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Biased estimates of fur seal pup mass: origins and implications

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(With 5 figures in the text)

The mass of fur seal pups weighed in different years can be used to estimate growth rates or compared with one another to make inferences about the relative condition of a population. However, unless appropriate precautions are taken, many factors can bias estimates of pup mass and lead to incorrect conclusions. Using data collected from tagged and untagged northern fur seal pups (*Callorhinus ursinus*) at the Pribilof Islands, Alaska, I assess how milk consumption, the timing of sampling, and the effects of growth and sample size influence the size of pups captured for weighing. Evidence is presented suggesting that pup mass may increase in a sigmoid fashion, with the most rapid rate of growth occurring when about two months old. This phenomenon can confound efforts to compare the masses of pups weighed on different days in different years, particularly if pups are weighed over the period of rapid growth. Variability in pup mass increases with time because growth rates of individuals vary and because the amount of milk pups consume increases with body size. Thus sample sizes must be increased as the pups grow older in order to detect statistically significant differences in mean body mass. There is also evidence that pups of different ages and sizes are not randomly distributed on the breeding beaches and are not randomly selected for weighing. It appears that the first pups captured for weighing are smaller and younger than subsequent captures, possibly because smaller pups are easier to handle and are segregated to the peripheral rookery regions where sampling begins. These hidden biases, related to sampling error and fur seal biology, must be considered and controlled for when weighing fur seal pups.

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Introduction

Pup mass is relatively easy to obtain and is available for all species of fur seals (King, 1983). Pups have been weighed over successive days to construct growth curves for northern fur seals, *Callorhinus ursinus* (Scheffer & Wilke, 1953), sub-Antarctic fur seals, *Arctocephalus tropicalis* (Kerley, 1985), Antarctic fur seals, *A. gazella* (Croxall & Prince, 1979; Doidge, Croxall & Ricketts,

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1984*a*; Kerley, 1985), Galapagos fur seals, *A. galapagoensis* (Trillmich & Limberger, 1985) and New Zealand fur seals, *A. forsteri* (Mattlin, 1981). For other species, such as the Cape fur seal, *A. pusillus pusillus* (Rand, 1956), only a single set of descriptive pup masses is available.

Growth curves can be contrasted with one another to make inferences about the life-history strategies of the different fur seal species. Similarly, growth curves can be used to compare the rate of pup growth of a single species between years (e.g. Kerley, 1985; Croxall *et al.*, 1988; Duck, 1990). Annual differences in the mean size of pups are also a potentially valuable management tool if, as believed, they reflect maternal competition for food and influence the future survival of the young animals (Scheffer, 1955; Chapman, 1961; Eberhardt & Siniff, 1977; Mattlin, 1981; Doidge *et al.*, 1984*a*; Kozloff & Briggs, 1986; Doidge & Croxall, 1989; Duck, 1990).

In order to construct growth curves properly or to compare the mass of fur seal pups born in different years, several factors, such as when the pups are weighed and the number of pups to be weighed, must be carefully considered and understood. Depending upon the rate of growth, it may be invalid to compare the mass of pups weighed on different days in different years. Similarly, difficulties may arise if samples contain primarily either fasting pups or pups that have recently fed. Finally, biases associated with sample sizes, behavioural segregation of different aged pups, and human error in randomly selecting pups for weighing need evaluation.

The present study brings together both published and unpublished data collected from northern fur seal pups born at St. Paul Island, Alaska, to evaluate potential biases associated with weighing fur seal pups. Three factors are considered: (1) the mass of milk consumed; (2) the rate of growth during the sampling period; and (3) the effect of different sample sizes. Biased estimates of pup mass can lead to improper conclusions unless appropriate precautions are taken. My goal is to review and document each of the three factors individually and provide an overview of the problems to consider when weighing fur seal pups.

Milk consumption

Errors in body mass associated with the mass of milk consumed by northern fur seal pups can be inferred from a study by Costa & Gentry (1986). These authors measured total water influx and determined that northern fur seal pups, on average, consumed a total of 3·5 litres of milk during the first 7 days following birth (2 males, 4 females) and 3·2 litres during each subsequent 2-day feeding bout (weighed mean: 2 males, 4 females). Their report contains 2 figures showing the volume of milk consumed per feeding bout plotted against (1) the age and (2) the mass of the pup.

TABLE I

Average density of northern fur seal milk determined from the specific density (Kleiber, 1961) and percentage composition of fur seal milk components (Costa & Gentry, 1986)

Components	Mean composition	Density	Density of milk
Water	44·4%	1·00	0·444
Fat	41·5%	0·89	0·369
Protein	14·2%	1·35	0·192
Ash	0·5%	3·10	0·016
Lactose	—	1·52	—
Total			1·021

Digitizing this data, a third figure was produced (body mass vs. age) and the volume of milk consumed per day of feeding was estimated. I then converted volume to mass by multiplying the components of milk by their specific densities (Table I).

On average, northern fur seal milk consists of 44·4% water, 41·5% fat, 14·2% protein, and 0·5% ash (Costa & Gentry, 1986), and has a density of 1·021 (Table I). Given that the mass of water at 28 °C is 0·9982 g ml^{-1} (Kleiber, 1961), the mean mass of fur seal milk is 1·019 kg l^{-1} (calculated as 1·021 × 0·9982 kg l^{-1}). The actual mass of milk consumed by the pup depends upon changes in milk composition that occur throughout lactation (Costa & Gentry, 1986), but is unlikely to vary much from the mean estimate. Note also that the estimate of mean density assumes that fur seal milk contains no carbohydrates (lactose), which is in keeping with the conclusions of Pilson &

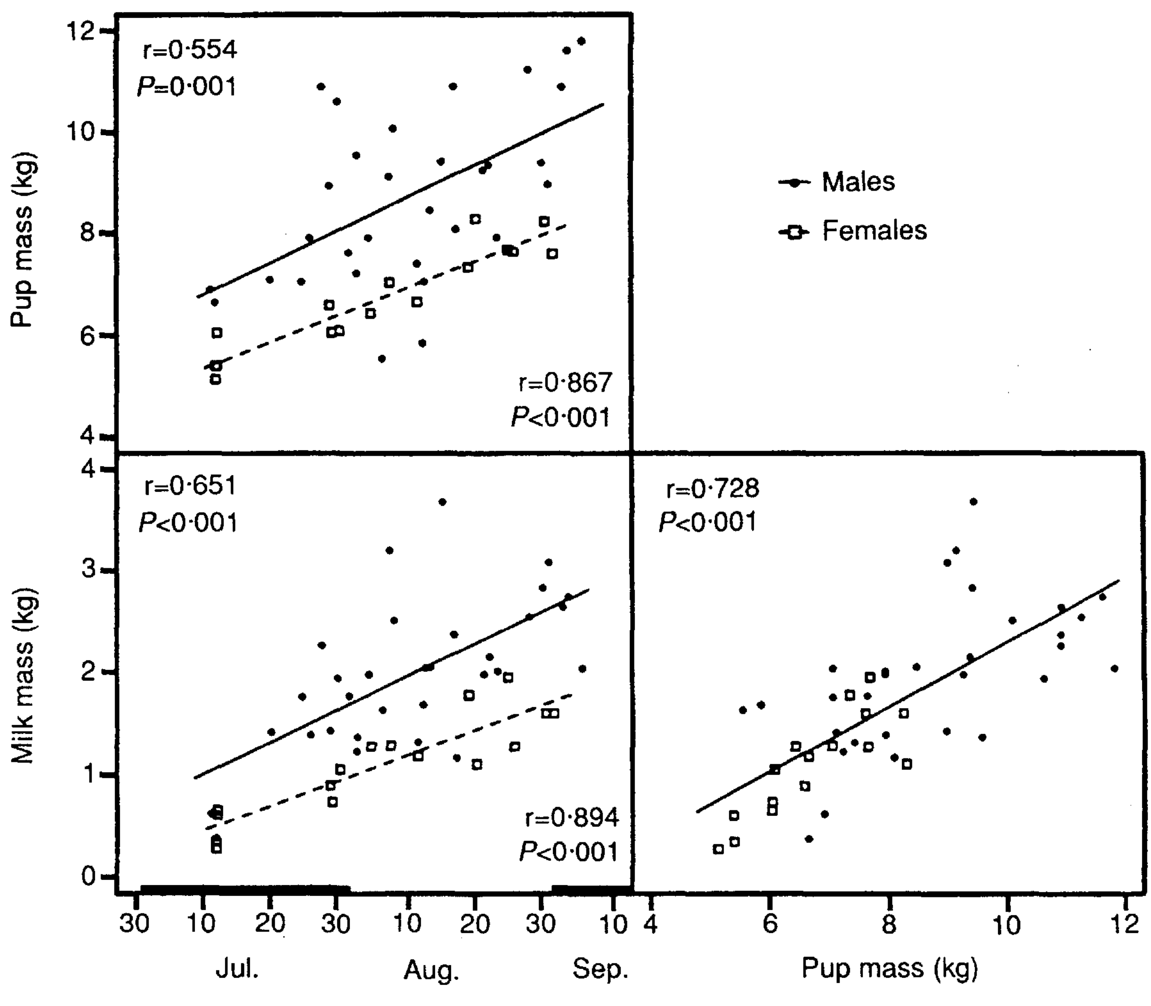

FIG. 1. Growth and milk consumption for male and female pups during one day of feeding. Males were significantly heavier than females (top left panel) and consumed greater amounts of milk (bottom left panel). The greater consumption of milk by males is related to their larger body size. Linear regressions applied to milk mass as a function of body mass for each sex separately were not significantly different (slope: $t_{45} = 1{\cdot}119$, $P = 0{\cdot}135$; elevation: $t_{45} = 1{\cdot}761$, $P = 0{\cdot}043$), indicating that males and females of comparable body sizes consumed the same amount of milk (bottom right panel). A linear regression is therefore shown for both sexes combined. The significance of the regressions is contained with each panel. The data shown in this figure were derived from the work of Costa & Gentry (1986) and were assumed to be from pups born on July 7, the mean date of birth (Trites, 1992).

Kelly (1962) and Pilson (1965). However, Schmidt, Walker & Ebner (1971) found low, but detectable lactose concentrations that suggest the above calculations are slightly underestimated, although not significantly so.

The mass of milk consumed by northern fur seals in one day of feeding varied between 0·2 and 3·8 kg d^{-1} depending upon a pup's size and sex (Fig. 1). Males seemed to consume more milk than females because they were physically larger, and consumption increased as the pups grew over time (*cf.* Costa & Gentry, 1986). Although the amount of milk consumed is shown in Fig. 1 as a linear function of time and body mass, it is more likely a nonlinear relationship which approaches an asymptote. Presumably, the capacity of lactating females to produce milk is limited at some point in time due to physiological constraints or the process of weaning.

Milk accounts for a large proportion of total body mass. For example, an average-sized male pup weighing 9 kg before feeding is likely to consume between 3·0 and 7·5 kg of milk over a 2-day feeding bout (Fig. 1). Thus the pup's mass could vary considerably depending upon whether the pup is weighed at the end of the 5-day fast or immediately after the 2-day suckling period. Such a large variance in body mass means that large sample sizes would be required to construct growth curves or to detect statistically significant differences in mean body mass between years.

Seasonal pup growth

A second major source of error in weighing pups can be attributed to the rate of growth during the sampling period. To assess the extent of this potential source of bias, the growth rate of northern fur seal pups was estimated from samples of tagged and untagged pups weighed at St. Paul Island, Alaska, since 1957.

Tagging and weighing were conducted between 1957 and 1971 by the United States Fish and Wildlife Service at 4 St. Paul rookeries: Zapadni Reef, Polovina, Reef and Northeast Point. Methods of data collection are contained in the annual 'Fur seal investigations' reports (e.g.

TABLE II

*Mean mass of male and female pups weighed between Aug. 29–Sept. 3. The mass of tagged pups, weighed from 1957–66, was compared to the mass of untagged pups weighed during the same time period using a Student's t-test. Probabilities associated with the sample statistic are enclosed in brackets (**P**). The mean mass of untagged males was compared to female mass over the years 1957–71, 1984 and 1987*

Mark	Sex	Mean mass (kg)	Standard deviation	*t*-test (*P*)	*d.f.*
no tag	M	9·47	1·98		
	F	8·30	1·74	35·10 (0·002)	12196
tagged	M	8·43	1·84		
	F	7·49	1·60	19·06 (<0·001)	4916
no tag	M	9·26	1·98		
tagged	M	8·43	1·84	16·36 (<0·001)	5697
no tag	F	8·14	1·75		
tagged	F	7·49	1·60	14·362 (<0·001)	5620

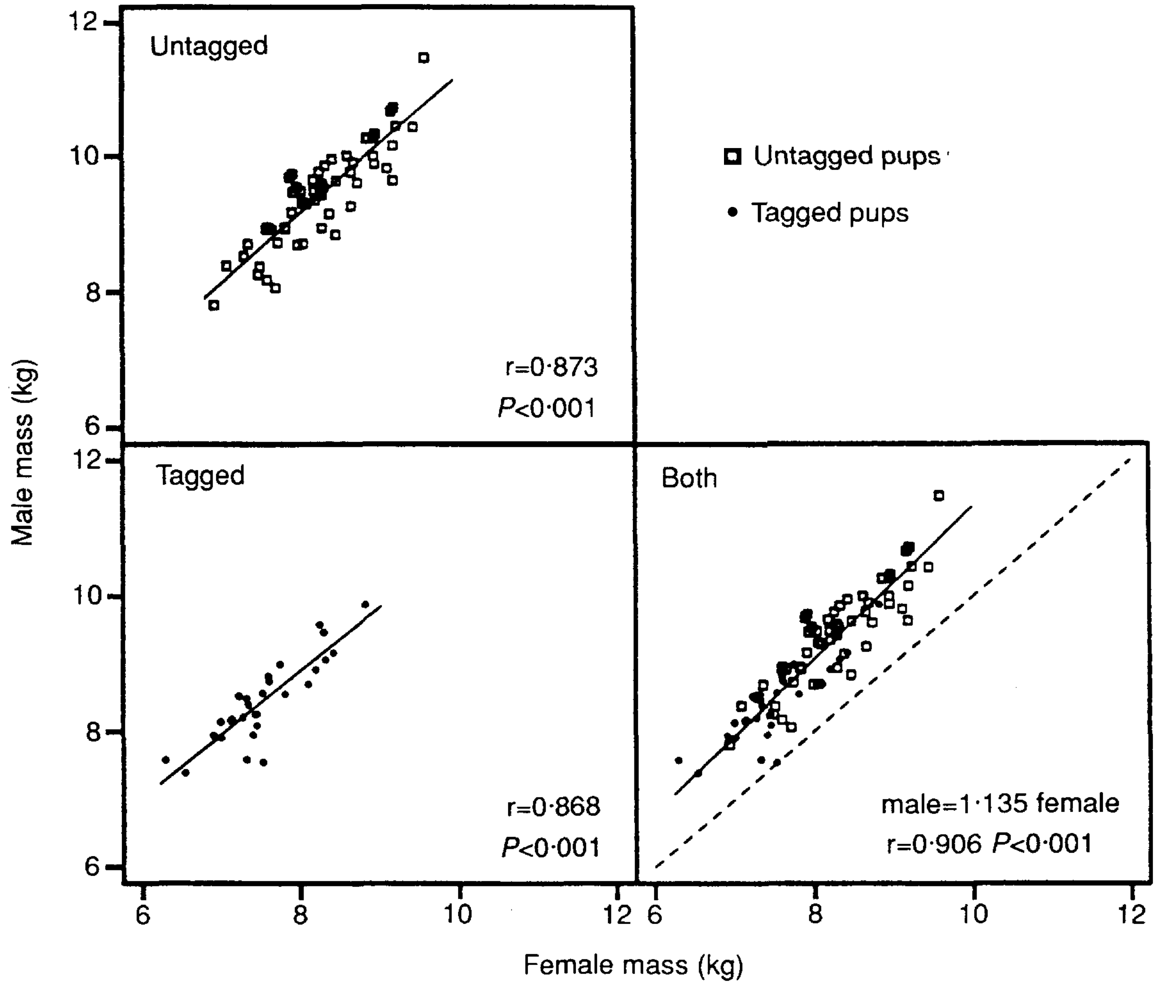

FIG. 2. Relationship between the mass of male and female pups. Each data point indicates the mean mass of at least 30 pups weighed between Aug. 29–Sept. 3 when approximately 2 months old and is specific to a given rookery in a given year (1957–71, 1984, 1987). Linear regressions were fitted separately to data from tagged and untagged pups. Neither of the intercepts was significantly different from zero (tagged: $t_{26} = 1{\cdot}745$, $P = 0{\cdot}092$; untagged: $t_{55} = 1{\cdot}446$, $P = 0{\cdot}154$). Nor did the slopes of the two regressions differ from one another ($t_{83} = 0{\cdot}629$, $P = 0{\cdot}266$). Thus, the two data sets were pooled and fitted with a zero constant (bottom right panel). The dashed line shows the expected 1 : 1 relationship. The significance of the regressions are contained within the panels.

MMBL, 1969) published by the United States Fish and Wildlife Service and are summarized in Trites (1991*a*). Data from 1984 and 1987 are from the files of the National Marine Mammal Laboratory, Seattle, WA.

Pups were tagged from 1957–66 when about 5–6 weeks-old and weighed 2 weeks later. Additional samples of untagged pups were weighed during 1967–71, 1984 and 1987. Since 1957, a total of 17,116 pups were weighed between Aug. 24 and Sept. 5, of which 4,918 bore a tag or mark.

The mass of pups weighed between Aug. 24–Sept. 5 was normally distributed and ranged from 1·0–18·8 kg with a mean of 8·7 kg (S.D. = 1·97, $n = 17{,}116$). The 2-month-old males were 13·5% larger than females (Table II, Fig. 2) and appeared to grow faster than female pups, given that the difference in size of northern fur seals at birth is only 10% (Trites, 1991*b*). This difference in growth rates of the sexes is consistent with the marked sexual dimorphism of fur seals, and has been demonstrated for a related species, the Antarctic fur seal (Payne, 1977, 1979; Doidge *et al.*, 1984*a*; Croxall *et al.*, 1988; Doidge & Croxall, 1989).

Tagged northern fur seal pups weighed less than untagged pups (Trites, 1991*a*), not because tagging affected growth but, presumably, because pups selected for tagging in mid-August were smaller and younger than average (Trites, 1991*a*). Additional studies of Antarctic fur seal pups (Kerley, 1985; Doidge & Croxall, 1989) and New Zealand fur seal pups (Mattlin, 1978, 1981) add further credence to the conclusion that tagging does not affect pup growth.

Since 1957, 90% of the pups weighed were sampled between Aug. 29–Sept. 3. During this period, untagged male and female pups grew an average of 0·131 and 0·121 kg d^{-1}, respectively (Fig. 3). Although males appeared to grow faster than females, the difference was not statistically significant (slope: $t_{110}=0{\cdot}130$, $P=0{\cdot}448$; elevation: $t_{111}=9{\cdot}548$, $P<0{\cdot}001$). Nevertheless, the growth rates were high and indicate potential problems in trying to contrast the mean mass of pups collected in different years if they were not sampled on the same day each year. For example, an average-sized male pup weighing 9·0 kg on Aug. 29 would weigh 9·7 kg on Sept. 3. Similarly, a female weighing 8·0 kg on Aug. 29 would gain 0·6 kg over the next five days.

There is curiously little information available on the seasonal growth of northern fur seal pups. In 1952, Scheffer & Wilke (1953) weighed pups at birth and again on Oct. 4. Assuming that 89 days had elapsed since July 7, the mean date of birth (Trites, 1992), the average growth rate was 0·096 kg d^{-1} for males and 0·081 kg d^{-1} for females. Costa & Gentry's (1986) data shown in Fig. 1 (top panel) suggest that growth over the first two months of life is linear and relatively slow (males grew 0·062 kg d^{-1} and females 0·051 kg d^{-1}). However, this growth curve is based on a few pups that were repeatedly weighed prior to feeding which means that there is less information in the figure than might appear. Nevertheless, the regressions are still significant when the degrees of freedom are reduced to account for the repeated measurements.

The initial rate of growth between July and August was in the order of 0·062 and 0·051 kg d^{-1} for male and female pups, respectively (Fig. 1). Between Aug. 29 and Sept. 3, however, growth rates more than doubled (0·131 kg d^{-1} males, 0·121 kg d^{-1} females, see Fig. 3 and above). Additional data (Trites, 1991*a*) suggest this high rate of growth drops off during the months of September and October. Growth rates of males weighed from Sept. 2–Oct. 3, 1962 averaged 0·092 kg d^{-1} and dropped to 0·046 kg d^{-1} from Oct 2–25 (Roppel *et al.*, 1963; Trites, 1991*a*). The suggestion from these three pieces of information is that pup growth is nonlinear with mass increasing in a sigmoid fashion from birth to weaning.

Several authors have concluded that fur seal growth from birth to weaning is linear. This has been reported for both sub-Antarctic (Kerley, 1985) and Antarctic fur seals (Doidge *et al.*, 1984*a*; Kerley, 1985; Doidge & Croxall, 1989). However, inspection of their data suggests growth is actually nonlinear and likely sigmoid (e.g. see fig. 1 in Doidge *et al.*, 1984*a*).

Sample size effects

Errors associated with sample sizes, behavioural segregation of different aged pups, and human error in randomly selecting pups for weighing were evaluated using the pup mass data base previously discussed and with independent studies.

On all rookeries, except Northeast Point, there was a positive relationship between the mean mass and the number of pups weighed (Fig. 4). This correlation between body size and sample size suggests that pups were not randomly chosen for weighing. Pups gather together in small pods on

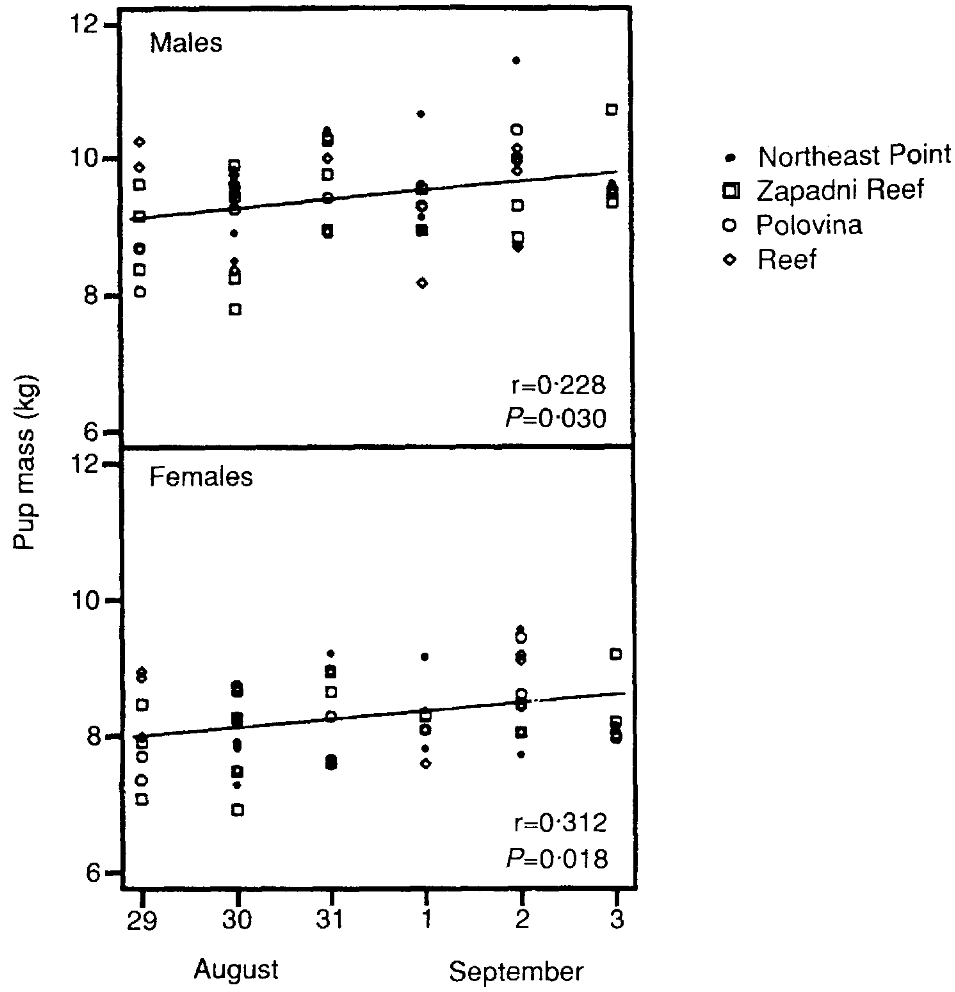

FIG. 3. Mean body mass of untagged pups weighed from Aug. 29–Sept. 3. Each point represents one rookery and one year (1957–71, 1984, 1987), where the sample size was greater than 30 pups. Note that in pooling the data I am assuming that no bias is introduced by the type of scale used, and that the sample size was large enough to reduce the effects of feeding and fasting. Linear regressions were fitted to the mean mass, rather than the raw values, to reduce the combined effects of annual differences in body mass and sample size. The significance of the regressions is shown at the bottom of each panel.

the rookery and pile up during weighing. As a result, smaller pups may be inadvertently taken by researchers from the tops of the piles. Evidence supporting this hypothesis was gathered in 1980 and reported by Roppel *et al.* (1981). They followed a shearing[1] crew through four rookeries at St. Paul Island and weighed the pups selected for shearing from pods of 10–200 pups. When the shearers were finished, the remaining unsheared pups in the pod were weighed. Roppel *et al.* (1981) concluded that sheared pups generally weighed less than unsheared pups and noted the difference in mass was somewhat greater for males than for females. Their results suggest that smaller pups are easier to handle and are subconsciously chosen before larger ones.

The correlation between body size and sample size shown in Fig. 4 could also be related to pups

[1]A mark-recapture experiment to estimate the numbers of pups born, done by clipping a patch of fur from the pup's head.

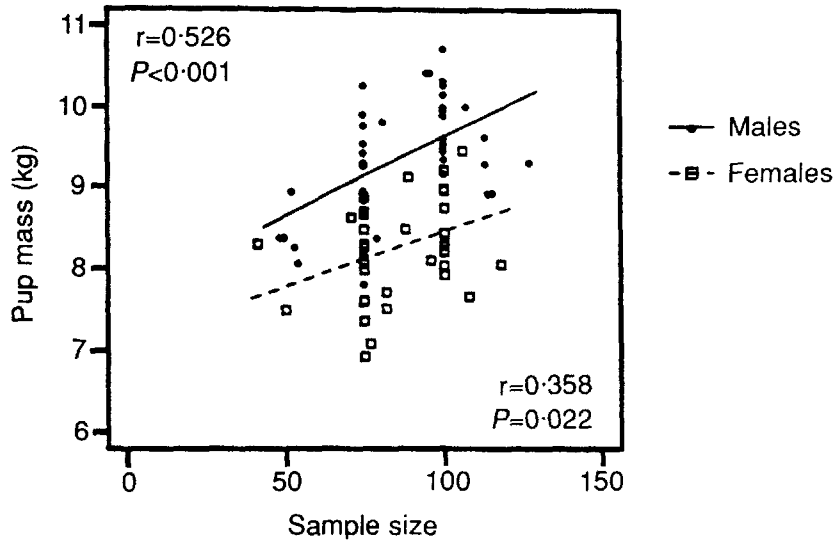

FIG. 4. Relationship between mean body mass and the number of untagged pups weighed on three rookeries: Zapadni Reef, Polovina and Reef. A positive relationship between pup mass and sample size was found for each rookery separately prior to pooling data, except at Northeast Point.

being segregated by size and age on the rookeries. Younger and smaller pups may be in the peripheral regions and more easily captured for weighing. Attaining larger sample sizes may require going further into the rookery, thereby rounding up older and hence larger pups. Support for this theory comes from a 1980 study reported by Gentry & Francis (1981). They marked northern fur seal pups shortly after birth on two rookeries, and calculated the median ages of those marked pups captured many weeks later for shearing, as well as the median ages of those marked pups not captured. They found that captured pups were significantly younger (by 4–5 days) than non-captured pups at both rookeries.

Further inferences about the spatial distribution of pups can be made from studies of Antarctic fur seals, since comparable data from northern fur seals are lacking. In one study, Boyd (1989) counted the number of pups inland and on the beach. He found the rise in numbers of pups using the inland area lagged behind the beach density by about three weeks. It appears that pups dispersed from the high density beach to the low density inland areas. In so moving, they probably improved their chances of survival, given that mortality rates are greater at high density sites than at low density sites (Doidge, Croxall & Baker, 1984*b*).

Another mechanism that might produce spatial segregation of fur seal pups relates to when pregnant females of different ages arrive on shore to give birth. Among Antarctic fur seals, the size and age of the females giving birth declines as the reproductive season progresses (Payne, 1979; Doidge *et al.*, 1984*b*; Boyd & McCann, 1989; Boyd *et al.*, 1990). There is also an increase over time in the proportion of primiparous females giving birth (Doidge *et al.*, 1984*b*). In northern fur seals, primiparous females are also thought to return late, and are known to give birth to smaller pups (Trites, 1991*b*). There is also evidence that younger females produce smaller pups that suffer higher mortalities than pups of older females (Calambokidis & Gentry, 1985). Perhaps there is a greater tendency for late arriving females to give birth in low density peripheral areas as the main breeding beaches fill. Such a strategy could improve the chances of a young inexperienced female

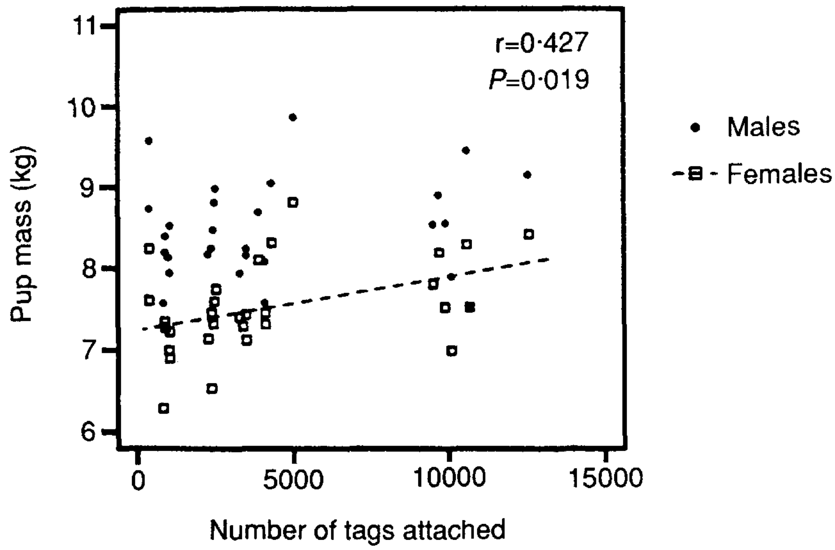

FIG. 5. Relationship between mean body mass of a sample of tagged pups and the total number of pups bearing tags. Each point represents one rookery in one year from 1957–66. Unlike the females, the male regression was not significant ($r = 0{\cdot}158$, $t_{28} = 0{\cdot}624$, $P = 0{\cdot}269$). This might be explained by the large variance of male mass and the small number of means.

successfully raising her pup. Such an hypothesis is supported by the observation that higher rates of starvation of Antarctic fur seal pups were recorded on high density breeding beaches because disturbances induced by the fighting and boundary displays of breeding bulls disrupted the establishment of mother–pup bonds (Doidge *et al.*, 1984*b*).

The possibility of spatial segregation of different sized pups could confound attempts to compare the mass of northern fur seal pups sampled during the high densities of the 1950s with that recorded in the 1980s when the population was considerably reduced. It could also confound making future comparisons between the size of Antarctic pups weighed at South Georgia as the population increases unless appropriate precautions are taken. Pups of different ages and sizes may be better mixed and less segregated at low densities. Furthermore, biologists are not restricted to the peripheral regions of the rookery at low densities and could presumably round up older and larger pups down at the water's edge.

Only the mass of northern fur seal pups from Northeast Point did not appear to be biased by the number of pups weighed (Fig. 4). This might be explained by the physical layout of this rookery which follows closely along the shoreline and has never extended far inland, such that a cross-section of pups could always be weighed down to the water's edge. There is presumably a threshold level beyond which weighing more pups would not increase the mean mass. Just exactly what the sample size is and how it relates to rookeries of different densities is not clear and should be further investigated. Perhaps subsections of the data could be grouped and analysed in the order collected.

An additional piece of evidence supporting the segregation theory is the positive correlation between the mean mass of tagged pups and the number of pups previously captured and tagged from 1957–66 (Fig. 5). The data suggest that bigger pups were captured and tagged when large numbers of tags were attached. This probably occurred because pups had to be driven from deep within the rookery to obtain large numbers of pups.

Overview

Several factors should be considered when weighing fur seal pups. If, for example, the intent is to make comparisons between the size of pups weighed in different years, then measurements should be made on the same day each year. This precaution assumes reproductive synchrony and controls for daily growth increments. It is also important to follow the same procedures each year when rounding up and weighing pups, so that any hidden biases (e.g. if pups of different ages are not well mixed) are consistent between years. Biases associated with spatial segregation of different aged pups can be particularly troubling if the size of the population changes rapidly. At high densities only seals in the peripheral regions of the rookery may be accessible, compared to a low density population where all individuals can be obtained.

Another important consideration is the sample size required to detect statistical differences in mean body mass, if they are indeed present. As a general rule, large samples are needed because of the large variability in body size that is attributed to such factors as the particular growth phase the pup is in, and whether or not a pup is currently fasting or has recently fed. Since variability in body size increases with time, the later the measurements are taken after birth, the greater the sample size required. Because females are on average lighter than males, differences in female mass can be detected with smaller sample sizes. Researchers may find that data from females are more reliable than data from males, if large samples cannot be obtained. The sample sizes needed can be deduced from power analysis (e.g. Zar, 1984), and should be estimated before investing time and effort into further pup weighing operations.

The fur seal pups were weighed by the United States Department of Fish and Wildlife (1957–71) and by the National Marine Mammal Laboratory, Seattle WA (1984, 1987). I am grateful to the Seattle Lab. for making their database available to me. Useful comments and suggestions on earlier drafts of this manuscript were made by the late Michael Bigg, Bill Doidge, Don Ludwig, Victor Scheffer, Carl Walters, and an anonymous reviewer.

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