperm between May 1 and September 30, that portion of the breeding season when all adults are thought to have sperm in their epididymides (Fig. 9). On this basis, males reach sexual maturity between 3 and 6 years of age, most maturing by 5 years.

An analysis of 46 males suggests that there is no spermatogenic activity in pups and 1- and 2-year-olds, only spermatogonia in the gonads (Table 2). Sexual activity begins at 3 years of age, 12% having sperm in the epididymis, and thus being mature, and most of the remainder having the germ cells in the seminiferous tubules developed to spermatocytes, spermatidia, or sperm. By 5 years of age, 72% of the males are mature; by 6 years, 100%.

In the same subspecies, Fisher (1952) compared baculum size with body size and suggested that males in British Columbia mature at 3 years. Bishop (MS, 1968), using the presence of abundant sperm in the epididymis as the criterion of maturity, concluded that all males in Alaska are mature by 6 years, some probably maturing at 5.

Males of the eastern Atlantic subspecies are thought to mature between 3 and 6 years of age (Havinga, 1933; Harrison, 1960).

FECUNDITY

The fecundity, or reproductive capacity, of females was determined from an examination of 66 adults, aged 2–28 years, collected between the time of implantation of the conceptus and that of the next ovulation (Table 3). This time interval was chosen to avoid assuming pregnancy in females taken during the delay of implantation. Reproductive failures were recorded in 7 out of 35 females from 2 to 7 years of age and in one 13-year-old out of 31 females from 8 to 28 years of age. For practical purposes, the average figure of 80% fecundity was used for age-groups 2–7 years and 97% for older seals. These percentages may be slightly high because many females examined were collected several months prior to parturition and some additional intrauterine mortality might be expected later in the pregnancy.

TABLE 3. Fecundity in 66 adult females collected between implantation time and the next ovulation.

Age at last mating season (*years*)	No. females in sample	Number pregnant	Fecundity (%)	Avg fecundity (%)
2	2	0	0	80
3	13	11	85	
4	4	4	100	
5	5	4	80	
6	5	5	100	
7	6	4	67	
8–28	31	30	97	97

These data indicate that the number of young born in a population depends upon the age distribution of adult females and that a meaningful estimate of fecundity can only be calculated from a sample of adults randomly collected (see

p. 23 for a discussion of random sampling). From the age distribution of 72 randomly collected adults and the fecundity rates at their ages, the average adult fecundity was calculated as 88% as follows:

Age at last mating season (*years*)	No. females in sample	% of sample	Fecundity (%)	
			Of age-group	Of random sample
2–7	40	56	80	45
8–28	32	44	97	43
Total	72	100		88

No comparable fecundity statistics are available for *P. v. richardi* in other regions. In Alaska, however, Bishop (MS, 1968) noted that two of six mature females taken about 1.5 months after implantation time were not pregnant and that 92% of females that had several pregnancies had either 2 successive pregnancies or 2 successive annual ovulations.

CAUSES OF REPRODUCTIVE FAILURE

The factors responsible for reproductive failure in females were classified as (1) an unsuccessful mating or failure of the blastocyst to implant; (2) embryonic resorption; or (3) abortion.

In the first category were three females that had ovulated for the first time and possibly one female that had had several pregnancies. The uteri of the three females ovulating for the first time, collected on February 24, March 18, and April 19, were juvenile in appearance suggesting that if pregnancy had occurred it was probably not maintained after implantation time. The uterine horn circumferences (range 23–27 mm) were slightly larger than those of immature females (range 16–23 mm), but much smaller than those of nonpregnant adults (range 48–70 mm) that had had several young. Their respective corpora albicantia were 9, 8, and 5 mm in diam and contained some tan coloration.

Failure in the female with several past pregnancies may have resulted from either of the first two causes listed. It is difficult to say, as the seal was collected on January 11, about 2 months after implantation time, and although no uterine evidence of pregnancy was found there may have been sufficient time for a small embryo to be resorbed. Its corpus luteum appeared normal and was about the same diameter (14 mm) as those of pregnant females taken at this time. Bishop (MS, 1968) reported that a female *P. v. richardi* taken in Alaska about 1.5 months after implantation time may have failed to implant or resorbed its foetus. He also noted that another female taken at the same time had resorbed the embryo, leaving only the foetal membranes. In the present study, an embryo was being resorbed in a female pregnant for the first time taken on March 1; the foetus showed signs of degeneration and was 8.4 cm long compared to the average embryonic size of about 37 cm at this time. The corpus luteum diameter (14 mm) and appearance were similar to those in females carrying healthy embryos in March.

Three females that had had several pregnancies, collected on May 21, May 29, and June 14, had resorbed or aborted their foetuses long enough prior to collection that the uterus showed no signs of pregnancy. The diameters of their corpora albicantia were 11, 14, and 10 mm, respectively. The presence of large corpora albicantia at these late dates implies that pregnancy was maintained for some time after implantation before embryonic loss.

GROWTH

The most pertinent investigations on prenatal growth of *P. v. richardi* are by Scheffer and Slipp (1944) and Bishop (MS, 1968); those on postnatal growth are by Scheffer and Slipp (1944), Fisher (1952), and Bishop (MS, 1968).

Observations on growth in the eastern Atlantic subspecies were made by Havinga (1933), Venables and Venables (1955), and Harrison (1960).

PRENATAL GROWTH

The gestation period, from fertilization to parturition, is about 10.5 months in southeastern Vancouver Island. As the conceptus develops to only the blastocyst stage during the 2-month delay of implantation, most growth occurs in the 8.5 months following implantation (Fig. 14). Embryo lengths from implantation to birth (Fig. 15) suggest that males and females grow at similar rates.

FIG. 14. A male embryo (specimen B151, collected December 31), 65 mm long, about 1.5 months after implantation time.

At birth, males and females are about the same size. The combined average length and weight of 6 males and 3 female newborn pups collected in British Columbia were 81.6 ± 6.2 cm (95% confidence limits) and 10.2 ± 1.5 kg.

In other studies, near-term and newborn lengths and weights of *P. v. richardi* are reported as follows: Washington State (Scheffer and Slipp, 1944), 87.5 cm and 10.9 kg for males (1 specimen) and 91.0 cm and 12.5 kg for females (1); Copper

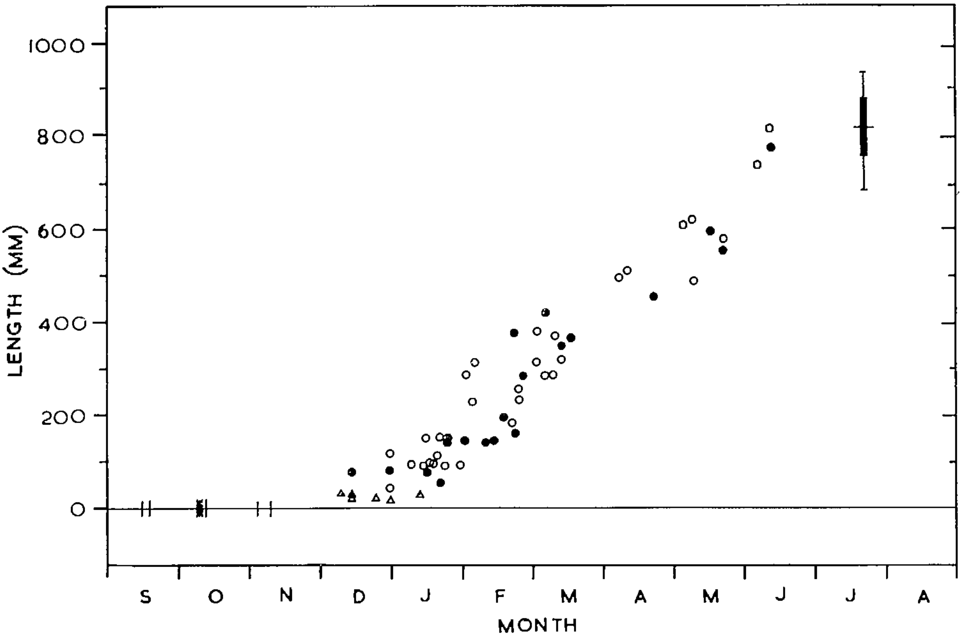

FIG. 15. Prenatal body growth in standard length for 74 seals collected in southeastern Vancouver Island. |, ovulation without implantation; ●, male; ○, female; △, sex unknown; summarized lengths at birth for both sexes show range (vertical line), mean for 95% confidence limits (box) and mean (horizontal line in box).

TABLE 4. Weights of 10 pups collected at weaning time in southeastern Vancouver Island.

Date	Sex	Wt (*kg*)	Stomach contents
Aug. 21	♀	20.9	Milk
Aug. 21	♀	20.9	”
Aug. 22	♂	22.7	”
Aug. 22	♂	19.1	Nothing
Sept. 2	♀	25.0	Milk
”	♀	25.0	Milk
”	♀	28.6	Nothing
”	♀	24.8	Milk
”	♀	25.0	Nothing
”	♀	28.1	Nothing
Avg		24.0	

River, Alaska (Imler and Sarber, 1947), 84.8 cm and 13.7 kg for males (1) and 73.0 cm and 7.5 kg for females (1); Skeena River (Fisher, 1952), 80.5–91.5 cm and 9.5–11.8 kg for males and females; and Tugidak Island, Alaska (Bishop, MS, 1968), 84.5 cm and 11.6 kg for males (2) and 76.5 cm and 11.8 kg for females (4).

In the eastern Atlantic subspecies newborn pups are 83–91 cm in length and 9–15 kg in weight (Havinga, 1933; Venables and Venables, 1955; Harrison, 1960).

Postnatal Growth

During the suckling period pups become very fat, more than doubling their birth weight to average 24.0 kg by weaning time (Table 4). Other workers on this subspecies noted that its weight is doubled (Fisher, 1952) or increased by 71–74%

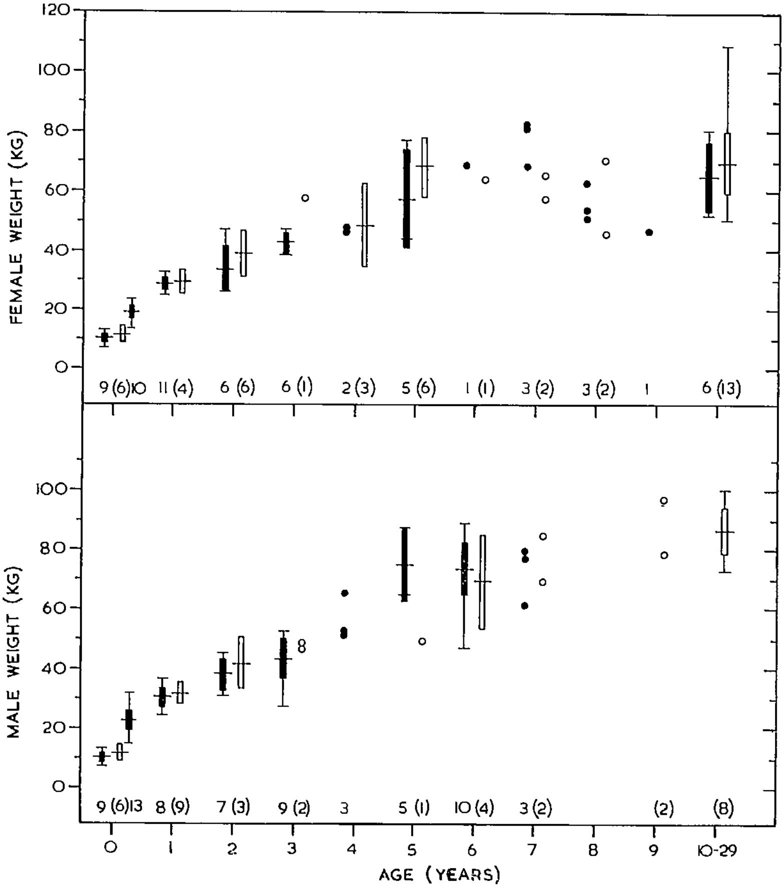

Fig. 16. Postnatal weights of males and females. Data from the present study are in black symbols with the numbers of seals below them and those of Bishop (MS, 1968) in light symbols with the numbers of seals in parentheses below them. Vertical line, range; box, mean with 95% confidence limits; horizontal line in box, mean.

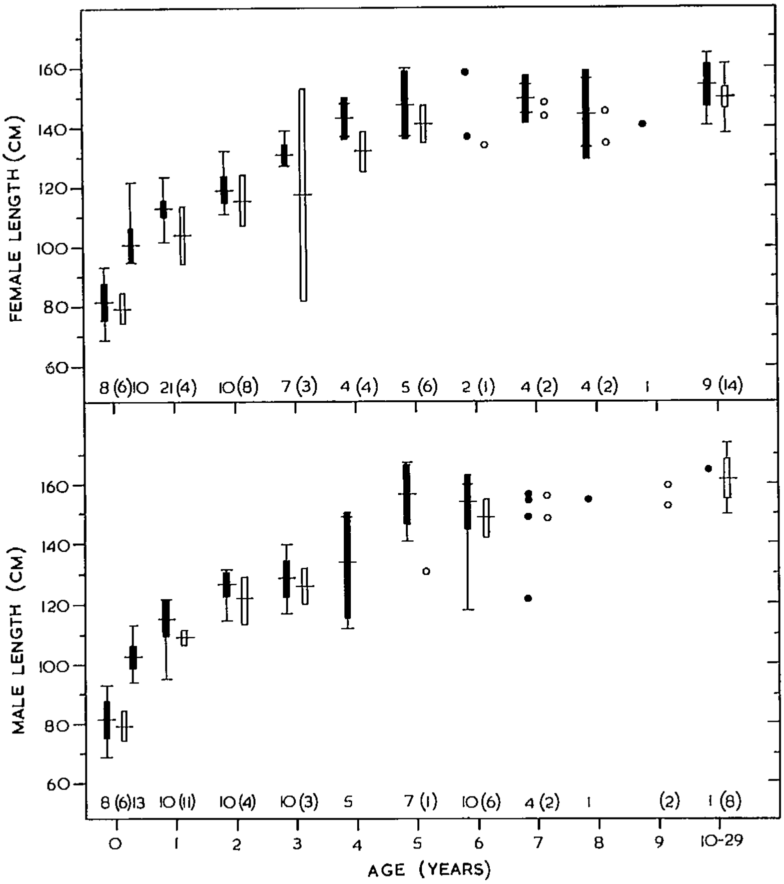

FIG. 17. Postnatal lengths of males and females. Symbols as in Fig. 16.

(Bishop, MS, 1968) by weaning. The rapid increase in weight results from the rich nature of the mother's milk, reported to contain 45% fat and 9% protein (Amoroso and Matthews, 1952, in Harrison, 1960).

Postnatal growth in *P. v. richardi* is described as follows from data collected in British Columbia and from Bishop's (MS, 1968) data taken in Alaska (Fig. 16, 17). From birth to 5 years of age, males and females grow at about the same rate. By 5 years most females are fully grown, averaging 147.7 ± 2.4 cm (95% confidence limits) in length and 64.8 ± 4.4 kg in weight; males continue growing until 9–10 years averaging 161.1 ± 4.9 cm and 87.0 ± 6.6 kg. Fully grown males, therefore, average about 9% longer and 34% heavier than fully grown females.

In Washington, Scheffer and Slipp (1944) concluded that adult males of this subspecies average 73 kg and adult females 59 kg. Fisher (1952) also commented that adult males in British Columbia average greater weights than females.

POPULATION ANALYSIS

Few data are published on population composition and dynamics of *P. v. richardi*. Imler and Sarber (1947) recorded population density in the Copper River, Alaska, and Bishop (MS, 1968) noted numbers and age and sex compositions on Tugidak Island, Alaska.

Havinga (1933) and Van Bemmel (1956) made theoretical estimates of population composition and dynamics for the eastern Atlantic subspecies.

SAMPLING

One of the main problems in seal population studies is determining if the specimens studied represent an unbiased sample of the population. Meaningful population statistics can only be derived from specimens randomly sampled with respect to sex and age.

Of the 336 postnatal seals collected in British Columbia, 245 from 1 to 29 years of age were considered sampled as near randomly as possible. The sample was thought random after a consideration of the seal's behaviour, the collecting technique, and known biasing factors.

In general, the harbour seal in British Columbia is dispersed fairly evenly along the coast with favoured areas where groups of up to 30 seals haul out each day (Fig. 18). In large river mouths and sand flats, groups may reach 100–150 seals. Throughout the year these groups appear to be composed of males and females of all ages. When not hauled out groups break up and individuals tend to disperse along the shore. Thus, the population is not organized into socially distinct groups or areas that could bias the age and sex composition during sampling.

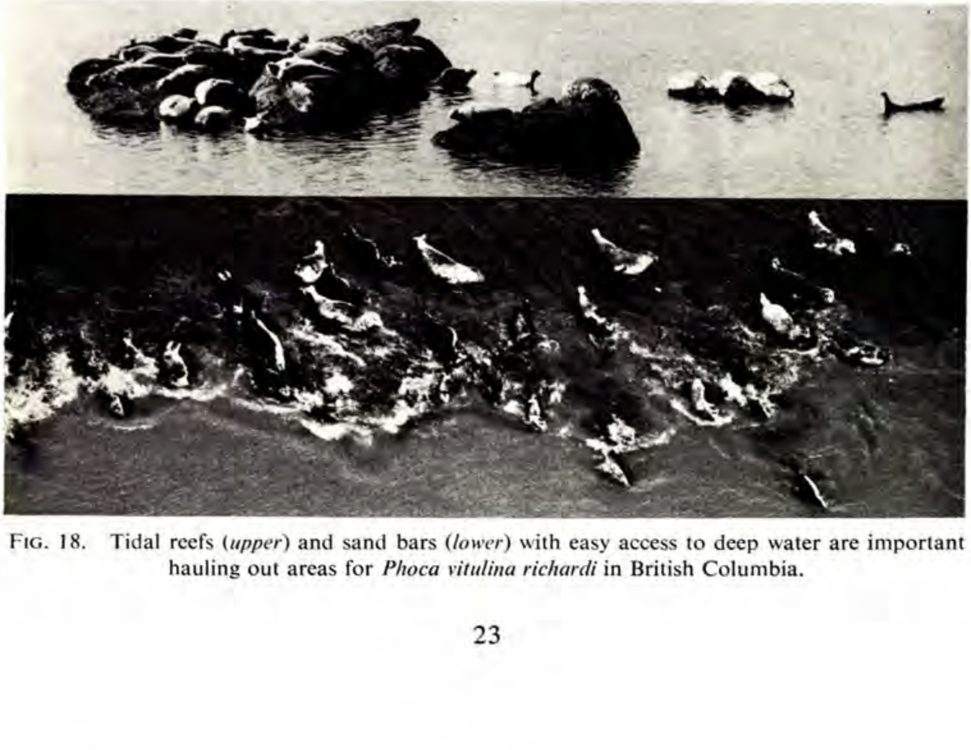

FIG. 18. Tidal reefs (*upper*) and sand bars (*lower*) with easy access to deep water are important hauling out areas for *Phoca vitulina richardi* in British Columbia.

Seals were collected mainly while they were dispersed and swimming, thus reducing the bias of knowing a seal's age and sex before collection. The possible effect of local population movements on sample composition was decreased by collecting specimens over a large area and sampling relatively evenly throughout the year.

To lessen the bias that the young, less wary seals tend to be collected more easily than the older seals, all pups (0.0–5.9 months of age) collected were eliminated from the analysis. In a few instances there were known biases for age or sex in collecting older individuals; these specimens were also excluded from the random sample.

Because population statistics are best given for specific times of the year, it was assumed that the sample of 245 seals represents the population just prior to the pupping season. The reasoning for the assumption was as follows: as ages of the seals were based on the closest birthday and seals were collected fairly evenly throughout the year (Table 5), the sample of 245 represents the population during the birth season; however, as no pups (0.0–5.9 months) were included in the analysis, the sample represents the population just prior to the pupping season.

TABLE 5. Monthly distribution of males and females taken in a random sample of seals 1–29 years of age.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Males	11	9	17	14	10	4	3	10	12	3	8	13
Females	8	14	25	18	15	8	9	10	10	5	3	6
Total:	19	23	42	32	25	12	12	20	22	8	11	19

The following population analyses were based mainly on the age and sex compositions of the sample of 245 seals (Table 6, 7).

SEX RATIO

Of 79 embryos collected during the study, 56% (44 specimens) were females.

In a sample of 289 pups (0.0–5.9 months) taken in the present study and several others, females comprised 50% (144) of the total, indicating that the early postnatal sex ratio is 1 male to 1 female. The numbers of males and females for the various studies were

	Author (s)					
	Scheffer and Slipp (1944)	Imler and Sarber (1947)	Fisher (1952)	Bishop (MS, 1968)	Present study	Total
Males	5	1	9	98	32	145
Females	1	1	11	99	32	144

TABLE 6. Life table for 163 females.

Age (*years*)	No. killed	No. killed/1000	No. survivors/1000	% mortality
Neonatal[a]	32	197	1000	20
1	36	221	803	28
2	17	104	582	18
3	11	68	478	14
4	15	92	410	22
5	5	31	318	10
6	6	37	287	13
7	6	37	250	15
8	5	31	213	15
9	3	18	182	10
10	3	18	164	11
11	2	12	146	8
12	6	37	134	28
13	5	31	97	32
14	1	6	66	9
15	0	0	60	0
16	3	18	60	30
17	0	0	42	0
18	0	0	42	0
19	1	6	42	14
20	3	18	36	50
21	0	0	18	0
22	1	6	18	33
23	0	0	12	0
24	0	0	12	0
25	0	0	12	0
26	0	0	12	0
27	1	6	12	50
28	0	0	6	0
29	1	6	6	100
Total:	163	1000	0	

[a]Estimated (p. 27).

In the sample of 245 seals, 53% (131) of those one or more years of age just prior to the pupping season were females. Bishop (MS, 1968) noted that a random sample of 50 harbour seals one or more years of age collected in Alaska contained 46% (23) females. In British Columbia, survival data derived from the sample of 245 seals (Fig. 19) suggest that the sex ratio changes with increasing age. From birth to 5 years of age males and females have similar survival rates suggesting a 1:1 sex ratio for this time. After 5 years, however, males die at a greater rate than females so that by 20 years of age the population consists almost entirely of females.

TABLE 7. Life table for 146 males.

Age (*years*)	No. killed	No. killed/1000	No. survivors/1000	% mortality
Neonatal[a]	32	219	1000	22
1	22	151	781	19
2	15	103	630	16
3	16	109	527	21
4	12	82	418	20
5	14	96	336	29
6	13	89	240	37
7	8	55	151	36
8	3	20	96	21
9	1	7	76	9
10	2	14	69	20
11	3	20	55	36
12	1	7	35	20
13	0	0	28	0
14	1	7	28	25
15	2	14	21	67
16	0	0	7	0
17	0	0	7	0
18	0	0	7	0
19	0	0	7	0
20	1	7	7	100
Total:	146	1000	0	

[a] Estimated (p. 27).

PER CENT MATURE

Of the 131 females in the sample of 245, 55% (72) had ovulated at least once and were thus mature. The per cent of mature males in the sample cannot be calculated directly because there is no method of establishing maturity in adults under 6 years of age, collected during the sexually inactive period. It can be derived indirectly, however, from the per cent males known to be mature in each age group and from the age distribution of males in the sample. It is estimated (Table 8) that 42% of males are mature just prior to the pupping season.

MORTALITY

In estimating the annual mortality rate, it was assumed that the population was not increasing or decreasing during the study period. Since pups are born during a short period of the year, the annual recruitment was estimated from the data on reproduction and age and sex compositions. As the sample of 245 seals contains 53% females, 55% of which are mature, and 88% of the mature females produce pups each year, the sample should produce 63 pups. The sample, therefore, theoretically varies from 308 seals at the end of the pupping season to 245

TABLE 8. Per cent of males mature just prior to the pupping season in a random sample of 114 males.

Age (*years*)	% of sample[a]	% mature Of age-group[b]	 Of sample
1	19	0	0
2	13	0	0
3	14	12	2
4	11	0	0
5	12	72	9
6-20	31	100	31
Total:	100		42

[a] From Table 7.
[b] From Table 2.

seals just prior to the pupping season. Since the annual recruitment through births should equal the annual loss through mortality, the annual mortality rate for all age-groups is estimated as 20%.

Mortality rates for each age from birth were calculated in life tables from the sample of 245 seals and the estimated number of pups it should produce. As there should have been 63 pups born in the sample with a sex ratio of about 1:1, the sample was considered to be increased by 32 female and 32 male pups during the pupping season to keep the calculations in whole numbers. The sample composition thus changes from 131 females and 114 males prior to the birth season to 163 females and 146 males immediately after the birth season. Life tables for the post pupping season were constructed for females (Table 6) and males (Table 7) on the format suggested by Quick (1965). The change in survival rate over the life span of each sex was determined by graphically representing the number of survivors found in each age on a semilogarithmic plot (Fig. 19). A change in survival rate is indicated by a change in the shape of the line connecting the numbers of survivors in the various age-groups.

Survival rates were similar and constant for the males and females in the sample from birth to 5 years of age. The average annual mortality for males during this time was 21% and for females, 20%. After 5 years, survival of males abruptly decreased and remained constant until the end of the life span, at about 20 years. Survival of females changed little, and remained constant until the end of the life span at about 30 years. The average annual mortality after 5 years was 29% for males and 15% for females.

It was worth noting that the mortality for males and females during the first year was only 21%. One expects that first-year seals are less experienced and therefore have a higher mortality than older seals. As the first-year mortality was

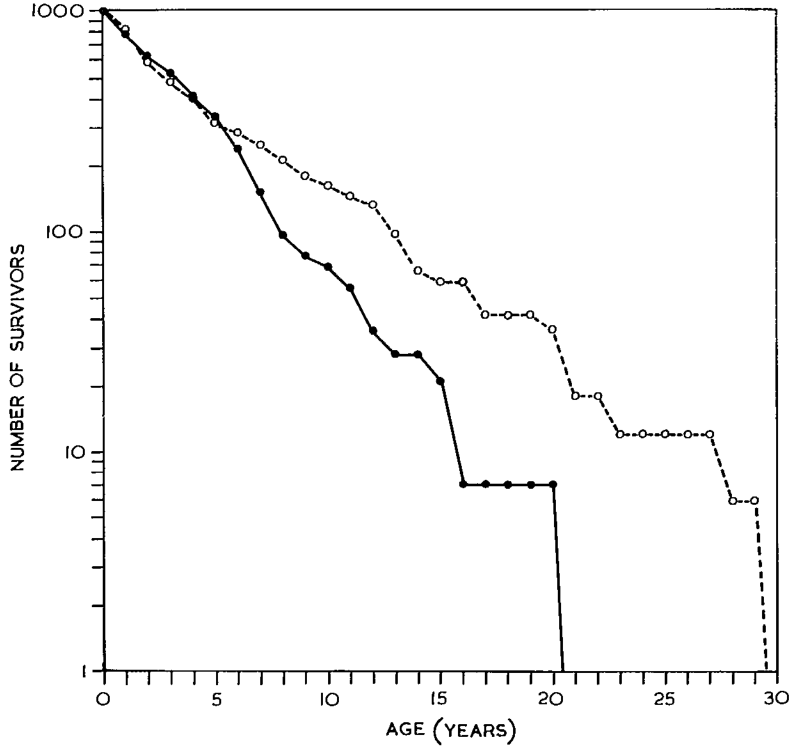

FIG. 19. Survival in males (●) and females (o). Data are from Tables 6 and 7.

a theoretical calculation, it is possible that the actual mortality was slightly higher. Van Bemmel (1956), however, assumed that the harbour seal in Holland had a 20% mortality during the first year and concluded from field counts and a series of theoretical mortality figures that it was 10% in later years.

Also noteworthy is the fact that mortality of males increased at 5 years of age, the same age that most males reach sexual maturity. The increased mortality may result from reproductive activities as males engage in fighting during the breeding season, being characteristically scarred around the face, neck, chest, and tail.

ESTIMATE OF POPULATION SIZE

It is difficult to estimate empirically the number of harbour seals in British Columbia as they do not congregate into large, observable herds. An estimate was made, however, by a method designed by Havinga (1933) for determining the number of harbour seals in Holland. He calculated the average number of seals collected for bounty each year and concluded that, because the kill was fairly constant over many years, the population was stable and could support the annual cropping. On the basis of assumed population statistics and compensations for natural mortality, reproductive failure and seals shot but not recorded for bounty, he estimated that an annual cropping of 1100 seals for bounty required a population of about 4000 seals of all ages in Holland. The same principle was used to estimate the number of harbour seals in British Columbia as bounty records have been kept over many years and most of the essential population statistics are known.

An average of 2913 harbour seals was reported killed for bounty each year in British Columbia from 1914 to 1964 (Table 9). This average does not include the years 1918–27, 1934–36, and 1940–41, when no bounty was offered. As the population withstood this level of cropping for many years without apparent decline, the 2913 seals killed annually represents the minimum annual mortality sustained by the population for the years recorded. Assuming that this number accounted for all deaths and that there was no strong hunting selection for a specific age-group, the population needed to replace this loss was large enough to produce 2913 pups a year as the number of births should equal the number of deaths in a stable population. Thus, to produce 2913 pups each year the population must have contained 3310 adult females because adult females are 88% fecund and produce only one pup a year. As 55% of all females are mature just prior to the pupping season,

TABLE 9. Numbers of bounty claims for harbour seals killed in British Columbia between 1914 and 1964. Bounty values from Fisher (1952) and unpublished data of the Department of Fisheries of Canada.

Year	No. of seals	Year	No. of seals
1914–15	2237	1944–45	961
1915–16	749	1945–46	1978
1916–17	785	1946–47	1639
1917–18	748	1947–48	2740
1918–27	No bounty	1948–49	2693
1927–28	567	1949–50	2556
1928–29	3209	1950–51	2289
1929–30	5944	1951–52	2791
1930–31	6308	1952–53	3397
1931–32	6084	1953–54	3257
1932–33	4300	1954–55	4333
1933–34	400	1955–56	3987
1934–36	No bounty	1956–57	3426
1936–37	1933	1957–58	4053
1937–38	4295	1958–59	3741
1938–39	4569	1959–60	3431
1939–40	3546	1960–61	2878
1940–41	No bounty	1961–62	2351
1941–42	3282	1962–63	2118
1942–43	1168	1963–64	4962
1943–44	1001		

Avg annual kill during bounty years = 2913 seals.

there were 6018 females of all ages. Since the population at this time contains 53% females the total number was at least 11,355 seals just before the pupping season.

The actual population size, however, must have been much larger as the 2913 seals killed annually do not represent all deaths, for several reasons. First, they represent only those seals for which a bounty was claimed and do not include those killed and not recorded because they sank into deep water, were wounded and died elsewhere, or no effort was made to collect the bounty. It is estimated from personal experience and conversations with seal hunters and Department of Fisheries personnel that only 50% of those killed were recorded in the bounty files. Second, it is unlikely that the harbour seal was cropped to its annual maximum as there was probably never a heavy hunting pressure on it. This was because most of the coast has remained unpopulated and accessible only by boat and because other livelihoods were more profitable than bounty hunting. Third, there must also be some mortality resulting from natural causes. It was, therefore, estimated that the actual mortality sustained by the population was closer to 9000 seals a year, or about three times the number noted in the bounty records. On the basis of the statistics previously mentioned for calculating the population required to produce pups, a more likely estimate of population size was about 35,000 seals just prior to the pupping season. This was an average density of 2.1 seals per mile of coast as there are about 16,900 statute miles of coastline in British Columbia (Canadian Department of Hydrographic Surveys, personal communication).

Other estimates of the population size in British Columbia were given by Spalding (1964), who stated that there were probably about 17,000 harbour seals during the late winter and quoted an estimate of 20,000 seals made by seal hunters Messrs B. and D. McNaughton. Scheffer (1958) wrote that *P. v. richardi* from Mexico to Alaska probably numbers between 50,000 and 200,000 seals. In Alaska, there appear to be larger numbers of the subspecies as Imler and Sarber (1947) reported at least 6000 seals inhabit the mouth of the Copper River alone and Bishop (MS, 1968) suggested that between 12,000 and 17,000 seals are found on Tugidak Island after the pupping season.

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GLOSSARY

annulus — a ringlike layer.
baculum — a bony structure in the penis of many mammals.
blastocyst — a hollow ball of cells destined to be implanted in the lining of the uterus and become an embryo.
cementum — a thin layer of bony substance covering the dentine on the root of a tooth.
conceptus — an organism between fertilization and birth.
corpus albicans — the remnants of a degenerated corpus luteum.
corpus luteum — a gland formed in the ovary at the site of an ovulation which secretes a hormone to maintain pregnancy.
dentine — a bony substance, ivory, surrounding the pulp cavity and forming the bulk of a tooth.
enamel — a thin, hard, calcareous covering on the crown of a tooth.
epididymis — a tubular structure that stores and ripens sperm, attached to the surface of the testis.
fecundity — the capacity of females to produce young.
implantation — the attachment of the conceptus to the lining of the uterus in preparation for placenta formation.
otolith — a granule of calcium carbonate in the inner ear of some vertebrates.
neonatal — at birth.
postnatal — after birth.
prenatal — before birth.
pulp cavity — the central cavity of a tooth, lined with dentine and containing blood vessels and nerves.
seminiferous tubules — convoluted tubules in the testis where sperm is produced.
spermatid — a developing male germ cell coming from a spermatocyte and giving rise to a sperm.
spermatocyte — a developing male germ cell coming from a spermatogonium and giving rise to a spermatid.
spermatogenesis — the process of sperm formation.
spermatogonium — an undifferentiated male germ cell giving rise to a spermatocyte.
uterine horns — the two anterior extensions of the uterus, each ending with an ovary.
vasa efferentia — ductules carrying sperm from the testis to the epididymis.

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