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Physical growth of northern fur seals (*Callorhinus ursinus*): seasonal fluctuations and migratory influences

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(With 10 figures in the text)

Growth curves are described for males, pregnant females, and non-pregnant females using morphometric measurements collected from over 18 000 northern fur seals (*Callorhinus ursinus*) shot at sea between California and the Bering Sea from 1958 to 1974. Seals of all ages experience seasonal increases and decreases in body mass and length. Seasonal fluctuations of body length may be an artefact of mass displacement caused by seasonal changes in mass. Rapid growth and gain in mass occur during a brief one to three month period as the population migrates northward through the coastal waters of northern British Columbia and Alaska on their way to the Pribilof Islands. Body mass of females and immature males is gradually lost while fasting on land and wintering along the coasts of Washington, Oregon, and California. Pregnant females are both heavier and longer than non-pregnant females of the same age. Body mass in pregnant females levels off with age in contrast with the increasing mass of non-pregnant females. Growth of northern fur seals does not appear to stop at an upper asymptote, but continues throughout their life spans.

Contents

[†] Deceased

Introduction

From 1958 to 1974, Canadian and American biologists, working under the auspices of the North Pacific Fur Seal Commission, recorded morphometric (body) measurements from over 18 000 northern fur seals (*Callorhinus ursinus*) shot at sea between California and the Bering Sea. Such an extensive dataset provides considerable information about physical growth and annual fluctuations in the mass and length of northern fur seals. It also offers insights into the processes underlying pinniped growth in general, and can be used to explore functional and evolutionary links among demography, energetics, sociobiology, and ecosystem processes (Bryden, 1972; Payne, 1979; McLaren, 1981, 1993; McLaren & Smith, 1985; Trites, 1991; Trites & Bigg, 1992).

Scheffer & Wilke (1953) were the first to describe growth of male and female northern fur seals from animals killed on land. Later, Nagasaki (1961) and Taylor, Fujinaga & Wilke (1955) constructed growth curves for females collected at sea, and noted that pregnant females were longer than non-pregnant females of the same age. This phenomenon was confirmed in subsequent pelagic studies by Fiscus *et al.* (1964, 1965) and further investigated by Bigg (1979) who also considered seasonal changes in the size of pregnant females. Concurrently, Lander (1979) summarized the 1958 to 1974 pelagic data by month and constructed monotonic growth curves by age and sex (cf. McLaren, 1993). In addition, growth curves were also drawn for Russian and Asian populations of northern fur seals (Ito, 1969; Bychkov, 1971*a*; Chelnokov & Chugunkov, 1971; Muzhchinkin, 1976; Boltnev, 1991).

The primary objective of our study was to construct growth curves for male and female northern fur seals from the Pribilof Islands (Fig. 1). Particular attention was paid to seasonal

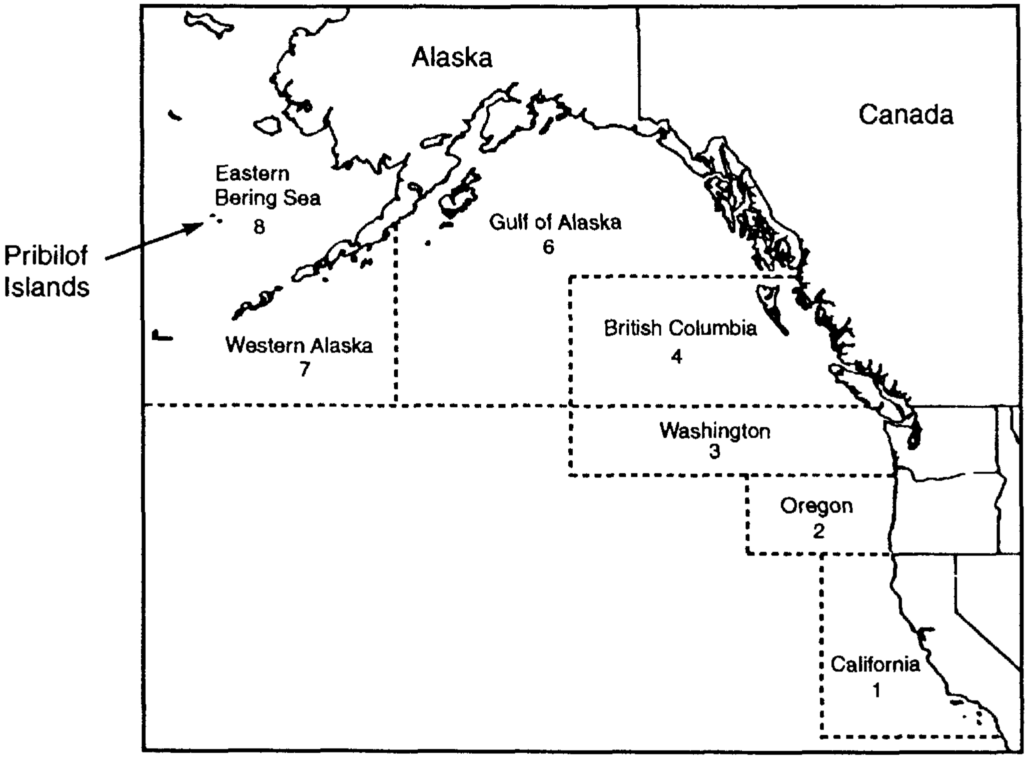

FIG. 1. Regions of the North Pacific where northern fur seals were collected from 1958 to 1974 (adapted from Kajimura, 1985).

fluctuations in length and body mass of sexually mature and immature seals. A second goal was to determine whether changes in body lengths and mass were related to the timing of migration and place of foraging.

Methods

Collection of data

Over 18 000 fur seals were shot and measured between California and the Bering Sea from 1958 to 1974 (Lander, 1980*b*; Scheffer, Fiscus & Todd, 1984). Most were thought to be from the Pribilof Islands, Alaska (Fig. 1), although a few undoubtedly originated from Russian populations (Lander, 1980*b*). The majority of seals were collected from January to September; few were taken from October to December. A breakdown of the numbers shot by year and month is contained in Lander (1979) and in Trites & Bigg (1992). Methods used to collect and prepare the samples are described by Lander (1980*b*) and are briefly summarized as follows.

Fur seals were shot from government and chartered vessels within the animals' known feeding range (Fig. 1). The number of fur seals collected between 1958 and 1963 was subject to annual minimum quotas. Times and areas of collections were not specified in the quota. Thus research during the quota years was concentrated in areas of known abundance, based on the experience of commercial pelagic sealers before 1911 and on pelagic research expeditions in 1952 and 1955. After the quota was removed in 1964, research vessels tended to follow systematic transects in some areas, but were still somewhat influenced by prior knowledge of expected distributions of fur seals.

Seals were sought and shot during daylight hours. They were processed as soon as possible after being taken aboard, before rigor set in. The seals were dropped on to a 'cradle' measuring board with their backs down. Length was measured from the tip of the tail to the tip of the nose (positioned to touch zero). Care was taken not to stretch the animal unduly. After 1967, the animals were not repositioned to touch the zero mark on the measuring board. Seals were weighed with spring, torsion, or platform scales (usually to the nearest 0.5 kg). Mandibles were taken and sent to laboratories to remove the canine teeth for age estimation. Reproductive condition (nulliparous, primiparous, or multiparous) of the females was determined aboard U.S. vessels from field examination of the uterine horns and superficial examination of ovaries for ruptured follicles, until 1962. Aboard Canadian vessels (1958 to 1974), and U.S. vessels (after 1962), the entire female genital tract was removed, placed on a metal stretcher to harden, and preserved in 10% formalin for later examination in the laboratory.

Analysis of data

The method used by the Canadian and American biologists to age the pelagic samples was not appropriate for analysing the growth data. The standard practice was to assign January 1 as date of birth, ignoring the true biological age of the animal (Lander, 1980*a*). In actual fact, dates of birth were assigned in November, such that a pup born in July and killed only 5 months later was recorded as a 1-year-old. Similarly, animals killed at 17 and 28 months were both considered to be 2-year-olds. We therefore adjusted the data to reflect the true biological ages of the samples, then determined the ages of all animals in days using July 1 as the mean date of birth.

Body mass and length were collated from 2 008 males, 6 493 non-pregnant females, and 9 630 pregnant females over the period 1958 to 1974. Females classified as pregnant included recently post-partum animals shot mainly during July and August in the eastern Bering Sea (see Lander, 1980*b* and Trites, 1991 for details). Data from all years and areas of the eastern Bering Sea and eastern North Pacific were combined and were plotted (i.e. length vs. mass) to identify unusual data points (outliers) which were later verified with the original field notes. A small amount of random variation was added to the plotted data to enhance visual acuity by reducing the overlap of data points caused by measurement roundoff. Thus many observations of a single measurement appear in the figures as a cloud of data rather than as a single point.

Growth in body length and mass over time was described by robust locally weighted regressions (*lowess*, Cleveland, 1979; Efron & Tibshirani, 1991). The *lowess* algorithm requires choosing a smoothness parameter f which is a number between 0 and 1. As f increases, the fitted curve becomes smoother. We began by choosing a small f value, and increased it until the curve was as smooth as possible. We then plotted and smoothed the residuals, to ensure no residual structure remained.

The linear relationship between body length (L) and mass (M) was estimated from the equation $\log(M) = \log(a) + b\log(L)$ where b is the slope, $\log(a)$ is the intercept, and $M = aL^b$.

It has been suggested that the geometric mean of the regression of mass on length and the inverse of the regression of length on mass should be used to give the appropriate linear regression for mass-length comparisons because length is not truly independent of mass (Ricker, 1979). However, others have indicated that ordinary least squares regression is appropriate and easier to interpret than geometric mean regression (Sprent & Dolby, 1980; Cone, 1989). Thus we used ordinary least squares regressions.

Seasonal fluctuations in body length and mass were analysed for 4 classes of fur seals: immature males (1.5–4.5 y), immature females (1.5–4.5 y), pregnant females (4.5+ y) and non-pregnant females (4.5+ y). Samples were insufficient to detect seasonal changes in body size of yearlings and mature males. We only considered the period between January and September, because fewer than 10 seals were collected for each month from October to December. Each dataset was smoothed using the robust locally-weighted *lowess* algorithm.

To determine the relationship between fur seal growth and geographic feeding location, we plotted the area sampled (grouped according to Fig. 1) against the Julian date of sampling for each of the 4 classes of fur seals previously mentioned. The data were smoothed (*lowess*) to show when and where the different classes of fur seals migrate. These migration plots were then compared with the timing of seasonal changes in body mass and length.

Results

Seasonal fluctuations

Growth curves for males (ages 6 mo to 17 y), non-pregnant females (6 mo to 25 y), and pregnant females (3 y to 23 y) are shown in Figs 2–5. Estimates of mean body size are contained in Table I. Maximum recorded lengths and weights were 208 cm and 221 kg (males), 147 cm and 67 kg (pregnant females), and 145 cm and 59 kg (non-pregnant females).

The growth curves reveal seasonal fluctuations in the body mass of immature males and females, with seasonal body mass peaking progressively earlier in the year as the animals grow older. However, seasonal changes known to occur in the body size of mature males ($\geqslant 9$ y) could

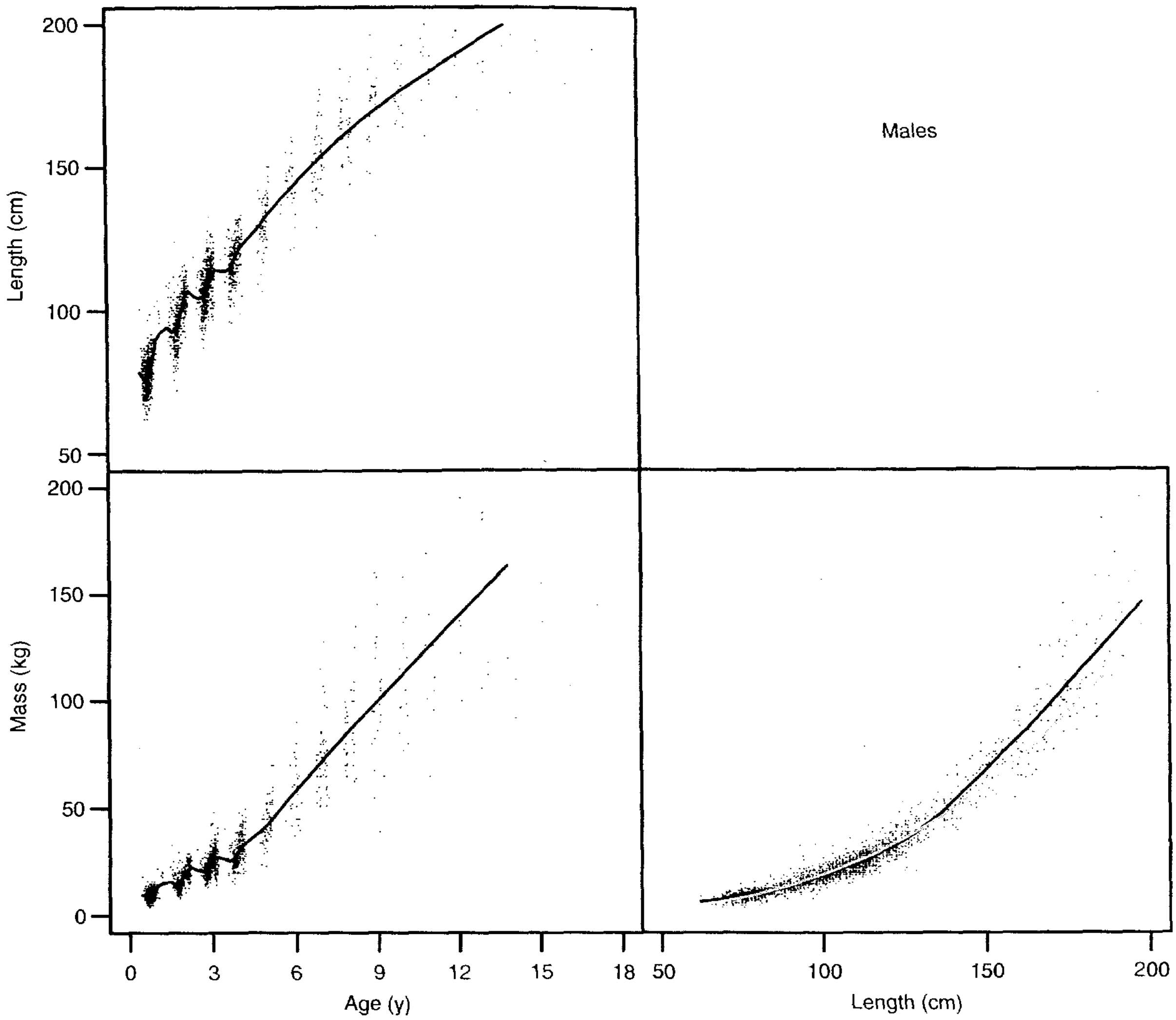

FIG. 2. Length and mass of 2008 males by age in days, where age 0 is July 1. A small amount of random noise was added to each variable to reduce the overlap caused by measurement roundoff. The growth curves were smoothed by *lowess* ($f = 0.15$). Seasonal changes in length and mass of young animals peak at progressively earlier times in the year as the animal grows older. Note also the absence of data from seals aged 1–1.5 y and the rapid increase in body mass that occurs between the ages of 4 and 5 y. The regression of mass on length (lower curve, right panel) failed to track the growth spurt shown by the *lowess* curve.

not be detected from the relatively few sets of morphological measurements recorded from bulls (Fig. 2). Annual changes in the body mass of mature non-pregnant females are less pronounced than in younger animals (Fig. 3), while changes in body mass of pregnant females reflect the development of the foetus, peaking near the mean date of birth, July 1 (Fig. 4). Pregnant females are both heavier and longer than non-pregnant females (Figs 5, 6).

Surprisingly, the data suggest that body length, like mass, also fluctuates instead of increasing monotonically as might be expected. Figs 2–4 (top panels) show apparent increases and decreases in body length within each age class. As with mass, there is a tendency for the apparent decrease in length to be more seasonally protracted with increasing age.

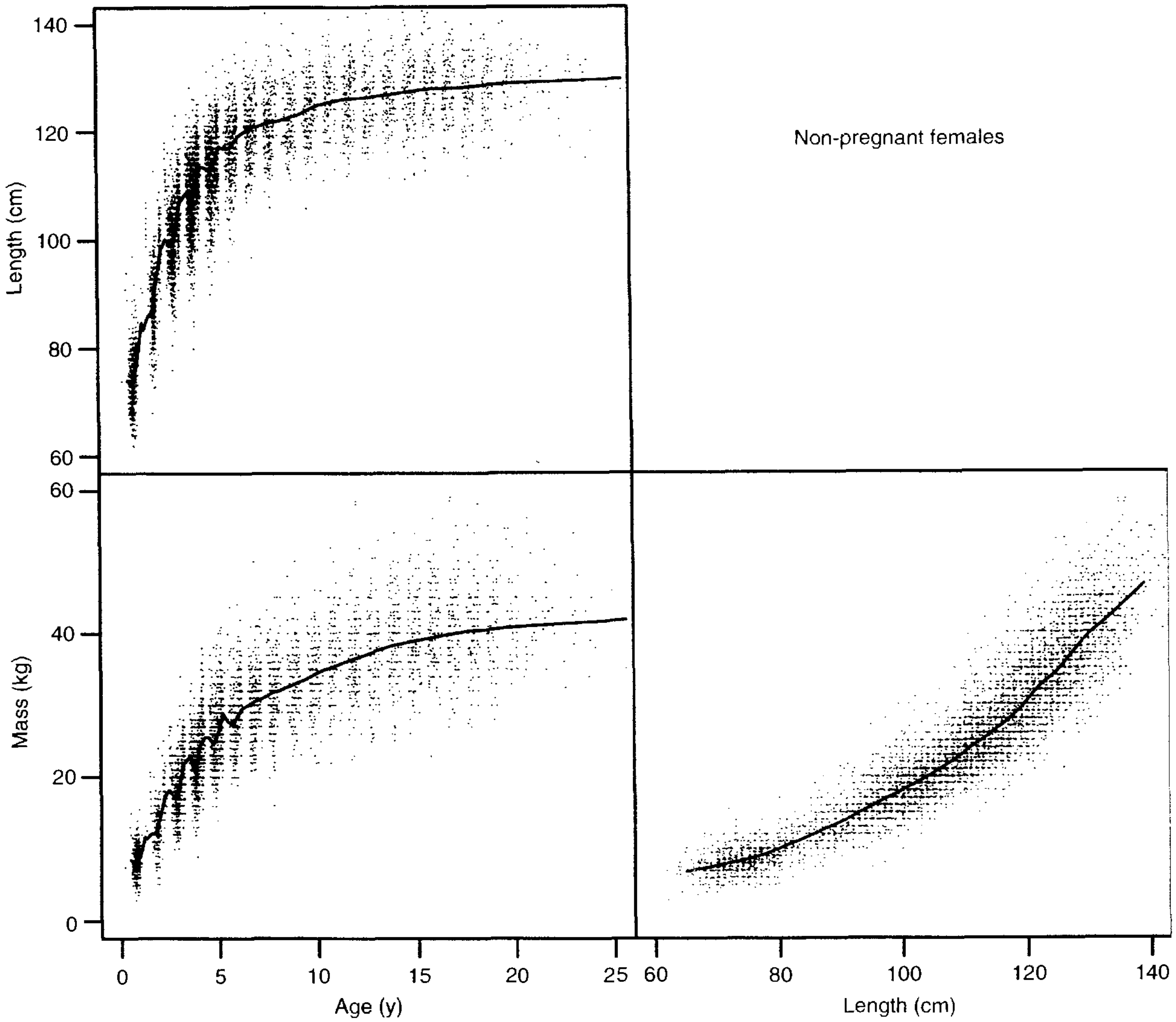

FIG. 3. Length and mass of 6 493 non-pregnant females by age in days. A small amount of random noise was added to each variable to reduce the overlap caused by measurement roundoff. Growth curves were drawn using *lowess* ($f = 0.08$ left panels, $f = 0.15$ right panel), with mean date of birth assumed to be July 1. Seasonal changes in length and mass of young animals peak at progressively earlier times in the year as the animal grows older, until virtually disappearing when sexually mature. Note also the absence of data from seals aged 1–1.5 y.

Seasonal changes in body mass and length are shown most clearly in Figs 7 and 8. Immature males gain mass from the beginning of May until the first week of July, after which they lose mass and apparently length. The few males captured at the beginning of the year suggest they continue to lose mass through the spring (January to March), as is the case for immature females (Fig. 7). Seasonal increase in the mass of immature females occurs from the end of May until late July, and lags behind that of immature males by about three weeks (Fig. 7).

Mature non-pregnant females (4.5+ y) lose mass from January to mid April. This gradual loss of mass is rapidly regained in 30 days from mid April to mid May. The large fluctuations in the size of pregnant females (Fig. 8) are related in part to the growth of the developing foetus. The

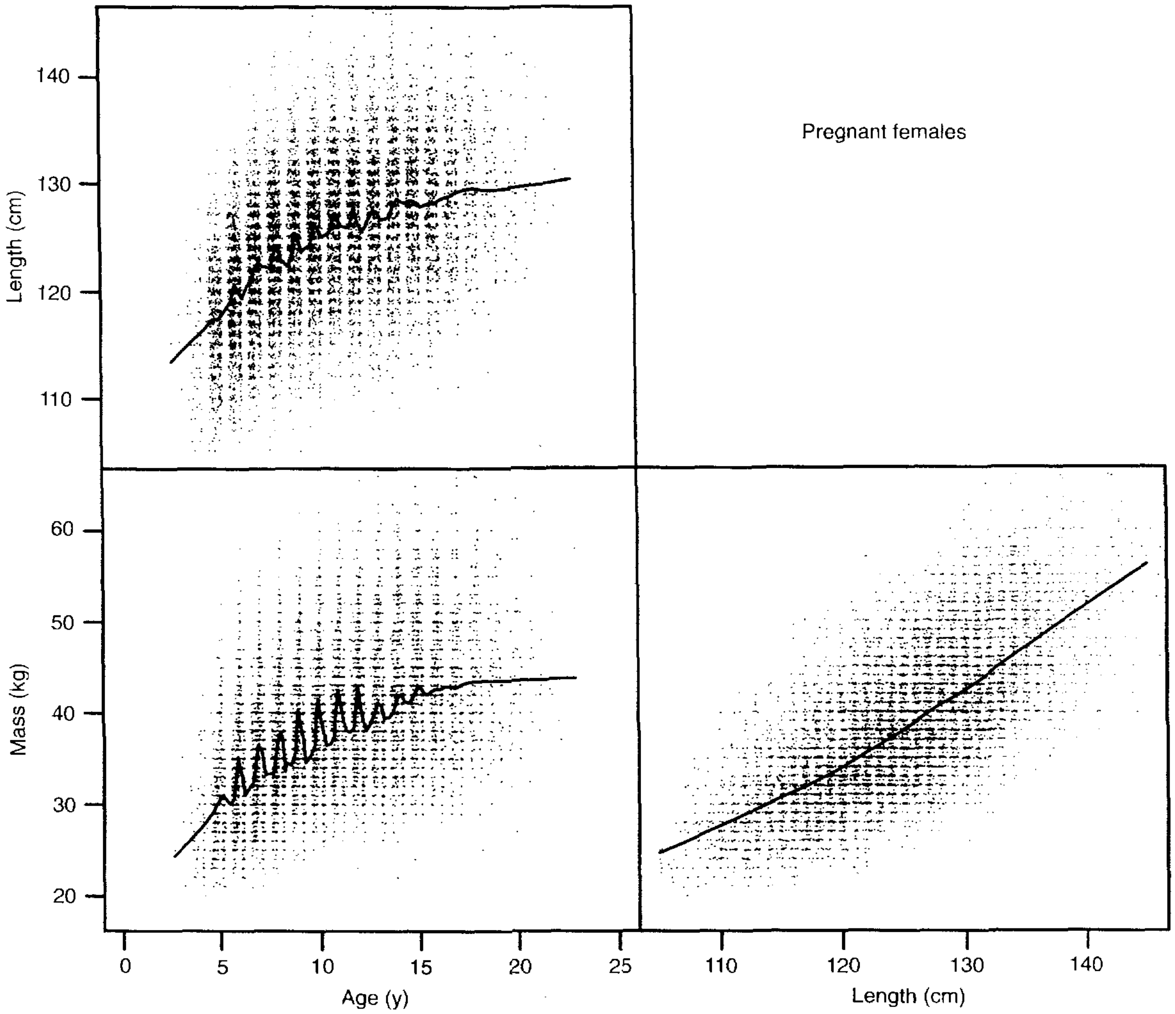

FIG. 4. Length and mass of 9 630 pregnant and postpartum females by age in days. A small amount of random noise was added to each variable to reduce the overlap caused by measurement roundoff. Growth curves were described by *lowess* ($f = 0.07$ left panels, $f = 0.15$ right panel). Note the seasonal changes in length and mass (which includes the foetus when present) peaks near July 1, the mean date of birth.

most rapid gain in mass begins in early April and peaks in mid June at the onset of the pupping season (late June to late July; Trites, 1991, 1992*a*).

Allometric relationships

The relationship between body mass (M in kg) and length (L in cm) is described by the equations: $M = 4.318 \times 10^{-5} L^{2.825}$ for males, $M = 6.081 \times 10^{-5} L^{2.740}$ for non-pregnant females, and $M = 9.794 \times 10^{-5} L^{2.666}$ for pregnant females. These predicted allometric relationships for pregnant and non-pregnant females were indistinguishable from those predicted by the *lowess* curves shown in Figs 3 and 4. However, the regression equation describing the mass-length relationship of males was inadequate to describe the male growth spurt (for males >1.4 m, Fig. 2).

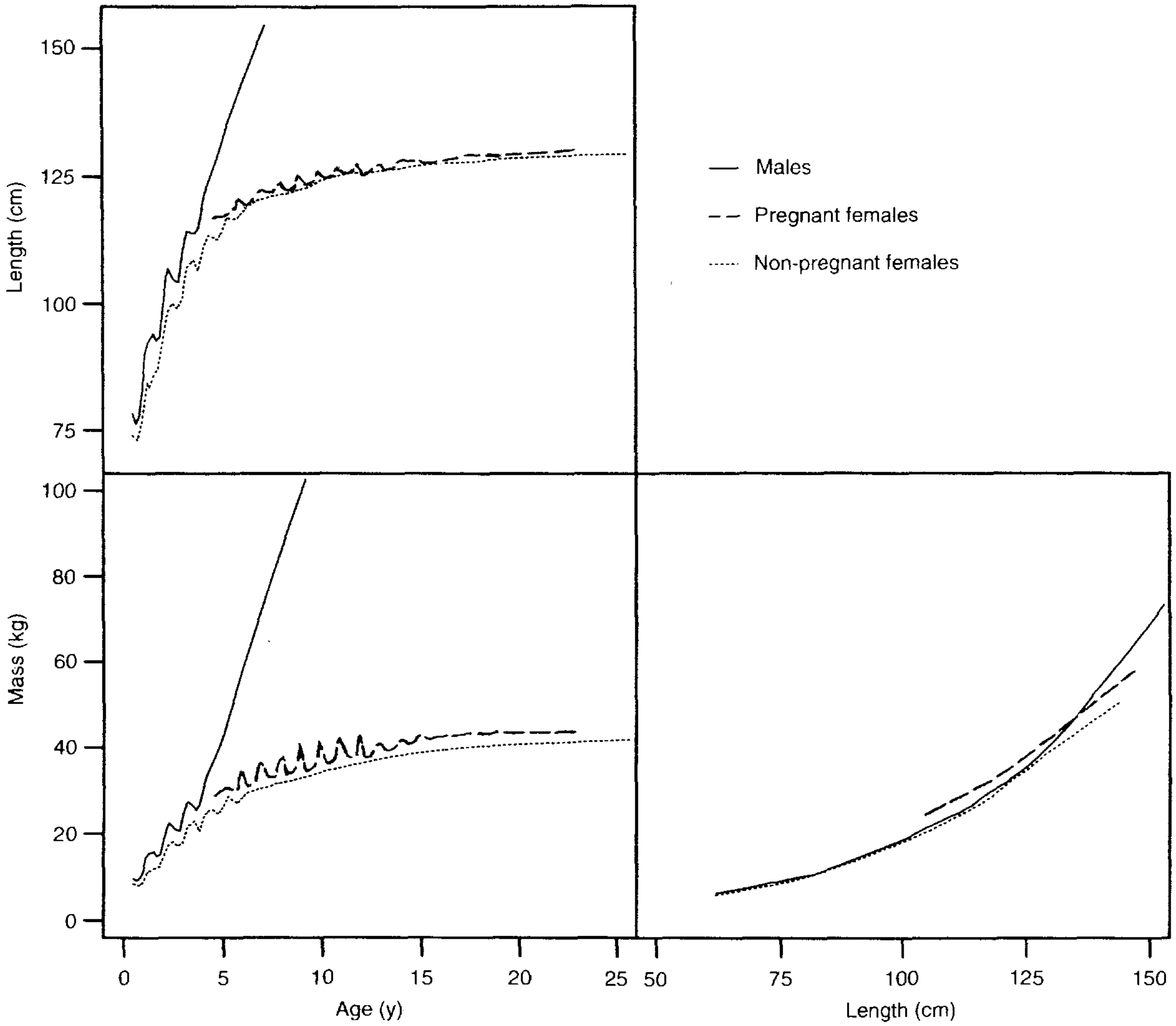

FIG. 5. Comparison of male, pregnant female, and non-pregnant female growth curves shown in Figs 2–4. Note the timing of the seasonal peaks in length and mass, and the similarity between the male and female allometric relationships.

Growth and migration

The migratory return of pregnant females to the Pribilof Islands is rapid (Fig. 9). In contrast, most non-pregnant females do not migrate as quickly northward through the coastal waters of Oregon and Washington, and complete their migration a few weeks after the pregnant females. Relative to pregnant females, most immature females (ages 2–4 y) delay their return by a month by remaining off the coast of Washington. Most young males also congregate off Washington, but typically depart for the Pribilofs before immature females.

The Washington coastal waters (Fig. 1) are a major transitional zone in the northern fur seal migration. Comparing the migration plots to the seasonal growth curves (Fig. 10) shows that fur seals maintain or lose mass while in Washington waters and areas further south. Only after each age group of northern fur seals has left Washington do they begin their period of seasonal fattening. In all cases, the seasonal peak in body mass and length occurs when the animals arrive on the Pribilof Islands.

TABLE I

Mean length (cm) and mass (kg) of males, non-pregnant females and pregnant females (including the foetus). Neonate data are from Trites (1991). All other data are from smoothed growth curves that removed the seasonal fluctuation. Mass and length of adult males are from animals collected prior to the breeding season

	Length			Mass		
Age	males	non-pregnant	pregnant	males	non-pregnant	pregnant
0	63.6	60.5	–	5.7	5.1	–
1	87.2	79.4	–	13.1	9.8	
2	100.5	93.1	–	19.1	14.8	–
3	110.9	103.1	–	25.5	19.2	–
4	119.9	110.6	115.9	31.3	23.8	27.4
5	132.5	114.8	117.4	43.2	26.8	30.7
6	143.2	118.2	120.2	58.3	28.7	33.6
7	153.1	120.1	122.5	72.8	30.7	35.9
8	162.0	121.7	124.0	87.3	32.0	37.9
9	169.6	122.8	124.9	100.1	33.2	38.4
10	176.4	124.4	125.7	113.1	34.5	39.5
11	183.0	125.5	126.6	125.6	35.6	40.8
12	188.7	126.0	126.7	139.7	36.6	40.8
13	194.9	126.3	127.3	151.8	37.6	40.9
14	201.1	126.8	128.2	167.2	38.4	42.0
15	206.7	127.4	128.2	179.1	39.0	42.7
16	212.9	127.8	128.3	192.9	39.5	42.6
17	–	127.9	129.0	–	40.0	43.0
18	–	128.2	129.3	–	40.4	43.4
19	–	128.5	129.4	–	40.6	43.5
20	–	128.8	129.5	–	40.9	43.5
21	–	129.0	129.7	–	41.1	43.6
22	–	129.1	130.0	–	41.2	43.7
23	–	129.2	130.3	–	41.4	43.8
24	–	129.4	–	–	41.6	–
25	–	129.5	–	–	41.7	–

Discussion

Life cycle

The annual autumn migration of Pribilof fur seals extends southward from the Bering Sea to California (Fig. 1), with the animals spending about 90% of their lives at sea and about one-third of the year in the Bering Sea near the Pribilof Islands (Lander & Kajimura, 1982; Gentry & Holt, 1986). Timing of migration and distance travelled appear to be a function of age, sex, and maturity (Fig. 9), as noted by Townsend (1899), Ognev (1935), Taylor *et al.* (1955) and Bigg (1986, 1990). On average, females migrate further south than males, with pregnant females going further south than non-pregnant females (Fig. 10).

The northward migration begins in February. Mature bulls are the first to arrive at the Pribilof breeding beaches in mid May and early June, where they fast for 1 to 2 months while defending territories (Kenyon & Wilke, 1953; Fiscus, 1978). The bulls are followed by the arrival of pregnant females in late June and early July (Bartholomew & Hoel, 1953; Peterson, 1968). Over 75% of females give birth during a three-week period from the end of June to the middle of July (Bartholomew & Hoel, 1953; Peterson, 1968; Trites, 1992*a*). Progressively younger animals arrive

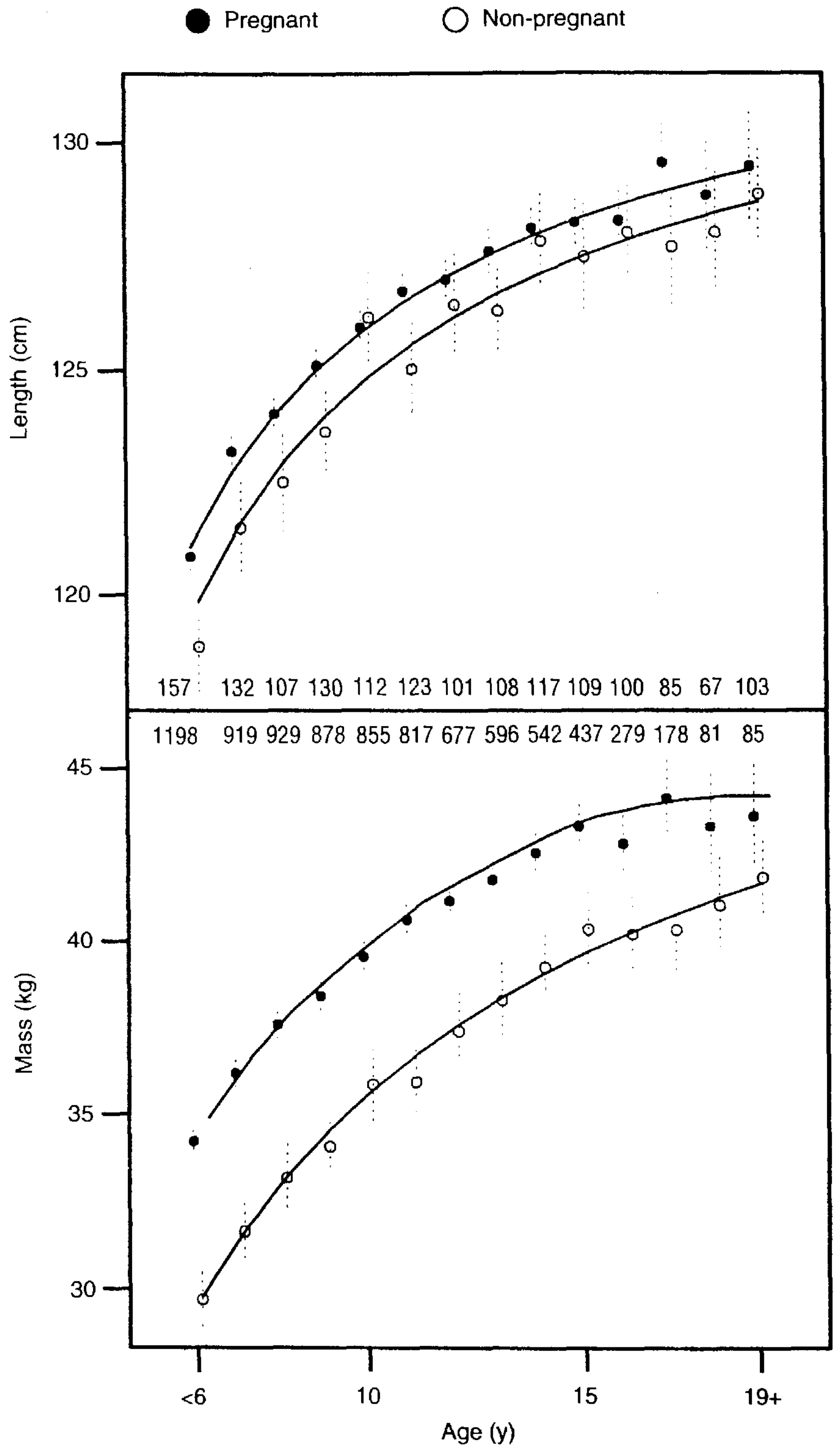

FIG. 6. Mean mass and length of multiparous females with 95% confidence limits. The growth curves were fitted with distance weighted least square smoothing (Systat, 1988). Age-specific samples sizes for the 1 551 non-pregnant and 8 471 pregnant fur seals are shown in the top and bottom panels, respectively. Asymptotic mass of pregnant females is due to senescent declines in the size of foetuses carried by mothers aged 11+ y.

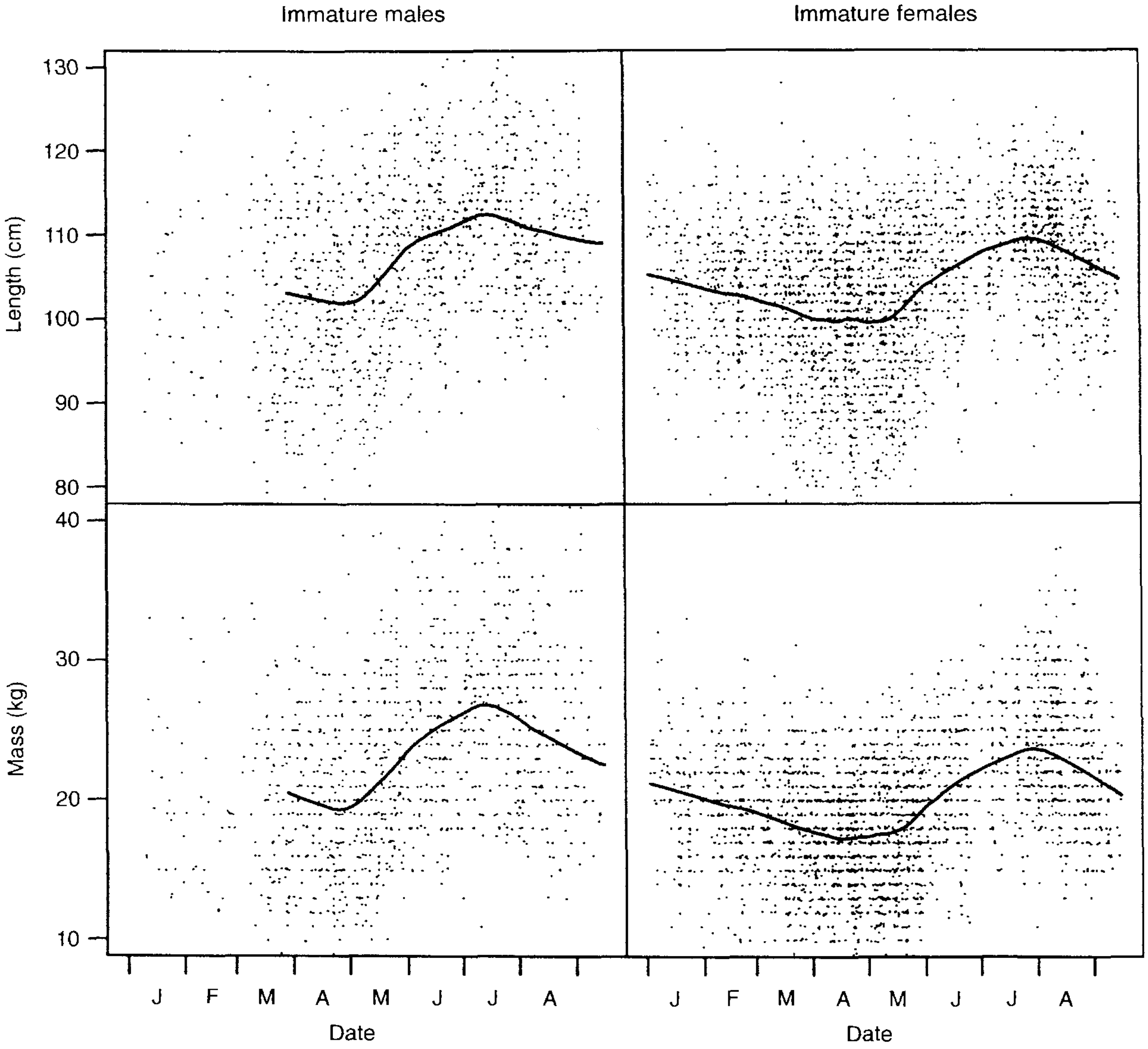

FIG. 7. Seasonal changes in the growth of immature males and females. Length and mass data were pooled for all animals between the ages of 1.5 and 4.5 y, and plotted against the day sampled. The smoothed *lowess* curves (male $f = 0.33$; female $f = 0.25$) show a decrease in length and mass of females through the spring, followed by an increase in the growth of both sexes beginning in May and peaking in July.

later in the breeding season (Bigg, 1986). Moulting begins in August (Scheffer & Johnson, 1963; Bychkov, 1971*b*), with the southward migration starting again in late October and November when the pups are weaned (Peterson, 1968).

Physical growth

Pregnant females are heavier and longer than non-pregnant females (Figs 5, 6). While the differences in mass are largely due to the presence or absence of the foetus, they can also be partly explained by physiological changes associated with pregnancy (Trites, 1991). Curiously, body mass

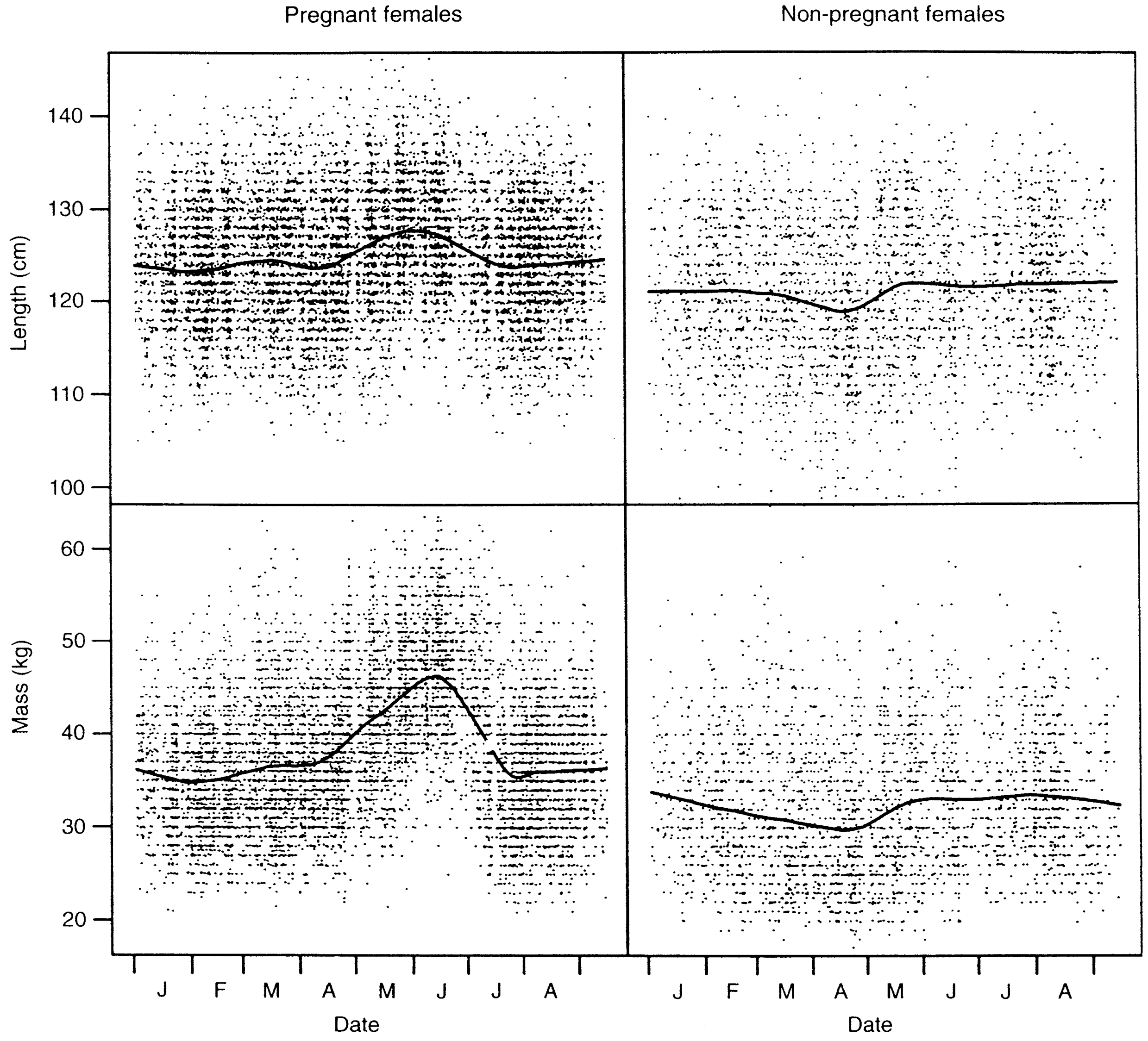

FIG. 8. Seasonal changes in the mass and length of pregnant and non-pregnant females. Data were pooled for all animals older than 4.5 y, and plotted against the day sampled. The smoothed *lowess* curves (pregnant $f = 0.20$; non-pregnant $f = 0.30$) show a small seasonal change in the size of non-pregnant females and marked changes in the size of pregnant females associated with foetal growth and parturition.

in old pregnant females levels off with age in contrast to the increasing mass of non-pregnant females. This is most visible in Fig. 6, and is related to a senescent decline in the size of young carried by females beyond 11 y of age, despite the fact that the mother continues to grow (Trites, 1991).

The seasonal peak in body mass of pregnant females (Fig. 8) occurs on average 1–2 weeks earlier than the peak timing of parturition. The most likely explanation for this is an over-representation of post-partum females in samples collected near the Pribilof Islands during late June and July. Pregnant females give birth shortly after arriving on land and lose a significant amount of mass with the birth of the pup. The post-partum females generally stay with their pup

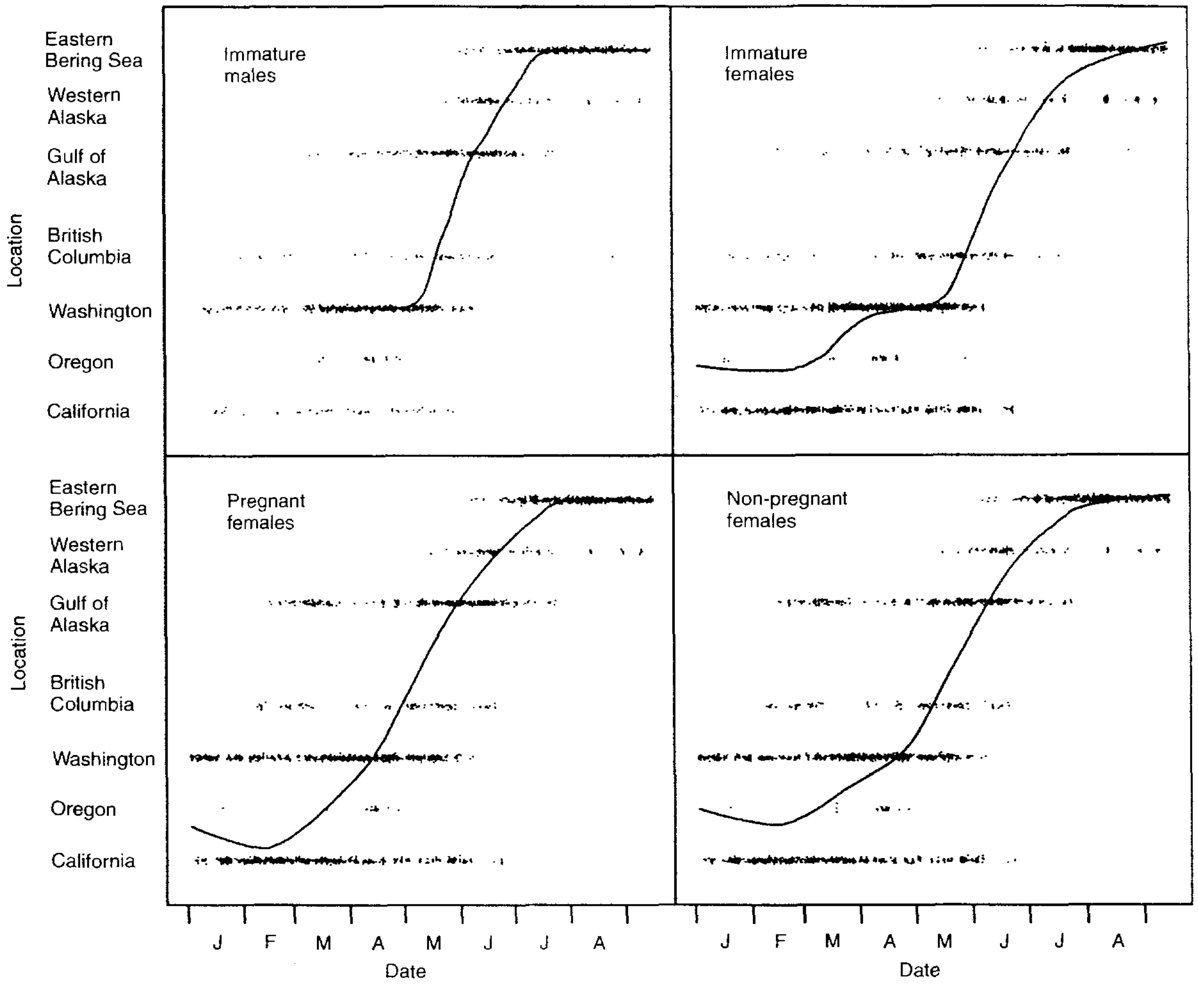

FIG. 9. Migration of northern fur seals by age and reproductive status through the North Pacific. Each data point represents the date and location a seal was shot. A small amount of random variation was added to each data point to reduce the overlap and show the relative density of data. The smoothed curves (*lowess*, $f = 0.33$) indicate the timing of the northward migration to the Pribilof Islands from California to the Bering Sea (see Fig. 1). The two age categories were 1.5–4.5 y for immature animals and 4.5+ y for pregnant and non-pregnant females.

for the first week following birth, then spend an average of 5 days at sea feeding and 2 days ashore suckling their pups (Gentry & Holt, 1986). Thus post-partum females, which are lighter than females still carrying foetuses, would have been over-represented in the samples collected near the Pribilof Islands.

The growth curves estimated for male northern fur seals (Fig. 2) do not show seasonal fluctuations in the size of mature males because of incomplete sampling over the male's migratory range, the difficulty of shooting mature males at sea, and the reduced numbers of males available for sampling caused by the commercial killing of males on land. The male growth curve probably represents the body size of mature males prior to spring fattening. The marked change in the male's growth rate (body mass) between the ages of 4 and 5 y corresponds with production of sperm and onset of puberty (Scheffer & Wilke, 1953). While male body mass increases rapidly with age beyond puberty, changes in the annual length increments are less pronounced (see Fig. 2).

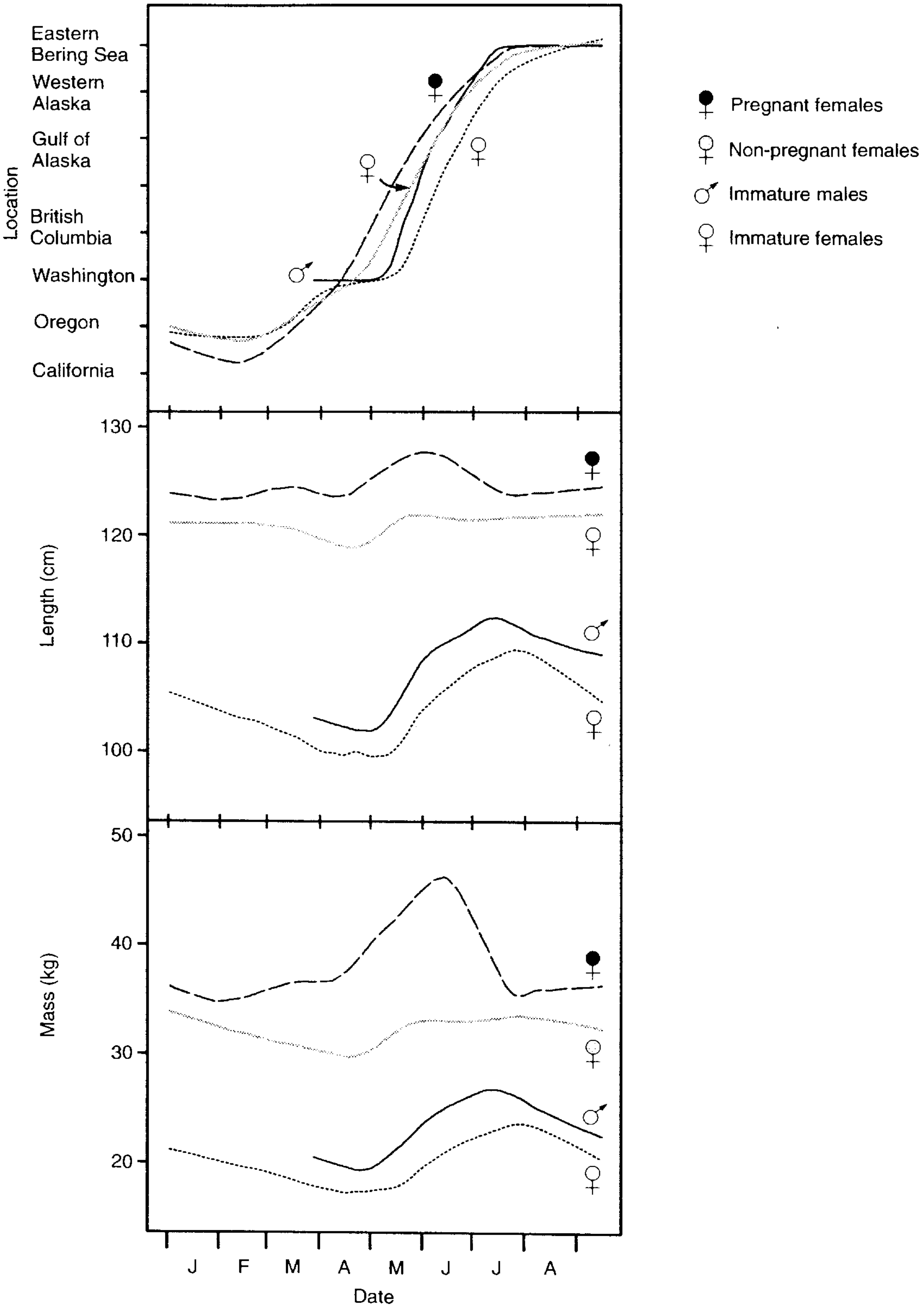

FIG. 10. Comparison of migratory tracts (Fig. 9) and seasonal changes in the mass and length of immature males, immature females, pregnant females, and non-pregnant females (Figs 7 and 8). Note that seasonal growth occurs as each group of animals leaves Washington waters.

The data suggest the male growth spurt occurs between the ages of 4 and 5 y, not between 7 and 8 y as contended by Lander (1981) and Scheffer & Wilke (1953). In all likelihood, the changes noted between the ages of 7 and 8 y are related to the seasonal fattening of breeding males, rather than growth. Johnson (1968) found the age composition of 249 territorial males that were shot, and of 156 that died of natural causes, ranged between 7 and 17 y (70% were aged 10–13 y; the modal age was 10 y). The males appeared to reach their prime condition in about their 10th year, based on the mass of their testes (Scheffer, 1950; Vladimirov, 1987). Adult females also appear to be in their reproductive prime at age 10 y, based upon the size of the foetuses they carry (Trites, 1991).

The mean mass of males 10–13 y is between 110 and 150 kg (from Fig. 2). Territorial males killed within one week of arrival weighed an average of 198 kg ($n = 180$).[1] Thus it appears that male body mass increases between 26% and 72% prior to the harem bulls arriving on land to defend breeding territories. This is in keeping with studies of captive male northern fur seals where body mass increased by 40% to 80% over two months and subsequently returned to its original level the following autumn (Spotte & Adams, 1979).

Captive male and female northern fur seals appear to reduce their food intake voluntarily from December to May (Spotte & Adams, 1979, 1981; Ohata & Miller, 1983; NPFSC, 1984). Increases in body mass occur from May onward, with marked synchrony between individuals. In the wild, the mass gain appears to occur until the seals arrive on land to breed and moult (Fig. 10). Lactating females haul out on 20–30% of the days between July–October to nurse pups (Bartholomew & Hoel, 1953; Peterson, 1968; Gentry & Holt, 1986). Immature males haul out on approximately 19% of the days (Gentry, 1981) and appear to fast for at least part of the time they are in the vicinity of the Pribilofs. Kenyon (1956) found that less than 0.06% (27 of 57 239) of the young males taken in the commercial harvest had eaten prior to roundup.

The average non-pregnant female in her reproductive prime weighs approximately 35 kg (Table I). A mature male is about 3.4 times heavier than the female prior to mating, and is 5.4 times heavier when defending a breeding territory. Such a high degree of sexual dimorphism has been positively correlated with the degree of polygamy of a species (Ralls, 1977; Alexander *et al.*, 1979).

Males and non-pregnant females appear to follow the same allometric relationship until males reach puberty between the ages of 4 and 5 y (Fig. 5). After this age, the male's allometric relationship departs significantly from that of the females as the male growth spurt begins. There is a remarkable consistency between postnatal and prenatal allometric curves. In the case of non-pregnant females, the equation describing the relationship between body mass and length ($M = 6.081 \times 10^{-5} L^{2.740}$) is very similar to that for female foetuses ($M + 6.607 \times 10^{-5} L^{2.740}$, from Trites, 1991).

Indeterminate growth

We did not describe fur seal growth with traditional growth curves such as the Richards, Gompertz, logistic, and von Bertalanffy models (see Zach *et al.*, 1984) because growth is not monotonic, but in fact has strong seasonal components that should not be ignored. Some standard growth models are based in part on the premise that final body size is asymptotic, which

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[1] Calculated from Scheffer & Wilke (1953; $\bar{x} = 188$ kg, $n = 12$), Lander (1979; weighed in 1965; $\bar{x} = 191$ kg, $n = 99$), and Gentry & Holt (pers. comm., cited by Lander, 1979, and weighed from 1975 to 1977; $\bar{x} = 209$ kg, $n = 69$)

may not be the case for northern fur seals. The large number of morphometric measurements suggests, rather unexpectedly, that growth in northern fur seals, and possibly in other pinnipeds, is indeterminate (i.e. growth continues throughout the life span of the individual[2]).

The annual increments in mass and length of fur seals decreases with age, but never reaches zero before the animal dies (Table I). This is shown in Fig. 6, which compares mass and length of physically mature females between the ages of 6 and 19+ y. The length and mass of these multiparous females increases throughout their life spans. Only the mass of pregnant females approaches a distinct asymptote due to the senescent decline in the mass of foetuses carried by mothers $\geqslant 11$ y old (Trites, 1991). Males may also grow continuously, but data from mature individuals are too scant to draw firm conclusions.

Energy allocations between growth and other activities may partly explain the indeterminate growth observed in northern fur seals. Marine mammals are fusiform with small appendages, living for most, if not all of their lives in an aquatic environment (Laws, 1956). Thus final body size may be related in part to body form and the effect of gravity on supporting parts of the body.

Bone is a dynamic tissue that undergoes continuous change and remodelling throughout the life of an individual. It not only functions to provide mechanical support and protection, but also regulates systemic concentrations of calcium. Comparative bone studies have revealed a number of significant differences between the skeletons of pinnipeds and terrestrial mammals. Most notably, they have shown that pinniped skeletons undergo accelerated growth in early development and that they retain some immature characteristics in adulthood (see review by Versaggi, 1981). In particular, many long bones and vertebrae from many pinnipeds have incompletely fused epiphyses or retarded ossification[3], even from animals well past the age of sexual maturity (Howell, 1930; Fawcett, 1942; King, 1972; Sumner-Smith, Pennock & Ronald, 1972; Briggs & Morejohn, 1975; Versaggi, 1981). The presence of incompletely fused epiphyses in pinniped bones suggests that skeletal growth in some, and perhaps all pinnipeds is continuous well past the attainment of sexual maturity when animals appear physically mature by external morphological criteria (Versaggi, 1981).

The differences between the skeletons of pinnipeds and terrestrial mammals suggest secondary aquatic adaptations. For example, the formation of a bone marrow cavity was probably deleted in pinnipeds to accelerate body growth and minimize heat loss (Versaggi, 1981). Similarly, skeletal neoteny may offer pinnipeds a direct physiological advantage, given that younger bones have lower mineral densities, higher amounts of interstitial water, and are more vascular compared to older bones. Thus, the physiological advantage for pinnipeds to retain immature characteristics, such as continual growth through retarded ossification, may be greater skeletal acid-based buffering capacities in response to respiratory and metabolic acidosis of prolonged and repetitive diving (Versaggi, 1981). Increased flexibility and compressibility of immature bone may also enable pinnipeds to withstand the pressures of deep dives better. Similarly, immature (red) bone marrow could repair damage to the endocortical surface of the bone (such as osteocytic necrosis) that might be caused by the pressures of deep dives.

Further evidence of indeterminate growth in marine mammals might be found by re-examining some of the historical pinniped data bases (e.g. grey seals; Mansfield, 1977; harbour seals: fig. 235

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[2] As defined by Lincoln, Boxshall & Clark, 1985

[3] Bone growth occurs as the cartilage cells that continuously grow away from the shaft are replaced by more bone. As ossification outruns cartilage growth, the bone ceases to increase in length (i.e. the epiphysis at the end of the bone closes and fuses). For most mammals, physical maturity is reached when all of the epiphyses have fused throughout the body.

in Naito & Nishiwaki, 1975; southern elephant seals: fig. 4 in Bryden, 1969; and northern elephant seals: fig. 5 in Reiter, Panken & Le Boeuf, 1981).

Fluctuations in body length

It has long been recognized that length is a more reliable indication of pinniped size than is mass because it varies less (Scheffer & Wilke, 1953; Laws, 1956; McLaren, 1993), and does not presumably fluctuate, at least not as much as mass. The discovery of seasonal decreases in body length of fur seals is therefore mystifying. The large samples of seals and variability in timing and location of sampling negate the possibility that the reported seasonal change in length is an artefact of sampling location or error in body measurement. Nor is it due to yearly changes in growth rates and sampling locations given that periodicity in length was evident in each year of sampling (Trites & Bigg, 1992).

A decrease in body length implies a decrease in the length of the vertebral column. Since the seasonal change is of a relatively large magnitude (7 to 8%), it is unlikely to result from deposition and resorption of bone in the vertebrae and intervertebral discs. Instead, it is probably related to factors that influence the spacing between the vertebrae discs. Three possible explanations are: (1) changes in body water composition; (2) gravity and the astronaut phenomenon; and (3) the displacement of body mass when out of water.

Bigg (1979) suggested there is seasonal variation in water content of the cartilage and connective tissues separating the bony components. The higher the water content, the more edematous the soft tissue, the longer the vertebral column might be. For example, the rapid increase in body length of females in late pregnancy followed by a rapid decline after parturition could be explained by the effects of pregnancy hormones, progesterone, and oestrogen, which increases extracellular water content (Guyton, 1961). Following parturition, the hormone levels would rapidly decline and cause a loss of body water. Support for this view is contained in Taylor *et al.* (1955), who report that the average right upper canine teeth of pregnant females weighed more than canine teeth from non-pregnant females. The difference in tooth mass is presumably related to water content. Thus pregnancy hormones could explain why pregnant females are longer than non-pregnant females of the same age. However, this explanation fails to account for the seasonal changes in male lengths.

The second hypothesis concerns the effect of gravity. Like astronauts that become physically taller while in space, the length of a seal's body might expand while supported in water, and contract during its residency on land. Thus seals collected near the Pribilof Islands might be longest after completing their annual migration (fur seals are at sea the entire time), and shortest when leaving the Pribilofs to begin their autumn migration.

Finally, changes in length could be an artefact of mass displacement, exerting stress upon the vertebral column of the seal lying on their backs on the 'cradle' measuring board. The greater mass of heavier seals would place greater force upon the vertebral column and increase the spacing between the vertebrae. Thus seasonal length fluctuations might be a product of the seasonal mass fluctuations. Support for this hypothesis comes from measurements of fur seals on their backs and bellies, made by Yoshida & Baba (1981). They found that 85% of the seals were longer when the animals were lying on their backs compared to lying on their stomachs. The increase averaged about 2% of body length (based on measurements from 1 024 females and 119 males).

We believe that all three factors contribute to the seasonal fluctuation in body length. Seals probably retain more body water as their mass increases on their return journey to the Pribilof beaches, in preparation for fasting on land, or as a direct result of pregnancy and the nutritional requirements of the foetus. However, the effect of fluid retention and gravity on the spacing of the vertebral discs is probably of minor consideration compared to how body mass could alter the length of seals measured on their backs.

The phenomenon of seasonal decreases in body length could be present in other species of wild mammals, but has not been detected because of insufficient sample sizes. It could also be missed because researchers have generally failed to consider length changes as a real possibility. Note for example when Olesiuk & Bigg (1993) considered seasonal changes in the length of male Steller sea lions, they found a tendency for the animals to be longer in the spring than in the autumn (adults were measured belly up). Finally, the observation that pregnant female fur seals are longer than non-pregnant females may also be true of other species and is deserving of further attention.

Growth and feeding location

Growth spurts and gains in body mass of all age groups only occur when the seals are north of Washington State (Fig. 1). Northern fur seals either lose or fail to gain body mass while in Washington and further south. Such changes in body mass are probably inherent, reflecting voluntary changes in consumption and/or difference in the quality and abundance of available prey. Reduction in feeding and loss of mass might well be evolutionary adaptations to lower seasonal abundances of prey encountered during this part of migration. They could also be mechanisms to pace physiology for a long migration.

Based on ocean circulation and distributions of commercially caught marine fish (Ware & McFarlane, 1989), the migrational range of the fur seal in the north-east Pacific Ocean can be divided into three major production domains: (1) the Central sub-Arctic Domain (Alaska); (2) the Central Coast Downwelling Domain (northern British Columbia); (3) the Coastal Upwelling Domain (southern British Columbia to Baja California). Fur seals gain body mass while in the first two domains. They lose it while in the third.

Fur seals feed upon small schooling fish and squid (Kajimura, 1985; Perez & Bigg, 1986). In the Upwelling Domain off California (where seals lose body mass), fur seals feed primarily upon northern anchovy. As the seals move northward along the coasts of Oregon and Washington, they feed upon a large variety of species including Pacific hake, jack mackerel, and Pacific herring. The greatest diversity of prey are consumed in Washington waters, with no single species dominating the diet (Kajimura, 1985; Perez & Bigg, 1986).

As the seals continue to migrate north into the Downwelling and sub-Arctic Domains, they begin to grow and gain body mass while feeding primarily on Pacific herring (British Columbia, Gulf of Alaska, Western Alaska), Pacific sandlance (Gulf of Alaska), and capelin (Western Alaska, Bering Sea). Their diet changes mainly to walleye pollock when the seals enter the Pribilof Islands region (Kajimura, 1985; Perez & Bigg, 1986).

Washington waters appear to be a major transitional zone in the migration of northern fur seals (see Fig. 10). It is not clear why immature animals spend so long here given that they do not grow until they leave this region. Perhaps water temperatures restrict the distribution of seals and therefore retard the northward migration of young animals. Energetic costs of heat regulation in colder northern waters may more than offset any gains made from going north earlier versus staying. Another possibility is that there are spatial and temporal differences in prey and in the foraging efficiency of seals of different ages and sizes.

By spreading out the migration, the total biomass of fur seals in any one area is probably never very high, which would reduce competition for food among the population as a whole. Upon arriving at the Pribilofs, most of the males appear to fast and reduce their food intake. Furthermore, a large biomass of pollock and other species in the Bering Sea can presumably support a large fur seal population and may well be the reason why large rookeries were established on the Pribilof Islands (Bigg, 1990).

Pinniped growth

The generally accepted view that pinniped growth is a monotonically increasing function of age (e.g. Scheffer & Wilke, 1953; Boulva & McLaren, 1979; Innes, Stewart & Lavigne, 1981; Lander, 1981; McLaren & Smith, 1985) appears to have resulted from a scarcity of data and/or the tabulation of body size by year rather than by day or month. Many studies have noted pronounced changes in the seasonal fat content of sexually mature phocids in connection with reproduction and moult (e.g. Bryden, 1968; Sergeant, 1973; Innes, Stewart & Lavigne, 1978; Ashwell-Erickson & Elsner, 1983; Stewart & Lavigne, 1984; Costa *et al.*, 1986; Pitcher, 1986; Bowen, Boness & Oftedal, 1987; Nordoy & Blix, 1988; Ryg, Smith & Oritsland, 1990). However, only one study has noted seasonal fluctuations in the size of immature phocids (Ryg *et al.*, 1990, for hooded seals); perhaps because subtle seasonal changes in core mass of immature phocids are more difficult to detect than the pronounced changes in blubber mass of mature individuals.

As with phocids, most otariid studies have also tended to focus upon seasonal fluctuations in the mass of sexually mature individuals (e.g. Scheffer, 1945; Rand, 1955, 1959; Vaz Ferreira, 1959; Fiscus, 1961; Bonner, 1968; Schusterman & Gentry, 1971; Bryden, 1972; Payne, 1979; Walker & Ling, 1981; Kastelein, Verhoeven & Wiepkema, 1990). Blubber thickness of mature female otariids increases only slightly with age, unlike mature males which experience a marked change with age in association with reproduction (Scheffer & Wilke, 1953; Thorsteinson & Lensink, 1962; Lander, 1979; Calkins & Pitcher, 1982). Studies of captive otariids indicate that males voluntarily regulate their food intake (Kastelein, Vaughan & Wiepkema, 1990; Kastelein, Verhoeven & Wiepkema, 1990), and increase body mass at the same time that wild populations approach the breeding beaches (Schusterman & Gentry, 1971; Spotte & Adams, 1979; Ohata & Miller, 1983). Weight gains appear to reflect the accumulation of fat over all parts of the body (except the flippers), as well as changes in core mass associated with increases in water content and/or proteinaceous tissue (Olesiuk & Bigg, 1993).

Conclusions

Estimates of pinniped population biomass may be useful for estimating food consumption and the amount of energy required for growth (e.g. Payne, 1979; Innes *et al.*, 1981; Fedak & Anderson, 1982). However, the strong seasonal and regional components of growth should be taken into account when assessing the role of pinnipeds as energy consumers in the ecosystem. This is particularly true if biomass estimates are based upon samples taken at or near breeding sites when pinnipeds are at maximal seasonal body size. Analysis of growth rates can also be confounded by seasonal fluctuations in body size unless appropriate precautions are taken. Furthermore, seasonal fluctuations can confound assessments of physiological condition based on length and mass measures.

The morphometric measurements indicate that northern fur seals gain body mass during a brief 1–3 month period each year prior to arriving on land. They appear to lose mass gradually during the rest of the year. Thus it appears that prey consumed by fur seals fulfil different needs in different regions of the migratory range. Food is important for the maintenance of body mass off California. But growth and increase in body mass occur while the fur seals are in the Gulf of Alaska and coastal waters of northern British Columbia. The importance of this food outside the Bering Sea has generally not been recognized before and should be given further consideration given the current depressed state of the Pribilof population (Trites, 1992*b*).

The extensive morphometric data from northern fur seals contain considerable information about growth and seasonal fluctuations in body size. They also reveal much about the relationship between prey type, physiology, and the timing of migration. Such insights into the physical growth of northern fur seals are likely to be applicable to other species of fur seals and perhaps to other pinnipeds as well.

The pelagic fur seal data were collected and prepared by Canadian (Department of Fisheries and Oceans) and American (National Marine Fisheries Service) biologists under the auspices of the North Pacific Fur Seal Commission. The data set represents thousands of hours of collection and preparation and has involved the efforts of many individuals. We are grateful to Mike Perez for helping to verify questionable data with the original field records. We would also like to extend our appreciation to Monique Bournot, Chuck Fowler, Roger Gentry, Harry Loe, David Lavigne, Don Ludwig, Carol Mace, Ian McLaren, Debbie Murie, Victor Scheffer, Carl Walters, and an anonymous reviewer for their constructive comments and suggestions on earlier drafts of this manuscript.

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